Interactive comment on "Comparing models of microbial-substrate interactions and their response to warming" *by* D. Sihi et al.

D. Sihi et al.

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General comments

Reviewer: Sihi and co-authors present a nice study examining soil C dynamics projected by a series of simple models that make different assumptions about heterotrophic respiration and enzyme production. At a high level their findings could be interpreted as: 1) Forward Michaelis-Menten (M-M) models are crazy 2) Reverse Michaelis-Menten models look more reasonable and 3) Reverse models approximate first-order models so why bother with these silly microbial models that are a pain to parameterize and run? I this this paper has more to offer, however, and my suggestions are intended to give the paper broader insight and appeal.

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Response: Thank you for these comments. This is perhaps a little bit too simplified. However, our work was intended to contribute to the discussion how microbial decomposition models and microbial enzyme models are similar (or dissimilar). The subsequent question the reviewer raises, however, are very much to the point, and help us tremendously to sharpen our manuscript.

Reviewer: The discussion around Model 4 (P 10885) may be the most interesting nuance of the paper, but I wonder if one has to invoke a optimized enzyme production model to get this same result? Could an empirical function between temperature and turnover accomplish the same goal? What if a larger (or temperature sensitive) Km value was chosen (implying a lower affinity for substrates with increased temperatures)? More importantly, how do we quantify the "real" μ value that should be used for Model 4, if that's the important value to differentiate between first order and microbial explicit models? What determines the cost of enzyme expenditures, and how may it be different in different soils.

Response: Perhaps the central motivation to put forward the model with optimised enzyme production is that earlier models link enzyme production directly with microbial biomass. What determines the level of enzyme production? The optimization of enzyme production may be viewed as an alternative to the "proportional" model, allowing microbes to adjust to the soil environment. Specifically, in our analysis, we show that if costs for enzyme production are small, enzyme production may be higher, which increases the overall affinity of microbes for substrates (by reducing K_m, see equation A30 with an increased b compared to assumptions in previous work (Schimel and Weintraub, 2003; Allison et al., 2010; German et al., 2012). At this point, we do not have a recipe to estimate the cost of enzyme expenditures.

We interpret enzyme expenditures in 2 ways: The cost per unit enzyme produced, which may be related to the enzyme specifically to solubilise a particular polymer. This may be the easier term to determine experimentally or even theoretically, but may also be a function of temperature. The cost of enzyme production relative to the amount

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of carbon depolymerised (roughly mu). Clearly, this depends on many parameters, including quality of the substrate, its accessibility, and the affinity of the enzyme for the substrate, none of which is easy to determine.

Given that all these parameter are unknown, the reviewer is right, there could be an empirical function that can get the same result. In fact, the first order solution is very close to the microbial model solution, particularly for small costs. Nevertheless, the microbial models and their analysis serve to lay theoretical fundament to understand microbial dynamics.

Reviewer: There are really two underlying modeling frameworks being used, the forward and reverse M-M kinetics (currently models 1 & 3 respectively). Overlying these basic structures the authors increase model complexity by adding maintenance respiration (Model 2), and enzyme production optimization (Model 4), but the order of these additions makes it unclear how maintenance respiration effects the reverse M-M model or how optimizing enzyme production may modify results from the forward model? I wonder if it makes more sense to restructure the results so we're able to: A) Compare forward vs. reverse configuration (these could be models 1a and 2a); then B) Layer on maintenance respiration costs (models 1b & 2b); and finally, C) Add Enzyme production optimization (models 1c & 2c).

Response: The Reviewer is right. Rearranging the discussion and the figures generates a much clearer picture. The biggest model alterations are forward versus backward model. The next alterations are maintenance respiration cost. In our improved version of the manuscript, we add a 3rd layer, in which we analyse the model behavior under the conditions that microbial biomass adjusts fast to new temperature and new carbon availability. We can show that decomposition in the reverse model can be more simplified, without much loss of information. The exception is the initial response to a temperature increase. In the early phase of the temperature response, the microbial decomposition model lags the sudden increase in depolymerisation higher v_max vs the model where microbes are assumed to equilibrate quickly with the supply (See

Fig 3). The fast adjustment models create a bridge between traditional and microbial model in an analytical fashion. This new set of analysis also highlights the use of the fast scale equilibrium for microbes in Table 3 in our improved manuscript, an issue raised by both reviewers.

