

Cover Letter

Dear Editor,

Thank you for giving us the opportunity to resubmit the revised version of the manuscript, “Comparing models of microbial-substrate interactions and their response to warming” by D. Sihi, S. Gerber, P. W. Inglett, and K. S. Inglett for consideration of publication in *Biogeosciences*.

The comments of both the reviewers in the 2nd round of the review helped to further improve the manuscript. In our current version, we followed comments from both of the reviewers. Both reviewers had questions on major implications/recommendation. To that end, we sought to further describe the main differences across the model, with respect to what the fundamental assumptions are, including enzyme vs. substrate limitation and assumptions about microbial enzyme production. The implications of these results are that the degree of enzyme limitation and the microbial response to enzyme limitation are potential areas that could help constrain the quantification of the long-term response of soil organic matter to warming. We added additional discussion on quasi-steady state model (based on the comments of Will Wieder) We also took care of (hopefully all) the language and grammatical errors based on the recommendations from both of the reviewers.

Below, you find a point by point response to all the reviewers’ comments, as well as a marked-up version that highlights the differences between the revised paper from the 1st round of review and this submission.

We believe that these improvements make our manuscript an excellent addition to *Biogeosciences*, particularly also because we show the mechanisms and consequences of different formulations of microbial carbon consumption resolved in current microbial models. The quantification and prediction of soil organic matter decomposition and its response to global change factor is critically important for global carbon cycle feedbacks, and therefore, the questions raised in our manuscript and our insights in decomposition models are important to the readers of this Journal.

We look forward to hearing from you soon.

Sincerely,
Debjani Sihi (corresponding author)

Response to Will Wieder

General comments

Sihi and co-authors have done a nice job revising their manuscript. The reorganization better leads the reader through the experiments & findings.

Specific comments

I'm not sure why the authors made the quasi-steady state assumption for microbial biomass in their microbial explicit model (Section 2.1.2 & 3.3)? I don't recall this analysis in the first submission, or see where previous reviews asked for the analysis? More, removing M as a state variable in the model hardly seems to simplify things, when M has to be approximated by the short time-scale equation in Table 2. The first half of the text in 3.3 seems more appropriate for the methods, and the second half of the text discusses results that are never show (as far as I can tell). This makes evaluating the claims being made challenging, but I think they are shown in Fig 3 (although this isn't referenced in the text)? Finally, these results are sparingly mentioned in the discussion, and I wonder if they contributed to, or distract from the story being presented here? If it's the former, minor changes are needed to better integrate these results throughout the paper.

We introduced the quasi-steady state (QSS) microbe model to make an explicit link to our first order decomposition model, which was requested by reviewer 1 in the first round of review. We explain now better, that under the quasi-steady state assumption the REV model and the OPT model will have identical formulation of decomposition as the FOD if a) K_e is approaching 0 in the REV model, or μ is approaching 0 in the OPT model. We discuss now the value of the QSS model, in that it is an extension of QSS for enzymes and DOC into the microbial timescale. As we show that the QSS microbe model is comparable to the base models, we can now express depolymerization based on microbial parameters instead of the microbial biomass itself. This allows to better compare rates of depolymerization across models and also compare the formulations with a first order model. This comparison then allows to better understand the parameter that defines affinity of enzymes to the substrate (K_e) and/or the role of microbial enzyme production optimization.

The ideas in the discussion are well developed and organized, but I find it helpful to refer to figures in the discussion w/ relevant text (same is true in the results).

We have introduced more references to Figures in both the Result and the Discussion section, where we thought it is helpful and appropriate.

I'm not really clear how these conclusions were reached. It seems like the authors are suggesting if we take a more complicated model (reverse M-M) and add even more complexity (optimized for yield) we can produce a model w/ identical form and function to a simple first order model. Why not just use a first order model? I wonder if those simplifying assumptions listed in the conclusion seem reasonable? Is this how we think soils work, or may the assumptions that led to this conclusion be unrealistic? How do they compare to assumptions behind a first order model? There seems to be some rich ideas here if you're interested in exploring them (although it may not be necessary in the text).

We have introduced a paragraph towards the end of the discussion that should shed some light on the value of microbial models vs. first order model. Even if a microbial model ultimately

shows a first order response, the black box behind the first order coefficient can be better understood. We add in this paragraph, that our transformation leads from a heavily enzyme limited model (FWD model), via the introduction of other limitations (REV and OPT models), to an entirely substrate limited FOD model (this is the assumption of a FOD model). At this point, we don't think we know how soils work, but the consideration of how the degree of enzyme limitation and how microbes respond are critical since it leads to a strong divergence in the response to warming.

There are distracting grammatical errors in the text, which should be carefully proofread before publication.

We have carefully read through our manuscript in order to find (hopefully) all the mistakes.

Technical corrections

P4 L5- The authors contend that “As microbial models are considered critical towards improvement of Earth System model”. I'm not sure this statement is widely agreed upon, it's also somewhat misleading for the scope of the study presented here. Instead, it may be safer to state “As microbial models are considered for broader application in models...”?

We incorporated this excellent suggestion.

P6 L10-21 The use of K_E and K_M (for forward and reverse models, respectively) in eq. 3 & 4, their subsequent description in the text, and in appendixes is somewhat confusing because it does not follow conventions used the papers on which this study is largely based. Specifically for the forward model, German and others (2012) state “ K_m is the substrate concentration at half-maximal velocity”, while the reverse model of Schimel and Weintraub (2003) use “ K_{es} half saturation constant for enzymes on substrate”.

In order to be consistent with the literature, we now use K_m in FWD and K_e for the REV model. We did not use K_{es} like Schimel and Weintraub (2003) as our unit of half-saturation constant for enzyme on substrate is different (not enzyme but microbe concentration).

Eq. 13. This isn't the first time someone has looked at temperature sensitive CUE. I see a reference in Table 3, but it's likely worth citing Allison et al. 2010 (or others) in the text here.

We have included the reference.

Section 3.4. also seems to refer to results, but never references a figure. I'm assuming it should refer to Fig. 3, but shouldn't have to.

We reference now to the figure in section 3.4, and also in the discussion section when we address the QSS-microbe model.

Discussion (and Fig. 2). I wonder what are we assuming by assigning really low K_m value for the OPT model- that the soil environment is basically saturated w/ respect to enzymes, such at addition of more microbes (or enzymes) yields no fitness advantage growth? I'm assuming you could parameterize a similar model with different V_{max} and K_m values that have non-zero K_m values, in which case the optimization would produce qualitatively different results? This is

suggested in the discussion, and while I'm not sure it needs greater attention in the text, seems like an interesting result.

We did not a priori assign a low K_m Value in the OPT model. Instead, the OPT model can be viewed as what is the optimal “flooding” of enzymes given a certain enzyme substrate affinity. This is where the product $K_p \cdot c$ is coming in. Clearly, depolymerization proceeds at a lower rate (per unit substrate) if this product is small (Table 2). We agree that this tradeoff is interesting.

P21, L21. Check accuracy of text in revering to K_M , K_E , and K_p values.

We have checked the subscript of the different half saturation constants throughout the text.

Table 2 What is the value for $K_p \cdot c$ in the OPT model? Also, check units for parameters that are given for accuracy.

Values of $K_p \cdot c$ are given in Table for scenarios of three different enzyme production costs. Thanks for catching the unit. It is a rate and the corrected unit is $mg\ S\ cm^{-3}\ hr^{-1}$ (see Table 3).

Fig. 1 Is kind of busy and difficult to understand. Several suggestions to bring greater clarity follow: Is that ‘decreasing marginal return’, green line in Fig 1, is also the reverse M-M model? If so, please use consistent language throughout (on the figure and in the caption)?

- Why are the E, E-S, and DOC pools shown at all, my reading is that these pools not actually being simulated? If so, it seems misleading to show these pools at all- or is the point to demonstrate that these pools are implicitly represented in the model, but because the ‘fast’ parts of the model each are assumed to be in steady state, and thus omitted from explicit representation. I think it's the later, but maybe this can be clarified in the text & caption?
- would mapping parameters from Table 1 onto Fig. 1 would be more useful for readers, or make the figure too busy?
- I'm also not sure Figs 1b and 1c are needed. Information about adding growth and maintenance respiration fluxes could be handled w/ small dashed lines or colored lines to communicate this relatively minor modification to the basic model structure.

We make sure we use now consistent language, referring to FWD, REV and OPT models. We mention in the caption, that E, E-S, and DOC are implicitly calculated. To make this distinction, they are circled with a dashed line. The reviewer is correct, they are represented based on quasi-steady state assumption. We still think they require to be there, because the associated parameters are enzyme-substrate reaction parameters. Also we can carry through with the theme (dashed circle), if we assume quasi-steady state for microbes in Figure 1b.

While Fig 1 and Table 1 share some information, we feel we would like to keep specific setup description separate from Fig. 1. We fear this would make the Figure too busy and distract from the conceptual ideas presented.

We separated out Figures b and c based on earlier review suggestion. We thought this is a good idea to show the sequence of the modeling layers. Figure 1a thus focuses on the main differences (FWD, REV, OPT), while b and c then highlight modifications, which are QSS-microbe and separation of respiration terms.

P47 L1- should be ‘growth’

Done

Fig. 3. As text introduces results from quasi steady-state results and then partitioning between maintenance & growth respiration should the caption for Fig. 3 be similarly organized?

Nice catch, we reorganized the caption and legend for Fig. 3.

Response to Referee 2

Sihi and co-authors present a nice overview and comparison of microbial-explicit soil C models. This is a timely study in light of the many recent papers presenting nonlinear microbial models and the recent efforts to integrate such models into Earth system models. The authors address the underlying assumptions that lead to Michaelis-Menten (MM) versus reverse-MM depolymerization kinetics, and explore how the underlying kinetics affect the projected response of soil C to warming.

The revised paper has been significantly improved in its organization and clarity. Following the recommendations of the previous reviewers, the presentation of each of the three nonlinear models and their comparison to the traditional linear model is much easier to follow. It would be useful to the community if the authors included a brief discussion in their conclusions regarding their recommendations for future nonlinear soil C models based on their findings. There are a number of instances that the text and methods are unclear, however, and could be better explained. This is especially true for the “tuning” of parameters, including temperature sensitivities. The paper also needs to be thoroughly proof-read for typos and grammatical mistakes.

Thank you for your positive comments. We have now added towards the end of the discussion how our research poses critical questions as microbial models are considered for Earth System Model. As these models move from basically enzyme limited (FWD model) to substrate and enzyme limitation (REV and OPT model) to purely substrate limited models (first order), we can conclude that the degree of enzyme limitation and the microbial response to enzyme limitation are central areas of research that could help constrain the quantification of the long-term response of soil organic matter to warming.

We have further clarified our tuning methods, and carefully checked for typos and mistakes.

Specific comments and technical corrections:

P1, L19-20: It would be good to briefly mention here what kind of interactions are needed to avoid oscillations. The current sentence “... limitations other than through enzyme-substrate interactions...” does not read very well and is not very informative.

We now list the specific mechanisms. The sentence now reads as “We show that several mechanisms, including substrate limitation, variable production of microbial enzymes, and microbes feeding on extracellular enzymes eliminate oscillations arising from a positive feedback between microbial biomass and depolymerisation”.

P2, L8, L14, etc. This is minor, but check punctuation for “ e.g., ” and “ i.e., ” throughout the text.

We took care of these punctuations in our revised manuscript.

P3, L1-2: Check sentence and verb tenses. “A comparison to traditional first order models further shows that microbial models display...”

It now reads as “A comparison to traditional first order model shows further that microbial models display an attenuated loss of soil organic matter to warming”.

P3, L10: What do you mean by quality here? Recalcitrance, nutrient content, type? Remove “and” from before soil quality and put “content” after the word “nutrient” in this sentence.

It now reads as “Temperature-dependence of CUE is typically not considered in traditional decomposition models, rather the ratios between respired CO₂ and the transfer to a different quality pool are mostly constant parameters, or vary based on soil texture, soil recalcitrance, and organic or inorganic nutrient content”.

P5, L5-6: This sentence doesn’t read well. Consider “... interaction between enzymes and substrate that results in the depolymerization ...”

The sentence now reads as “All models also implicitly take into account interaction between enzymes and substrate that results into depolymerisation of substrate into a DOC pool on which microbes can feed”.

P5, L14: Check sentence. Consider “... both fresh and microbial ... before they can ...”

It now reads as “In contrast to Allison et al. (2010), but congruent with German et al. (2012), there is no “free” DOC, both fresh litter and microbial necromass need to be depolymerised before they can be ingested by microbes”.

We keep the term litter here in order to emphasize the fresh plant material as an external input.

P7, L1-3: Consider revising sentence to “... derived for the case where an enzyme can adsorb to only a fraction ...”

Done. It now reads as “A version of the reverse Michaelis-Menten model also has been derived for the case where an enzyme can adsorb to only a fraction of soil organic matter due to inaccessible binding sites from surface limitation or physical protection”.

P7, L4: “appearing” instead of “appears”.

We changed the sentence slightly. It reads now “...is included in the denominator”.

P8, L21-22: Drop the s from “becomes”. Please revise comma placements and tenses.

Done

P9, L19: traditional decomposition models (plural)

Done

P10, L2-3: I wonder, how much would your results change with a first order model that

contains multiple pools? Traditional models generally have multiple pools with different temperature sensitivities.

Typically, first order models do not have different temperature sensitivities, although it has been suggested that they should (Knorr et al., 2005, Davidson and Janssens, 2006).

Obviously the dynamics would change, too, where multiple decomposition time scales are considered. However, this is beyond the scope of the paper, as it also would require the consideration of multiple pools in all other models. However, traditional decomposition model can also be viewed as an assembly of parallel pools, where all the fluxes and rates are basically additive (Bolker et al., 1998).

P11, L17: “Modifications” should be plural.

Done

P12, L17-19: This sentence is a little awkward. What do you mean by “working their tuning factors directly into these two parameters”? By “tuning factors” do you mean temperature sensitivities?

German et al. (2012) had tuning factors that related the measured V_{max} to substrate processing rates, when we wrote tuning factors, we referred to these. We attempted to clarify this by writing as “Here, we report $V_{max,FWD}$ and K_m by considering 15°C as our reference temperature and by incorporating German et al. (2012) tuning coefficients (a_K , a_V) directly into these two parameters. In other words, $V_{max,FWD}$ and K_m are the product of the reference values in German et al. (2012), their adjustment to our reference temperature, 15°C and the German et al. 's (2012) tuning parameters.”

P12, L4-5: How do you choose this precise value of 0.37 for the parameter K_m ? From what I can tell, there isn't much support in the text for this value, other than it being smaller than M . How does this compare to K_m in other modeling studies and from experiments?

If K_e (renamed from K_M) is very small, it becomes a first order model. On the other hand, if K_e is very large that leads to oscillations which defies our idea of other limitations. Thus, we chose it to be a good deal (but not diminishingly smaller) than the microbial biomass ca. 3/8. Further we show in the appendix how K_e is derived (it is a composite parameter, see Appendix B).

P12, L7: When you say $V_{max,REV}$ is tuned, do you mean the underlying $V_{max,i}$ and Q_{10} values? How do you tune $V_{max,REV}$? Similarly for $V_{max,OPT}$ on P12, L9-10.

We sought to clarify by writing: “This leaves the determination of $V_{max,REV}$ which is tuned here to such that the REV model yields equivalent equilibrium values of S at the reference temperature as the FWD model.”

We adjust $V_{max,OPT}$ (in the same manner as in the REV model) such that the system again yields equilibrium values for S at the reference temperature (15°C) and the same initial response to warming as in the other models.

P13, L21: Do any of the “traditional models” have temperature sensitive CUE?

A temperature sensitive CUE is not a typical feature in traditional models, but see Frey et al. (2013) where a variable CUE has been introduced in CENTURY model. We lay this out in the introduction.

P 14, L3-6: This paragraph is confusing. How exactly do you perform your parameter adjustments? What do you mean by not allowing Q_{10} to differ? Do you mean that the values are the same across the models or at initial times? Please be clear on your methods here.

