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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: As the authors mention, the behavior of models 1 and 2 is very similar [P10872, L23]. How does the additional complexity mathematically manifest itself in the emergent dynamics? Can the similarity be explained by the structure of the models? In the case of models 1 and 2, it seems that they share the same mathematical structure, in that model 2 can be reduced to model 1 as follows:

dS/dt = I – lambda_d*M – D where D = V_max*S*M/(K_E + S) [same in models 1 & 2]

dM/dt = (D - lambda_r *M)*(1-g) – lambda_d *M [form of model 2] = (D – D*g - lambda_r *M + lambda_r *g*M) – lambda_d *M = (D(1-g) – M(lambda_r - lambda_r

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*g + lambda_d) = alpha*D – beta*M [same form as model 1]

Where alpha = (1-g) and beta = (lambda_r - lambda_r *g + lambda_d) for model 2. How do these relate to epsilon and lambda_d in model 1, respectively? The authors briefly discuss concerns associated with adding parameters [P10873]. Is introducing uncertainty through extra parameters warranted here? The temperature sensitivity of the partitioned respiration model is indeed different, but the model structure is the same. Additional discussion on how the models relate when reduced mathematically would be a great addition to this manuscript. For example, why does model 4 with mu=0 behave so similarly to model 5?

Response: Thank you for your detailed comments, which help us greatly to improve our Manuscript. In response to the suggestions from Reviewer 2, in our improved manuscript, we change the presentation of the models. We first introduce forward (FWD) vs. reverse (REV and OPT) Michaelis-Menten models, where the main difference is a decreasing marginal return in the reverse model and the subsequent optimization of enzyme productivity. Basically, these are the results of model 1, and model 3 to 5 without separating out maintenance respiration (Fig 2). We then compare each of the model to a variant where we first introduce a separation between growth and maintenance respiration. Finally, we assumed for the REV and OPT models, that microbial biomass is at quasi-steady state with substrate supply (See Fig 1). Both reviewers mention that they have trouble seeing the value of the short-term equilibrium in Table 3. We explain this better in our improved manuscript. 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 (quasi)-equilibrate with the current level of soil organic matter (see also Menge et al., 2009). We can then substitute the expression for microbial biomass as obtained from dM/dt = 0 into the function of depolymerisation and, microbial death, and respiration,

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which is the microbial quasi-steady state. In the improved manuscript, we will add a figure (see Fig 3 in this response), that shows how the assumption of microbial equilibrium compares well against the fully dynamic models, with respect to the dynamics of decomposition and CO2 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 (D) in Model 3 (now REV model) now becomes

D = V_max*S – K_M*lambda_d/ epsilon

Where V_max is a maximum depolymerisation rate, S soil organic matter carbon, k_M the half saturation constant for microbes, and epsilon is carbon use efficiency.

The expression of depolymerisation above becomes independent of microbial biomass. This expression becomes a first order model, if k_M * lambda_d « V_max *(1-g). Similarly, in model 4 (now, OPT model) under mu = 0, and dM/dt = 0 (quasi-steady state) depolymerisation becomes

D = V_max*S Microbial death = V_max*S* epsilon And thus dS/dt = I – V_max*S*(1-epsilon)

where I is the input.

As for the reviewer's analysis above, the reduction show requires a temperature sensitivity of the term beta (instead of alpha, as used in model 1 in our discussion paper), and is important on the short microbial time scale. We are convinced that our reorganisation of first considering a microbial model without maintenance respiration, then adding maintenance respiration, and ultimately assuming microbial steady state helps to explain how nuances of microbial models impact the temperature response, and how they compare analytically to traditional first-order (FOD) models.

Reviewer: Overall, this manuscript is well-written and presents an interesting modeling analysis. It could be improved by providing a perspective on future models and giving

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specific recommendations that the reader could take away for model development.

Response: Thank you for your positive review! This comment has also been raised by reviewer 2. 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 easy to decompose (or to access), plays an important role on carbon storage (and on the response to temperature on decadal scale). Secondly, the work clearly shows dynamical differences whether substrate-enzyme reactions are considered a rate limiting step, resulting in forward (Models 1 and 2 in the discussion paper) vs. reverse models (Model 3 and 4 in the discussion paper). We show that there are potential mechanisms that support a reverse model. The results then resemble more closely to the traditional first order models. Further, we discuss 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 larger scale models.

