

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

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## 7 **Abstract**

8 Recent developments in modelling soil organic carbon decomposition include the explicit  
9 incorporation of enzyme and microbial dynamics. A characteristic of these models is a  
10 positive feedback between substrate and consumers, which is absent in traditional first order  
11 decay models. Under sufficiently large substrate, this feedback allows an unconstrained  
12 growth of microbial biomass. We explore mechanisms that curb unrestricted microbial growth  
13 by including finite potential sites where enzymes can bind and by allowing microbial  
14 scavenging for enzymes. We further developed a model where enzyme synthesis is not scaled  
15 to microbial biomass, but associated with a respiratory cost and microbial population adjusts  
16 enzyme production in order to optimise their growth. We then tested short and long-term  
17 responses of these models to a step increase in temperature, and find that these models differ  
18 in the long-term, when short-term responses are harmonized. Oscillations that arise from a  
19 positive feedback between microbial biomass and depolymerisation are eliminated if  
20 limitations other than through enzyme-substrate interactions are considered. The model,  
21 where enzyme production is optimised to yield maximum microbial growth shows the  
22 strongest reduction of soil organic carbon in response to warming, and the trajectory of soil  
23 carbon largely follows that of a first order decomposition model. Modifications to separate

1 growth and maintenance respiration generally yield short-term differences, but results  
2 converge over time, because microbial biomass approaches a quasi-equilibrium with the new  
3 conditions of carbon supply and temperature.

4

## 5 **1 Introduction**

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

14 In traditional models, microbes are only considered as a simple donor-controlled pool (i.e.,  
15 microbial biomass has no impact on decomposition), or in an implicit manner (Gerber et al.,  
16 2010). In contrast, in microbial models, decomposition rates become a function of enzyme  
17 activity that is linked to microbial biomass. This leads to more complex dynamics because  
18 decomposers feed back into soil organic matter degradation via microbial enzyme production  
19 affecting depolymerisation. This positive feedback between microbial biomass and  
20 depolymerisation causes soil organic carbon stocks and microbial biomass to oscillate after a  
21 perturbation (Li et al., 2014; Wang et al., 2014). Nevertheless, microbial decomposition  
22 models have been shown to improve the prediction of soil carbon and perform well when  
23 compared against decomposition experiments (Lawrence et al., 2009; Wieder et al., 2013;  
24 Wieder et al., 2014a; Wieder et al., 2014b; Wieder et al., 2015b). A comparison to traditional

1 first order model show further that microbial model display an attenuated loss of soil organic  
2 matter to warming (Allison et al., 2010; Wieder et al., 2013).

3 Moreover, the response of soil organic matter to warming is very sensitive to microbial  
4 carbon use efficiency (CUE), because this parameter and its climate sensitivity defines the  
5 fraction of carbon remaining in the soil as processed organic matter vs. carbon removed via  
6 respiratory CO<sub>2</sub> (Allison et al., 2010; Frey et al., 2013; Kivlin et al., 2013; Tucker et al., 2013;  
7 Wang et al., 2013; Li et al., 2014). Temperature-dependence of CUE is typically not  
8 considered in traditional decomposition models, rather the ratios between respired CO<sub>2</sub> and  
9 the transfer to a different quality pool are mostly constant parameters, or vary based on soil  
10 texture, and soil quality, and organic or inorganic nutrient (Parton et al., 1987; Gerber et al.,  
11 2010; but see Frey et al., 2013). Microbial respiration can be partitioned into a series of  
12 carbon expenditures that do not contribute to growth. These expenditures include growth  
13 respiration, maintenance respiration, respiratory cost for enzyme production, and overflow  
14 respiration (Manzoni et al., 2012; Moorhead et al., 2012). Each type of respiratory carbon  
15 expenditures may differ in its response to temperature. In addition, respiration may be  
16 parameterised based on different microbial properties: Maintenance respiration is assumed to  
17 scale with microbial biomass (Chapman and Gray, 1986; Fontaine and Barot, 2005) while  
18 growth respiration may scale to the amount of new tissues built. On the other hand, overflow  
19 respiration occurs during stoichiometric adjustment (Russell and Cook, 1995; Schimel and  
20 Weintraub, 2003; Frost et al., 2005; Franklin et al., 2011) whereas costs related to enzyme  
21 production may be governed by microbial demand and substrate availability and quality,  
22 resource diffusion, and microbial diversity (Allison, 2005). This differentiation can impact the  
23 dynamics of the microbial biomass: For example, maintenance respiration costs would incur  
24 even in the absence of carbon uptake, which can lead to a reduction in microbial biomass. In  
25 contrast, growth respiration is only due when substrate for growth is available. However,

