

Authors Response to Reviewer 1

R1: In this manuscript, Wutzler et al. present a simplification of the previously published model SEAM by assuming a quasi-steady state for the extracellular enzyme pool. The SESAM model builds upon the SEAM model with additional modifications to the enzyme allocation mechanism for the decomposition of litter and residue pools. The main results include reducing SEAM model complexity while retaining long-term (decadal) SOM dynamics (C and N) and microbial adaptation to nutrient-limited conditions using overflow respiration and dynamic enzyme allocation. Overall, I appreciate how the authors retained the effects of microbial diversity and kept a simpler model structure. Moreover, I admire the authors for their thoroughness of the analysis, especially on the bias with quasi-state assumptions. The methods and results are sound; however, the introduction and discussion need some attention.

The major shortcoming of the manuscript is the writing style. The discussion section needs significant revision. I have the following suggestion to improve the quality of the manuscript further; afterward, the manuscript should be reconsidered for publication.

Authors: Thanks reviewer R1 for these encouraging comments. In the revised manuscript we work on the writing style, taking into account these helpful comments.

R1-1: Consider modifying the title because the manuscript is more of a simplification of SEAM rather than upscaling. Or be specific what is being upscaled.

Authors: We strive to introduce the SESAM model without requiring the reader to be familiar with the SEAM model. Hence, we want to not make the title specific to the simplifications going from SEAM to SESAM. Both, SESAM and SEAM, deal with upscaling microbial dynamics from pore to pedon scale with a focus on longer-than-seasonal time scale. Simplifying assumptions additionally constrain the SESAM model to potentially not accurately predict processes operating at time-scales shorter than the dynamics of the enzyme pool, i.e. shorter than seasonal.

In the revised manuscript we better clarify between first, the abstracting purpose of both models, which is mainly about scaling up from detailed subseasonal microbial processes at pore scale to general dynamics at pedon scale, and second, the time scale constraint which is introduced by the enzyme quasi-steady-state (QSS) assumption in SESAM. We also clarified in the aims of the manuscript “The aim of this paper is to present the SESAM model without pre-knowledge of the SEAM model, ...” (p2L30)

Furthermore, we adopted a longer but more specific title: “Simulating long-term responses of soil organic matter turnover to substrate stoichiometry by abstracting fast and small scale microbial processes: The SESAM Soil Enzyme Steady Allocation Model (v3.0).”

R1-2-1: The first paragraph of the abstract deals with the spatial scale of the microbial processes, and then SESAM is proposed to fix issues with temporal scale (decadal dynamics). Please fix this. The same issue is in the introduction; first, the spatial scale is introduced, then a solution for the temporal scale. A better explanation is needed to link how pore-scale processes affect SOM dynamics at different time scales to motivate the simplification of SEAM.

Authors: see also R1-1. We further split the first part of the discussion into two subsections, with the first subsection summarizing the abstraction purpose again and motivating why the

SESAM should therefore be driven by annually averaged litter inputs, and second, a subsection focusing on bias due to averaging model inputs (p.12 l.5).

R1-2-2: P1L22: What is that discrepancy? Provide examples with references. Some introductory sentences are missing on how current "global models" implement microbial processes and what is already feasible. Without this context, the development of the proposed model does not make sense.

Authors: The development of microbial formulations in SOM dynamic models and discrepancies is described in the paragraphs following this sentence (p2l5ff "At the micro-pore scale ..."). We start the section with giving the main message before going to the details. In the revised version we extended the sentence to "However, relevant processes happen at the pore scale and processes strongly vary between microsites and sites. On the other hand we are concerned with dynamics at the pedon or ecosystem scale and strive for general predictions that do not depend on the varying details. Hence, there is a discrepancy in detail and scale between process understanding and what is feasible to implement in global models." (p.1 l.23ff)

R1-3: Define what the temporal scale of processes is. Authors often use short-term and long-term vaguely.

Authors: In the revised manuscript we detailed "The SESAM model is intended to capture the longer-term, i.e. decadal dynamics of SOM decomposition and abstracts from short-term dynamics, i.e. shorter than seasonal, by applying ..." (p.2 l.27)

R1-4-1: sensitivity analyses often depend on the sample size. I wonder if 5000 was sufficient.

Authors: The Sobol-Touati methods generates design matrix of 80000 parameter combinations to evaluate from the two samples of each 5000 records depending on the number of parameters. During pre-studies we experimented with different sensitivity methods and sizes of the input samples. Using 10000 instead of 5000 records input for the two sample input matrices did not alter the mean estimates and decreased the uncertainty of the sensitivity estimates only marginally.