Specific comments

Reviewer: P10858, L8: It may be more appropriate to say that you “analyse five microbial decomposition models”, as this is not a general analysis of all existing models, nor of models with multiple pools.

Response: This will be changed according to the suggestion.

Reviewer: P10858, L10-15: How does your proposed model compare to models that

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explicitly represent enzyme dynamics with finite potential binding sites, such as the MEND and DEB models?

Response: To our knowledge the MEND model does not have finite potential binding sites, based on our reading of Wang et al. (2013). Their steady-state solution is fairly similar to our model 1 and 2, although the MEND model considers additional pools. We haven't found any reference of the DEB model. Perhaps of critical importance to the difference between forward and reverse models, which – based on your comments elsewhere, and based on Reviewer 2, we are hashing out much more.

Reviewer: P10858, L15: "fast responses" in relation what?

Response: We will change this to "immediate response".

Reviewer: P10858, L16: Why "short-term adjustment in microbial growth"? From the figures it appears that microbial biomass, as with carbon storage, reaches a new (long-term) steady-state.

Response: The response to this question should come out of one of the major changes of the manuscript. We try to motivate a short (microbial) timescale and a longer (soil organic matter) timescale. On the short timescale, microbial biomass adjusts quickly to new environmental conditions (temperature), and on the long timescale, microbial biomass only adjusts to the slow decrease of soil organic matter (it is in quasi-equilibrium with soil organic matter). See also our response to the main concern above.

Reviewer: P10859, L17: Can add citation for Wieder et al. 2015 here.

Response: We will add this reference in our new submission.

Reviewer: P10859, L20: The citation for Li et al. 2014 would be appropriate here regarding CUE response to warming across models.

Response: We will add this reference in our new submission.

Reviewer: P10860, L15: Although additional parameters were added to separate mi-

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crobial respiration sources, the form of model 2 can be reduced back to model 1, as shown in the main comments above. Does the parameterization drive the difference in decomposition dynamics, since the model structure is the same?

Response: It is actually the model structure that drives the difference, since now different terms are temperature sensitive. That is, in the mathematical derivation under "main comments" parameter beta, instead of parameter alpha becomes temperature sensitive, when moving from model 1 to model 2.

Reviewer: P10861, L8: For clarity, it would be good to note that enzyme concentrations and microbial biomass go together and that you do not represent them as separate pools in the simulated differential equations; rather, you focus on the response of 2-pool, substrate-microbe models to warming. Can you confidently capture microbe and enzyme allocation/reaction/production dynamics without an explicit enzyme pool?

Response: We will make more clear that we assume that the enzyme pool is assumed to be at steady state with respect to the microbial biomass. That is, the enzyme pool does not change unless microbial biomass changes. Given, the simple mechanisms that describe enzyme production and turnover, our equilibrium assumption is a valid simplification.

Reviewer: P10861, L19: It would be good to clarify that the "tendency" is the "derivative" when you first use it, as I feel that the latter is more commonly used among BG readers.

Response: We add in parenthesis "derivative with respect to time".

Reviewer: P10863, L19: To be consistent with the literature, it may be good to mention here that the final form you use for model 3 is a reverse Michaelis-Menten formulation, as in Schimel and Weintraub 2003.

Response: We will add the reference in the method, and now make explicit distinction between forward and reverse Mechaelis-Menten models.

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Reviewer: P10865, L3: Is there a negative sign missing in Eq. 14? Otherwise, dS/dt = constant*S with a constant > 0 would increase exponentially. Also, please check your mass balance: if a (1-epsilon) fraction leaves to respiration, then should a net –(1-epsilon) be leaving S, since –k*S +epsilon*ks in the mass balance?

Response: Thank you for catching this! This equation should correctly say: dS/dt = I –(1- epsilon (del_T))*k*Q_10^(del_T/10)

where I is input of fresh litter.

Reviewer: P10865, L10: Which are the traditional models (cite a few) and how do they represent the temperature sensitivity of CUE? Often CUE decreases linearly with temperature in simple models and often 'traditional', Century-type models include more than one pool of carbon.