Based on the reviewer's suggestion we propose new figures to replace previous Figs 2 to 4 (See new Figs 2 to 4 in this response).

Reviewer: The model simulations nicely compare results of the models evaluated here, but given the choice to modify parameters to achieve the same initial and final values of CUE, M, and S (P 10869, L 21) it's unclear how much the results in Fig 2 emerge because of the parameter values chosen vs. differences in model structure. Is there some apriori reason to expect these predefined responses of CUE, and substrate pools to warming? I realize that Fig. 4 and section 4.2 tries to address this concern, but it's too derived to make much intuitive sense (beyond forward M-M models seem really wacky)- but that's a point already made in Fig. 2 and elsewhere (Wang et al. 2014).

Response: Our challenge has been to parameterise each of these different models, such that they are comparable to each other. We chose in our first submission that to parameterise in order to create the same long-term response. We realize that this may be 'too derived' in order for the reader to be able to critically compare the models based on the figures themselves. Here we present an alternative: In layer 1, we adjust model parameter that

a) microbial biomass,CUE, and soil organic carbon are equivalent at reference temperature as in our first submission, and b) that the initial response of respiration is the same across models.

This second parameterisation may be motivated, that short-term respiration responses are often measured in laboratory settings. This second requirement can be met by simply keeping the temperature sensitivity of maximum depolymerisation and of carbon use efficiency the same across models. As a result, the long term changes in soil

organic matter differs across the models (but not microbial biomass, see Table 3) and Figure 2 in this response. When we add the additional layers of maintenance respiration and microbes in quasi-steady state, we do not change the parameters to fulfill requirement b) nor do we change requirement a) when we add enzyme production cost in the enzyme optimisation model, keeping the format of our previous submission.

Because both short-term and long-term responses can now be inferred directly from the new figures, the previous figures with the apparent Q_{10} become obsolete.

Reviewer: Would it be more illustrative to explore the parameter space that allows each model to hit the same initial conditions, but then potentially diverge in their responses to warming? This would provide more of a sensitivity analysis for the respective models, and illustrate potential issues with equifinality in the more complicated model (#4). Such considerations seem important, because I would assume that different parameterizations may project either an increase or decrease in microbial biomass, but currently only one set of parameters are used for each model (e.g. Model 3, discussed in the middle of page 10870).

Response: Based on the previous comment (see above) we did change the models to hit the same initial conditions, and they now diverge in the long-term. We kept the setup for model 4 (OPT model), where the initial conditions are different, based on the cost for enzyme production. I think this has value in that it shows, that at higher cost i) fewer microbes are able to live off a given supply of carbon, and ii) the rate of decomposition is lower, which then translates into overall higher soil organic carbon. To address equifinality of the different cost models, we compare the relative change in soil organic matter and microbial biomass, which are smaller the higher the cost is. Similar values indeed suggest similar model behavior as in the no-cost model. We also found interesting dynamics with respect to CUE: CUE sharply decreases, as in previous models. Yet in the model associated with cost, CUE further declines, as the substrate depletes. Lower SOM increases the fraction of carbon used towards enzyme production.

Specific comments

Introduction:

Reviewer: There are so many clauses in the text that they become distracting to the main message being communicated. I understand this is highly editorial, but I'd recommend using more direct, precise language throughout the manuscript to directly convey the authors' intent.

Response: We will re-address our introduction, and will use shorter sentences to more clearly convey our message. We hope that it helps to pose the questions that we address in this manuscript which are: Microbial models suffer from oscillation, because there is a positive feedback between depolymerisation and microbial biomass. How do alternative formulations of depolymerisation affect this feedback? Simple microbial decomposition models consider 1 respiration term. Does the separation of temperature dependent maintenance respiration and temperature-independent growth respiration affect response to warming? How do different microbial decomposition models compare against the traditional first order models?

Reviewer: Paragraph starting on P 10859, L 19-30: I'm not sure these features are unique to microbial models alone. (see Frey et al 2013 cited here, which uses CENTURY). Moreover, much of the partitioning of respiration fluxes could be done in first-order and microbial models. Separately, it's somewhat misleading to cite Hagerty et al. 2014, which is an observation based paper that doesn't really deal with models (the topic of the sentence here). Finally, is seems odd to cite Schimel 2013, which is a non-peer reviewed opinion / summary of Wieder et al. (2013).