We changed the wording of this paragraph significantly. We wanted to reiterate some of the methods here to clarify that the models were equalized for the state variables and for the initial response. It reads now:

“Fig 2 shows the transient response of the different models (FWD, REV, OPT, and FOD) to a temperature step from 15°C to 20°C . Recall, that the perturbation occurs, after all models were equilibrated at 15°C , and are forced through the same initial values of M , S , and CUE by way of parameter adjustments. Also, by identical Q_{10} of V_{max} and CUE’s the initial response to a warming is equal across the models.”

P15, L1-2: “dynamics are...” (plural)

Done

P16, L14-17: What conditions or parameters would lead to such an imbalance that would cause M to decay or grow indefinitely?

We clarify the implications of the imbalance. Because the parameters are independent of each other the likelihood of a balance approaches zero. We further say that a positive balance causes exponential growth or decay in the short term. Please see Table 2 footnote.

P18: It seems that you should refer to Fig. 3 in the text here.

We include now a reference to Fig. 3

P18, L6: In Fig. 3, it looks like the dashed “with MR” lines for FWD (blue) are much more oscillatory (in frequency and magnitude) than the solid line. Maybe I’m missing something, but does including MR really decrease the oscillation frequency as stated in L6?

This is a mistake. We mentioned in the discussion that oscillation frequency and amplitude increases in FWD model with MR.

P18, L24: “resulted in a” instead of “into”

Done

P19, L10: You could cite Hararuk et al. GCB 2015 here.

We included this citation.

P19, L16-17: The first part of this sentence doesn't seem to be “evidenced” by the second part of the sentence. Also, just a note that oscillations can be stable (and often are in these models) in that they eventually approach a steady-state.

We change “evidenced” by caused. Also we made sure that we refer to short term instability – as even the FWD model eventually approaches steady state.

P19, L18: Interplay of soil organic matter with what? Microbes? Please clarify.

We changed to “...stabilization only occurs via the slow changing soil organic matter pool”.

P20, L10-14: You may also want to cite and take a look at the Equilibrium Chemistry Approximation (ECA) kinetics as proposed in Tang & Riley 2013 and Tang 2015, which can be thought of as a hybrid between MM and reverse MM depending on the conditions.

We added “Transitions between FWD and REV model behaviour has also been detailed out in the more complex Equilibrium Chemistry Approximation model that also include sorption of enzymes and substrates to mineral surfaces (Tang and Riley, 2015).“

P20, L16: Does your analysis robustly show this or just from the figures? All of your models are in fact stable dynamical systems given the chosen parameters. Even the models that oscillate are dampened and eventually approach a stable steady state.

We want to emphasize that M can be in quasi-equilibrium in the REV model on a microbial time-scale, but not in the FWD model. M will decay or grow indefinitely in short-term for in the FWD model in the absence of a perfect balance of parameters (Please see Table 2 footnote). To clarify our points, this now reads as “Our analysis shows that the positive feedback between decomposition and microbial growth is removed, as our REV model has now a stable short term QSS”.

P21, L7: Tang & Riley 2015 may also fit here given their incorporation of dynamic energy budget theory.

We added this reference.

P21, L18: ... cost approaching zero...

Done

P21, L21: remove “a” from “via a half saturation constants”

Done

P21, L22-24: Consider revising this sentence.

We changed this paragraph significantly to hash out the main features of the OPT model, thereby removing some duplication w.r.t the role of the half saturation constants. This sentence was removed in the process.

P21, L3: Sentence fragment.

Sentence removed in the process of rewriting the paragraph.

P24, L6-7: Is this assumption justified?

We added references (German et al., 2012, and Moorhead et al., 2012) where this fast enzyme and DOC turnover has been used. The next sentence then provides some rationale:

„...we assumed that depolymerised carbon in soil solution (DOC) is always at steady state with the microbial biomass (see also German et al., 2012 and Moorhead et al., 2012). This simplification can be justified with fast and efficient scavenging of microbes and thus fast turnover of the DOC pool.“

P24, L18: Check grammar/wording. Remove “to” and comma after complex, and add a period at the end of the sentence.

Done

The conclusions section could benefit from a brief discussion on where such models are going and what recommendations the authors have for the community based on their findings.

We demonstrate possible mechanisms that need attention for developing future decomposition models as these can lead an enzyme-limited microbial decomposition model to a substrate-limited first-order kinetic model. We modify the conclusion accordingly.

Check grammar and content of the Fig. 1 caption, particularly (b) and (c).

Done

Fig. 2 (d) the color of the initial straight line looks purple. It might also be good to add a note in the caption that the value of CUE is the same across the models, since the lines completely overlap.

Thanks for catching this, we change the color of the initial straight line to black for Fig. 2 (d). We also add a note that CUE of OPT model is superimposed on FWD and REV models.

P47, L1: Fix “growth”.

Done

Fig. 3: This graph is a little busy with so many lines. Why do some of the modified models start from different microbial biomass conditions? You may want to use SS Microbe instead of Eq. Microbe in the legend.

This figure compares the difference between our different model families. In order to emphasize the results of Quasi-steady state (QSS) microbe models and models with growth and maintenance respiration, we try to modify the thickness (thin and thick) and type (solid, dashed, or dotted) of lines here.

The modified models do not start from different microbial biomass conditions. Rather, the higher M in QSS microbe models compared to other models results from a greater response of M immediately after warming.

We now use QSS microbe in the legend for models with quasi-equilibrium of microbial biomass.

References included in the response

Bolker, B.M., Pacala, S.W. & Parton Jr, W.J.: Linear analysis of soil decomposition, insights from the century model, *Ecological Applications*, 8, 425–439, 1998.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, 440, 165-173, doi:10.1038/nature04514, 2006.

Knorr, W., Prentice, I. C., House, J. I., Holland, E. A.: Long-term sensitivity of soil carbon turnover to warming, *Nature*, 433, 298-301, 2004.

1 Comparing models of microbial-substrate interactions and their response to warming

2
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8 9 **Abstract**

10 Recent developments in modelling soil organic carbon decomposition include the explicit
11 incorporation of enzyme and microbial dynamics. A characteristic of these models is a positive
12 feedback between substrate and consumers, which is absent in traditional first order decay
13 models. Under sufficiently large substrate, this feedback allows an unconstrained growth of
14 microbial biomass. We explore mechanisms that curb unrestricted microbial growth by including
15 finite potential sites where enzymes can bind and by allowing microbial scavenging for enzymes.
16 We further developed a model where enzyme synthesis is not scaled to microbial biomass, but
17 associated with a respiratory cost and microbial population adjusts enzyme production in order to
18 optimise their growth. We then tested short and long-term responses of these models to a step
19 increase in temperature, and find that these models differ in the long-term, when short-term
20 responses are harmonized. Oscillations We show that arise several mechanisms, including
21 substrate limitation, variable production of microbial enzymes, and microbes feeding on

1 ~~extracellular enzymes eliminate oscillations arising~~ from a positive feedback between microbial
2 biomass and depolymerisation ~~are eliminated if limitations other than through enzyme-substrate~~
3 ~~interactions are considered.~~ The model, where enzyme production is optimised to yield
4 maximum microbial growth shows the strongest reduction of soil organic carbon in response to
5 warming, and the trajectory of soil carbon largely follows that of a first order decomposition
6 model. Modifications to separate growth and maintenance respiration generally yield short-term
7 differences, but results converge over time, because microbial biomass approaches a quasi-
8 equilibrium with the new conditions of carbon supply and temperature.

10 **1 Introduction**

11 Traditional soil organic matter decomposition models are based on first order kinetics, where
12 decomposition scales to the pool size. The scaling factor represents recalcitrance of a specific
13 pool, and is modified by soil temperature, moisture, and other soil properties (e.g., van Veen et
14 al., 1984; Parton et al., 1987; Molina et al., 1990; Li, 1996; Chertov and Komarov, 1997). Recent
15 modelling efforts have specifically included catalysis of polymeric soil organic carbon to
16 dissolved organic carbon (DOC) by extracellular enzymes. This depolymerisation step is thought
17 to be a rate-limiting step in organic matter decomposition ~~processes~~ (Schimel and
18 Weintraub, 2003; Fontaine and Barot, 2005).

19 In traditional models, microbes are only considered as a simple donor-controlled pool (i.e.,
20 microbial biomass has no impact on decomposition), or in an implicit manner (Gerber et al.,
21 2010). In contrast, in microbial models, decomposition rates become a function of enzyme
22 activity that is linked to microbial biomass. ~~(Allison et al., 2010; German et al., 2012).~~ This leads
23 to more complex dynamics because decomposers feed back into soil organic matter degradation

1 via microbial enzyme production affecting depolymerisation. This positive feedback between
2 microbial biomass and depolymerisation causes soil organic carbon stocks and microbial
3 biomass to oscillate after a perturbation (Li et al., 2014; Wang et al., 2014). Nevertheless,
4 microbial decomposition models have been shown to improve the prediction of soil carbon and
5 perform well when compared against decomposition experiments (Lawrence et al., 2009; Wieder
6 et al., 2013; Wieder et al., 2014a; Wieder et al., 2014b; Wieder et al., 2015b). ~~A~~
7 ~~comparison~~ Furthermore, when compared to a traditional first order ~~model~~ ~~show~~ ~~further~~
8 ~~that~~ ~~models~~, microbial ~~model~~ models also display an attenuated loss of soil organic matter to
9 warming (Allison et al., 2010; Wieder et al., 2013).

10 Moreover, the response of soil organic matter to warming is very sensitive to microbial carbon
11 use efficiency (CUE), because this parameter and its climate sensitivity ~~defines~~ define the
12 fraction of carbon remaining in the soil as processed organic matter vs. carbon removed via
13 respiratory CO₂ (Allison et al., 2010; Frey et al., 2013; Kivlin et al., 2013; Tucker et al., 2013;
14 Wang et al., 2013; Li et al., 2014). Temperature-dependence of CUE is typically not considered
15 in traditional decomposition models; ~~(but see Frey et al., 2013)~~, rather the ratios between respired
16 CO₂ and the transfer to ~~a~~ different quality ~~pool~~ pools are mostly constant parameters, or vary
17 based on soil texture, ~~and~~ soil ~~quality~~ recalcitrance, and organic or inorganic nutrient content
18 (Parton et al., 1987; Gerber et al., 2010; ~~but see Frey et al., 2013~~). Microbial respiration can be
19 partitioned into a series of carbon expenditures that do not contribute to growth. These
20 expenditures include growth respiration, maintenance respiration, respiratory cost for enzyme
21 production, and overflow respiration (Manzoni et al., 2012; Moorhead et al., 2012). Each type of
22 respiratory carbon ~~expenditures~~ expenditure may differ in its response to temperature. ~~In addition,~~
23 respiration

1 Respiration may be parameterised based on different microbial properties: ~~Maintenance.~~ For
2 example, maintenance respiration is assumed to scale with microbial biomass (Chapman and
3 Gray, 1986; Fontaine and Barot, 2005) while growth respiration may scale to the amount of new
4 tissues built. On the other hand, overflow respiration occurs during stoichiometric adjustment
5 (Russell and Cook, 1995; Schimel and Weintraub, 2003; Frost et al., 2005; Franklin et al., 2011)
6 whereas costs related to enzyme production may be governed by microbial demand and substrate
7 availability and quality, resource diffusion, and microbial diversity (Allison, 2005). This
8 differentiation can impact the dynamics of the microbial biomass: For example, maintenance
9 respiration costs would ~~new~~ be incurred even in the absence of carbon uptake, which can lead to
10 a reduction in microbial biomass. In contrast, growth respiration is only due when substrate for
11 growth is available. ~~However~~ Because of the explicit and mechanistic link between microbial
12 activity and soil organic matter degradation, inclusion of microbial models in Earth System
13 Models may have the potential to ultimately reduce uncertainty of climate-carbon feedback in
14 the face of climate change, because of the explicit link between microbial activity and soil
15 organic matter degradation (Todd-Brown et al. 2012, 2013; Wieder et al., 2015a).

16 As microbial models are considered ~~critical towards improvement of~~ for broader application in
17 Earth System ~~model~~ Models, it is key essential to analyse and understand their structure and their
18 dynamics. Here, we compare a series of microbial decomposition models with each other.
19 Specifically, we analyse feedbacks between depolymerisation and microbial growth, consider
20 constraints on depolymerisation and enzyme—substrate interactions, investigate the
21 parameterisation of microbial enzyme productivity, and ~~investigate~~ address the representation of
22 microbial respiration and CUE.

23 Our main questions are:

1 a) How do different model implementations of depolymerisation affect the feedback between
2 microbial biomass and soil organic matter, if subjected to warming?

3 b) How does the consideration of functional respiration terms (growth, maintenance, and carbon
4 acquisition expenditures) affect decomposition dynamics?

5 We organise the paper in the following way. In the next section, we introduce 3 simple models
6 that differ in their representation of depolymerisation. Each model will be further modified for
7 different representation of microbial dynamics and respiration. To analyse model behaviour, we
8 will evaluate the response of respiration, microbial biomass, CUE, and soil organic matter to a
9 step increase in temperature. We will then discuss the models' ~~behavior by comparing~~
10 ~~against~~ behaviour and compare their results with the dynamics of a traditional first order model.

12 2 Materials and methods

13 2.1 Model descriptions

14 We first introduce three model families that differ in the way depolymerisation is handled.

15 In all models, the setup consists of a single soil organic matter pool and a single microbial pool
16 (Fig. 1). ~~However, all~~ All models also implicitly take into account interaction between enzymes
17 and substrate; that results into depolymerisation of substrate into a DOC pool on which microbes
18 can feed. Enzyme-substrate reactions are based on Michaelis-Menten kinetics (see Appendix A,
19 Michaelis-Menten kinetics with enzyme denaturation). We do not consider a specific enzyme
20 pool, nor a specific DOC pool, but assume that the enzyme and DOC ~~pool~~ pools are in a quasi-
21 steady state (see Appendix A, DOC and enzyme dynamics). Thus, the amount of enzyme
22 produced equals the amount of enzyme decay at every time step. Similarly, the amount of DOC

1 produced is the same as the amount of DOC consumed by microbes. In contrast to Allison et al.
 2 (2010), but congruent with German et al. (2012), there is no “free” DOC, both fresh litter, and
 3 microbial necromass need to be depolymerised before ~~it~~they can be ingested by microbes.
 4 ~~Further, both~~In all models depolymerisation and microbial respiration are temperature
 5 dependent, causing increased depolymerisation and reduced microbial CUE with warming.

6 **2.1.1. Base Models**

7 The tendency (derivative with respect to time) for soil organic carbon and microbes in all of the
 8 models are described with:

9
$$\frac{dS}{dt} = I + \lambda_d * M - D \tag{1}$$

10
$$\frac{dM}{dt} = D * \epsilon - \lambda_d * M \tag{2}$$

11 where S and M are the soil organic matter and the microbial pool, respectively, I is the input of
 12 fresh litter, λ_d is the death rate of microbes, D is the rate of depolymerisation, and ϵ is the
 13 microbial CUE.

14 ***Forward M-M Model (FWD)***

15 In the forward model (FWD), depolymerisation is represented as a Michaelis-Menten process,
 16 and stems from the simple microbial-enzyme decomposition model as proposed by Allison et al.
 17 (2010) and modified by German et al. (2012) (Fig 1a).

18
$$D = \frac{V_{max,FWD} * S * M}{K_E + S} \frac{V_{max,FWD} * S * M}{K_m + S} \tag{3}$$

19 Where D is the rate of ~~depolymerization~~depolymerisation, $V_{max,FWD}$ is the maximum
 20 depolymerisation rate and K_E, K_m the half saturation constant ~~for~~of enzymes. Appendix A shows
 21 the derivation of this function, based on enzyme-substrate dynamics.