Response: We changed the description of how we set up model 5 in that we explicitly mention how this setup differs from traditional models such as CENTURY and Roth C. The two major differences are that our model only considers a single pool, while traditional models consider a series of different quality pools feeding into each other. We also mention that with a temperature dependent carbon use efficiency, a temperature increase changes the fraction of carbon processed becoming CO2. This is not typical to traditional models, as the fraction respired is not a function of temperature.

Reviewer: P10865, L21: What do you mean by tuning factors for V_max1 and K_E and what are they tuned to for model 1 in addition to the German et al. parameters?

Response: We have changed the formulation, such that it becomes clear that we did not tune this part of the model, but instead worked the tuning factors directly into the parameters. It now reads: "We start off with model 1 where we use the parameters as reported in German et al. (2012), however, we report V_max1 and K_E by considering 15°C as our reference temperature and by working their tuning factors directly into these two parameters."

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Reviewer: P10866, L7: I think “maintenance estimation” should be “maintenance respiration”. Also, why one-third of the death rate? Please provide a reference or more reasoning.

Response: Yes, a typo. We re-addressed the partitioning of maintenance vs. growth respiration. We had a hard time finding specific values in the literature, but motivated the partitioning based on vegetation models. LPJ (Sitch et al., 2003) and ED (Moorcroft et al., 2001) have a growth respiration factor of one-third. We then constrain the overall respiration by the carbon use efficiency in German et al., 2012, and obtain a maintenance respiration rate that is now close to the microbial death rate (lambda_r =1.25 * lambda_d)

Reviewer: P10866, L16: Here you say that you match the equilibrium values for CUE, M, S and decomposition. Matching equilibrium decomposition rates had not been mentioned before?

Response: In the discussion paper, matching decomposition is actually not necessary, as it results from matching CUE, M, and S. You will notice, though, in our improved manuscript, it is our goal to match depolymerisation immediately after the temperature increase, and let the long-term responses deviate.

Reviewer: P10868, L5-15: This confuses me a little, as the two differential equations are coupled and respond together by necessity. The magnitude of change within each pool differs, as the pool sizes are significantly different. Please provide a bit more explanation and rationalization for this part of your analysis. In calculating the true equilibrium, dM/dt = 0 and dS/dt=0.

Response: This confused both reviewers and we take great care in our improved manuscript to show the use of short-term (quasi) vs long-term (true) equilibrium. The turnover of soil organic matter is much slower than that of microbe. Therefore, over the timescale of microbial adjustment, there is little change in S. It therefore allows microbe to almost equilibrate with S. In other words, microbes are at quasi-steady state.

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As soil organic matter changes, the short-term equilibrium of microbial biomass (or the quasi-steady state) is changing along. In our improved manuscript, we will show a plot (Fig 3), with the equilibrium microbial biomass as a function of time. We show that, over mid- to long-term the quasi-steady state of microbes is a good approximation of the actual microbial biomass. This paragraph will be entirely rewritten in the improved manuscript.

Reviewer: P10870, L22: Can you show mathematically how model 4 reduces to the linear model when mu=0?

Response: Equation 12 has the depolymerisation as D = Vmax * S – sqrt(K_P*c*V_max*S).

Where the second term on right hand side is the reduction of depolymerisation if there is a cost associated with decomposition (i.e. mu>0). If mu is 0, D becomes V_max*S, which is the form of the first order model. We will reference the equation and how it changes under zero cost, in order to clarify and support our assertion.

Reviewer: P10875, L18: Considering putting (mu=0) for the negligible costs scenario, just to be clear.

Response: We will do so in our improved manuscript, whenever we refer to negligible, or a similar term.

Reviewer: P10876, L1: How realistic are the equilibrium values you fit to and how much do these vary in reality? If the parameters are fit to different values, how much might the dynamics and conclusions change? For example, the enzyme-substrate model in Allison et al. 2010 may or may not oscillate depending on the parameters.

Response: The equilibrium values can vary a great deal across the globe, depending on climatic conditions and soil quality. Perhaps equally important is the question, how much the parameters are constrained which determine the equilibrium values. We find that these values are fairly uncertain. As we compare models with each other,

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we felt that we should not pick arbitrary parameters, but choose them that the models are comparable in some way. In our discussion paper, we chose to force the model through equilibrium values. Reviewer 2 pointed out that some of the results were too derived (in particular the apparent Q_10, Fig 4 in our discussion paper). We agree with reviewer 2, and we changed the parameterisation such that the equilibrium at reference temperature are the same, and that the initial response to a temperature perturbation is equal across the model.