R1-4-2: The maintenance does not require N in SEAM/SESAM, right? What would be consequence of if it did?

Authors: Correct. Maintenance costs are modeled to be carbon only. This is because most of the material of degraded and rebuild proteins are reused within the cell and energetic costs are covered by catabolic respiration, i.e. carbon mineralization. Intracellular protein synthesis and protein destruction (which is recycled in the cell) is covered by the biomass synthesis and only catabolic energy requirements are modeled. Elemental costs of producing extracellular enzymes are modeled explicitly and are therefore not part of the modeled maintenance. In the unlikely case that microbes would produce N-intensive extracellular polymers that are not recycled, the model needed to take into account another N-mineralization flux in addition to the three fluxes detailed in Fig A.1. This would trigger changes in the N-mass balance equations and further in the N-limitation. In rare conditions this could shift the system to a different elemental limitation causing large changes. Otherwise, we expect effects to be smaller than the difference between SESAM3 and NoEnzFlux in Fig. 5. Because we think that it is reasonable to neglect the elemental contributions to maintenance at the modeled scale, we do not extend the manuscript but explicitly document this assumption: "Eq. A9 assumes that the N taken up is only used for enzyme production and biomass synthesis. A potential contribution of N to maintenance processes is neglected." (p.24 l.18)

R1-D-1: The first paragraph in most discussion sections reads as the introduction. This should be deleted or put in context with the manuscript's results.

Authors: We believe that it is very helpful to the readers to remind them of the settings of this paper before discussing the results of the paper in detail, and therefore prefer to keep the manuscript structure. We restructured and rewrote the beginning of the discussion. We can of course remove these if the editor feels they are redundant.

R1-D4.1-1: L5 "At the heart of the interactions are soil microbial processes, and hence, these processes need to be represented in models of SOM dynamics". Is that a good enough reason?

Authors: We agree that this is not sufficient reason and indeed strive for formulations that abstract again. We reformulate: "Hence, a more mechanistic representation of microbial processes should improve dynamic SOM models and their applicability across different sites." (p.12 l.10)

R1-D4.1-2: L6 check patters - **Authors:** We corrected the typo.

R1-D4.1-3: L7 Which microbial processes are being referred to here? Please be specific.

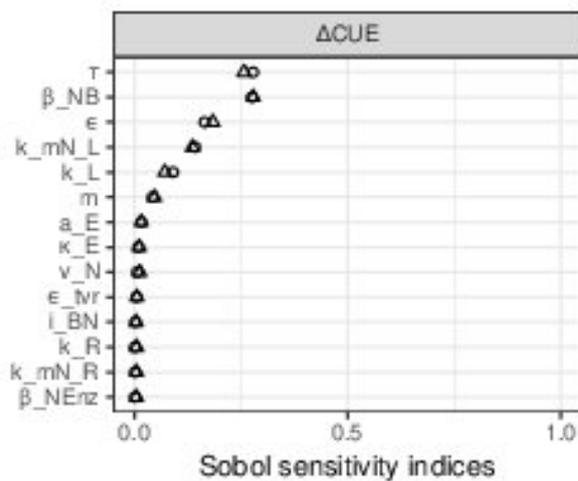
Authors: We detailed "SOM formation and turnover are expected to be controlled by microbial processes, such as depolymerization of SOM, respiration, mineralization/immobilization, and microbial turnover" (p.12 l.8)

R1-D4.1-4: L8 missing subject. - **Authors:** We corrected the typo.

R1-D4.1-5: L9: "Many of these processes work on small" define small - **Authors:** We detailed "pore spatial and hourly to daily temporal scale" (p.13 l.1).

R1-D4.1-6: L11: In my opinion, "abstract" is misused throughout the manuscript. I would prefer simplification of the model rather than abstraction. Quasi-state assumption leads to a simpler model structure. All models are abstract anyway.

Authors: To abstract means neglecting some of the details and finding more general descriptions. To simplify is a more general term that can also be used for just transforming an equation without chaining its meaning. While the QSS of enzyme levels neglects the fast-term dynamics of enzyme production and turnover, the entire SESAM model is about abstracting away details of microbial dynamics, which may be relevant at pore-scale and at sub-seasonal scale, and find general formulations that hold for systems/sites that differ in many microbial details. We argue that "to abstract" is the more appropriate term here. However, in the revis



ed manuscript we replaced “abstracted” by “simplified” when specifically referring to the QSS.