1 ***Diminishing Return (REV) Model***

2 In Appendix B, we derive two depolymerisation models which show a diminishing increase of
3 depolymerisation as microbial mass increases. These models include a) a case where microbes
4 are scavenging for free enzymes, and b) where potential sites ~~offor~~ enzyme-substrate reactions
5 are finite. The ~~implementations~~implementation of these factors lead to a reverse Michaelis-
6 Menten type model (REV) as in Schimel and Weintraub (2003):

7
$$D = \frac{V_{\max,REV} * S * M}{K_M + M} \frac{V_{\max,REV} * S * M}{K_e + M}$$

8 (4)

9 Where ~~K_M~~V_{max,REV} is the maximum depolymerisation rate for this model, K_e is a half saturation
10 constant that determines the diminishing return function. In the cases developed in the Appendix,
11 ~~K_MK_e~~ incorporates factors indicating the finite sites for enzyme substrate interactions (Appendix
12 B, model with limited available substrate), or the efficiency with which microbes scavenge for
13 free extracellular enzymes (Appendix B, microbial consumption of enzymes). A version of the
14 reverse Michaelis-Menten model also has been derived ~~if-for the case where an enzyme can~~
15 ~~adsorb to~~ only a fraction of ~~the-soil organic matter due to inaccessible~~ binding sites ~~where-a~~
16 ~~particular enzyme can adsorb to-from surface limitation or physiscal protection~~ (Wang and Post,
17 2013). A major difference ~~tofrom~~ the FWD model is ~~that-now~~ the ~~microbial-biomass,~~
18 ~~insteadinclusion~~ of the amount of ~~soil-organic-matter-appears~~microbial biomass in the
19 denominator: ~~in lieu of soil organic matter~~. Therefore, the depolymerisation per unit biomass
20 decreases as biomass increases, plateauing at V_{max,REV}*S (diminishing return).

21 ***Optimised Enzyme Production (OPT) Model***

1 In ~~this~~our OPT model, we relax the condition that microbial enzyme production scales to
 2 microbial biomass, an assumption that is present in many microbial models and which is also
 3 assumed in the FWD and the REV model above. Instead, we probe a model where microbial
 4 enzyme production is optimised for growth. We motivate this by microbial competition (Allison,
 5 2005), which ~~will allow~~allows microbes to succeed if microbial enzyme production allows the
 6 highest possible return. Optimisation only has meaningful results for the case of limited substrate
 7 availability (i.e. a diminishing return, possibly through constraints in potential sites for enzyme-
 8 substrate reaction) and if there is a cost associated with microbial enzyme production.

9 Depolymerisation as a function of enzyme production can be represented by

$$10 \quad D(P) = \frac{P \cdot V_{\max,OPT} \cdot S}{K_p + P} \cdot \frac{P \cdot V_{\max,OPT} \cdot S}{K_p + P} \quad (5)$$

11 $V_{\max,OPT}$ is the maximum rate of depolymerisation, P is the enzyme production rate, and ~~K_p~~ K_p
 12 carries information on the affinity of the enzyme for the substrate and longevity of the enzyme
 13 (see Appendix C, for full derivation of depolymerisation in the OPT model).

14 Microbial growth (G) is as in previous models but accounts for carbon expenditure of enzyme
 15 production:

$$16 \quad G = \varepsilon * (D(P) - Pc) \quad (6)$$

17 Where c is the respiratory cost per unit enzyme produced (Schimel and Weintraub, 2003).

18 Optimising growth by setting $\frac{dG}{dP} = 0$ yields:

$$19 \quad D = V_{\max,OPT} * S - \sqrt{K_{pp} * c * V_{\max,OPT} * S} \quad (7)$$

20 And the cost per unit carbon depolymerised is then:

$$\frac{P_c}{D} = \frac{\sqrt{\frac{K_{pe}}{S V_{max,OPT}}}}{\sqrt{\frac{K_{pc}}{S V_{max,OPT}}}} \quad (8)$$

2.1.2. Equilibrium microbial Quasi-steady state (QSS) microbe models

While the previous models are fairly simple, we further reduce the complexity by removing microbial biomass as a state variable; but instead consider M at a quasi-steady state: (QSS). In the equilibrium microbial QSS microbe models, the microbial uptake at each time step is thus equal to the microbial carbon loss via death or respiration (Fig 1b). This is similar/identical to our treatment of DOC and enzymes, where production and removal of these substances are always balanced. This simplification is motivated by the fact that microbial biomass turns over much faster than soil organic matter, and therefore microbial biomass adjusts much faster to changes in environmental conditions than soil organic matter itself. The fast turnover of M compared to S allows microbial biomass to (quasi)-equilibrate with the current level of soil organic matter (see also Menge et al., 2009).

In our equilibrium microbial QSS microbe models, we solve $\frac{dM}{dt} = 0$, in order to obtain a quasi-steady state microbial biomass, \bar{M} . \bar{M} substitutes/replaces the state variable M in the functions for depolymerisation and microbial death. We note that this is only possible for the REV and the OPT model. The as the FWD model yields no solution for M in $\frac{dM}{dt} = 0$, and the first order model does not consider a microbial biomass in the first place. The equilibrium. The QSS microbe models; effectively becomes/become a one-pool model, where depolymerisation is not a direct function of microbial biomass, but an expression of S and a series of parameters. Table 2 (see formulations for Short/Fast timescale) shows the quasi-steady state for M, and the resulting depolymerisation function for the equilibrium models. QSS microbe models. \bar{M} can be diagnosed at each time step based on S and parameters that determine depolymerisation and microbial

1 turnover (Table 2, second column). In the QSS microbe models a fraction $(1 - \epsilon)$ of
2 depolymerisation is immediately recycled back into the soil organic matter pool, thus the
3 dynamics of the soil pool becomes

$$4 \frac{dS}{dt} = I - (1 - \epsilon) * D \quad (9)$$

5 In turn, depolymerisation is immediately partitioned into respiration and a returning carbon flux,
6 which mimics microbial death.

7 **2.1.3. Partitioning between maintenance and growth respiration**

8 While the dynamics of the soil organic matter pool remains the same as in the base model setup,
9 we alter ~~the forward and the reverse Michaelis-Mentenall~~ models ~~as we make distinction~~
10 ~~between(FWD, REV, OPT) to treat~~ growth and maintenance respiration as separate processes
11 (Fig 1c). Partitioning of microbial respiration into growth and maintenance respiration
12 characterise the microbial pool as follows:

$$13 \frac{dM}{dt} = (D - \lambda_r * M)(1 - g) - \lambda_d * M \quad (910)$$

14 Where g is the growth respiration fraction and λ_r the maintenance respiration rate. The separation
15 of microbial respiration in growth and maintenance terms is motivated by a similar formulation
16 in other microbial (Beefing et al., 1990; Van Bodegom, 2007), vegetation growth (Foley et al.,
17 1996; Cannell and Thornley, 2000; Arora, 2002; Thornley, 2011; Pretzsch et al., 2014), and
18 ecosystem-scale (Sistla et al., 2014) models. Growth respiration is applied after requirements for
19 maintenance respirations are met: and is proportional to new microbial tissues built. Maintenance
20 respiration (respiration related to non-growth components) is typically proportional to microbial
21 biomass (Van Bodegom, 2007).

22 **2.1.4. First-Order Decomposition (FOD) Model**

1 The last model represents the structure of traditional decomposition ~~model~~models such as
2 CENTURY (Parton et al., 1987) or Roth-C (Coleman et al., 1996) and their derivatives, where
3 decomposition is considered as a first-order reaction:

$$4 \frac{dS}{dt} = I - S * k * (1 - \epsilon) \quad (411)$$

5 where k is the first order decomposition constant. The two major differences between our first-
6 order decomposition (FOD) model and traditional models are that we consider only a single
7 carbon pool whereas traditional models consider ~~several quality~~multiple pools with different
8 turnover times that feed into each other. We also consider a temperature-dependent CUE on top
9 of a temperature-dependent processing rate (k, see parameterisation and implementation
10 section). This increases the fraction of carbon processed with warming to become CO₂.

11 Respiration (R) is then

$$12 R = S * k * (1 - \epsilon) \quad (412)$$

13 2.2 Temperature response

14 We implement the response of decomposition to warming by modifying the depolymerisation
15 and the microbial respiration.

16 In the FWD, REV and OPT model, V_{max} is modified as

$$17 V_{\max,i}(\Delta T) = V_{\max,i} * Q_{10}^{\left(\frac{\Delta T}{10}\right)} \quad (4213)$$

18 Where V_{max,i} and V_{max,i}(ΔT) are the reference and ~~the~~temperature-dependent maximum
19 depolymerisation rate of the model i = (FWD, REV, OPT, see Table 3). Similarly, the
20 decomposition rate k is modified by the Q₁₀ function in the FOD model.

21 Further, we also parameterise CUE as a linear function of the temperature change, following
22 Allison et al. (2010) and German et al. (2012)

1 $\varepsilon(\Delta T) = \varepsilon_0 + \Delta T * \varepsilon_{\text{slope}}$ (1314)

2 where ε_0 is the CUE at reference temperature, and $\varepsilon_{\text{slope}}$ is the change in CUE per °C
3 temperature (ΔT) change. Finally, in the models where we partition growth and maintenance
4 respiration, we formulate maintenance respiration as a Q_{10} function of temperature

5 $\lambda_r(\Delta T) = \lambda_{r,0} * Q_{10}^{\left(\frac{\Delta T}{10}\right)}$ (1415)

6 Where $\lambda_{r,0}$ and $\lambda_r(\Delta T)$ are maintenance respiration rate at reference and elevated temperature.
7 Growth respiration is typically much less sensitive to warming than maintenance respiration
8 (Frantz et al., 2004), and we therefore do not consider a temperature dependence of this
9 particular respiration term.

10 In our simplified model we further neglect the weaker temperature dependence of the half
11 saturation constants (see Davidson et al., 2012; German et al., 2012; Stone et al., 2012), and also
12 do not consider changes in cost of enzyme production as temperature increases in the case of the
13 OPT model.

14 2.3 Parameterisation and implementation

15 All models are implemented in STELLA, version 10.0.3. To enable comparison among the
16 models, we adjust parameters in the following way: The models have the same initial soil
17 organic carbon and the same initial microbial biomass. Both CUE (ε_0), and its temperature
18 dependence ($\varepsilon_{\text{slope}}$) are the same across models. Further, the temperature sensitivities of V_{max}
19 are identical across models so that we obtain the same increase of depolymerisation in the
20 first time step after the temperature perturbation. We motivate this kind of parameterisation by

1 acknowledging that many of these parameters are largely unknown, but it will provide us with
2 the possibility of comparing the functional response to long-term warming across these models.

3 We use parameters as reported in German et al. (2012), with a few ~~modification~~modifications.
4 Here, we report $V_{\max, \text{FWD}}$ and $K_E K_m$ by considering 15°C as our reference temperature and by
5 ~~working their~~incorporating German et al. (2012) tuning factors~~coefficients~~ (a_K, a_V) directly into
6 these two parameters: (Table 3). In other words, $V_{\max, \text{FWD}}$ and $K_E K_m$ are the product of the
7 reference values in German et al. (2012), ~~their respective tuning parameters and~~ their adjustment
8 to our reference temperature, 15°C, and the German et al.'s (2012) tuning parameters. Further,
9 we have converted the exponential temperature sensitivity of $V_{\max, \text{FWD}}$ into a Q_{10} term.

10 To allow a diminishing return mechanism, we assumed that most of the enzyme decay/loss in a
11 scavenging model is attributed to microbial consumption instead of denaturation. Alternatively,
12 under conditions of limited enzyme-substrate reaction sites, we assumed that there is an excess
13 of free enzymes, and therefore, enzyme concentrations are higher than their corresponding half
14 saturation concentrations. Overall, these assumptions would suggest a $K_M K_e$ that is smaller than
15 M ($K_M K_e < M$). Here, we chose K_M to be 0.37 of K_e considerably but not diminishingly smaller
16 than M equilibrated at the reference temperature: ($K_e = 0.37$ times equilibrated M). Note, that the
17 half saturation constant in the REV model has a different unit (mgMmg M cm^{-3}) than in the
18 FWD model (mgSmg S cm^{-3}) (see Appendix A for the FWD model and Appendix B for the REV
19 model). This leaves the determination of $V_{\max, \text{REV}}$ are then, which is tuned to yield here to such
20 that the REV model yields equivalent equilibrium values of S at the reference temperature as the
21 FWD model.

22 In the OPT model, we adjust $V_{\max, \text{OPT}}$ (in a similar~~the same~~ manner as in the REV model) such
23 that the system again yields equilibrium values for S at the reference temperature (15°C) and the

1 same initial response to warming as in the other models. In the OPT model, we have to work
 2 ~~inwith~~ two additional parameters, namely the cost of enzyme production (c), and the term that
 3 contains the affinity of enzymes for the substrate (~~$K_p K_p$~~). We chose to have the OPT models
 4 comparable to others if the cost (c) is zero. Higher costs ($c > 0$) therefore, will yield different
 5 equilibrium result of S and a different response to warming, depending on the cost of enzyme
 6 production. ~~Both, the half saturation constant (affinity parameter, K_p) and the cost per enzyme~~
 7 ~~produced are parameters that are hard to come by. Instead, the solution allows us to quantify~~
 8 ~~these based on how much of carbon depolymerised is allocated to enzyme production (see Eq. 8~~
 9 ~~in the main text).~~

10 ~~Here, we analyse the OPT model based on different levels~~ Both, the half saturation constant
 11 (affinity parameter, K_p) and the cost per enzyme produced are parameters that are hard to come
 12 by. Instead, the relationship between enzyme production cost and overall depolymerisation
 13 allows us to quantify the product of K_p and c . (see Eq. 8 in the main text). We define a fractional
 14 expense μ that quantifies the enzyme expenditures and expressed as enzyme costs per unit
 15 carbon depolymerised ($\mu = \frac{Pc}{D}$), where relative to overall depolymerisation at the base
 16 temperature steady state, and at zero cost ($\mu \equiv \frac{Pc}{D} \Big|_{Eq, \Delta T=0}$). We chose μ to be 0, 10, and 50
 17 percent of the depolymerisation rate at the reference temperature and at steady state. ~~This~~
 18 ~~yields~~ Based on the relationship given in Eq. 8 we then obtain an expression for the combined
 19 cost (c) and the half saturation constant (~~K_p~~) (~~K_p~~) without having to specify the value of the
 20 individual parameters (see also the variable Y in Table 2):

$$21 \quad \del{K_p} K_p * c = \mu^2 * D_{Eq, \Delta T=0} \quad (4516)$$

22 Where $D_{Eq, \Delta T=0}$ is the rate of depolymerisation at zero enzyme cost and reference temperature.

1 | When separating growth and maintenance respiration, we sought to equalise steady state CUE,
 2 | M, and S by tuning g and λ_r . We first parameterised maintenance respiration, where, the
 3 | coefficient for maintenance respiration is scaled to microbial turnover (Van Bodegom, 2007).
 4 | We motivate the partitioning between growth and maintenance respiration based on vegetation
 5 | models. LPJ (Sitch et al., 2003) and ED (Moorcroft et al., 2001) have a growth respiration factor
 6 | of one-third of the carbon allocated to growth. We then constrain the overall respiration by the
 7 | CUE in German et al. (2012), and obtain a maintenance respiration rate by difference. This
 8 | yields a maintenance respiration rate that is close to the microbial death rate such that:

9 |
$$\lambda_{r,0} = 1.25 * \lambda_d \tag{4617}$$

10 | The second parameter, g is adjusted, such that the CUE at the steady state and reference
 11 | temperature remains the same. This constrains g to

12 |
$$g = \frac{\lambda_d - \varepsilon_0 * (\lambda_d + \lambda_{r,0})}{\lambda_d - \varepsilon_0 * \lambda_{r,0}} \tag{4718}$$

13 | To obtain the same equilibrium values of CUE at 20°C as in the base models, we adjust Q_{10,λ_r}
 14 | such that models with maintenance respiration ~~hashave~~ have the same CUE as ~~in~~ the base models.