As for the oscillation, Wang et al. (2014) showed the parameter space with respect to the oscillatory behavior. Large V_max compared to K_m dampens oscillation quickly. On the other hand, in the Allison et al. (2010) model, a large fraction of the input and microbial necromass was assumed to become DOC, which does not require enzymes for microbial consumption. This assumption also reduces the positive feedback between microbial growth and decomposition, because microbial growth can occur independent of enzyme production via consumption of readily available DOC. We will briefly explain and refer the oscillatory behavior as a function of parameterisation in the discussion.

Reviewer: P10878, L2: Is there a +kr[ES] term missing from the expression given for d[E]/dt? If the reversibility of enzyme binding removes –kr[ES] from d[ES]/dt, then where does it go? Also, reversibility is not shown in the diagram of Fig. 1.

Response: Yes, this is missing, but the mistake is editorial and does not affect the subsequent math. We will show the reversibility in our new Fig 1.

Reviewer: P10878, L6: Please explain a little more in the text what P is and that it changes; i.e., that it is a rate proportional to microbial biomass.

Response: Our improved manuscript will say that P is the production of enzymes, and that in most microbial decomposition model, this is assumed to microbial biomass. However, our model 4 (OPT model) will relax this assumption and P will be optimized.

Reviewer: P10878, L13: Why are you most interested in E_t? The Michaelis-Menten

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derivation using the quasi-steady state approximation for short-lived intermediates (i.e., d[ES]/dt = 0) is very standard in textbooks, but could be better explained here.

Response: Starting from line 13 we will rearrange to the following:

The Michaelis–Menten approximation for depolymerisation assumes that the system is in quasi-steady state in which the tendency d[ES]/dt and d[E]/dt are zero. This implies also that tendency of the total enzyme concentration dEt/dt (with Et = ES + E) becomes zero.

Here we include also that the total available sites do not change (S is constant) within the timescale of enzyme reactions. This implies that Eq. (A2) becomes zero as the different reactants will approach a steady state and in therefore the concentration of the free enzymes and the enzyme substrate complex can be expressed as a function of the total enzyme concentration.

Reviewer: P10878, L15-16: This sentence seems to cut off prematurely, in which E_t . . . is?

Response: This is now taken care of with the new formulation.

Reviewer: P10878, L17-19: Consider using S_t for total sites instead of [S] which is also used as the transient free sites and is certainly not constant, otherwise d[S]/dt=0 would defeat the purpose. I think that the condition on S or St is not necessary for the derivation; Eq. (A2) = 0 by the quasi-steady state assumption of fast-reacting intermediates. Also note the missing period.

Response: The S stands for the total substrate, and we would like to keep that in the main text. We will mention in the derivation of the Michaelis-Menten equation (currently p 10878) that the amount of substrate is much bigger than the amount of enzyme substrate complex. Because S_tot = S_free + ES and ES « S_free, S_free ∼= Stot ∼= S. You are correct, the condition on S_tot is not necessary. And thus we delete this part. What we meant though, S_tot changes only marginally (quasi-steady state of E

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and ES) so that the relative concentrations of ES and S do not lag the substrate.

Reviewer: P10879, L10: Similarly to what? I would suggest moving P10879 L18 – P10880 L5 to above P10879 L10. It might be better to introduce the previous method and then what you do, instead of switching back and forth.

Response: We agree. In our new manuscript we now deal with the quasi-equilibrium of the total enzyme concentration first and then talk about how we deal with the DOC sink.

Reviewer: P10879, L13: Is Eq. (A7) missing a term? From [Et] = [E]+[ES], taking the derivative and substituting Eq. (A1) and (A2), you would get d[Et]/dt = P – lambda_E1*[E] – kcat + lambda_E2)*[ES]. This would then add a term to the denominators of (A8) and (A9) and carry through the expressions presented to (A25), etc. It would also be good to be consistent with your Et and [Et] notation, as they are used interchangeably in the appendix.

Response: Introducing k_cat*[ES] in this equation would imply that the enzymes are destroyed when the product is formed. Likely, both is happening, some enzymes are destroyed, and some can be recycled. lambda_E2 is thus a parameter that includes both, the destruction of enzymes when products form, as well as denaturizing of enzymes while they are complexed with substrate. We will also make sure to maintain consistency on [E_t] notation.

