

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

Anonymous Referee #1

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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 ap-

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proach, 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!

Nonetheless, the findings that EC and ECA models were better than MM kinetics have some caveats. . .

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.

I enjoyed the comparison to predator-prey relationships (bottom of page 6, top of page 7).

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.

Equation 7 doesn't make the loss of product clear, and line 5 on this page should probably be expanded a bit.

It would be appropriate to reference Wang and Post (2013 RMM) in the first paragraph (already included in the reference list).

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

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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.

Wang and Post (2013 RMM) should probably also be noted in the first paragraph on page 15, for their discussion of the relationship between the RMM and Languir isotherms.

I did smile when I read lines 12-13 on page 16, because it's a tall order to define reaction coefficients properly for all such equations. However, it's the best we can do in such circumstances.

I again appreciated the reference to trait-based models in section 2.4 on page 17. This was a very solid example of how such EC and ECA approaches could be used.

The discussion of soil properties at the top of page 18 also reduced the complexity of the system to an unrealistic degree. Most water movement in most soils simply isn't by diffusion. Nonetheless, this assumption makes a more tractable problem. Similarly, the relationship to cell size (page 19) was mathematically elegant, but highly unlikely to be so consistent. The authors might want to recognize the practical limitations of such assumptions while pointing out these attractive mathematical features.

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

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.

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

In lines 7-8 on page 26, the conclusion about mineral enzyme binding should again reference Wang and Post (2013 Ecol Appl).

The next couple of lines on page 26 highlight a very useful result of this model with regard to depth-specific parameterization.

The last word on page 26 should be "weak", not "week".

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 cross-linkages 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.

On page 28, line 9, did the authors mean that biomass was usually within 10% of the total organic carbon in the system? As written, the statement didn't make sense because substrate isn't alive, i.e., it's not part of the "bio"-mass.

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.

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

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modeling example that I've seen.

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

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