15 | Finally, in the FOD model, the traditional decomposition model, we adjust the parameters k and
 16 | ε_0 to obtain the same S, and CUE as in all other models at 15°C and employ a $Q_{10,k}$ value
 17 | identical to the Q_{10} values of V_{max} in the other models. We keep the decreasing CUE – a feature
 18 | not typically set up in traditional models.

19 | All parameter values are given in Table 3. –
 20 |

1 3 Results

2 3.1 Base Model Simulations

3 ~~Fig. The-2 shows the~~ transient response ~~for~~of the different models (FWD, REV, OPT, and FOD)
4 to a temperature step from 15°C to 20°C ~~is shown in~~. Recall, ~~Fig. 2~~. We note that the
5 perturbation occurs after all models were equilibrated at 15°C and are forced through the same
6 initial values of M, S, and CUE by way of parameter adjustments. ~~Further~~Also, by identical Q_{10}
7 of V_{max} and CUE's, the initial response to a warming is equal across the models ~~by not allowing~~
8 ~~Q_{10} of V_{max} and Q_{10} of CUE to differ.~~

9 In all models, warming leads to a decline of soil organic matter and microbial biomass (Fig. 2).
10 In this initial comparison, we assume that there is no cost associated with microbial enzyme
11 production. Across all the models, microbial biomass first increases because of higher
12 depolymerisation. Increased depolymerisation causes soil organic matter to decrease. In the
13 longer term, M decreases as rates of depolymerisation decline due to a reduction in S, and due to
14 lower CUE. We note that M becomes identical across all models in the long term, when soil
15 organic carbon has equilibrated with ~~the~~ microbial processing at higher temperature (see also
16 Table 2).

17 The FWD Model shows the oscillations in M and S, as noted earlier (Wang et al., 2014). The
18 warming triggers an increase in depolymerisation, which in turn feeds microbial biomass,
19 causing an even higher rate of depolymerisation. This positive feedback experiences a break only
20 when the substrate (S) is sufficiently depleted, such that microbial biomass begins to decline.
21 Thereafter, the positive feedback takes over again, the decreasing microbial biomass spirals
22 down along with depolymerisation until microbial biomass is low enough for soil organic matter

1 to recover. The amplitude of the oscillations dampens over time (Fig. 2). Rates of respiration
2 oscillate along with microbial biomass, before settling at the initial rate in the long-term (after
3 ca. 200 years).

4 The transient dynamics in the REV model with a diminishing return as enzyme (or microbial)
5 concentration increases, ~~is~~ are smoother compared to FWD model (Fig. 2). The mechanism of
6 allowing a finite site for enzyme-substrate reaction or microbial scavenging for enzymes curbs
7 the growth of microbial biomass. Warming still leads to an initial increase of microbial biomass,
8 owing to the fact that the gains of depolymerisation outweigh losses from increased respiration
9 (i.e. decreased CUE). As soil organic matter depletes, microbial biomass is reduced, ultimately
10 below the initial levels.

11 The OPT model considers the metabolic cost of enzyme production and allows
12 ~~optimising~~ optimisation of microbial growth. In Fig. 2, the temporal evolution of M, S,
13 respiration, and CUE is shown for a setup without any costs associated with enzyme production.
14 Among the 3 microbial models presented here (FWD, REV, OPT), the OPT model shows the
15 strongest soil organic matter decrease in response to warming. The response in the OPT model is
16 also almost identical with the traditional FOD model. The transient response also shows a
17 smaller initial growth of M in the OPT vs. the REV model.

18 **3.2 Analytical steady state solutions**

19 The analysis of equilibria helps to understand the model behaviour. We first address the “long
20 time scale” in Table 2 where we solve for the steady state of the entire system (i.e. $\frac{dM}{dt} = 0$ and
21 $\frac{dS}{dt} = 0$). In the long-term, the steady state microbial biomass is identical in the FWD and the
22 REV model and depends on the input of fresh organic matter, the microbial CUE, and microbial

1 turnover (Table 2, right-most column). The same microbial biomass is also realised in the OPT
2 model under zero cost ($\mu=0$) (see Eq. 4516 and Table 2, right-most column). In contrast, the
3 analytical steady state solutions of S are different among the models: For the REV and the OPT
4 model, the input of fresh litter is a determining variable for the steady state, but not for the FWD
5 model. In the OPT model the resulting equilibria of S and M end up being complex expressions,
6 and we did not calculate the long-term equilibria of M; but expressed them simply as a function
7 of soil organic matter. ~~The OPT model has —under the assumption of marginal costs ($\mu \rightarrow 0$) the~~
8 ~~same steady state solution for M as the other models.~~ Further, the steady states of S are the same
9 in the traditional first order model (FOD) and the OPT model with zero cost. As expected, the
10 effect of enzyme production cost has a negative impact on microbial biomass.

11 The analysis of the short-term quasi-steady state of the microbial biomass ($\frac{dM}{dt} = 0$) is useful to
12 understand the trajectory of the coupled S-M system. Typically, microbial turnover is much
13 faster than the turnover of bulk soil organic matter (Stark and Hart, 1997; Schmidt et al., 2007).
14 Thus, we would expect that microbial biomass is approaching a quasi-steady state given any
15 level of S.

16 In the FWD model, we find that the quasi-steady state for M requires a perfect balance of
17 parameters that govern growth- and death rates (Table 2, second column). ~~In absence of such a~~
18 ~~balance (This has been~~ referred to as knife-edge equilibrium, ~~see~~ (Schimel and Weintraub,
19 2003), ~~M would therefore grow~~). ~~The absence of such a balance leads to either an exponential~~
20 ~~growth (if positive balance) or decay indefinitely (if balance is negative) of the microbial~~
21 ~~biomass in the short term, where changes in S are small.~~ It becomes clear that the soil organic
22 matter pool must respond on a similar time scale aswith microbes in order to maintain microbial
23 biomass within acceptablerealistic boundaries. In the REV and the OPT models, the short-term

1 equilibria are a function of soil organic matter (Table 2, second column). In the REV₇ and the
2 OPT model, \bar{M} is strongly determined by the rate of depolymerisation at a given S, the CUE and
3 the microbial death rate. A weaker affinity for the substrate (larger half-saturation constant) and
4 higher enzyme production cost act to reduce \bar{M} in these models.

5 3.3 **3.3 Quasi-Steady State (QSS) of Microbial Biomass**

6 Given the quasi-equilibrium biomass, and the resulting decomposition at quasi-steady state, we
7 set up a second line of modelling experimentexperiments, where depolymerisation rates₂ as well
8 as microbial respiration and death₂ are calculated based on microbial biomass at quasi-steady
9 state (QSS microbe, Table 2, second and third columns). ~~It follows that a fraction $(1 - \epsilon)$ of~~
10 ~~depolymerisation is immediately recycled back into the soil organic matter pool, yielding the~~
11 ~~equation $\frac{dS}{dt} = (1 - \epsilon) * D$. Depolymerisation is immediately partitioned into respiration and into~~
12 ~~a returning carbon flux, which mimics microbial death. In this modelling setup, microbial~~
13 ~~biomass is thus no longer a state variable and the models are reduced to single pool setup (Fig.~~
14 ~~1b). \bar{M} is diagnosed from S and parameters that determine depolymerisation and microbial~~
15 ~~turnover (Table, see also method section 2, second column.1.2). Compared to the base models,~~
16 the steady-stateQSS-microbe models yield very similar results for S and respiration, but they do
17 not reproduce the early adjustment of the microbial biomass to the temperature step- (Fig 3).

18 Instead of a slow adjustment to the sudden warming, \bar{M} increases with the

19 instantaneousinstantaneous increase of depolymerisation. However, over a timescale of <1 year,
20 \bar{M} and R converge to the values of the base models in REV and the OPT model, and therefore₂,
21 the quasi-steady state appears to be an acceptable assumption over medium to long time scales.

22 Our results further show that the depolymerisation in the OPT model at quasi-equilibrium and at

1 marginal enzyme production cost ($\mu \rightarrow 0$) yields a depolymerisation formulation that is
2 functionally the same as a first order decomposition model. Depolymerisation in the OPT model
3 becomes $V_{\max} * S$ in absence of enzyme production cost (see Table 2), and therefore ~~respiration~~
4 and, the entire dynamics ~~of S are the same for~~ has the ~~quasi-steady state OPT model and the~~
5 ~~traditional~~ familiar first order ~~model~~. characteristics (compare Eqs. 9 and 11).

6 **3.4.3.4 Partitioning between maintenance and growth respiration**

7 In the third modification of our base models, we partition respiration in our models into a
8 temperature independent growth respiration and a temperature (and biomass) dependent
9 maintenance respiration. This affects the transient pattern of the FWD in that it increases the
10 feedback between microbes and substrate (evidenced by higher amplitudes in M, S, and
11 respiration, Fig. 3). This is because part of respiration is now tied to microbial biomass, which
12 lags depolymerisation. CUE ~~initially decreases less than in the base model, because as~~
13 maintenance respiration lags the growing microbial biomass. The maintenance term also
14 introduces ~~also~~ a mild oscillation into CUE, as microbial biomass waxes and wanes.
15 Interestingly, ~~including the inclusion of~~ maintenance respiration ~~decreases~~ increases oscillation
16 frequency and amplitude of S and M. In the REV and the OPT model, microbial biomass is
17 slightly higher and respiration is slightly below the values of the base models shortly after the
18 step increase, however, this difference diminishes over time. (Fig. 3). The nuanced consideration
19 of microbial respiration causes CUE to decline in 2 stages. The initial drop occurs via the
20 immediate increase in maintenance respiration. This drop is followed by further changes in CUE
21 as M oscillates (FWD model), or as M net growth is diminishing (REV and OPT). Similar as in
22 ~~the case with equilibrium microbes~~ to microbial biomass, differences disappear within < -1 year
23 after the step warming. We note that in our modelling setup, we adjusted the temperature

1 sensitivity of the maintenance respiration such that CUE is the same at the reference (15°C) and
2 the elevated (20°C) temperature.

3 **3.5. Enzyme production expenditures**

4 Finally, we analyse in the OPT model how levels of costs associated with enzyme production
5 affects soil carbon storage and response to temperature (Fig. 4). Because of largely unknown
6 parameters we express enzyme expenditures as the fraction of respiratory carbon for enzyme
7 production per unit carbon depolymerised at the reference state (see Eq. 8 and Eq. 16). We tested
8 3 levels of enzyme production cost: 0%, 10%, and 50% of equilibrium depolymerisation at our
9 reference condition (i.e. 15°C). As expected, increasing enzyme production cost reduced the rate
10 of depolymerisation, and S is therefore maintained at a higher level. The increasing costs also
11 resulted intoin a smaller relative decline of S in response to warming, whereas the absolute loss
12 is larger, as indicated by the consistently higher rates of respiration. Similarly, the response of
13 CUE to warming is smaller and the decline of M is less pronounced if enzyme production costs
14 are considered.

16 **4 Discussion**

17 Recently developed microbial decomposition models (Schimel and Weintraub, 2003; Allison et
18 al., 2010; German et al., 2012) highlight the importance of microbial processes and microbial
19 physiology during decomposition. Their application specifically highlights the role of
20 extracellular enzymes during decomposition and how these constraints will further affect the
21 release of soil organic matter as a consequence of warming. While microbial decomposition
22 models are able to improve prediction of organic carbon stock globally, and can successfully
23 recreate litter decomposition dynamics, the long-term trajectory of a warming response needs

1 further evaluation (Wang et al., 2014); ~~Hararuk et al., 2015~~). In particular, a positive feedback
2 between depolymerisation and microbes can only be curbed via the longer term adjustment of
3 soil organic matter and therefore lead to oscillation in both microbial biomass and soil organic
4 matter (Wang et al., 2014). ~~The oscillation is the consequence of a positive feedback between~~
5 ~~depolymerisation and microbial growth, and is evidenced caused~~ by a knife's edge or unstable
6 equilibrium ~~under constant substrate condition (in the short term (unstable QSS for microbes,~~
7 Schimel and Weintraub, 2003). A break in this feedback and stabilisation only occurs via
8 ~~interplay with the reduction of slow changing~~ soil organic matter.
9 ~~Such interplay occurs on a longer timescale than that of microbial turnover, causing the swings~~
10 ~~in M and S pool~~. We note that some attenuation of the oscillation may occur via direct input into
11 a DOC pool that does not require depolymerisation (Allison et al., 2010), a feature not
12 considered here.

13 The display of oscillation in the FWD model has been a point of critique as it has not been
14 observed in laboratory and field incubation studies (Wang et al., 2014). Here, we introduce
15 mechanisms that curb the positive feedback between substrate and microbial biomass. We portray
16 two scenarios, where each increment in microbial biomass or enzyme concentration yields a
17 smaller increase in depolymerisation than the previous increment (i.e. diminishing return). The
18 scenarios we worked out are 1) microbial biomass feeds on active extracellular enzymes, and 2)
19 limited sites for substrate/enzyme reactions (see Appendix B). We derived the forms of
20 depolymerisation from the original Michaelis-Menten kinetics and the resulting formulations
21 presented in the method section are simplified and more illustrative versions of more complex
22 functions. ~~Wang and Post (2013) arrived at the same function for depolymerisation of the reverse~~
23 ~~Michaelis-Menten model, where an enzyme only adsorbs to a fraction of binding sites because of~~

1 | ~~complex substrates.~~ The simplified formulation of depolymerisation and microbial consumption
2 | we ~~arrived at~~obtained has been dubbed a reverse Michaelis-Menten formulation (Schimel and
3 | Weintraub, 2003), because microbial biomass (or enzyme concentration) instead of the substrate
4 | concentration is now occurring in the denominator of the depolymerisation term, invoking the
5 | diminishing return. Wang and Post (2013) arrived at reverse Michaelis-Menten depolymerisation
6 | function if enzymes only adsorb to a fraction of binding sites because of complex substrates.
7 | Transitions between FWD and REV model behaviour has also been detailed in the more complex
8 | Equilibrium Chemistry Approximation model that also included sorption of enzymes and
9 | substrates to mineral surfaces (Tang and Riley, 2015; Tang, 2015). Our analysis shows that the
10 | positive feedback between decomposition and microbial growth is removed, as our REV model
11 | now has ~~now~~ a stable ~~equilibrium~~short-term QSS.

12 | Limited sites may play a role if the substrate has a high volume to surface ratio, or if the
13 | substrate is associated with minerals (Davidson and Janssens, 2006; Gillabel et al., 2010; Conant
14 | et al., 2011; Davidson et al., 2012, 2014; Cotrufo et al., 2013; Wagai et al., 2013; Benbi et al.,
15 | 2014; Wieder et al., 2014a; Tang and Riley, 2015). Our implementation of limited substrate
16 | causes a surplus of free enzymes that compete ~~among themselves~~ for binding to substrates
17 | similar to the Langmuir adsorption isotherm theory (Vetter et al., 1998; Schimel and Weintraub,
18 | 2003, Wang and Post, 2013, and see Appendix B, Model with limited available substrate~~)-),~~
19 | leading to diminishing depolymerisation returns and a REV model formulation. Effects of
20 | microbial scavenging for enzymes cause a diminishing return because more microbial biomass
21 | will lead to an increased probability of enzymes being consumed before they interact with soil
22 | organic matter. Other mechanisms of diminishing return as enzyme increase may be the
23 | stabilisation of enzymes into organic matter-humate complex (Allison, 2006), or sorption to

1 minerals, soil organic matter, or microbes (Tang and Riley, 2015). Diminishing returns also
2 occur with rate-yield tradeoffs (Allison, 2014).