Response: The reviewer is right. The sensitivity to carbon use efficiency is not restricted to microbial models. In our improved manuscript we will change that to:

Further, the response of soil organic matter to warming in models is sensitive to microbial carbon use efficiency (. . ...), because this parameter defines the fraction of carbon

remaining in the soil as processed organic matter vs carbon removed via respiratory CO2.

We will remove the Schimel (2013) reference and add wieder et al. (2013). We also remove the Hagerty et al. (2013) reference as it also does not deal with carbon use efficiency, but evaluates the effect of microbial turnover.

Reviewer: The paragraphs at end of the Introduction and beginning of the Materials & Methods section are nearly identical and summarize the modifications to the basic "German model". I appreciate the clear organization, but wonder if some redundancy can be removed.

Response: In our new submission we shorten the end of the introduction, and provide the details in the beginning of the method section. The end of the introduction will read like: "We organise the paper in the following way: We apply and develop a series of microbial decomposition models which differ with respect to formulations of soil organic matter depolymerisation and respiration. We then evaluate the different models to a step increase in temperature and compare the results against traditional, first order decomposition models. " We keep the more detailed general model description at the beginning of the method section.

Methods:

Reviewer: I really appreciate Figure 1, which nicely summarizes the model modifications being investigated here. Is it worth adding Fig. 1b that shows the first-order model (#5) used too? Alternatively, this could be described more completely in the text (is it just a two pool model with SOM and microbial biomass (that doesn't do anything?)

Response: We have changed Fig 1 now to explicitly show the different model families: Different formulations of depolymerisation (Fig 1a), partitioning between maintenance and growth respiration (Fig 1b), and equilibrium microbial model, where the microbial uptake at each time step is equal the microbial carbon loss via death or respiration (Fig

1c), which in the special case of Model 4 is the first order decomposition model.

Reviewer: Model 3 is a reverse Michaelis-Menten models, which has been proposed and used in other microbial explicit models (e.g. Schimel & Wientraub 2003), as opposed to the forward configuration used by Allison et al 2010, on which the German model is built. References to models and the theory behind forward vs. reverse Michaelis-Menten models are likely relevant here.

Response: We will add the Schimel and Weintraub (2003) reference to the reverse Michaelis-Menten model in the beginning of the model description section in the improved manuscript.

Results:

Reviewer: The 'knife edge' results are mentioned in both results and discussion, but I'm not really clear what this refers to? Is it obvious is any of the display items? If not, could it be- it's such a strongly visual phrase it seems like it should be obvious in a figure?

Response: In both instances, we refer to Schimel and Weintraub (2003), who used this term, and also showed the instability of the system. We feel it is not necessary to add a graph, particularly we do not want to create the impression that this finding is new (which it is not).

Reviewer: In Table 3 and results I'm not clear of the utility of the short times scale steady-state solution for M? Is this just to show that the forward models (#1 & 2) aren't stable & oscillate over short times scales (as evident in Fig 2b)? I'm also curious what causes the shift in the steady state equation for M in model 3 over longer times scales? It's also not clear what part of Table 3 if being reference in the results (P 10868, L 10-12), specifically what's independent of 'M', steady state S pools? This is generally true of other microbial explicit models (see Wang et al. 2014). I'd suggest dropping the shorter times scale M response to focus on the longer time scale dynamics, or spend

time discussing both.

Response: Both reviewers mention that they have trouble seeing the value of the short-term equilibrium in Table 3. The timescale of the microbial turnover is much shorter than the time scale of soil organic matter turnover. That is microbial biomass adjusts much faster to changes in environmental conditions than soil organic matter itself. Thus, over the timescale of microbes, soil organic matter can be approximated by a constant (it does not change that much). This allows microbe to equilibrate with the current level of soil organic matter (quasi-steady state, see also Menge et al., 2009). We can then substitute the quasi-steady state expression for microbes into the function of depolymerisation and, microbial death, and respiration. In the improved manuscript, we will add a figure (Fig 3 here in this response), that shows how the assumption of microbial equilibrium compares against the fully dynamic models with respect to the dynamics of decomposition and CO_2 flux. Further, this analytical trick helps to build the bridge to traditional first order models, because the formulations of decomposition are now independent of the microbial biomass. For example depolymerisation in Model 3 now becomes:

$D = V\_max * S * epsilon - K\_M * lambda\_d$

Reviewer: The authors never refer to Fig. 3 in the results, but I assume the first paragraph on P 10871 refers to these results?