R1-D4.1-7: L12: what is meant by mean effects?

Authors: We detailed “effects that are most important when averaged across pedon and years” (p.13 l.3)

R1-D4.1-8: P13L3: “neglects smoothing dynamics that occurs when explicitly modeling DOM and enzyme pools”. Add reference.

Authors: We did not find a good reference. With the QSS and jumps in input to enzyme pools, enzyme levels also immediately jump to respective steady states, giving a wrong impression of the dynamics. Contrary, with explicitly modeling the enzyme pools, they increase slowly and by internal feedback and buffering mechanisms they often do not reach the extreme values as predicted by QSS immediately after the input jump. In effect they act as a buffer that smoothes the dynamics similar to the other effects described in the paragraph (p.13, l.15). We argue that explaining these dynamic details in the manuscript distracts from the overall message and story of the paragraph and do not adapt the sentence. Its a typical case of introducing divergences (see R-8) during revisions of the manuscript.

R1-D4.1-9: P13L7: it is confusing to read input along with fluxes because 'decomposition functions' are functions of stocks, not inputs. If you mean litter input, then write litter input/s.

Authors: Yes. Here we write about input arguments to a function but should better use “stocks”. We corrected to “Specifically, the mostly concave functions of decomposition according to Michaelis-Menten kinetics yield a higher decomposition flux of the average stock (input argument to the decomposition function) compared to the average of the fluxes computed using the fluctuating stocks.” (p.13 l.15)

R1-D4.1-10: P13L8: “The fluctuation analysis revealed....” Convolved sentence. Split into two sentences. - **Authors:** We split into two sentences.

R1-D4.1-11: P13L11: What are those certain conditions?

Authors: That could be a topic of further research beyond this paper. We just picked reasonable conditions for the fluctuation experiment and did not observe the expected nonlinear bias. In the revised manuscript we replaced “certain conditions” by “some conditions” (p.14, l6).

R1-D4.2-1: “Competition between microbial groups and adaptation of the microbial community is one of those detailed processes that have been shown to exert strong control on decadal-

term SOM dynamics". Which of those detailed processes? Also, add references for "strong control on decadal-term SOM dynamics"

Authors: Its explained in the that clause. We replaced "those" by "the" and added reference to Kaiser et al. 2014 (p.14 l.10).

R1-D4.2-2: P14L5: delete "instead of respiring it to the atmosphere after those pulses" -

Authors: We deleted the subclause.

R1-D4.2-3: Delete: "Studying and discussing how these pathways can be modeled and clarified using SESAM warrants a dedicated manuscript" - **Authors:** We deleted the sentence.

R1-D4.2-4: P14L13-14, why and how is this related to the results from this manuscript?

Authors: We try to find scenarios where SESAM predictions can be falsified or corroborated by observations. Here, we identify such potential observations based on stocks versus CN-ratios predicted in all the studied scenarios (p.14 l.23).

R1-D4.3-1: "short time scales" vague - **Authors:** replaced by "hourly to seasonal time scales"

R1-D4.3-2: "Hence, microbial parameters need to be constrained by inverting models to larger scale observations". What is meant by inverting here?

Authors: An inverse problem in science is the process of calculating from a set of observations the causal factors, i.e. model parameters, that predict given uncertain observations. Although we think that "inverting" is the more precise term, we replaced "inverting" by "calibrating" to avoid technical jargon (p.15 l.1).

R1-D4.3-2: "Currently, the free air enrichment time series are running about 20 years are getting long enough to calibrate and test models at decadal time scale" This sentence seems to be disconnected from the entire paragraph.

Authors: We are discussing that decadal-term observations are required and point to sources that can potentially be used to calibrate and corroborate or falsify the model assumptions. Therefore, we argue that referencing the FACE experiments is warranted here (p.15 l.10).

R-D4.4-1: "We think of ways how let it change together with other microbial properties of enzyme allocation". How does this sentence contribute to the manuscript?

Authors: It relates to the insights from sensitivity analysis. If the assumption that the C/N ratio of microbial biomass parameter cannot be fixed to a general constant is wrong, we have to think about ways forward. Either we have to calibrate it at each site again or we can come up with a more general solution. Our suggestion, here, is trying to relate it to the dynamic state variable of enzyme allocation. We wrote "Hence, the assumption that it can be fixed because its range is rather constrained has to be revisited. We think of future developments to let it change together with other microbial properties of enzyme allocation." (p.15 l.15)

R1-D4.4-2: The third paragraph in this section is not a discussion of results. It can go in the outlook, but it can also be removed entirely.