3 Many microbial decomposition models work under the assumption that enzyme production is
4 proportional to microbial biomass. ~~It, however it is~~ also conceivable that microbes are adjusting
5 production to maximise return or growth (Cooney, 2009; Merchant and Helmann, 2012). Tang
6 and Riley, 2015). In our OPT model, we relax the proportionality of microbial enzyme
7 production and microbial biomass ~~but~~ and instead allow a best possible return; given the cost of
8 enzyme synthesis. While the exact cost of enzyme production is not known, we fixed parameters
9 (the product of ~~$K_p K_p$~~ and c) that relate to the fractional expense of carbon depolymerised upon
10 initialization (i.e. at steady state and reference temperature, Eqs. 8 and ~~15~~ 16). Importantly,
11 enzyme production optimisation is not possible for some of the models presented here. Higher
12 enzyme production would always lead to further microbial growth in the FWD model, and the
13 highest yield would occur with infinite enzyme production. Similarly, in the case of microbial
14 scavenging for enzymes, additional investments into enzymes always increases
15 depolymerisation.

16 The response to temperature in our OPT model closely resembles the traditional first order decay
17 model (FOD). In the limit of enzyme production cost ~~is~~ approaching zero, depolymerisation
18 occurs at the maximum rate ($V_{\max} * S$), ~~confirming essentially turning the~~ resemblance to the OPT
19 model into a first order model. ~~This model shows (Fig. 2). In the strongest response to~~
20 warming OPT model, reductions in the long term because the temperature dependence of
21 depolymerisation ~~is not reduced via a half saturation constants (K_E in forward, K_M in OPT, via K_p~~
22 are alleviated when enzyme synthesis is inexpensive, where the reduction of the maximum
23 depolymerisation rate becomes a function of the product of $K_p * c$ (Eq. 7 and K_p in OPT model) as

1 ~~in the FWD or REV model. We note that half saturation constants in our~~ Table 2). The results of
2 the OPT model also show the effects on assumptions on microbial enzyme production rates. In
3 many microbial models combine several parameters such as enzyme productivity relates, enzyme
4 production is scaled to microbial biomass, ~~and turnover of the enzyme pool. In the REV and the~~
5 ~~OPT model, smaller the half saturation constant is, the closer we arrive at the formulation.~~
6 Lifting the tight coupling between microbial biomass and enzyme production leads to a more
7 dynamic enzyme concentrations and ultimately affects the temperature sensitivity of
8 decomposition ~~in a first order model, this occurs via an increase of enzyme concentration by way~~
9 ~~of higher production or reduced enzyme turnover. Both, parameter are hard. Thus, the cost and~~
10 trade-offs associated with microbial enzyme production are potential important areas to better
11 quantify the long-term response of soil carbon storage to ~~come by~~ climate change.

12 The response of decomposition to warming can be viewed as a response ~~occurring~~ occurring on
13 multiple ~~timescales~~ timescales. For example, while enzyme activity likely produces ~~likely~~
14 immediate response, microbial respiration responses may also be triggered quickly, although
15 longer term acclimation may occur (Frey et al., 2013). It may take longer for microbial biomass
16 to respond to ~~the~~ temperature changes (weeks to months). Finally, because the rate of
17 decomposition is slow compared to the overall abundance of soil ~~organic~~ organic matter,
18 discernible changes in this pool occur on timescales of months to years. Based on the distinct
19 rates of ~~adjustments~~ adjustments, timescales can – in principle – be separated by assuming a
20 quasi-steady state of pools that turn over fast.

21 The assumption that both enzyme concentrations and DOC (i.e. the depolymerisation products)
22 are at quasi-steady state cuts across all models presented here (FWD, REV and OPT, see
23 Appendix A). When we extend our assumption of steady state to the microbial timescale (quasi-

1 | steady state of microbial ~~biomass~~biomass), we find that for both the REV and the OPT model,
2 | the short-term response of microbial biomass and respiration is influenced by the adjustment of
3 | microbial dynamics to the warmer temperature- (Fig. 3). Because microbial biomass jumps
4 | immediately to a higher level after the temperature increase in ~~such an equilibrium~~our QSS
5 | assumption, depolymerisation₂ and thus respiration₂ are affected. However, the ~~equilibrium~~QSS
6 | assumption ~~does not affect~~affects the trajectory of the soil carbon pool, ~~S~~ only minimally. At
7 | timescales that allow microbes to turn over a couple of times (several months), the quasi-steady
8 | state poses a suitable approximation to represent respiration and microbial biomass, even after a
9 | sharp perturbation in ~~form of a step change. Perhaps more intriguing is the fact that a traditional~~
10 | ~~first order model is the special case of the OPT model with microbial quasi-steady state and with~~
11 | ~~marginal enzyme production costs ($\mu \rightarrow 0$). Here, we maintain reduction of CUE under increasing~~
12 | ~~temperature in the FOD, a feature typically not include in traditional first order models.~~the form
13 | of a step change. In the QSS assumption, depolymerisation becomes independent of the
14 | microbial biomass (but is still dependent on a combination of microbial parameters, see Table 2).
15 | The introduction of QSS microbial biomass allows addressing and comparing the long-term
16 | responses of the different models to warming. In particular, the comparison of the QSS derived
17 | depolymerisation of the FOD with the REV and the OPT directly show the effect of how
18 | enzyme-substrate affinity and enzyme production costs dampen the rate of depolymerisation and
19 | its response to temperature. In other words, the long-term response of the FOD is equivalent to
20 | the long-term response of our OPT or REV model, when 1) K_e is low (high enzyme production,
21 | high enzyme-substrate affinity, and low enzyme turnover), and/or 2) costs of enzyme
22 | productions are low, and 3) and CUE (the fraction of depolymerised not respired but cycled back

1 into soil organic matter pool) is also temperature dependent in the FOD, a feature typically not
2 included in traditional decomposition models.

3 CUE ultimately is the result of different microbial respiration terms. Here, we
4 ~~considered~~consider 3 processes that may affect microbial respiration under a warming scenario.
5 We first ~~considered~~consider a partitioning into growth and maintenance respiration across our 3
6 models. Growth respiration ~~was~~is simply assumed to be a proportion of carbon allocated to
7 microbial growth. In contrast, maintenance respiration scales ~~in our models~~ to microbial biomass
8 in our models, where the proportionality factor increases with temperature. We motivate the
9 partitioning by formulations of plant respiration in terrestrial biosphere models. We find that this
10 separation affects the short-term responses of respiration, because microbial biomass lags the
11 increase of depolymerisation. The temperature response of CUE is thus delayed. The partitioning
12 of the respiration terms ~~has particularly~~ also has a particular impact on the transient dynamics
13 of the FWD model, in that the lag in maintenance respiration amplifies the oscillation- (Fig. 3).
14 However, in the REV and the OPT model, effects of separation are only discernible on the
15 microbial time scale, before microbial biomass is approaching quasi-steady state values.

16 In the OPT model, we introduce an additional respiration term, namely the cost of enzyme
17 production, ~~which.~~ In this model, we allow microbes to adjust enzyme production in order to
18 optimise growth.- It is interesting that increasing costs lead to a smaller immediate response in
19 respiration and more resilient soil organic matter pool in the long term, when subject to warming-
20 (Fig. 4). The early respiration response in the OPT model is both a product of higher rates of
21 depolymerisation, (increased V_{max}), but also a higher rate of enzyme production. However, the
22 enhancement relative to the rates at the reference temperature ~~is~~becomes smaller, ~~the~~ with higher
23 ~~the~~ enzyme production cost. In the long term, the decrease in soil organic matter ~~decreases much~~

1 ~~lessis reduced~~ when enzyme production costs are considered. This ~~reduction is accompanied by a~~
2 ~~smaller reduction in CUE under higher enzyme production, even though there is a subsequent~~
3 ~~CUE reduction occurring as S declines. The changing~~ yield tradeoff ~~thus act~~overall acts to buffer
4 respiration increases that could be expected from physiological responses alone (V_{\max}), although
5 the effects are smaller and may be well within the uncertainty of the temperature response of any
6 parameters considered here. We note that enzyme expenditure relative to depolymerisation is a
7 function of the product of K_p and c .

8 We acknowledge that we used a simplified set-up of our model suite. For example, we assumed
9 that depolymerised carbon in soil solution (DOC) is always at steady state with the microbial
10 biomass. ~~We justified this~~ (see also German et al., 2012 and Moorhead et al., 2012). This
11 simplification ~~by assuming~~ can be justified with fast and efficient scavenging of microbes. ~~and~~
12 thus, fast turnover of the DOC pool. Further sensitivity analysis may shed ~~further~~ light on the
13 dynamics across the full parameter space, while using the simplified linear terms (Appendices B
14 and C, Tang, 2015), particularly also because many of the parameters are ~~hard~~difficult to ~~come~~
15 by estimate. We further did not include nutrient requirements of microbes. ~~Considering, where~~
16 considering the stoichiometric requirements can ~~in particular~~ change the allocation of resources
17 to optimise enzyme synthesis. Finally, our model does not include interaction that may occur
18 with adsorption to mineral surfaces, which may occur with the substrate, the enzymes and
19 microbial biomass, and which has important short and long-term consequences to temperature
20 fluctuations and changes (Wieder et al., 2014a; Tang and Riley, 2015). Nevertheless, our suite of
21 models ~~show~~shows the importance of ~~how~~formulating the depolymerisation step ~~is formulated~~ in
22 mathematical models when evaluating the response of decomposition under warming, ~~and it~~
23 ~~provides ecosystem modelers a mechanistic handle when expanding microbial frameworks into~~

1 ~~to more complex, models with multiple substrates of different quality and different propensities~~
2 ~~to microbial processing.~~

3 Microbial models are considered to be more realistic because of mechanistic representation of
4 the decomposition steps, yet the oscillatory behavior has been viewed as an unrealistic response
5 to perturbation (Wang et al., 2014). Perhaps on a more fundamental level, first order
6 decomposition models inherently assume substrate limitation while the FWD model incorporates
7 enzyme availability (and enzyme production) as the limiting step during decomposition. Here,
8 we show that first order models can be viewed as a special case of a microbial model that
9 considers limitation other than enzyme availability (i.e., diminishing returns) and low values of
10 the half saturation constant (REV Model), or alternatively, a decoupling of microbial enzyme
11 production from microbial biomass (OPT model). While moving from the FWD to the REV
12 model (diminishing return) introduced a form of substrate limitation, optimising enzyme
13 production can be viewed as a further alleviation (or removal under marginal production cost) of
14 enzyme limitation. Since the response to warming is vastly different across our suite of models,
15 our results suggest that the degree of enzyme limitation and the microbial response to enzyme
16 limitation are potential areas that could help constrain the quantification of the long-term
17 response of soil organic matter to warming.

19 **5 Conclusions**

20 Our findings suggest that different formulation of ~~how microbes acquire~~microbial substrate
21 acquisition will have a significant impact on the short vs. long-term consequences of warming.

22 Here, we present simple, yet feasible mechanisms of microbial dynamics. We show that substrate
23 limitation in the form of decreasing marginal return can create a break in the positive feedback

1 between microbial biomass and depolymerisation, turning a forward Michaelis-Menten model
2 into a reverse model. We further ~~seperate~~separate out 3 types of respiration, that ~~possibly~~have
3 possible have consequences on the temporal trend of CUE in response to warming. Although
4 such ~~seperation~~separation is more mechanistic, it remains open whether the addition of extra
5 parameters is justified at this point, given the uncertainty in models, and because much of the
6 effects of this separation diminishes on timescales longer than the microbial lifespan. Finally, ~~our~~
7 ~~OPT model is~~ among our suite of models, ~~the one that our~~ OPT model most closely resembles
8 the traditional first order decomposition model, ~~and can be converted to such.~~ In our modeling
9 framework, a first order model ~~by applying is~~ a ~~series~~special case of ~~tangible a microbial~~
10 decomposition model where 1) mechanisms ~~and simplification. These include 1) mechansims~~ of
11 ~~dimishing~~diminishing returns ~~that breaks~~break the feedback between substrate and microbes, 2)
12 ~~relaxing~~ the proportionality of enzyme production and microbial biomass is relaxed and adjusted
13 to yield optimum return of enzyme investments, 3) ~~small cost~~costs associated with enzyme
14 synthesis, are small (and/or enzyme-substrate affinity is high), and 4) ~~assumption of microbial~~
15 ~~quasi-steady-state and microbes turn over relatively fast compared to soil organic matter. Our~~
16 results thus suggest that a better grasp of the limiting steps of decomposition and mechanisms of
17 microbial enzyme production will help to constrain the long-term response to warming.

18

19 **Appendix A**

20 **Michaelis-Menten kinetics with enzyme denaturation**

21 The dynamics of the enzyme-substrate complex are

$$22 \frac{d[E]}{dt} = P - K_S[S][E] - \lambda_{E1} * [E] + K_r + K([ES]) \quad (A1)$$

$$\frac{d[ES]}{dt} = -(K_{cat} + K_r + \lambda_{E2})[ES] + K_S[S][E] \quad (A2)$$

Where P is the microbial production of new enzymes, [S] is the concentration of the substrate, [E] the concentration of enzymes, [ES] the substrate-enzyme complex, K_S , K_{cat} , and K_r are reaction constants that denote substrate-enzyme binding, actual depolymerisation rate, the reversibility of the enzyme-binding process. λ_{E1} and λ_{E2} are enzyme decay parameters that lead to enzyme denaturation or render enzymes inactive in the free enzyme pool or in the enzyme-substrate complex, respectively. In the FWD and REV model, P is proportional to microbial biomass. The Michaelis–Menten approximation for depolymerisation assumes that the system is in quasi-steady state in which the tendency $\frac{d[ES]}{dt}$ and $\frac{d[E]}{dt}$ are zero. This implies also that tendency of the total enzyme concentration $\frac{d[Et]}{dt}$ (with $[Et] = [ES] + [E]$) becomes zero.

Setting Eq. (A2) to zero, and substituting $[Et] = [ES] + [E]$, it follows

$$[E] = \frac{[Et] - K_E K_m}{([S] + K_E K_m)} \quad (A3)$$

$$[ES] = \frac{[Et] [S]}{([S] + K_E K_m) ([S] + K_m)} \quad (A4)$$

And the rate of depolymerisation

$$D = \frac{[Et] + V_{max} [S]}{([S] + K_E K_m)} \frac{[Et] * V_{max} [S]}{([S] + K_m)} \quad (A5)$$

where D is the familiar Michaelis-Menten equation with $K_E K_m = \frac{K_{cat} + K_r + \lambda_{E2}}{K_S}$ and V_{max} is equivalent to K_{cat} .

DOC and enzyme dynamics

1 We assumed that DOC concentrations are in equilibrium with substrate and microbial uptake. In
 2 microbial decomposition models, the only DOC sink is microbial consumption, which by way of
 3 mass conservation, leads to microbial consumption being equivalent to the rate of
 4 depolymerisation.

5 Previous models (Allison et al., 2010; German et al., 2012) assumed a general decay of the total
 6 enzyme pool, where:

$$7 \quad \frac{d[E_t]}{dt} = P - \lambda_E * [E_t] \quad (A6)$$

8 Because enzyme turn over fast, we can assume a quasi-steady state of the total enzyme pool by
 9 setting Eq. A6 to zero. We obtain:

$$10 \quad [E_t] = \frac{P}{\lambda_E} \quad (A7)$$

11 And depolymerisation as:

$$12 \quad D = \frac{\frac{P}{\lambda_E} * K_{cat} * [S]}{[S] + K_E} = \frac{\frac{P}{\lambda_E} * K_{cat} * [S]}{[S] + K_m} \quad (A8)$$

13 Finally, microbial decomposition models assume that enzyme production is proportional to the
 14 microbial biomass (M): $P = b * M$, hence:

$$15 \quad D = \frac{V_{max} * M * [S]}{[S] + K_E} = \frac{V_{max} * M * [S]}{[S] + K_m} \quad (A9)$$

16 With $V_{max} = \frac{b * K_{cat}}{\lambda_E}$

17 Yet, it is conceivable, that the enzyme-substrate complex, and free enzymes decay at
 18 different rates (see also Eqs A1 and A2-).

$$19 \quad \frac{d[E_t]}{dt} = P - \lambda_{E2}[ES] - \lambda_{E1}[E] \quad (A10)$$

1 Substituting Eq. A3 and Eq. A4 for [E] and [ES], and applying a quasi-steady state as before
 2 yields:

$$3 \quad [E_t] = \frac{P([S]+K_E)}{\lambda_{E1}K_E + \lambda_{E2}[S]} \frac{P([S]+K_E)}{\lambda_{E1}K_m + \lambda_{E2}[S]} \quad (A11)$$

4 And the overall depolymerisation is thus:

$$5 \quad D = \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E1}K_E + \lambda_{E2}[S]} D = \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E1}K_m + \lambda_{E2}[S]} \quad (A12)$$

6 Which can be converted into a Michaelis-Menten form

$$7 \quad D = \frac{V_{max} \cdot M \cdot [S]}{[S] + K_S} \quad (A13)$$

8 where $V_{max} = \frac{b \cdot K_{cat}}{\lambda_{E2}}$ and $K_S = K_E \frac{\lambda_{E1}}{\lambda_{E2}} K_m = K_m \frac{\lambda_{E1}}{\lambda_{E2}}$

9 Appendix B

10 Microbial consumption of enzymes

11 Microbes feeding on free enzymes can be represented as:

$$12 \quad F = \lambda_{E,M} \cdot [E] \cdot M \quad (B1)$$

13 Where F is microbial enzyme consumption and $\lambda_{E,M}$ the feeding rate. We can then represent the
 14 decay of the free enzymes with

$$15 \quad [E] \cdot \lambda_{E1} = [E](\lambda_{E1,0} + \lambda_{E,M} \cdot M) \quad (B2)$$

16 where the total $\lambda_{E,0}$ is the spontaneous enzyme decay rate.