Response: Yes, that is correct, this paragraph describes the Fig 3 results. We will make sure our improved manuscript has all figures referenced.

Reviewer: I wonder if the lack of apparent changes of Q_10 in the first order model (#5) are an artifact of the analysis done here, or the very simplified model structure being considered (see Koven et al. 2015).

Response: Q_10 in the first model is higher than 1, so there is a (albeit small) temperature response also in model 5. The much lower Q_10 stems from our initial modeling

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setup to force the results to the same beginning and end values for CUE, soil organic carbon and microbial biomass. This required us to set Q_10 for Vmax to be 1, while only respiration was temperature sensitive. Based on the reviewer's suggestion, we now do not force the model to the same end-points, but through the same initial response to temperature. The apparent Q_10 figure (Fig 4 in the discussion paper) was intended to compare short-term vs. long-term responses. The new modeling setup allows us now to compare short-term vs. long-term responses in a more direct fashion. Thus the 'too derived' Fig 4 in our initial manuscript becomes obsolete.

Discussion:

Reviewer: The beginning of the discussion reads too much like the introduction. In my mind, the discussion should highlight key finding of the work presented here, not a literature review on microbial models.

Response: In our improved manuscript, we will shorten the first paragraph of the discussion. It was our intention to acknowledge earlier work. We will tip our hats to these researchers now in appropriate places throughout the section, and more directly in conjunction with the discussion of our results.

Reviewer: I wonder if you really need the nuances of maintenance respiration and CUE to get a reverse Michaelis-Menten model to approximate a first order model? Just looking at equation 9, if Km is small (relative to M [P 10866, L 23]) then $D = V\_max * S$ (basically eq. 14).

Response: This is correct, there is no need of nuanced respiration and CUE to get a first order model. We can show that now even better, with the suggested layering of the model. In previous model 4 (in absence of enzyme production cost), the decomposition equation is exactly a first order model. However, what needs to be considered in some way is a temperature dependent CUE. That is how much carbon is being rerouted back into soil organic carbon pool. This point is important and we will add it to the result and discussion sections.

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Reviewer: Material in the Appendix is frequently referred to in the discussion; however, it's not really clear what part of the Appendix readers should direct their attention. Moreover, it's not really clear if or how the mathematical derivations in the Appendix are (or are not) used in the main display items and results of the paper. If the material in the Appendixes are being used for simulations presented they should be clearly referenced in the main text. In my mind the Appendixes should NOT be used as a large parenthetical to house fancy mathematical derivations that don't inform the larger manuscript.

Response: Our intention of the appendix was to not clutter the method section with detailed mathematical derivations, but provide the readers with the necessary tools to recreate the differential equation for microbial biomass and soil organic matter. However, in retrospect we can relate to the reviewer (and readers) not seeing the link between the method and appropriate parts and equations in the appendices. In our improved manuscript, we will have the appendix clearer referenced.

Reviewer: I appreciate the need to use simple models like this to understand the mathematical dynamics of microbial explicit models, but how much do we lose by using such a simple model that it doesn't really represent soil C dynamics at large spatial, or long temporal scales? There's some of this at the end of the discussion, but greater introspection into how this study may inform ecosystem scale models (or larger) that are used for soil C projections would be helpful.

Response: We will add to the discussion, and more importantly in the conclusion how the evaluation of simple models can serve larger scale models. We do this in a series of questions. First, in current models, soil organic matter is represented as a suite of pools feeding into each other, and representing different recalcitrance. In this simple model, microbial death leads feeds back into the soil organic carbon pool, but in large scale decomposition model microbial necromass and processed carbon feeds into a different quality pool. Whether this secondary material is easily to decompose (or to access), plays an important role on carbon storage (and on the response to tem-

perature on decadal scale). Secondly, the work clearly shows dynamical differences whether substrate-enzyme reactions are considered a rate limiting step, resulting in forward vs. backward model. We show that there are potential mechanisms that support a backward model. The results then resemble more closely first order models. Further, we show that even in simple models, the response to temperature is a composite of parameters that are hard to come by, including half saturation constants, sensitivity of microbial respiration to temperature, the amount of enzyme produced by microbes, as well as enzyme activity. Finally, our work shows mathematical linkages between first order decomposition model and microbial models, which help to understand and potentially improve first order models, as more nuanced microbial models are being developed.