Authors: The sensitivity analysis showed that results are strongly dependent on parametrization of microbial turnover. We use this finding to conclude that it is an important process which warrants further discussion on how to model it in alternative better ways. We therefore believe that it is an important part of the discussion section (p.15 l.17ff).

R1-D4.4-3: It would be interesting to see how the sensitivity of selected parameters varies in the short-term simulation, e.g., for the time scale of Figure 4, substrate pulse simulation. This would add interesting analysis to the sensitivity section comparing short and long-term sensitivity patterns in parameter space.

Authors: We performed the suggested sensitivity analysis of the substrate pulse simulation with the same method as described in the manuscript. We explored the sensitivity of the range of CUE (maximum – minimum) over time for the simulation with substrate C/N=50. The following figure displays the results:

The magnitude of CUE variation across time was most sensitive to turnover and the C/N ratio of microbial biomass. We observed lowest range with parameter combinations that led to only a weak N-limitation after substrate pulse addition, such as high C/N ratio of microbes. Similarly, we observed highest range with parameters leading to strong N-limitation, such as low C/N ratio of microbes, low turnover of microbial residues, and high microbial turnover with high carbon use efficiency. In order to prevent the results to be distorted by CUE of cases where the parameterization led to a system which was C-limited after the initial pulse, we prescribed a lower initial residue pool and lower initial inorganic N compared to the substrate pulse simulation described in the paper.

Although interesting, we do not see how this sensitivity analysis adds to the message of the paper and did not include it in a revised version.

R1-Outlook: Delete it or rewrite it. In its current shape, it is not adding anything to the story. It reads like a to-do list.

Authors: We omitted the outlook section from the manuscript.

R1-F-1: SOM should be the sum of all C pools, right? Even if microbial biomass, DOM, and enzyme pools are small.

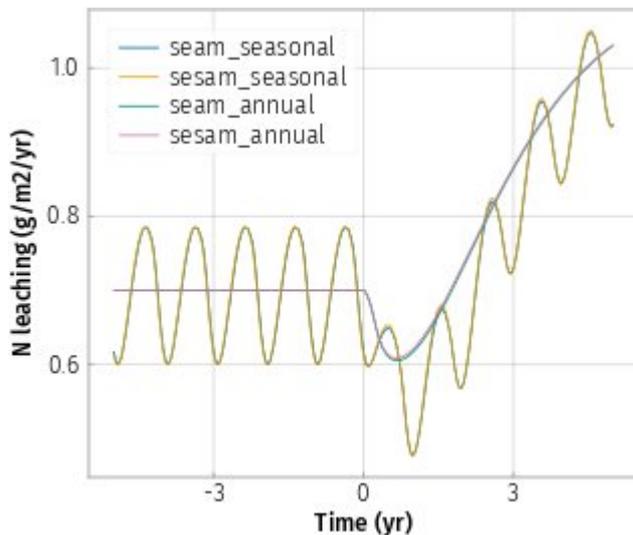
Authors: Yes. We clarified : “SOM Stocks, here approximated by the sum of litter, L, and residue, R ...”, because the other pools are magnitudes smaller. (Fig. 3)

R1-F-2: Figure 4: How does CUE compare with different model formulations SEAM/SESAM/SESAM_NoEnzFlux for this simulation?

As detailed in the methods, these substrate-pulse simulations have only been performed with the SESAM with two parametrizations selected for the purpose of the experiment. We expect only negligible changes to the presented simulation if we would repeat the experiment with the other variants and the performed model experiment already suffices for the message of the paper. Hence, we so far did not invest the work to repeat the experiment with the other variants.

R1-F-3: Figure 6. Why are seasonal patterns for SESAM not shown?

Authors: Because of overplotting. In the following figure with all four variants, SESAM_seasonal is virtually indistinguishable from SEAM_season.



Three model variants presented in the paper are enough to convey the two messages of the figure. First, we show differences between season vs. annual patterns and used the SEAM for this. Second, we wanted to show potential bias between SEAM and SESAM at annual scale.

R1-A-1: A3b It is best to avoid syn_Enz , because when discussing NoEnzFlux scenario, it gets confusing that dec will zero.

