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Interactive comment on "A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial litter decomposition" *by* J. Y. Tang and W. J. Riley

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Below we respond in italic by following the comments.

General comments: Although I generally understood the rationale for most of the mathematical derivations in this paper, and the resulting equations, I could not follow all of the mathematical details nor was I familiar with all of the referenced derivations. This would have required much more than the already lengthy amount of time I spent reviewing this manuscript, so I must leave that aspect of the review to others. Otherwise,

this is one of the most thorough, mechanistically based, mathematical descriptions of the biogeochemistry of decomposition that I've ever read. The mathematical rationale, rigor and logic are formidable. I very much appreciated the generic approach, placing the substrate-enzyme reaction within the larger donor-recipient framework of equilibrium chemistry. Ecological modelers should appreciate the historical context of such physical-chemical models to quantitative ecology. This is an intellectually provocative paper. Excellent work!

Response: *We thank the reviewer's very positive comments. We will answer the raised concerns below.*

Comment: In some respects, the mathematics of the system includes some unrealistic possibilities. On page 6 on line 4, the velocity of the reaction never approaches infinity because enzyme concentration does not. Similar issues emerge elsewhere in the manuscript, such as lines 13-14 on page 9, because I don't think that high enzyme concentrations are typical of in situ litter decay of SOM dynamics, so while it's an interesting point, it may not be particularly useful. Also lines 8-19 on page 15, because enzymes rarely exceed substrate pool size. Again in the third paragraph on page 24, because substrate: enzyme ratios of 1 are not likely.

Response: *While we in general agree with the reviewer's comments on the enzyme-substrate ratio, we feel our assumption is valid given we are putting our developments in a much broader context than the enzymatic decomposition of SOM. For instance, in an interactive protein network, where our approach is also applicable, the enzyme-substrate ratio could be over a very large range (Ciliberto et al., 2007). Even for SOM decomposition, the microbes are selecting between different substrates, and there are chances that the enzyme-substrate ratio is high, though the ecological significance is low. Our general treatment is also meaningful for the predator-prey problem or more generally food-web dynamics. It is known that the assumption of small ratio between predator and prey (analogous to that between enzyme and substrate) cannot always hold and it leads to dynamical instability when the ratio approaches very high values* *because the substrate is depleted too rapidly (e.g. Borghans et al., 1996). We have added one sentence at the end of the description of the random sampling experiment (paragraph 2 in section 2.5) to ensure that other readers understand the broader context of our results.*

Comments: The authors should mention the relevant points of the MEND model developed by Wang et al. (2013 Ecol Appl 23:255-272) in the second paragraph on page 7. They also addressed adsorption/desorption of enzymes on soil particles and made different conclusions. These results should also be revisited in the discussion section.

Response: *We followed the suggestion and revised accordingly.*

Comments: I didn't understand the rationale for why inactive enzymes would compete for binding sites (second paragraph, page 13; again on page 14, lines 13-14). If the enzyme can bind, it seems likely to catalyze the reaction regardless of whether it's associated with a live or dead cell. Enzyme activity is often independent of the cell, at least for a period of time.

Response: *This is an issue we took from the paper by Suzuki et al. (1989). While it was a suspected mechanism, there is evidence to indicate that enzymes can bind to substrates and still not process them (e.g. Koshland, 1994).*

Comments: I was surprised to see the parameters of Moorhead and Sinsabaugh (2006) used in this exercise, given that those parameters were almost entirely arbitrary.

Response: *We used the published parameters just for a qualitative assessment of our developments. Unfortunately, there are no non-arbitrary parameters in the published literature for this application. We have added a sentence to the text indicating this problem.*

Comments: The "shielding" relationship between lignin and cellulose is due to the biochemical cross linkages between hemicellulose and lignin moieties. These relationships are well known to plant cell wall biochemists and those who study ruminant digestion, although few decomposition studies recognize them. I'd suggest the authors cite work by Bertrand and her student, Machinet, which are among the first forays into this arena for decomposition studies. In any case, the rise in lignin concentration is entirely explainable.

Response: *We read and cited some of the recommend references appropriately in the revision.*

Comments: Why is a half-hour iteration sufficient? Please be more specific about your selection criteria.

Response: *We added an explanation in the revision that this half-hour iteration is selected through trial-and error by looking at the differences when using different time steps.*

Comments: On page 27, some of the unrealistic results for the MM model must have resulted from the absence of other controls normally included, such as the lignocellulose crosslinkages mentioned above. Also, the unreasonable biomass:substrate ratios imply that the relative turnover rates were unrealistic. These are dynamic characteristics of the system, albeit not described as such in this model.

Response: *We agree with the reviewer that the MM model lacks the necessary mechanisms to obtain stable results. This is why other studies have to explicitly impose an LCI function to have their model behave properly. Our model is more parsimonious and can deal with the problem correctly using the same number of parameters as the MM model. So it is reasonable to suspect the MM model is less appropriate for the decomposition problem we are studying here.*

Comments: On page 28, line 9, did the authors mean that biomass was usually within 10

Response: *We reworded the sentence to make it clearer.*

Comments: Lines 9-11 on page 29: although MM kinetics were not the best choice within the constraints that your approach imposed on modeling decomposition, part of this conclusion results from some of the unrealistic features of your modeling approach. It would be more accurate to say that within the framework of your approach, it didn't perform as well. It would also be reasonable to point out that your framework is more parsimonious than that of most models, including those you cite.

Response: *Yes, we stressed in the revision that our model is more parsimonious than the MM model and that our results are consistent within the framework of our approach.*

Comments: Your statements on page 30 are entirely consistent with the general scatter of LCI values reported for well-decomposed litter. I recall that Osono reported values of 0.8, although anything less than 0.7 could be attributed to earlier stages of decay. However, your results are clearly consistent with the emerging consensus in the literature about the importance of initial litter chemistry and microbial interactions. This is the first modeling example that I've seen.

Response: *Thanks for the appraisal; we were equally excited when we made our discovery during this study.*

Comments: Your statement in section 3.3.3 on page 31 is very well made. You might mention Herman et al. (2008, SBB), who showed that the lignin decay threshold was variable and responded to such factors as N concentration. This is generally consistent with your results.

Response: *We added this citation to the revision.*

We carefully incorporated other minor comments from Reviewer 1 into our revision.

References

Borghans, J. A. M., DeBoer, R. J., and Segel, L. A.: Extending the quasi-steady state approximation by changing variables, B Math Biol, 58, 43-63, doi: 10.1007/Bf02458281, 1996.

Koshland, D. E.: The Key-Lock Theory and the Induced Fit Theory, Angew Chem Int Edit, 33, 2375-2378, 1994.

Suzuki, I., Lizama, H. M., and Tackaberry, P. D.: Competitive-inhibition of ferrous iron oxidation by thiobacillus-ferrooxidans by increasing concentrations of cells, Applied and environmental microbiology, 55, 1117-1121, 1989.

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