Reviewer: P 10858, L 5-6 This sentence is somewhat awkward and doesn't seem grammatically correct.

Response: Changed to "Under sufficient substrate availability, this new feedback allows an unconstrained growth of microbial biomass."

Reviewer: P 10858, L 6 I'd recommending modifying the beginning of this sentence by adding 'often' or some other qualifier. For example: "A second phenomenon 'often' incorporated in microbial decomposition models"

Response: Will be changed

Reviewer: P 10859, L 29 Wieder et al. 2014a doesn't deal with microbial models (as implied by the text in the sentence. A better references may be Wieder et al. 2015, Geoscientifc Model Development.

Response: We will substitute the reference as suggested.

Reviewer: L 10860, L 6 What are "dynamical consequences"?

Response: We will change that to "This differentiation can impact the dynamics of the microbial biomass".

Reviewer: I appreciate thorough documentation supplied in the Appendix, but to aid in reader understanding can specific parts of the Appendix be referred to in the main body of the text where appropriate (e.g., sections 2.1.3 & 2.1.4)? Were are A1, A2:: etc. referred to in the text? (see also P 10873 L 23 and P 10874 L 10)

Response: Our improved manuscript will have a clearer link to the specific parts in the appendix in the method section and throughout the text.

Reviewer: P 10869, L1-2 this statement is not obviously supported by results presented in this paper.

Response: This part of the result section is different in the improved manuscript, due to the altered modeling setup.

Reviewer: Figure 3: It's not immediately obvious to what model this figure refers? The green color chosen is painful to look at.

Response: We will change the caption to make clear that the simulations refer to OPT model. We also have changed the color scheme (see Fig 4 in this response)

Reviewer: P 10873 L 23: It's nice that the authors derived a reverse M-M model (from the forward configuration), but it seems like a lot of work to replace a term in the denominator of an established model seem like a lot of work. I'm not sure how much the derivation is warranted in the Appendix.

Response: Respectfully, we would like to keep this part in the appendix, since we explicitly point to two specific mechanisms that can change a forward M-M model into a backward model. Showing the full derivation helps the reader to understand that transition.

Reviewer: Paragraph beginning on P 10875, L 10 should reference Fig 3.

Response" This paragraph has changed. The warming response in model 4 is now not confined to the temperature sensitivity of microbial respiration, but also to the depoly-

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merisation rate.

Reviewer: P 10877 L 17-19 This sentence is completely unsubstantiated and should be qualified & reference or removed.

Response: The reviewer is right. Through the modifications of the modeling setup, this sentence is not needed.

Reviewer: P 10877 L 20-21 This seems like completely throw away sentence that should be removed since no discussion of experiments and observations are used or discussed earlier in the paper.

Response: Both comments are taken care of by rewriting the conclusion. The conclusion links our work with large scale models and the challenges to incorporate microbial models in there. (see also our response to the earlier comment on the use of simple microbial models).

References cited in the response to reviewer comment:

Allison, S. D., Wallenstein, M. D., and Bradford, M. A.: Soil-carbon response to warming dependent on microbial physiology, Nature Geosci., 3, 336–340, doi:10.1038/ngeo846, 2010.

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Hagerty, S. B., van Groenigen, K. J., Allison, S. D., Hungate, B. A., Schwartz, E., Koch, G. W., Kolka, R. K., and Dijkstra, P.: Accelerated microbial turnover but constant growth efficiency with warming in soil, Nature Clim. Change, 4, 903-906, doi:10.1038/nclimate2361, 2014.

Koven et al. (2015) Controls on terrestrial carbon feedbacks by productivity ver-

sus turnover in the CMIP5 Earth System Models. Biogeosciences, 12, 5211-5228, doi:10.5194/bg-12-5211-2015

Menge, D. N. L., S. W. Pacala, and L. O. Hedin. 2009. Emergence and maintenance of nutrient Limitation over multiple timescales in terrestrial ecosystems. The American Naturalist, 173:164–175.

Schimel, J.: Soil carbon: microbes and global carbon, Nature Clim. Change, 3, 867-868, doi:10.1038/nclimate2015, 2013.