Authors: We could replace syn_Enz in eq. A3b by its definition $a_B B$. However, the naming also conveys meaning that with the proposed change gets lost. The NoEnzFlux simulation scenario is a special case and should not compromise the description of the SESAM model. Instead we tried to improve the description of the NoEnzFlux scenario: "This has been accomplished by using $\text{syn}_{\text{Enz}} = 0$ instead of (A2a) and using $a_E B$ directly in computation of decomposition (A3b) and subsequent in computation of revenue (A13).

R1-8: I strongly advise using a formal writing approach as text occasionally reads colloquial, and often author deviates from the main ideas. Streamlining the text and avoiding such diversion would help the reader better understand take-home messages.

Authors: We have edited the text to remove colloquial language.

Authors Response to Reviewer 2 (Nadezda Vasilyeva)

R2-General-1: The study presents an upscaling of a short-term (enzyme turnover time) SEAM model of C and N dynamics in soil to a decadal scale. This is done by one of the valid procedures - the simplification of short-term model equations, while retaining discussed microbial mechanisms. The study shows that the performed modification of the model equations did not change long-term effects of those mechanisms in specific scenarios, and the SESAM model is interesting for further studying the effects of these mechanisms on regional scale.

Authors: We thank R2 for the constructive summary.

R2-General-2: The authors mention having already tried implementing SESAM into a land model and that this trial initiated several reformulations of model aspects. It would be interesting to know which kind of aspects were revealed necessary to reformulate.

Authors: A variant of SEAM is part of the Jena soil model (Ye et al 2020), where we tried to adapt the formulations also for phosphorous (P). Since the current manuscript does not introduce the P cycle in SESAM we will not detail the following explanations in the paper. There were two basic problems. First, although soil microbes were mostly simulated to be P-stressed in organic layer, the model did not show much P-limitation as there was virtually no cost attached to producing enzymes under P stress. This is because with former SEAM the investment was computed for the limiting element only, and because enzymes have a very low P-content there is only a very low P-cost. The presented version computes a limitation-weighted investment across all elements, so that carbon also contributes to cost under P-limitation (eq. A13c). Second, JSM described biomineralization, i.e. the cleavage of P from organic matter without depolymerizing organic matter independent of enzyme modeling while former SEAM could only handle a single dimension of enzymes (L vs. R). The model version presented in the manuscript allows for additional enzymes that do not depolymerize (extension of A3b that we decided to add only to a forthcoming P-related manuscript), but more importantly this manuscript already introduces a new formulation of elemental limitations that can handle several dimensions of enzymes (A15).

Yu L, Ahrens B, Wutzler T, Schrumpf M & Zaehle S (2020) Jena Soil Model (JSM v1.0 revision 1934): a microbial soil organic carbon model integrated with nitrogen and phosphorus processes. Geoscientific Model Development, Copernicus GmbH, 13, 783-803 10.5194/gmd-13-783-2020

R2-General-3: The basis of the model in adapting microbial consumption of SOM driven by their stoichiometry and resulting CUE as emergent property of microbial community is a very sensible approach and a valuable result. While it looks questionable whether the stoichiometrically excess C should indeed go into respiration overflow, this mechanism is worth testing.

Authors: There are alternatives for excess C whose discussion goes beyond the current manuscript. First, microbes could reduce uptake and decomposition so that immobilization N flux can match stoichiometry. However, this usually leads to lower microbial growth rates which we interpret as evolutionary inferior to the overflow approach. Second, microbes could invest into C-storage. However, storage primarily buffers up-to-seasonal term fluctuations in stoichiometry of inputs and we hypothesize that effects on decadal-term cycling are not large, after storage capacity becomes exhausted. Third, microbes could produce extracellular polymeric substrates (EPS). This option does make a difference, because the C can be recycled

instead of being lost to the atmosphere. Studying this option, however, will need a dedicated study including observational evidence. However, EPS studies on longer-than-seasonal scale are rare to our knowledge.

Minor questions:

R2-1: p.2 l.20: it would be good somewhere in the beginning to explain in a few words what is “banking mechanism” same as done for “N priming”.

Authors: We now explain in the introduction “the banking mechanism (Perveen et al., 2014; Wutzler et al., 2017), where excess available N is stored by SOM buildup and made available again by increased SOM decomposition during periods of N limitation.” (p.2 l.23)

R2-2: p.5 l.10 “..SEAM required model parameters for enzyme turnover.” You could make it more clear - that SESAM now requires only one instead of two enzyme parameters in SEAM, if this is what you mean.