Reviewer: P10882, L4: It would be nice to keep consistent notation for [S]; for example, St = theta (S+ES), where S represents free, available sites.

Response: We would like to keep S for the total amount of substrate, to be consistent with the main text. But we make sure, here and in the discussion of the Michaelis-Menten equiation, to inform the reader how S (all forms of S) relates to the available and complexed sites.

Reviewer: P10882, L8-9: Can you explain a bit more why you take a Taylor series ex-

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pansion (linearize) around the total sites S=0 versus linearizing around the equilibrium S? Also, you alternate between kE and KE.

Response: We will expand there. We assume that enzyme concentrations are much bigger than the potential reaction sites. That is E_t + K_E » S/theta. Thus the term S/theta is in the vicinity of zero if compared to E_t + K_E. This allows us to expand around zero. We will also add, that we obtain the same result, if S_f « K_E in Equation A21, (small amount of free sites) and thus

Equation A21

$S_f = S/\theta - S_f*E_t/(K_E + S_f) \sim= S/\theta - S_f*E_t/K_E$

Therefore

$S_f = S/\theta * K_E/(E_t + K_E)$ We will also make sure to maintain consistency on K_E notation.

Reviewer: P10882, L12: Could you explain why the S/theta term is much smaller than E_t and K_E (as on P10883, L1) and dropped from the denominator of Eq. (A24)?

Response: We will add, that this particular solution is for a small amount of binding sites, and enzymes compete for free sites. Thus E_t » S/theta, and it can be dropped from the denominator.

Reviewer: P10884, L5: Is the final expression missing an M in the numerator?

Response: Correct and nice catch! We will add the microbial biomass as a factor.

Reviewer: P10885, L1-3: If P is a function of M as before, then M can also be written as a function of P. When taking the derivative of G in Eq. (A32) with respect to P, does the lambda_r*M term come into play? Similarly with substituting a function of M for P in the denominator of D (A35) when determining if an optimum exists.

Response: In this solution, where the microbial community optimizes enzyme produc-

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tion, P is independent of the microbial biomass, therefore the derivation of lambda_r*M is zero.

Reviewer: P10892, Table 2: For model 4, the value of KP is not given, does this mean that it carries over from the fitting of the other models? For clarity, please addïĂă μ to the table where Pc/D is given for model 4.

Response: We realize, the ratio Pc/D in the table is confusing. We will use mu, as suggested, and motivate it usage better in the method section (10867 L8-10). Values for both parameter KP and c are hard to come by. But in our solution they always occur together in a product (K_P*c). Moreover, the fraction of enzyme expenditures in relation to depolymerisation can easily be expressed as a function of maximum depolymerisation (V_max*S) and the product K_P*c (Equation A34). Mu is then the fraction of carbon that is used for enzyme production compared to the potential depolymerisation rate, as it would occur without cost, evaluated at steady state. With think this makes enzyme expenditures a bit more tangible because we relate these costs to processing rates. Once we defined mu, we can easily derive K_P*c. We note that the potential depolymerisation rate at steady state is also the input of fresh litter (I). We added the values of K_P*c to the table.

Reviewer: P10893, Table 3: Should the short/fast time scale and long time scale have the same conditions (namely, S =eq. S) in the caption? Please clarify the methodology in the caption.

Response: We improve Table 2, also in response to the improved modeling setup. In the short-term equilibrium, we let microbial biomass equilibrate with S (any potential value of S). This is motivated by the fact that microbial biomass turns over much faster than soil organic matter. We added a new column, that calculates depolymerisation if M is at equilibrium (with any given S). We also have carried out additional simulations, that show the dynamics of soil organic carbon, respiration, and the diagnostic equilibrium microbial mass. We can show, that the assumption of a microbial steady-state leads to

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similar results in the medium to long-term (but not in the short-term, see our new Fig 3). We will explain the assumption of the short-term equilibrium (quasi-steady state) in the new method section (see also our response to an earlier comment to P10868, L5-15).