1 inclusion of microbial models in Earth System Models may have the potential to ultimately  
2 reduce uncertainty of climate-carbon feedback in the face of climate change, because of the  
3 explicit link between microbial activity and soil organic matter degradation (Todd-Brown et  
4 al. 2012, 2013; Wieder et al., 2015a).

5 As microbial models are considered critical towards improvement of Earth System model, it is  
6 key to analyse and understand their structure and their dynamics. Here, we compare a series of  
7 microbial decomposition models with each other. Specifically, we analyse feedbacks between  
8 depolymerisation and microbial growth, consider constraints on depolymerisation and enzyme  
9 substrate interactions, the parameterisation of microbial enzyme productivity, and investigate  
10 the representation of microbial respiration and CUE.

11 Our main questions are:

- 12 a) How do different model implementations of depolymerisation affect the feedback between  
13 microbial biomass and soil organic matter, if subjected to warming?
- 14 b) How does the consideration of functional respiration terms (growth, maintenance, and  
15 carbon acquisition expenditures) affect decomposition dynamics?

16 We organise the paper in the following way. In the next section, we introduce 3 simple  
17 models that differ in their representation of depolymerisation. Each model will be further  
18 modified for different representation of microbial dynamics and respiration. To analyse model  
19 behaviour we will evaluate the response of respiration, microbial biomass, CUE, and soil  
20 organic matter to a step increase in temperature. We will then discuss the models' behavior by  
21 comparing against a traditional first order model.

22

## 1    2    **Materials and methods**

### 2    2.1    **Model descriptions**

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

4    In all models the setup consists of a single soil organic matter pool and a single microbial pool  
5    (Fig. 1). However, all models also implicitly take into account interaction between enzymes  
6    and substrate, depolymerisation of substrate into a DOC pool on which microbes can feed.  
7    Enzyme-substrate reactions are based on Michaelis-Menten kinetics (see Appendix A,  
8    Michaelis-Menten kinetics with enzyme denaturation). We do not consider a specific enzyme  
9    pool, nor a specific DOC pool, but assume that the enzyme and DOC pool are in a quasi-  
10    steady state (Appendix A, DOC and enzyme dynamics). Thus, the amount of enzyme  
11    produced equals the amount of enzyme decay at every time step. Similarly, the amount of  
12    DOC produced is the same as the amount of DOC consumed by microbes. In contrast to  
13    Allison et al. (2010), but congruent with German et al. (2012), there is no “free” DOC, both  
14    fresh litter, and microbial necromass need to be depolymerised before it can be ingested by  
15    microbes. Further, both depolymerisation and microbial respiration are temperature  
16    dependent, causing increased depolymerisation and reduced microbial CUE with warming.

#### 17    **2.1.1. Base Models**

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

$$20 \quad \frac{dS}{dt} = I + \lambda_d * M - D \quad (1)$$

$$21 \quad \frac{dM}{dt} = D * \varepsilon - \lambda_d * M \quad (2)$$

1 where S and M are the soil organic matter and the microbial pool, respectively, I the input of  
2 fresh litter,  $\lambda_d$  the death rate of microbes, D the rate of depolymerisation, and  $\epsilon$  the microbial  
3 CUE.

#### 4 ***Forward M-M Model (FWD)***

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

$$8 \quad D = \frac{V_{\max, \text{FWD}} * S * M}{K_E + S} \quad (3)$$

9 Where D is the rate of depolymerization,  $V_{\max, \text{FWD}}$  is the maximum depolymerisation rate and  
10  $K_E$  the half saturation constant for enzymes. Appendix A shows the derivation of this  
11 function, based on enzyme-substrate dynamics.

