

We thank anonymous reviewer #2 for their supportive comments and stimulating thoughts.

We address each individual comment below. The original reviewer's comments are stated in regular typeface and our responses in italic.

General Comments

Schwartz et al. present a thorough and robust stability analysis of microbial-explicit biogeochemical models, showing how model structure, kinetics, and parameter space can create unstable equilibria. The phenomenon of instability in microbial models has been mentioned in passing in existing literature (e.g. Schimel and Weintraub 2003, Georgiou et al., 2017) but the analysis presented in this manuscript represents the most thorough investigation of this phenomenon to date. This makes the manuscript novel and interesting to the community of people interested in developing microbial-explicit soil carbon models. I have two main areas of feedback to improve the manuscript.

First, I would like the authors to make sure that this manuscript is accessible to the community of researchers who would benefit from understanding its main conclusions. To this end, I count 46 numbered equations in the manuscript in addition to those contained in tables, which is really quite a lot. I appreciate that these equations build support for the main findings of the paper, but I suspect that very few people will read this paper and work through all these equations. There is a significantly broader audience that will benefit from understanding the outcome of this analysis without working through all the math. With this in mind, I suggest the authors take steps to ensure that the main findings are easy to locate and understand for this audience. Although the supplement is quite large already, moving some of the less crucial equations to the supplement could improve readability. In the figures, finding ways to represent data in less abstract ways and providing conceptual interpretations will make the conclusions more actionable for readers of the manuscript. Specific comments below.

Thank you very much for this helpful suggestion. We agree that accessibility of the paper and its conclusions could be broadened. We suggest to move less crucial equations currently contained in the main text to the Appendix (appearing at the end of the main text) rather than the supplemental information, where they might be easier to locate for interested readers. Specifically, we suggest to move the Jacobian matrixes and technical details on the derivation of stability criteria. Additionally, we will extend Table 3 to include parameter groups (explaining their meaning were appropriate – see specific comment below).

My second main comment is that the paper could benefit from some discussion of stability as a realistic ecological/biogeochemical phenomenon. We should expect microbial-explicit models to produce realistic predictions at the scale of the mechanisms that they represent. Generally, the mechanisms in these models can be described over very small spatial scales where conditions can be assumed to be homogenous. Directly upscaling non-linear uptake and depolymerization kinetics in heterogenous environments does not preserve model behavior (Chakrawal et al., 2020). It is probably worth some discussion then whether equilibrium is a realistic way to represent microbial dynamics in soil at all. Microbial populations in reality may very well oscillate and exhibit instability at the scale of mechanisms represented in microbial models, while still producing stable emergent behavior at larger scales.

We agree that the behaviors these models produce – including oscillations and instability – can very well be realistic at the microscale (i.e. the scales of the processes they describe). We touch on this in lines 35-39 and 551-554. Still, if these models are without further modifications used to describe processes at larger spatial scales (as commonly done), these behaviors are no longer realistic. I.e. models used to simulate SOC fate at the large scale must have stable equilibrium points to prevent erratic simulation outcomes (see also response to reviewer 1). We agree that this discrepancy might be indicative of a scaling problem. If non-linear microbial-explicit models accurately describe processes at the small scale – at which oscillatory and unstable behavior might occur – we need to adapt these formulations before applying them at larger spatial scales where we do not observe these behaviors. In this light, the approaches to avoid instability could inform development of suitable upscaling approaches. I.e. suitable upscaling approaches might lead to formulations that simplify the non-linear dynamics (such as approaches 1 & 2 in section 4.2) or that acknowledge spatial (and temporal) heterogeneity and ecology of microbial communities (approach 3).

Regarding the scaling relations established by Chakrawal et al. (2020) we note that it can be a very interesting exercise to plug their upscaled kinetic descriptions into our stability criterion (substituting any of their upscaled kinetic descriptions to represent the depolymerization rate P and then taking the respective partial derivatives). However, the lack of a closure of the equations presented by Chakrawal et al. (2020) limits meaningful insights from this exercise – i.e. we would need to know how the variance and covariance terms of their equations scale with state variables (as terms such as $\frac{\partial}{\partial s} cov(S, E)$ would need to be evaluated - $cov(S, E)$ being the spatial covariance between SOC (S) and extracellular enzyme (E) concentration). Considering such scaling relations as a potential solution to avoid instability could be regarded as a special case of adapting kinetic formulations to avoid instability. Though, as it does not directly emerge from our analysis we refrain from listing it in line with the other approaches we suggest in section 4.2. Still we agree that this is an important notion and we suggest to extend the discussion to acknowledge it.