Reviewer: P10895-10897, Figures 2-4: Could you include a short descriptive model name for the four models in the legend or in the captions and briefly discuss why you chose a logarithmic x-axis? The log axis makes it harder to think through the dynamics and build intuition for shorter time scales; consider changing to a regular axis. 1,000 years is very long! Also, it looks like models 4 and 5 have the same orange color in the legend. Please make sure the five colors used are clearly distinguishable.

Response: We changed the model names such that they are more descriptive (now FWD, REV, OPT, and FOR) for the forward, and reverse Michalis Menten, model, for optimizing enzyme production, and for the traditional first order Model. We will add 'Logarithmic axes are chosen' to better highlight differences in short-term responses' to the figure caption. If we switch to regular axis, differences with respect to the implementation of respiration (explicit growth and maintenance respiration), and with respect to the equilibrium assumption simply disappear. We truncated our time axis 200 years when the system final equilibrium. We have changed the color scheme to better highlight the differences between models.

Technical corrections

All technical corrections will be addressed in the improved manuscript.

References cited in the response to reviewer comment:

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Please also note the supplement to this comment:
http://www.biogeosciences-discuss.net/12/C6726/2015/bgd-12-C6726-2015-supplement.pdf

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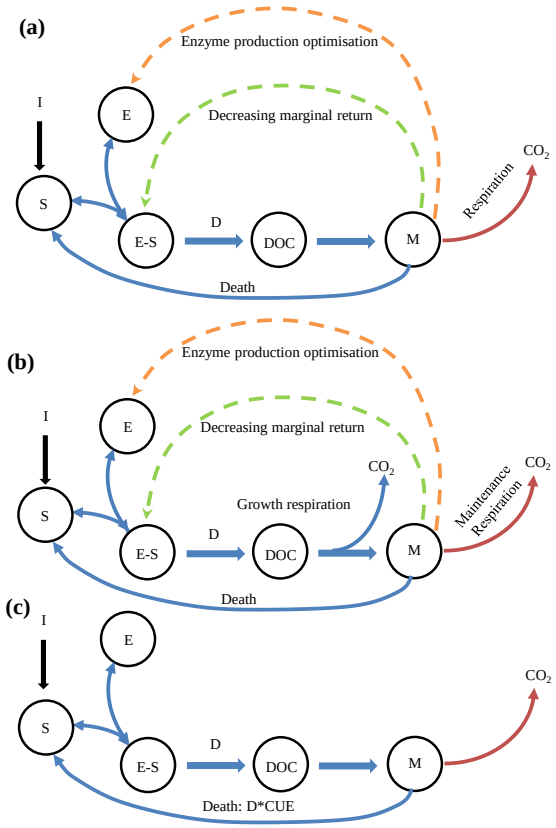

Fig. 1.

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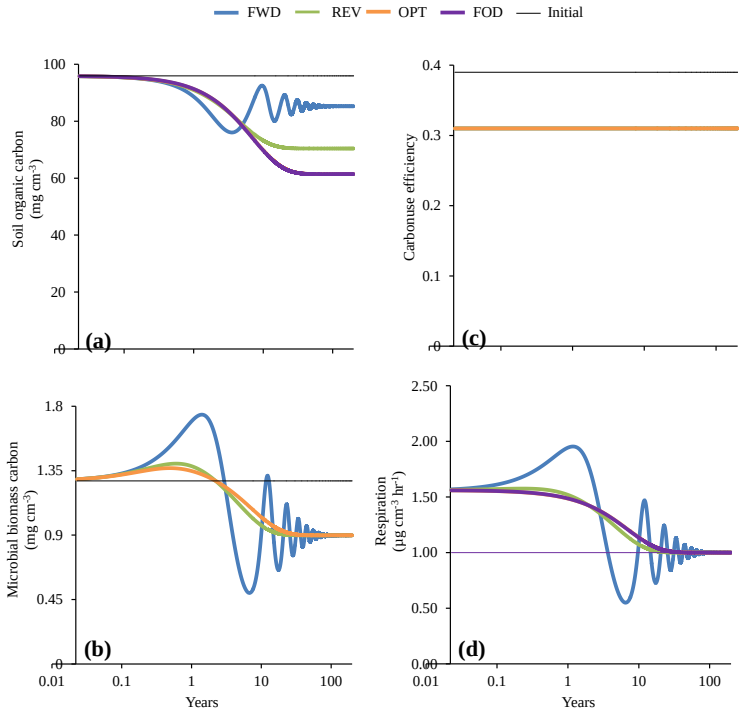

Fig. 2.