#### 12 ***Diminishing Return (REV) Model***

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

$$18 \quad D = \frac{V_{\max, \text{REV}} * S * M}{K_M + M} \quad (4)$$

19 Where  $K_M$  is a half saturation constant that determines the diminishing return function. In the  
20 cases developed in the Appendix,  $K_M$  incorporates factors indicating the finite sites for  
21 enzyme substrate interactions (Appendix B, model with limited available substrate), or the  
22 efficiency with which microbes scavenge for free extracellular enzymes (Appendix B,

1 microbial consumption of enzymes). A version of the reverse Michaelis-Menten model also  
2 has been derived if only a fraction of the binding sites where a particular enzyme can adsorb  
3 to (Wang and Post, 2013). A major difference to the FWD model is that now the microbial  
4 biomass, instead of the amount of soil organic matter appears in the denominator. Therefore,  
5 the depolymerisation per unit biomass decreases as biomass increases (diminishing return).

### 6 ***Optimised Enzyme Production (OPT) Model***

7 In this model, we relax the condition that microbial enzyme production scales to microbial  
8 biomass, an assumption that is present in many microbial models and which is also assumed  
9 in the FWD and the REV model above. Instead we probe a model where microbial enzyme  
10 production is optimised for growth. We motivate this by microbial competition (Allison,  
11 2005), which will allow microbes to succeed if microbial enzyme production allows the  
12 highest possible return. Optimisation only has meaningful results for the case of limited  
13 substrate availability (i.e. a diminishing return, possibly through constraints in potential sites  
14 for enzyme-substrate reaction) and if there is a cost associated with microbial enzyme  
15 production.

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

$$17 \quad D(P) = \frac{P \cdot V_{\max, \text{OPT}} \cdot S}{K_P + P} \quad (5)$$

18  $V_{\max, \text{OPT}}$  is the maximum rate of depolymerisation and  $K_P$  carries information on the affinity  
19 of the enzyme for the substrate and longevity of the enzyme (see Appendix C, for full  
20 derivation of depolymerisation in the OPT model).

21 Microbial growth ( $G$ ) is as in previous models but accounts for carbon expenditure of enzyme  
22 production:

$$23 \quad G = \varepsilon * (D(P) - P_c) \quad (6)$$

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

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

$$3 \quad D = V_{\max,OPT} * S - \sqrt{K_P * c * V_{\max,OPT} * S} \quad (7)$$

4 And the cost per unit carbon depolymerised is then

$$5 \quad \frac{Pc}{D} = \sqrt{\frac{K_P c}{S V_{\max,OPT}}} \quad (8)$$

### 6 **2.1.2. Equilibrium microbial models**

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

17 In our equilibrium microbial models, we solve  $\frac{dM}{dt} = 0$ , in order to obtain a quasi-steady state  
18 microbial biomass,  $\bar{M}$ .  $\bar{M}$  substitutes state variable  $M$  in the functions for depolymerisation  
19 and microbial death. We note that this is only possible for the REV and the OPT model. The  
20 FWD model yields no solution for  $M$  in  $\frac{dM}{dt} = 0$ , and the first order model does not consider a  
21 microbial biomass in the first place. The equilibrium models, effectively becomes a one-pool  
22 model, where depolymerisation is not a direct function of microbial biomass, but an

1 expression of S and a series of parameters. Table 2 (see formulations for Short/Fast timescale)  
2 shows the quasi-steady state for M, and the resulting depolymerisation function for the  
3 equilibrium models.

### 4 **2.1.3. Partitioning between maintenance and growth respiration**

5 While the dynamics of the soil organic matter pool remains the same as in base model setup,  
6 we alter the forward and the reverse Michaelis-Menten models as we make distinction  
7 between growth and maintenance respiration (Fig 1c). Partitioning of microbial respiration  
8 into growth and maintenance respiration characterise the microbial pool as follows:

$$9 \quad \frac{dM}{dt} = (D - \lambda_r * M)(1 - g) - \lambda_d * M \quad (9)$$

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

### 18 **2.1.4. First-Order Decomposition (FOD) Model**

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

$$22 \quad \frac{dS}{dt} = I - S * k * (1 - \varepsilon) \quad (10)$$

1 where  $k$  is the first order decomposition constant. The two major differences between our  
 2 first-order decomposition (FOD) model and traditional models are that we consider only a  
 3 single carbon pool whereas traditional models consider several quality pools that feed into  
 4 each other. We also consider a temperature dependent CUE on top of a temperature dependent  
 5 processing rate ( $k$ , see parameterisation and implementation section). This increases the  
 6 fraction of carbon processed with warming to become  $\text{CO}_2$ . Respiration ( $R$ ) is then

$$7 \quad R = S * k * (1 - \epsilon) \quad (11)$$

## 8 **2.2 Temperature response**

9 We implement the response of decomposition to warming by modifying the depolymerisation  
 10 and the microbial respiration.

11 In the FWD, REV and OPT model,  $V_{\max}$  is modified as

$$12 \quad V_{\max,i}(\Delta T) = V_{\max,i} * Q_{10}^{\left(\frac{\Delta T}{10}\right)} \quad (12)$$

13 Where  $V_{\max,i}$  and  $V_{\max,i}(\Delta T)$  are reference and the temperature dependent maximum  
 14 depolymerisation rate of the model  $i = (\text{FWD}, \text{REV}, \text{OPT})$ . Similarly,  $k$  is modified by the  $Q_{10}$   
 15 function in the FOD model.

16 Further, we also parameterise CUE as a linear function of the temperature change

$$17 \quad \epsilon(\Delta T) = \epsilon_0 + \Delta T * \epsilon_{\text{slope}} \quad (13)$$

18 where  $\epsilon_0$  is the CUE at reference temperature, and  $\epsilon_{\text{slope}}$  the change in CUE per  $^{\circ}\text{C}$   
 19 temperature ( $\Delta T$ ) change. Finally, in the models where we partition growth and maintenance  
 20 respiration, we formulate maintenance respiration as a  $Q_{10}$  function of temperature

$$21 \quad \lambda_r(\Delta T) = \lambda_{r,0} * Q_{10}^{\left(\frac{\Delta T}{10}\right)} \quad (14)$$

22 Where  $\lambda_{r,0}$  and  $\lambda_r(\Delta T)$  are maintenance respiration rate at reference and elevated temperature.  
 23 Growth respiration is typically much less sensitive to warming than maintenance respiration

1 (Frantz et al., 2004), and we therefore do not consider a temperature dependence of this  
2 particular respiration term.

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

### 7 **2.3 Parameterisation and implementation**

8 All models are implemented in STELLA, version 10.0.3. To enable comparison among the  
9 models we adjust parameters in the following way: The models have the same initial soil  
10 organic carbon and the same initial microbial biomass. Both CUE ( $\epsilon$ ), and its temperature  
11 dependence ( $\epsilon_{\text{slope}}$ ) are the same across models. Further, the temperature sensitivities of  
12  $V_{\text{max}}$  are identical across models so that we obtain the same increase of depolymerisation in  
13 the first time step after the temperature perturbation. We motivate this kind of  
14 parameterisation by acknowledging that many of these parameters are largely unknown, but it  
15 will provide us with the possibility of comparing the functional response to long-term  
16 warming across these models.

17 We use parameters as reported in German et al. (2012), with a few modification. Here, we  
18 report  $V_{\text{max,FWD}}$  and  $K_E$  by considering 15°C as our reference temperature and by working  
19 their tuning factors directly into these two parameters. In other words,  $V_{\text{max,FWD}}$  and  $K_E$  are the  
20 product of the reference values in German et al. (2012), their respective tuning parameters and  
21 their adjustment to our reference temperature, 15°C. Further, we have converted the  
22 exponential temperature sensitivity of  $V_{\text{max,FWD}}$  into a  $Q_{10}$  term.

23 To allow a diminishing return mechanism, we assumed that most of the enzyme decay/loss in  
24 a scavenging model is attributed to microbial consumption instead of denaturation.