Schimel, J. P. and Weintraub, M. N.: The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model, Soil Biol. Biochem., 35, 549-563, doi:10.1016/S0038-0717(03)00015-4, 2003.

Wang, Y. P., Chen, B. C., Wieder, W. R., Leite, M., Medlyn, B. E., Rasmussen, M., Smith, M. J., Agusto, F. B., Hoffman, F., and Luo, Y. Q.: Oscillatory behavior of two nonlinear microbial models of soil carbon decomposition, Biogeosciences, 11, 1817-1831, doi:10.5194/bg-11-1817-2014, 2014.

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Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G., Bonan, G. B. 2015. Representing life in the Earth system with soil microbial functional traits in the MIMICS model. Geosci. Model Dev., 8:1789-1808.

Figure Captions

Figure 1. Conceptual diagrams for the microbial-enzyme models applied. Solid lines represent material flow (in FWD and FWD model with maintenance respiration) and dashed lines represent information flow (in Rev and OPT models). E, S, E-S, D, DOC, M represent enzyme, substrate, enzyme-substrate complex, depolymerisation, dissolved organic carbon, and microbial biomass carbon, respectively. We analyse the

different models in three ways: a) Base models of forward vs reverse formulation of depolymerisation. In the forward version, depolymerisation scales microbial biomass via enzyme production. In the reverse formulation the decreasing marginal return curbs rates of depolymerisation. This decreasing marginal return can partly be overcome by enzyme production optimisation. b) For all models we introduce partitioning between maintenance and growth respiration. c) Microbes are instantaneously in steady with substrate delivery (reverse models only).

Figure 2. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d) respiration to a 5°C warming in base models (forward vs reverse). The black line represent initial values, which are model equilibria at15°C. (Note: Differences in simulated soil organic carbon and respiration by OPT and the FOD are almost equal, and therefore not discernible. In the OPT model, simulations are carried out at zero enzyme production cost, i.e. $\mu = 0$).

Figure 3. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d) respiration to a 5°C warming for all models, if separation of maintenance and growth respiration are considered, and if microbial biomass is assumed to be at quasi-steady state. Black thin line represent initial values, where equilibria @ 15°C. Colored thin lines represent base models. Dashed lines (growht and maintenance) and dotted lines (quasi-steady state) represent modifications for REV and OPT models respectively. (In the OPT model, simulations are carried out at zero enzyme production cost, i.e. $\mu = 0$).

Figure 4. Long-term responses of optimized enzyme production (OPT) model to a 5°C warming in a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d) respiration operating at different relative enzyme production costs (μ), see Equation 13. Thick lines represent warming response and thin lines represent corresponding equilibrium at reference temperature.

Please also note the supplement to this comment:

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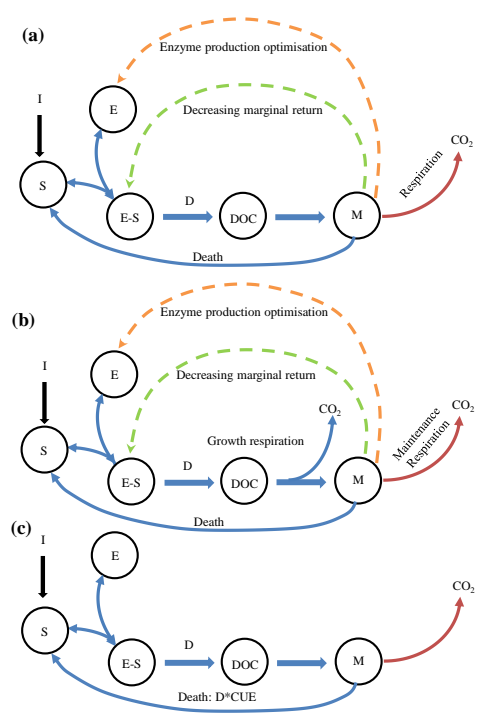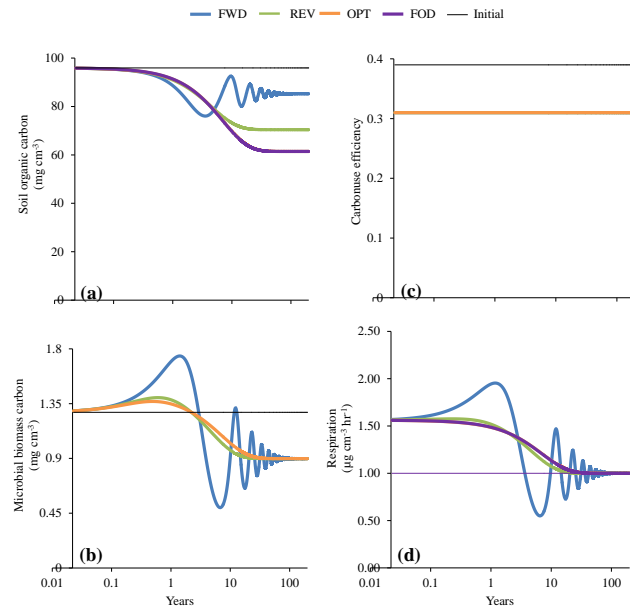**(a)**