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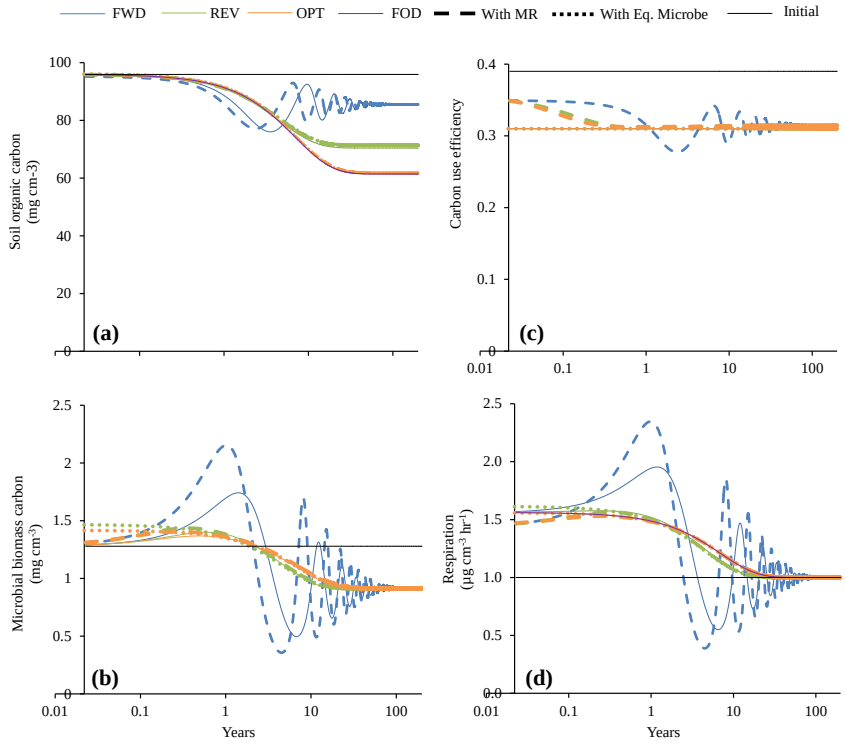

Fig. 3.

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Discussion Paper

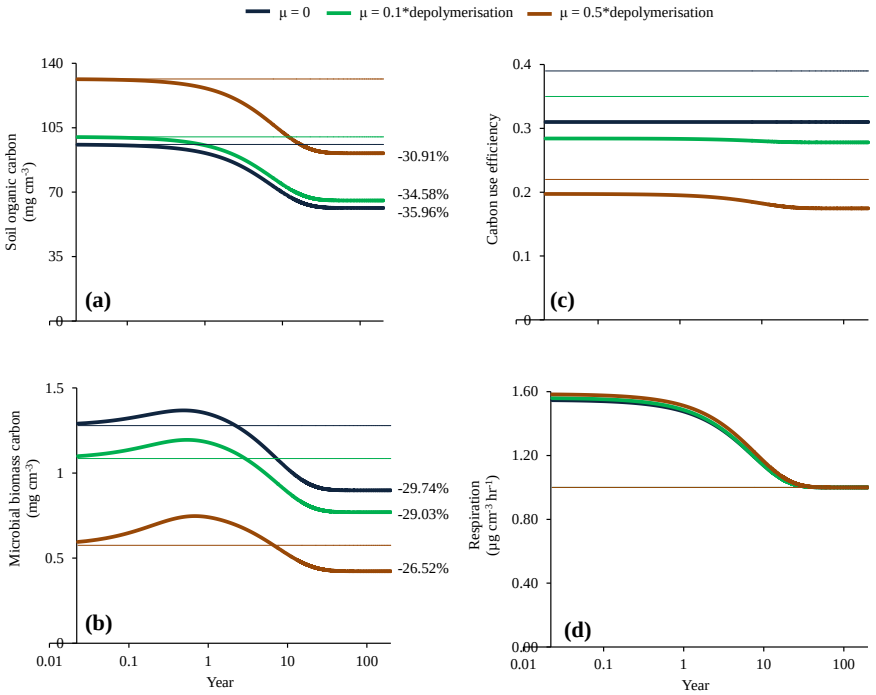

Fig. 4.

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