Specific Comments

218-222: This is one place where grouping parameters helps express the equilibrium solutions in a concise way, but it becomes very difficult for me to interpret any of these equations with the added layers of abstraction. When the authors then mention $\omega > 0$ or , the significance of this fact is not clear because the expression is hidden behind a layer of abstraction. Is there any conceptual interpretation that can be added to help readers understand? Similar issue lines 285-290.8

The grouping parameters were primarily introduced to express steady states in a concise way. These groups don't necessarily have a specific conceptual meaning. We state that $\omega > 0$ not to give an interpretation of ω , but only to understand under what conditions steady states are positive (and thus physically meaningful). On the other hand, e.g. α and β can be identified as "enzyme turnover" and "microbial biomass turnover", respectively. We suggest to add meaningful descriptions to parameter groups where appropriate and to further move the definitions of these parameter groups to Table 3 in order to not break the text flow unnecessarily.

Table 5 and 6: What do the vertical bars in the B and E columns signify?

Vertical bars were supposed to indicate that the expressions for $B_{k,i}^*$ and $E_{k,i}^*$ apply to all used kinetic formulations. We suggest to use curly brackets to indicate this more clearly. E.g. for Table 5:

Table 5. Summary of steady state solutions of the three-pool SBE model for different kinetics of depolymerization. The “biotic” equilibrium solutions for microbial biomass and extracellular enzymes have the same form for any chosen kinetic.

	Kinetic (i)	$S_{k,i}^*$	$B_{k,i}^*$	$E_{k,i}^*$
abiotic ($k = 0$)	i	$\frac{I}{l_S}$	0	0
biotic ($k = 1$)	m	$\frac{\alpha\beta}{v_m\eta}$	$\frac{\alpha\eta B}{\omega} l_S (S_0^* - S_{1,i}^*)$	$\frac{\eta}{\alpha\eta B} B_{1,i}^*$
	f	$\frac{\alpha\beta}{v_f\eta} \frac{K_f^p}{1 - \frac{\alpha\beta}{v_f\eta}}$		
	r	$\frac{\alpha\beta}{v_r^p\eta} \frac{K_r^p\omega + I\eta}{\omega + l_S \frac{\alpha\beta}{v_r^p}}$		
	e	$\frac{\alpha\beta}{v_e^p\eta} \frac{K_e^p\omega + I\eta}{\omega - \omega \frac{\alpha\beta}{v_e^p} + l_S \frac{\alpha\beta}{v_e^p}}$		

339-340: This feedback is interesting because it makes mathematical sense but I’m not sure if it makes sense in an eco-evolutionary view. Doesn’t this imply that microbes could decrease constitutive or inducible enzyme production rates without losing access to SOC? If depolymerization is substrate-limited at equilibrium, then isn’t producing extracellular enzymes a losing strategy from an individual fitness perspective? Discussion of this potential paradox could strengthen the paper and help identify future lines of research.

This is a very interesting notion and points to a very interesting paradox – i.e. that in fact “producing extracellular enzymes [is] a losing strategy from an individual fitness perspective”. Importantly, the model as it is currently formulated and applied (e.g. by Hararuk et al. (2015) but also in the original model described by Allison et al. (2010)) does not consider any competition for SOC substrate. Thus, the only alternative to enzymatic degradation of SOC is its accumulation. This means, in an eco-evolutionary perspective (e.g. if maximizing the growth rate of microbes), that microbes would reduce their enzyme investment to a minimal amount, SOC would accumulate dramatically, but microbes could still attain high growth rates, though at low per-biomass cost for enzyme production. The eco-evolutionary perspective only becomes relevant (and applicable) once there is a competing process that removes SOC. In theory this could either be competition for SOC by other (micro)organisms or abiotic processes that remove (accessible) SOC (erosion, leaching, occlusion, sorption, ...). This outcome emerges also from a mathematical analysis of optimal substrate utilization—without losses of substrate due to abiotic processes or competition, decomposers do not have any reason to invest in resource acquisition (Manzoni et al., 2023).

Thus, an eco-evolutionary optimization approach might not be readily implemented with the current model structure but would require extension of the model to account for competition for SOC. Our analysis demonstrates instead how (given the model structure) microbes might adapt to environmental conditions not to maximize their fitness, but to attain a stable population (e.g. by adapting microbial parameters accordingly; 3rd approach described Section 4.2). Whether stability and fitness maximization are convergent (and e.g. an organism at a fitness maximum would also be able to establish a stable population) would warrant an own dedicated paper. We will include this important notion in our discussion. We note that Abs et al. (2022) in their pre-print are exploring the effect of eco-evolutionary

dynamics on soil carbon fate by explicitly considering competition between microbes (using an adaptive dynamics approach).