Authors: Yes. We now adapted to “SEAM required two model parameters for the dynamics of the enzyme pools. These parameters are hard to measure and added complexity to model-data-integration. The presented SESAM model uses only one enzyme production related parameter, while the enzyme turnover parameter merges with the half-saturation parameter of the SOM decomposition.” (p.5 l.19)

R2-3: p.7 l.24: “with scenario of varying initial C/N ratio with otherwise very low rate of L input” not very clear what is meant here by “otherwise”.

Authors: We split into sentences “In this experiment microbial community decompose a carbon rich chunk of initial litter whose initial C/N ratio varied by simulation scenario. Continuous L input rate was set close to zero to 40 gm -2 yr^{-1} and N leaching rate was set to zero.”. (p.7 l.29)

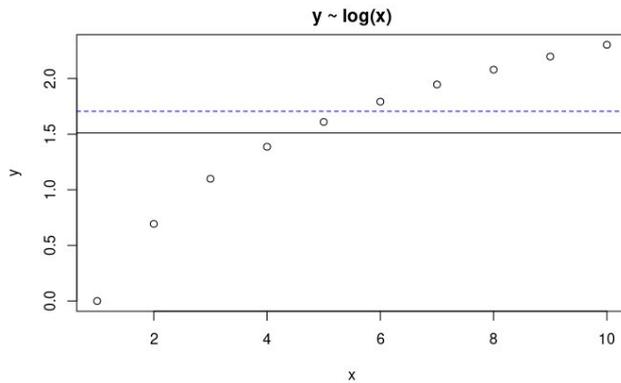
R2-4: p.10 Figure 3: the legend covers the figure - **Authors:** We put the legend to the side of the figure.

R2-5: p.11 Figure 4: what do numbers 50,70,90 in the legend mean? is it C/N ratio if yes, why is it so high?

Authors: Yes its C/N ratio of initial litter as described in the figure caption. In hindsight it is really at the high side of inputs, however, a ratio of 90 is not uncommon for wheat straw. I do not remember specific reasons for choosing these scenarios. The effects are best visualized with a large range of C/N ratios. (Fig 4)

R2-6: p.13 l.6: “The mostly concave functions of decomposition according to Michaelis-Menten kinetics yield a lower flux of the average input compared to the average of the fluxes on varying input. Hence, we expected slightly higher decomposition rates and lower stocks with the average litter input scenario.” Not very clear how the averaging of inputs should cause ‘higher decomposition’.

Authors: We got it the wrong way in the first sentence. The issue is best shown at a blackboard but an additional figure in the paper would distract from the main story.



The black line is $\text{mean}(y)$, the blue line $\log(\text{mean}(x))$. Hence applying the concave log function to averaged inputs yields a higher value than taking the average of the function values.

We adapted the text to “Specifically, the mostly concave functions of decomposition according to Michaelis-Menten kinetics yield a higher decomposition flux of the average stock (input argument to the decomposition function) compared to the average of the fluxes computed using the fluctuating stocks. Hence, we expected slightly higher decomposition rates and lower stocks with the average litter input scenario” (p.13 l.15ff).

R2-7: p.14 l.12: “While the relative changes in SOM pools are so small that are very hard to directly measure, changes can potentially be detected by a changing C/N ratio of the total SOM”. What result of SESAM model one can expect in the scenario of no litter input on decadal scale for C/N of the pools and C stock?

Authors: For this specific scenario C stocks decline. Given that external inputs and outputs of mineral N are negligible, then SESAM predicts C/N of total SOM to decrease, because the N-poorer labile parts are depleted first. For the single pools: C/N of labile pool does not change. C/N of residue pool is difficult to predict in general because it depends on many factors like abiotic N balance or the ratio of microbial turnover to enzyme turnover. In order to not distract, we did not include this discussion in the manuscript.

R2-8: p.15 l.27: here for the first time “conserving CUE” is used. The CUE was discussed as an emergent property of the model. How to interpret “conserving”? Does it mean optimal for survival?

Authors: We used misleading terminology. Here, specifically it means CUE is less fluctuating, i.e. it is buffered against fluctuations in C/N of substrate and in turn to fluctuating stoichiometry of litter input. It refers to the experiment of Fig 4. In the revised version we changed “conserved” to “dampened fluctuation” throughout the text.

R2-9: Thanks for noting the typos. We corrected them.