17 Substituting the new enzyme decay formulation into the depolymerisation (Eq. A12) yields

$$18 \quad D = \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E2}[S] + \lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E2}[S] + \lambda_{E1,0} \cdot K_m + \lambda_{E,M} \cdot M \cdot K_m} \quad (B3)$$

1 For the REV model, we simplify Eq. B3 and assume that enzymes associated with substrate do
 2 not undergo denaturation ($\lambda_{E2}=0$), which yields:

$$3 \quad D = \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \frac{P \cdot K_{cat} \cdot [S]}{\lambda_{E1,0} \cdot K_m + \lambda_{E,M} \cdot M \cdot K_m} \quad (B4)$$

4 And, in the case where enzyme production scales to microbial biomass ($P = b \cdot M$)

$$5 \quad D = \frac{M \cdot V_{max} \cdot [S]}{K_m + M} \quad D = \frac{M \cdot V_{max} \cdot [S]}{K_{es} + M} \quad (B5)$$

6 Which is again the familiar Michaelis-Menten function with $V_{max} = \frac{b \cdot K_{cat}}{\lambda_{E,M} \cdot K_E}$ and $K_{es} = \frac{\lambda_{E1,0}}{\lambda_{E,M}}$

7 **Model with limited available substrate**

8 Access to substrate might be finite, for example, if organic matter is associated with mineral soil
 9 or if the rate of depolymerisation is constrained by the surface area. In this case, the relationship
 10 between the total available substrate and the free sites can be calculated as

$$11 \quad [S] = \theta * ([S_f] + [ES]) \quad (B6)$$

12 Where S_f are the available sites for enzyme reaction, θ a scalar relating the total amount of
 13 substrate to the total potentially free sites (e.g. a surface to mass conversion), and $[ES]$ represents
 14 the sites with enzyme-substrate complexes. We note that $[S]$ in this case is not the available
 15 substrate anymore, but reduced by a fraction θ .

16 Substituting $[ES]$ from Eq. A4, but knowing that $[S]$ has now become $[S_f]$, we obtain:

$$17 \quad [S_f] = \frac{[S]}{\theta} - \frac{[S_f][E_t]}{K_E + [S_f]} \frac{[S_f][E_t]}{K_m + [S_f]} \quad (B7)$$

18 $[S_f]$ is thus the solution of a quadratic polynomial:

$$[S_f] = \frac{1}{2} \left\{ - \left([E_t] + K_E - \frac{[S]}{\theta} \right) \pm \sqrt{\left([E_t] + K_E - \frac{[S]}{\theta} \right)^2 + 4 * \frac{[S]}{\theta} * K_E} \right\} \left\{ - \left([E_t] + K_m - \frac{[S]}{\theta} \right) \pm \sqrt{\left([E_t] + K_m - \frac{[S]}{\theta} \right)^2 + 4 * \frac{[S]}{\theta} * K_m} \right\} \quad (B8)$$

The scenario of limited reaction site is relevant if $\frac{[S]}{\theta}$ is small (i.e. $\frac{[S]}{\theta} \ll [E_t]$). Under this scenario, we simplify Eq. B8 using a Taylor expansion around ($\frac{[S]}{\theta} = 0$)

$$[S_f] = \frac{[S]}{\theta} * \left(\frac{K_E}{[E_t] + K_E} \right) \left(\frac{K_E}{[E_t] + K_m} \right) + O\left[\left(\frac{[S]}{\theta}\right)^2\right] \quad (B9)$$

Plugging this into the depolymerisation

$$D = \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E + \frac{[S]}{\theta}} \cong \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E} \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_m + \frac{[S]}{\theta}} \cong \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_m} \quad (B10)$$

which has a Michaelis-Menten form with a saturating enzyme concentration. This particular solution is for a small amount of binding sites, and enzymes compete for free sites. Thus $[E_t] \gg \frac{[S]}{\theta}$, and it can be dropped from within the denominator. On a side note: we obtain the same expression if we approximate from Eq. B7:

$$[S_f] = \frac{[S]}{\theta} - [S_f] \frac{[E_t]}{[S_f] + K_{Em}} \quad (B11)$$

$$[S_f] \cong \frac{[S]}{\theta} - \frac{[S_f][E_t][S_f][E_t]}{K_E K_m} \quad (B12)$$

Which assumes very few free sites ($[S_f] \gg K_E K_m$). Therefore:

$$[S_f] = \frac{[S]}{\theta} \frac{K_E}{[E_t] + K_E} \frac{K_m}{[E_t] + K_m} \quad (B13)$$

We can also include equations for enzyme turnover (Eq. A7) to calculate $[E_t]$:

However, we need to substitute $[S]$ in this equation with $[S_f]$, and thus:

$$\frac{d[E_t]}{dt} = P - \frac{\lambda_{E2} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E + \frac{[S]}{\theta}} - \frac{\lambda_{E1} * [E_t] * ([E_t] + K_m)}{[E_t] + K_E + \frac{[S]}{\theta}} - \frac{\lambda_{E2} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_m + \frac{[S]}{\theta}} \quad (B14)$$

Maintaining $\frac{[S]}{\theta} \ll ([E_t] + K_E + K_m)$ we obtain

$$\frac{d[E_t]}{dt} \cong P - \frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_E} - \lambda_{E1} * [E_t] \quad (B15)$$

The quasi-equilibrium solution ($\frac{d[E_t]}{dt} = 0$) yields a quadratic expression for $[E_t]$, however, we can evaluate the following scenarios:

a) suppose $\frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_E} \gg \lambda_{E1} * [E_t]$, this assumes that enzyme decay occurs mainly when bound to the substrate.

setting $\frac{d[E_t]}{dt} = 0$, we obtain

$$[E_t] = \frac{K_E * P}{\lambda_{E2} * \frac{S}{\theta} - P} - \frac{K_m * P}{\lambda_{E2} * \frac{S}{\theta} - P} \quad (B16)$$

and with P proportional to microbial biomass (M)

$$D = \frac{K_{cat} * P}{\lambda_{E2}} = V_{max} * M \quad (B17)$$

Where $V_{max} = \frac{K_{cat} * b}{\lambda_{E2}}$

In this case, depolymerisation and microbial consumption is independent of the substrate but is determined by the relative rate of catalysis and irreversible destruction of the enzyme-substrate complex.

b) suppose $\frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_E} \ll \lambda_{E1} \ll \frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_m} \ll \lambda_{E1} * [E_t]$

1 This implies that enzymes mainly decay if they are not associated with the substrate and that
 2 there is an appreciable amount of free enzymes. This is realistic under substrate limiting
 3 conditions, as there will be a sizeable amount of free enzymes compared to enzyme substrate
 4 complexes.

5 We then obtain: $[E_t] = \frac{P}{\lambda_{E1}}$

6 And

$$7 \quad D = \frac{K_{cat} * P * \frac{S}{\theta}}{P + \lambda_{E1} * K_{Em}} \quad (B18)$$

8 With $P = b * M$, we have

$$9 \quad D = \frac{M * V_{max} * S}{K_M + M} * \frac{M * V_{max} * S}{K_e + M} \quad (B19)$$

10 Where $V_{max} = \frac{K_{cat}}{\theta}$, and $K_M K_e = \frac{\lambda_{E1} * K_E}{b} * \frac{\lambda_{E1} * K_m}{b}$

11 **Appendix C**

12 **Optimising depolymerisation**

13 Microbes may be able to optimise their growth, and thus, depolymerisation becomes a function
 14 of the metabolic costs of enzyme production. Depolymerisation based on enzyme production,
 15 assuming fixed turnover of free enzymes yields:

$$16 \quad D(P) = \frac{P * V_{max} * [S]}{K_{Pp} + P} \quad (C1)$$

17 Where P is the amount of new enzyme produced, V_{max} is $\frac{K_{cat}}{\theta}$ and $K_P = \lambda_{E1} * K_E * K_p = \lambda_{E1} * K_m$,
 18 based on the model with limited available substrate.

19 Microbial growth (G) will be

1 $G = (1-g) * (D-Pc-\lambda_r * M)$ (C2)

2 Where g is the growth respiration factor, c the respiratory cost per unit enzyme production, and
 3 λ_r the maintenance respiration factor.

4 Enzyme production (P) can be optimised by substituting Eq. C1 into Eq. C2 and setting $\frac{dG}{dP} = 0$.

5 This yields:

6 $Pc = -\frac{K_p c}{\sqrt{V_{max} * [S] * K_p c}} + \frac{K_p c}{\sqrt{V_{max} * [S] * K_p c}}$ (C3)

7 The proportion of carbon expended for enzyme production relative to depolymerisation is

8 $\frac{Pc}{D} = \frac{\sqrt{\frac{K_p c}{[S] V_{max}}}}{\sqrt{\frac{K_p c}{[S] V_{max}}}}$ (C4)

9 Instead of specifying c , we used Eq. C4 to express overall microbial carbon expenditure for
 10 enzyme production. After assigning a value to μ , we calculate c based on equilibrium S at
 11 reference temperature.

12 In contrast, the microbial scavenging scenario does not provide an optimum enzyme production.

13 In this case, depolymerisation is:

14 $D = \frac{P * V_{max} * [S]}{(K_M + M) * \lambda_E} \frac{P * V_{max} * [S]}{(K_e + M) * \lambda_E}$ (C5)

15 And thus, $\frac{dG}{dP}$ will yield a constant where growth scales with the rate of enzyme production.

16

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Table 1. Key features of the microbial decomposition models and subsequent modifications
presented in this study.

FWD Model

German et al., 2012

FWD Model with maintenance respiration

As FWD model but microbial respiration is partitioned into temperature insensitive growth and temperature sensitive maintenance respiration terms.

REV Model

Depolymerisation and uptake relative to microbial biomass decreases with increasing M (diminishing return mechanism).

REV Model with equilibrium microbes

As REV model but fast microbial adjustments.

REV Model with maintenance respiration

As REV model but maintenance respiration added.

OPT Model

Optimisation of microbial enzyme production to maximise microbial growth, and consideration of carbon costs associated with enzyme synthesis.

OPT Model with equilibrium microbes

As OPT model but fast microbial adjustments.

OPT Model with maintenance respiration

As OPT model but maintenance respiration added.

FOD Model

First order decomposition model, modified to account for temperature sensitive carbon use efficiency.

1 Table 2. Quasi-steady state values ~~for~~ for microbial biomass (M), and decomposition at the short/fast timescale (at any given S) and
 2 “true” long-term equilibria for M and S across the models. Note, for simplicity, we did not substitute S in the long-term microbial
 3 equilibrium for OPT model.

4

Model	Short/Fast time scale		Long time scale	
	M	Decomposition	S	M
FWD	no solution *	no solution *	$\frac{\lambda_d K_E}{V_{\max, \text{FWD}} \varepsilon - \lambda_d}$	$\frac{I \varepsilon}{(1 - \varepsilon) \lambda_d}$
REV	$\frac{V_{\max, \text{REV}} S \varepsilon - K_M \lambda_d}{\lambda_d}$	$(V_{\max, \text{REV}} S - K_M \lambda_d / \varepsilon)$	$\frac{I}{V_{\max, \text{REV}} (1 - \varepsilon)} + \frac{K_M \lambda_d}{V_{\max, \text{REV}} \varepsilon}$	$\frac{I \varepsilon}{\lambda_d (1 - \varepsilon)}$
OPT	$\frac{(X - Y)^2 \varepsilon}{\lambda_d}$	$X^2 - XY$	$\frac{1}{2 V_{\max, \text{OPT}} (1 - \varepsilon)^2} [-Y (2\varepsilon - 1) \sqrt{4IY (1 - \varepsilon) + Y^2} + (1 - \varepsilon) (2I - 2\varepsilon Y^2) + Y^2]$	$\frac{(X - Y)^2 \varepsilon}{\lambda_d}$

5 $X = \sqrt{S V_{\max, \text{OPT}}}$, $Y = \sqrt{K_P * c}$

6 * requires $\lambda_d = \frac{V_{\max, \text{FWD}} S \varepsilon}{S + K_E}$

1 Table 3. Parameters used in microbial decomposition models (~~In subsequent models~~Down the
 2 model list, we provide only those parameters where modifications have been made.)

	Parameter	Unit	Value	Description	Source
FWD Model					
	I	mg <u>S</u> cm ⁻³ hr ⁻¹	0.001	Input of fresh litter	
	λ_d	hr ⁻¹	0.0005	Death rate of microbes	
	$V_{max, FWD,0}$	(mg em ⁻³ M) ⁻¹ hr ⁻¹	0.0049	Maximum catalytic rate @ 15°C	
	$Q_{10, Vmax, FWD}$	-	1.9	Q_{10} of maximum catalytic rate	
	$K_E K_m$	mg S cm ⁻³	270	Half-saturation constant @ 15°C	German et al., 2012
	ϵ_0	-	0.39	Microbial growth efficiency @ 15°C	
	ϵ_{slope}	°C ⁻¹	-0.016	Microbial growth efficiency temperature slope	
FWD Model with maintenance respiration					
	$\lambda_{r,0}$	hr ⁻¹	0.0006	Maintenance respiration @ 15°C	
	Q_{10, λ_r}	-	2.2	Q_{10} of maintenance respiration	This study
	gG	-	0.24	Growth respiration coefficient	
REV Model					
	$V_{max, REV}$	mg ⁻¹ M em ⁻³ hr ⁻¹	2.61*10 ⁻⁵	Maximum catalytic rate @ 15°C	
	$K_M K_e$	mg M cm ⁻³	0.68	Half-saturation constant @ 15°C	This study
OPT Model					
	$V_{max, OPT}$	mg ⁻¹ M em ⁻³ hr ⁻¹	1.71*10 ⁻⁵	Maximum catalytic rate @ 15°C	
	μ	=	0, 0.1, 0.5	Enz production cost <u>costs</u> (as % of decomposition @ 15°C steady state)	This study
	$K_P K_p * c$	mg MS ⁻³ <u>hr</u> ⁻¹	0, 1.64*10 ⁻⁵ , 0.0004 , <u>4*10⁻⁴</u>	combined <u>Combined</u> cost and the half saturation constant <u>constants</u> at $\mu = 0, 0.1, \text{ and } 0.5, \text{ respectively.}$	
FOD Model					
	k^*	hr ⁻¹	1.71*10 ⁻⁵	First order decay constant @ 15°C	This study

1 * k in FOD model is identical to $V_{\max, \text{OPT}}$ in OPT model.