Figure 3: There are a few ways that labeling and captioning on this figure could be clarified to help readers interpret the figure

- For figure 3a, I think it may be useful to label the axes with a conceptual description of the mathematical expression. If I understand correctly, I think we are seeing the sensitivity of depolymerization to changes in soil carbon on the x axis and sensitivity of depolymerization to changes in enzymes on the Y. Points below the line fit the conservative condition for stability, but points with damping values > 1 are stable (if oscillatory). Clearly indicating this in the figure labels, axes, and caption will help readers interpret this figure independently, even if they haven't worked through all equations. It may also be helpful to specify in the caption that the proposed condition isn't arbitrary and rather an extension of the criteria found in the simpler model.
- It is confusing that 3b and 3c have essentially the same axis but are shown on two graphs. Figure should include a color legend for stability instead of explaining in the caption. Alternatively, can the same color gradient be used in 3b and 3c that is in 3a?

We suggest to update the figure according to the reviewer's comments. Panels b and c are different in that they represent steady states that fulfill (b) or do not fulfill (c) the stability criterion. Hence the x-axes either have positive (b) or negative values (c). We indicated this difference more clearly now. We replaced absolute numbers of stable and unstable points now by their relative occurrence (%-values in b and c).

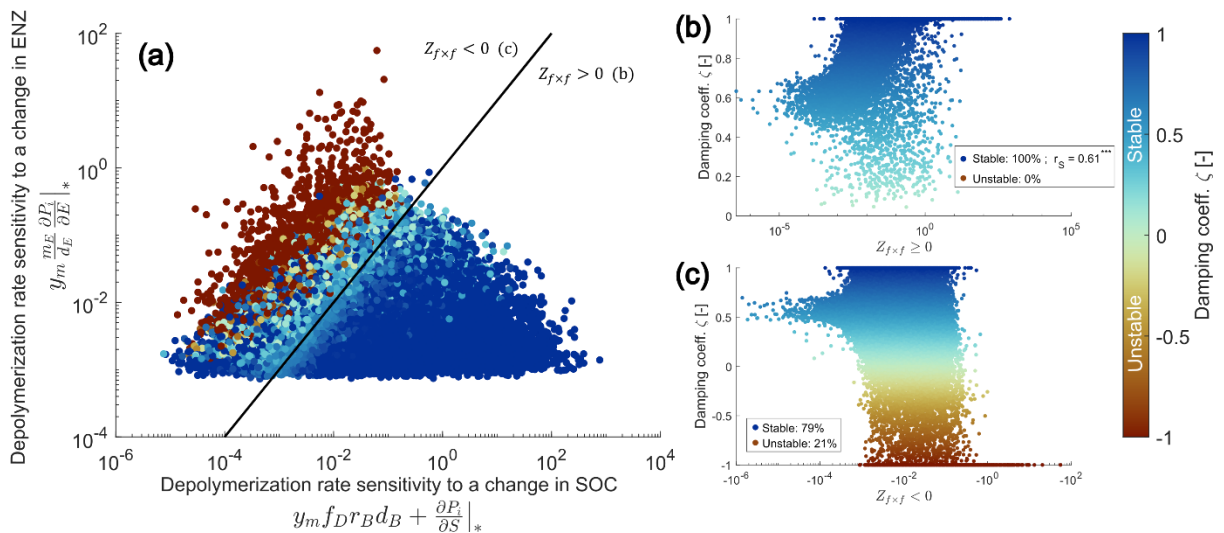


Figure 4: Color scheme for 4b-d would benefit from a legend on the graph rather than in-text description. It is also confusing that the color scheme is the same as 4a, but corresponds to a different variable. I would also suggest labeling axes with variable names instead of single letters (i.e. Biomass decay rate) so that readers don't have to refer back to the parameter table to interpret the figure.

We suggest to update the figures according to the reviewer's comments. Instead of using a legend for the color code of lines in b-d we prefer to have the description directly at the lines. We now swapped panels b and c so that this description together with the legend describing the different line styles appears in the upper right corner where it might be more intuitively found by readers.