Enzyme production optimisation

Decreasing marginal return

CO_2

Respiration

I

E

S

E-S

D

DOC

M

Death

(b)

Enzyme production optimisation

Decreasing marginal return

CO_2

CO_2

Maintenance Respiration

Growth respiration

I

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D

DOC

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Death

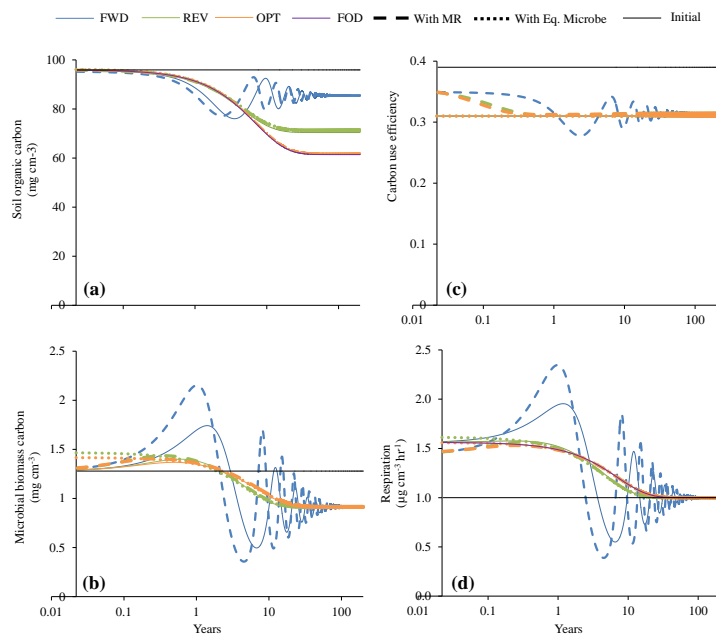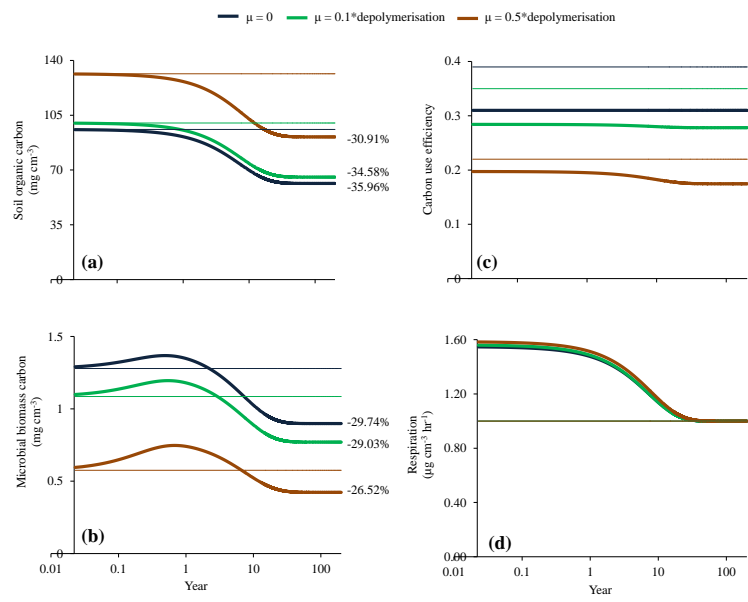**(c)**

CO_2

I

E

S

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D

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M

Death: D*CUE

Fig. 1.

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Fig. 2.

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Fig. 3.

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Fig. 4.

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