1 **Figure Captions**

2 Figure 1. Conceptual diagrams ~~for the of our~~ microbial-enzyme models ~~applied~~. ~~Solid lines~~
3 ~~represent material flow~~ (~~).~~ ~~The difference across the models is in FWD and the formulation of~~
4 ~~depolymerisation of soil organic matter (S), where the FWD model with maintenance~~
5 ~~respiration) and dashed lines represent information flow (in Rev and is based on German et al.~~
6 ~~(2012), the REV model considers diminishing return and the OPT models).~~ ~~model includes~~
7 ~~optimised enzyme production to maximise microbial growth~~. E, S, E-S, D, DOC, M represent
8 enzyme, substrate, enzyme-substrate complex, depolymerisation, dissolved organic carbon, and
9 microbial biomass carbon, respectively. ~~We analyse the different models in three ways: a) Base~~
10 ~~models of forward vs reverse formulation of depolymerisation. In the forward version,~~
11 ~~depolymerisation scales microbial biomass via enzyme production. In the reverse formulation the~~
12 ~~decreasing marginal return curbs rates of depolymerisation. This decreasing marginal return can~~
13 ~~partly be overcome by enzyme production optimisation. b) For all models we introduce~~
14 ~~partitioning between maintenance and growth respiration. c) Microbes are instantaneously in~~
15 ~~steady with substrate delivery (reverse models only).~~ ~~I denotes input from fresh litter and D~~
16 ~~represents depolymerisation. Solid lines represent material (carbon) flow and dashed lines~~
17 ~~represent information flow affecting enzyme concentration (in microbial enzyme predation in~~
18 ~~REV model and enzyme production rate in OPT models). E, E-S, and DOC pools were implicitly~~
19 ~~represented in the model but not explicitly simulated based on the assumption of quasi-steady~~
20 ~~state. We analyse the different models in three ways: a) Comparison among different~~
21 ~~parameterisation of depolymerisation (FWD, REV and OPT models), b) A second suite of~~
22 ~~simulations operate under the assumption, that microbes are instantaneously in steady with~~
23 ~~substrate delivery (similar to the treatment of enzymes and DOC, for REV and OPT models~~

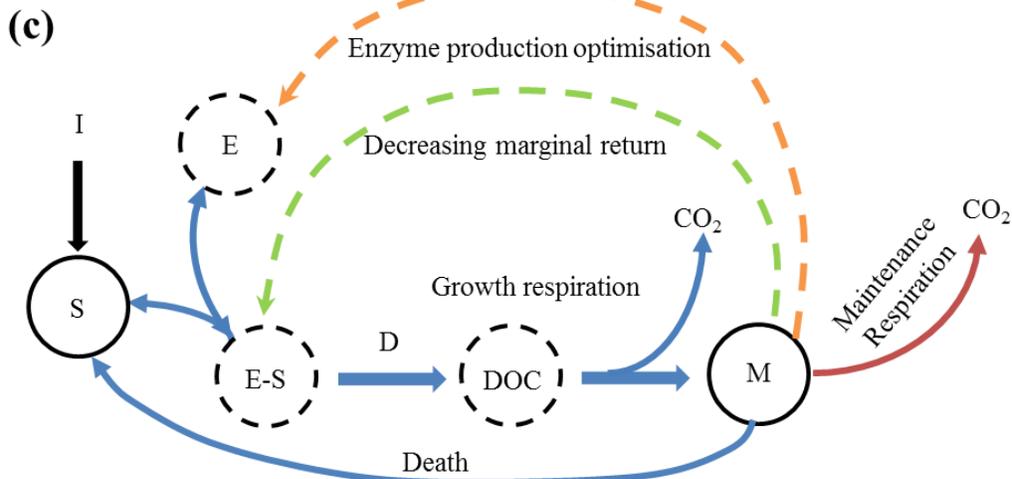
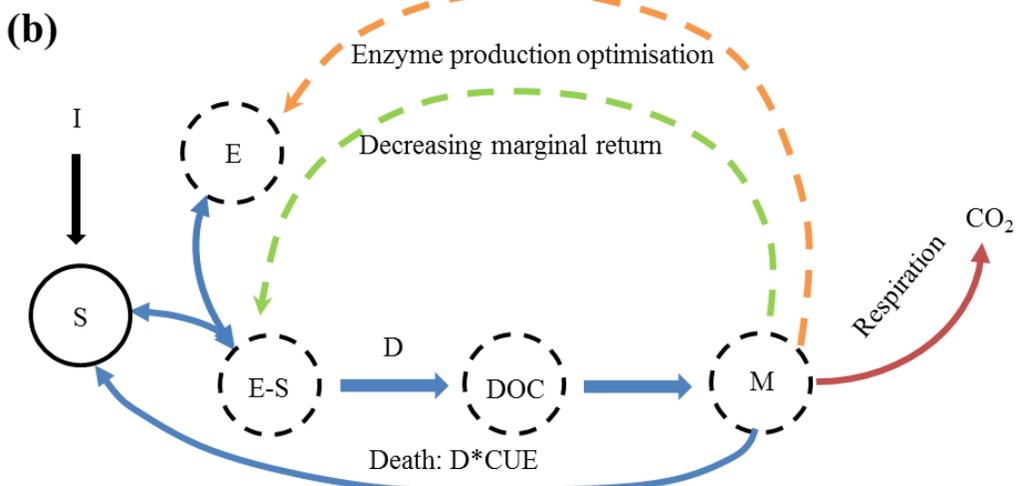
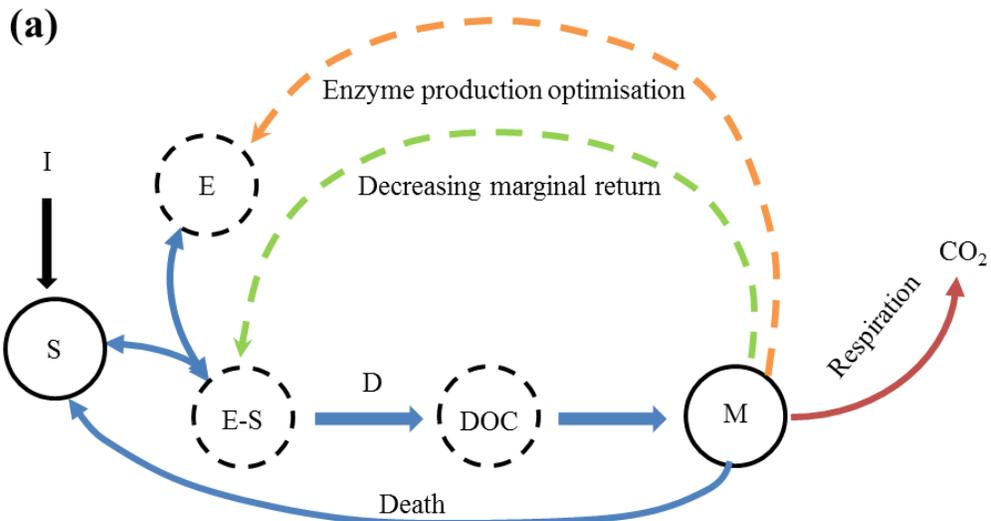
1 only, indicated by dashed outline of the pools), c) A third series of simulations considered
2 partitioning between a biomass-dependent maintenance respiration and a growth respiration that
3 scales to new tissues built, applied to all (FWD, REV, and OPT) models.

4 Figure 2. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d)
5 respiration to a 5°C warming in the base models (~~forward~~FWD vs ~~reverse~~)-REV and OPT, Fig.
6 1a). The black line ~~represent~~represents initial values, which are model equilibria at 15°C. We
7 chose logarithmic ~~axis~~axes for time to better highlight the differences in short-term responses.
8 ~~(Note: Differences~~We note that the differences in simulated soil organic carbon and respiration
9 ~~by~~for the OPT and the FOD are almost equal, and therefore not discernible. Also, values of CUE
10 at warmed temperature are identical in all models, and therefore, the orange line is superimposed
11 on blue and green lines. In the OPT model, simulations are carried out at zero enzyme production
12 cost, i.e. $\mu^2 = K_p * c = 0$).

13 Figure 3. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d)
14 respiration to a 5°C warming for all models, if microbial biomass is assumed to be at quasi-
15 steady state (QSS, dotted lines), and if separation of maintenance and growth respiration are
16 considered, ~~and if microbial biomass is assumed to be at quasi-steady state. Black thin line~~
17 ~~represent initial values, where equilibria @ 15°C. (dashed lines).~~ Colored thin lines represent
18 base models. The black thin line represents initial values, equilibrated at 15°C. Dashed lines
19 ~~(growth~~growth and maintenance) and dotted lines (quasi-steady state) represent modifications for
20 REV and OPT models respectively. ~~(In the OPT model, simulations are carried out at zero~~
21 enzyme production cost, ~~(i.e. $\mu^2 = k_p * c = 0$).~~

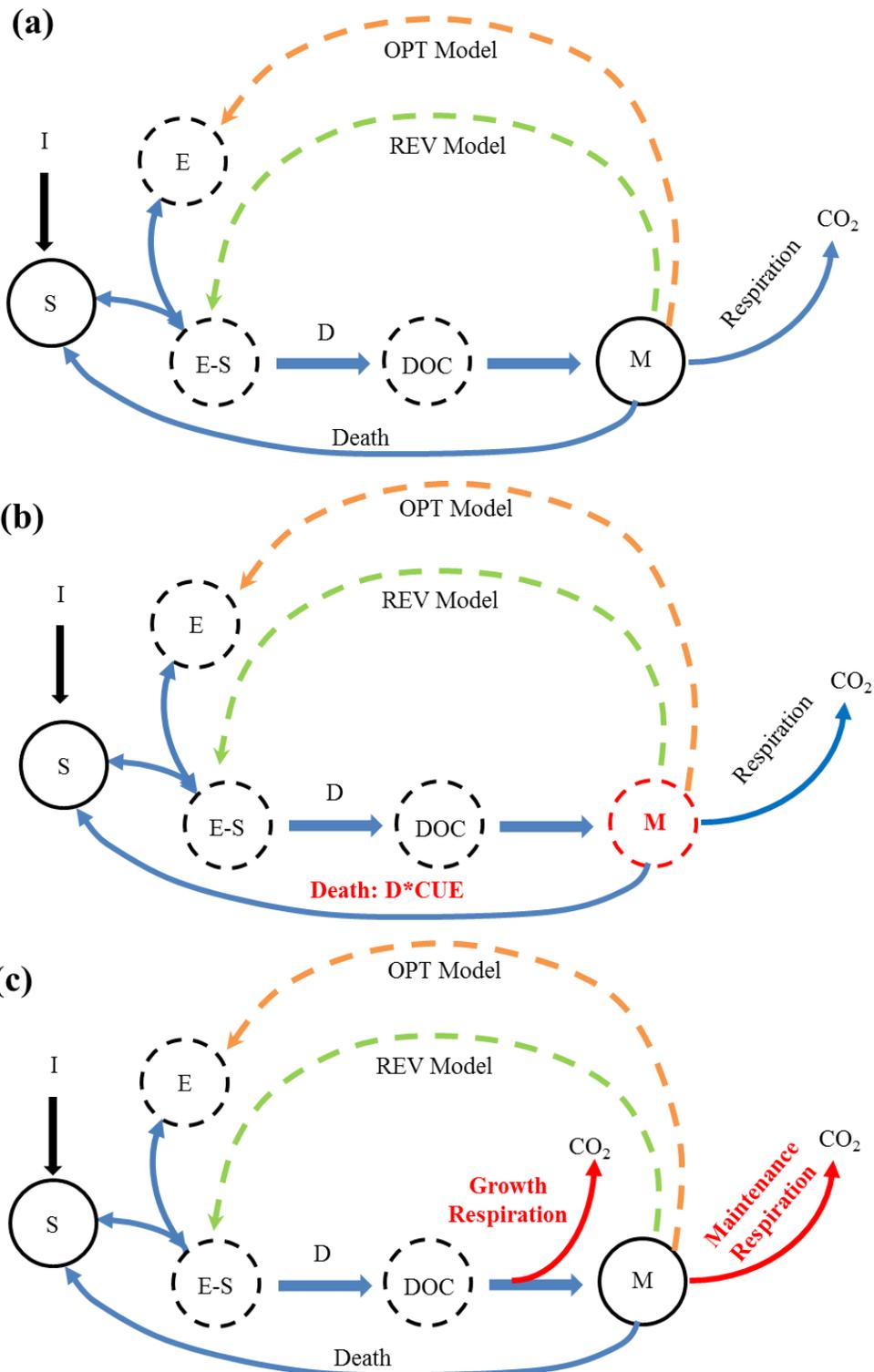
1 | Figure 4. Long-term responses of ~~optimized~~optimised enzyme production (OPT) model to a 5°C
2 | warming in a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d) respiration
3 | operating at different relative enzyme production costs (μ), see ~~Equation 13~~Eq. 16. Thick lines
4 | represent warming response and thin lines represent corresponding equilibrium at the reference
5 | temperature.