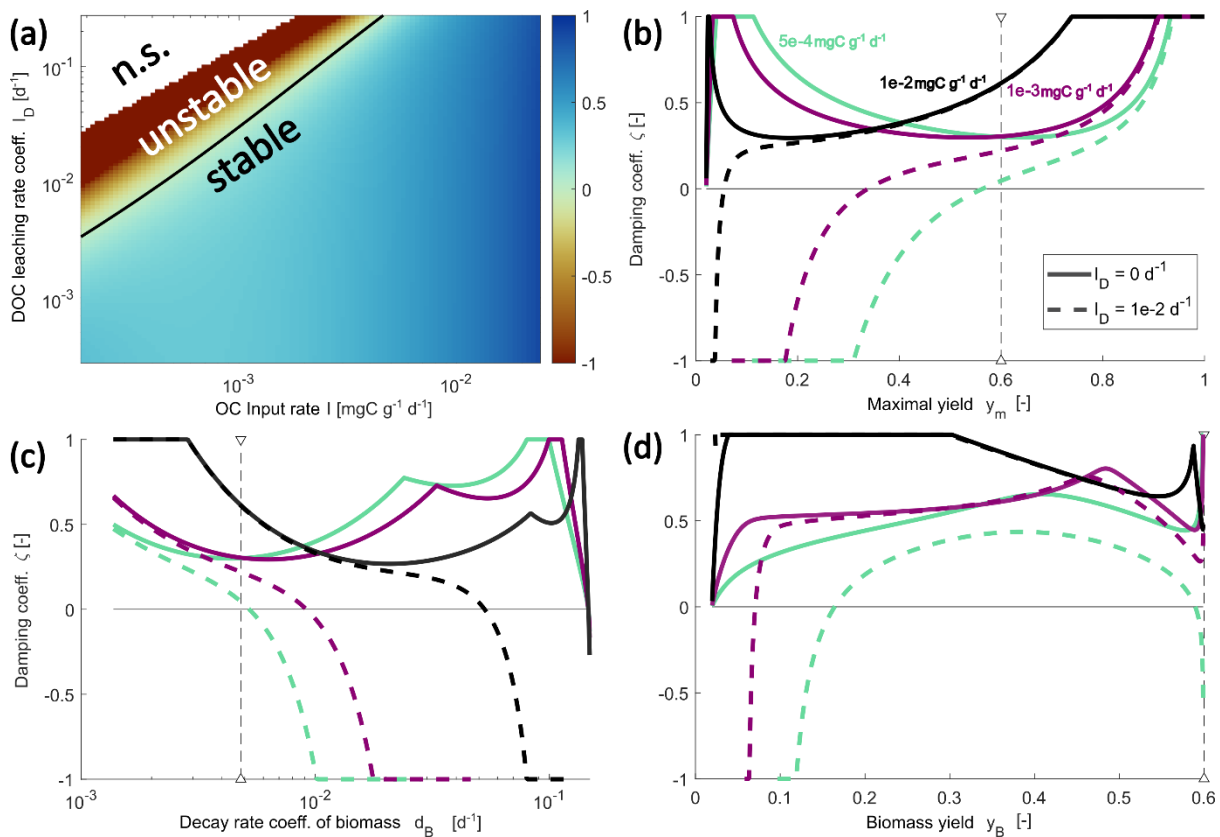


Figure 5: Please clarify – are grey points stable but not plausible?

Correct, we suggest to adapt the caption text as following to make this clearer:

“Color-coded points are stable and plausible steady state solutions, the color code indicating the value of the damping coefficient. Grey points are stable but not plausible steady state solutions and black points are physically meaningful but unstable steady state solutions.”

465: This is good and helpful for readers. It would be helpful to add 1-2 sentences in the abstract that summarize these approaches to avoiding instability.

*We propose to change lines 11-13 and add to it (altered text is **highlighted**):*

*Principally, three distinct strategies can avoid instability: 1) negligence of explicit DOC dynamics, 2) biomass independent uptake rate or 3) co-variance between parameter values to obey the stability criterion. While the first two approaches simplify some mechanistic processes, the third approach points to the interactive effects of environmental conditions and parameters describing microbial physiology, **highlighting** the relevance of basic ecological principles for avoidance of unrealistic (i.e. unstable) simulation outcomes.*

515: This may be a good place to include some discussion about whether microbial equilibrium is, either as a scale issue, or an eco-evolutionary issue, as discussed in comments above.

We suggest to expand the discussion on the above points either here or where it comes naturally considering all arguments.

Technical Corrections

382: analytical analysis is redundant

Done.

Citation

Chakrawal, A., Herrmann, A. M., Koestel, J., Jarsjö, J., Nunan, N., Kätterer, T., & Manzoni, S. (2020). Dynamic upscaling of decomposition kinetics for carbon cycling models. *Geoscientific Model Development*, 13(3), 1399-1429.

References used in replies

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- Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, *3*(5), 336–340. <https://doi.org/10.1038/ngeo846>
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- Manzoni, S., Chakrawal, A., & Ledder, G. (2023). Decomposition rate as an emergent property of optimal microbial foraging. *Frontiers in Ecology and Evolution*, *11*, 1094269. <https://doi.org/10.3389/fevo.2023.1094269>