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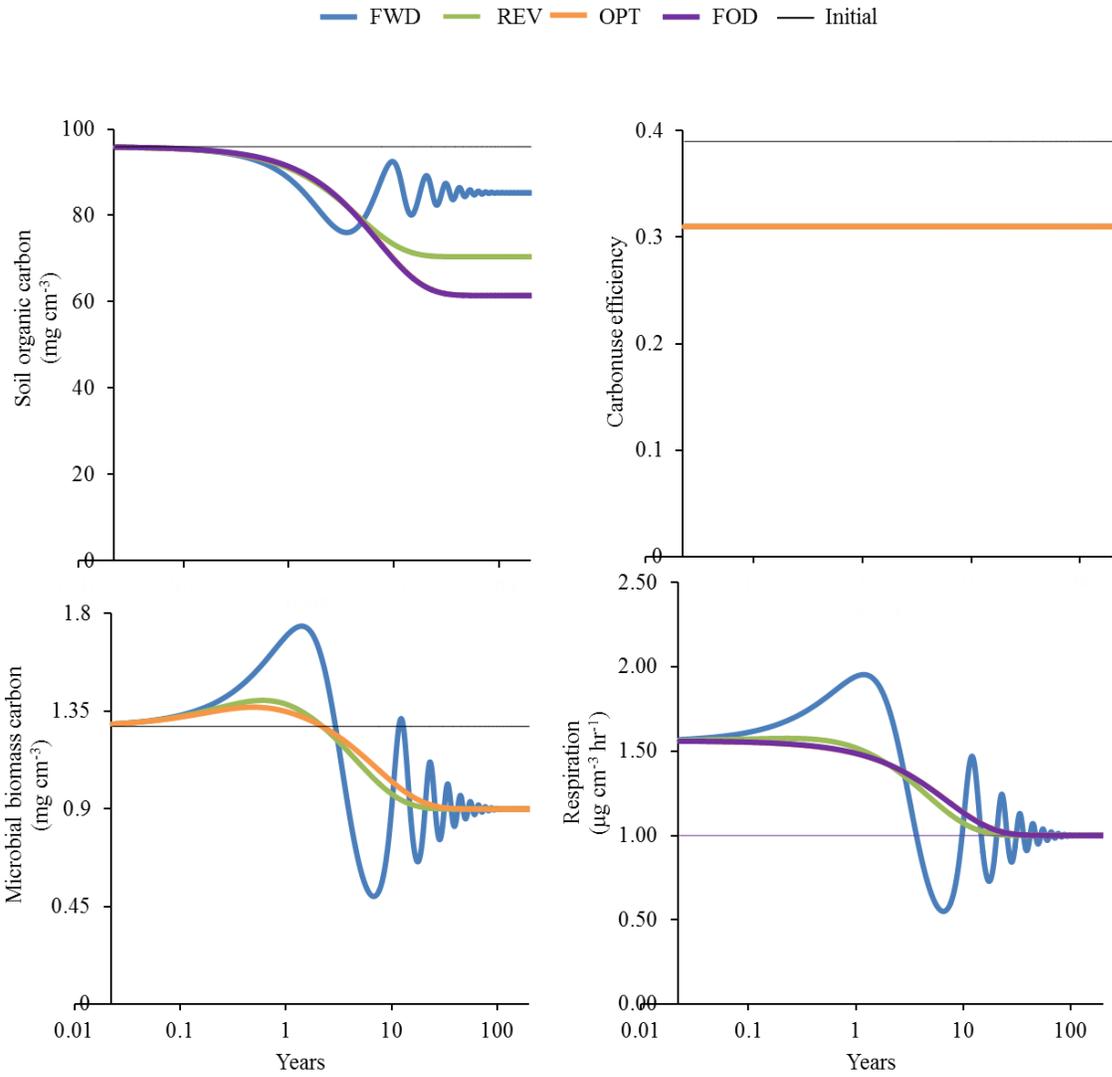
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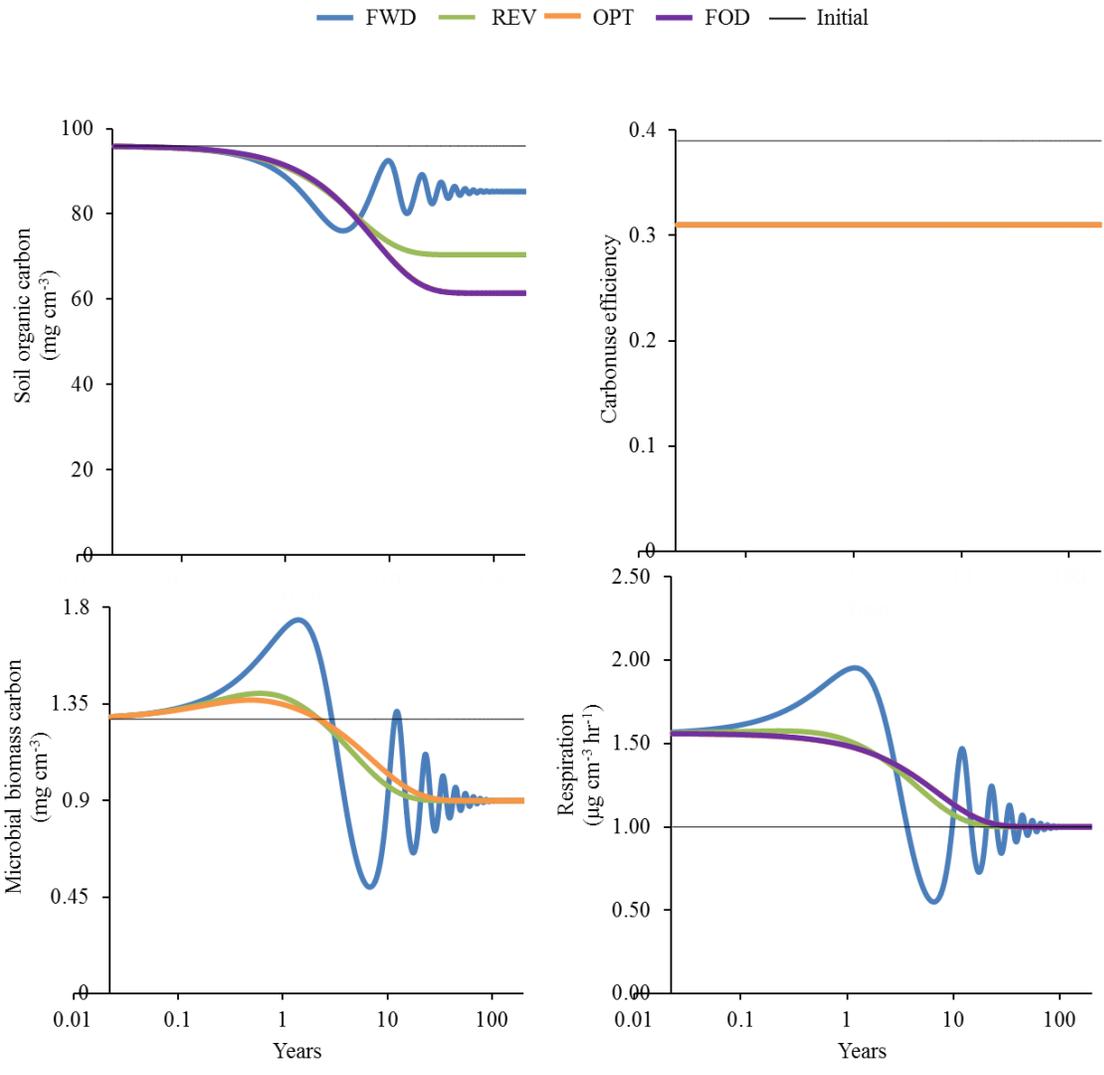


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2 Fig. 1

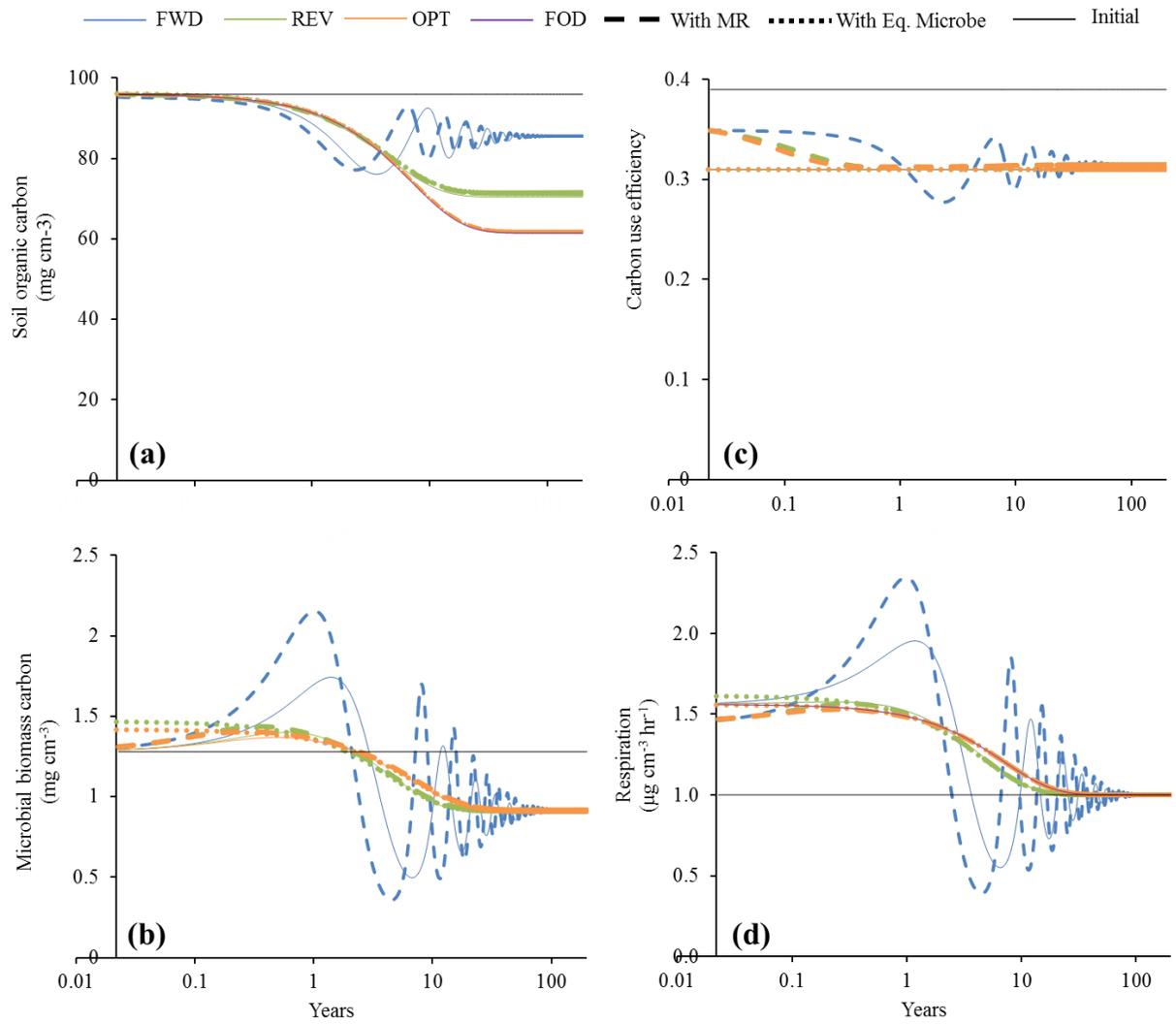


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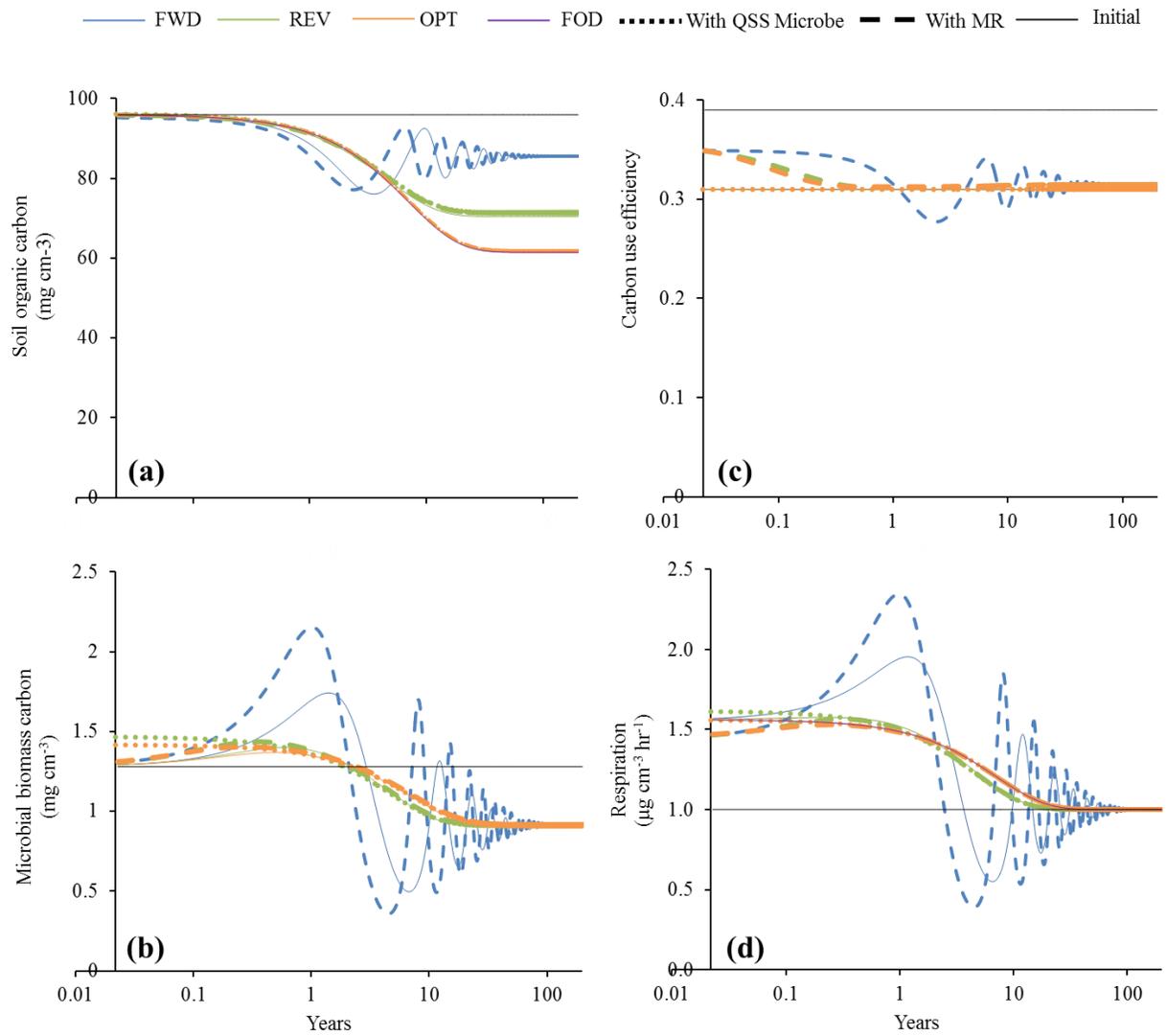


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2 Fig. 2

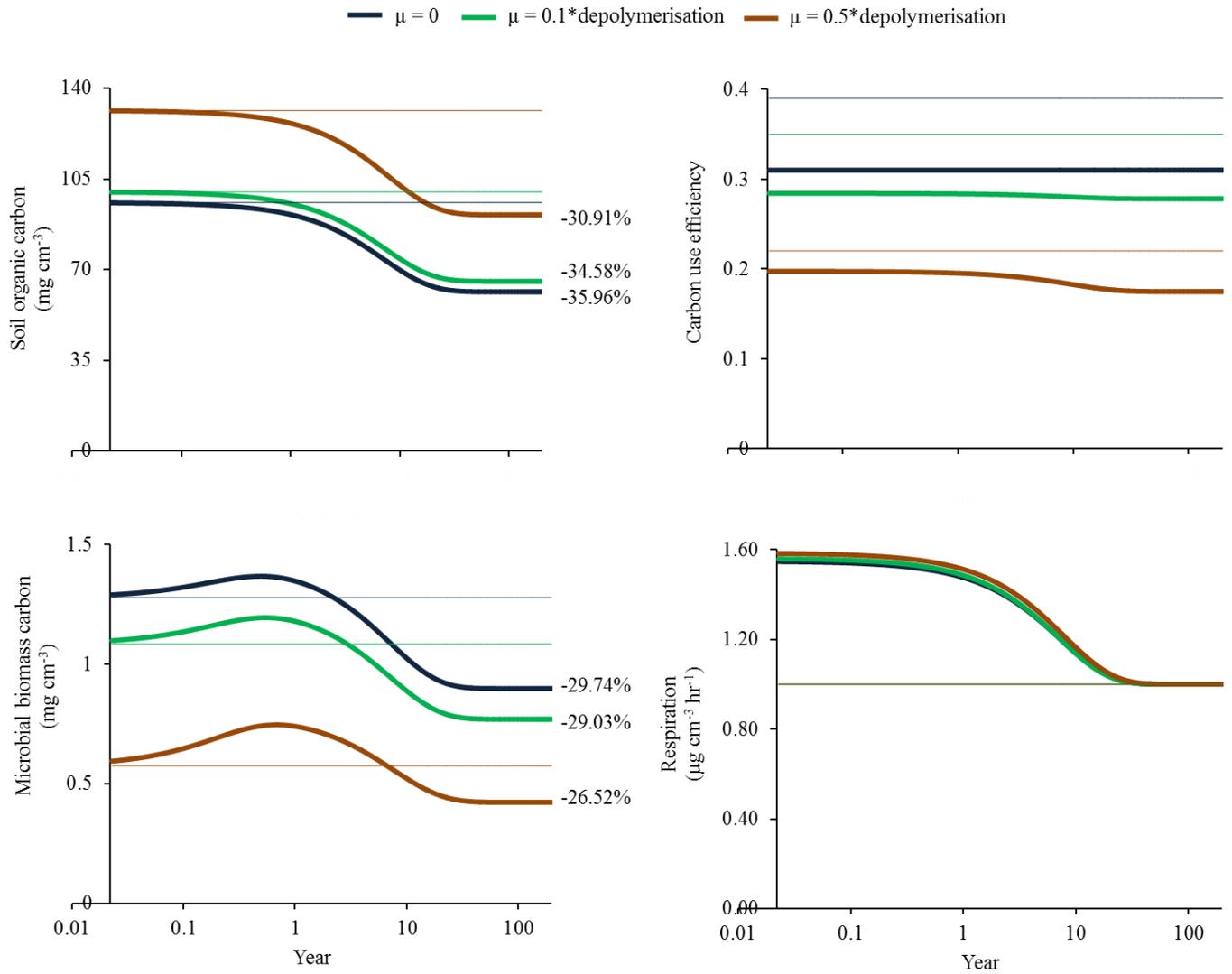


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2 Fig. 3



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2 | Fig. 4

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