1 Alternatively, under conditions of limited enzyme-substrate reaction sites, we assumed that  
2 there is an excess of free enzymes, and therefore, enzyme concentrations are higher than their  
3 corresponding half saturation concentrations. Overall, these assumptions would suggest a  $K_M$   
4 that is smaller than  $M$  ( $K_M < M$ ). Here, we chose  $K_M$  to be 0.37 of  $M$  at the reference  
5 temperature. Note, that the half saturation constant in the REV model has a different unit  
6 ( $\text{mgM cm}^{-3}$ ) than in the FWD model ( $\text{mgS cm}^{-3}$ ) (see Appendix A for the FWD model and  
7 Appendix B for the REV model).  $V_{\text{max,REV}}$  are then tuned to yield equivalent equilibrium  
8 values of  $S$  at the reference temperature.

9 In the OPT model, we adjust  $V_{\text{max,OPT}}$  (in a similar manner as in the REV model) such that the  
10 system again yields equilibrium values for  $S$  at the reference temperature ( $15^\circ\text{C}$ ) and the same  
11 initial response to warming as in the other models. In the OPT model, we have to work in two  
12 additional parameters, namely the cost of enzyme production ( $c$ ), and the term that contains  
13 the affinity of enzymes for the substrate ( $K_P$ ). We chose to have the OPT models comparable  
14 to others if the cost ( $c$ ) is zero. Higher costs ( $c > 0$ ) therefore will yield different equilibrium  
15 result of  $S$  and a different response to warming, depending on the cost of enzyme production.  
16 Both, the half saturation constant (affinity parameter,  $K_P$ ) and the cost per enzyme produced  
17 are parameters that are hard to come by. Instead, the solution allows us to quantify these based  
18 on how much of carbon depolymerised is allocated to enzyme production (see Eq. 8 in the  
19 main text).

20 Here, we analyse the OPT model based on different levels of enzyme expenditures and  
21 expressed as enzyme costs per unit carbon depolymerised ( $\mu = \frac{Pc}{D}$ ), where  $\mu$  is 0, 10, and 50  
22 percent of the depolymerisation rate at reference temperature and at steady state. This yields  
23 an expression for the combined cost ( $c$ ) and the half saturation constant ( $K_P$ ) (Y in Table 2):

$$24 \quad K_P * c = \mu^2 * D_{\text{Eq}, \Delta T=0} \quad (15)$$

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

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

$$12 \quad \lambda_{r,0} = 1.25 * \lambda_d \quad (16)$$

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

$$15 \quad g = \frac{\lambda_d - \varepsilon_0 * (\lambda_d + \lambda_{r,0})}{\lambda_d - \varepsilon_0 * \lambda_{r,0}} \quad (17)$$

16 To obtain the same equilibrium values of CUE at 20°C as in the base models, we adjust  $Q_{10,\lambda_r}$   
17 such that models with maintenance respiration has the same CUE as in the base models.

18 Finally, in the FOD model, the traditional decomposition model, we adjust the parameters k  
19 and  $\varepsilon_0$  to obtain the same S, and CUE as in all other models at 15°C and employ a  $Q_{10,k}$  value  
20 identical to the  $Q_{10}$  values of  $V_{max}$  in the other models. We keep the decreasing CUE – a  
21 feature not typically set up in traditional models.

22 All parameter values are given in Table 3.

23

## 1   **3   Results**

### 2   **3.1   Base Model Simulations**

3   The transient response for the different models to a temperature step from 15°C to 20°C is  
4   shown in Fig. 2. We note that all models are forced through the same initial values of M, S,  
5   and CUE by way of parameter adjustments. Further, the initial response is equal across the  
6   models by not allowing  $Q_{10}$  of  $V_{\max}$  and  $Q_{10}$  of CUE to differ.

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

15   The FWD Model shows oscillations in M and S, as noted earlier (Wang et al., 2014). The  
16   warming triggers an increase in depolymerisation, which in turn feeds microbial biomass,  
17   causing an even higher rate of depolymerisation. This positive feedback experiences a break  
18   only when the substrate (S) is sufficiently depleted, such that microbial biomass begins to  
19   decline. Thereafter, the positive feedback takes over again, the decreasing microbial biomass  
20   spirals down along with depolymerisation until microbial biomass is low enough for soil  
21   organic matter to recover. The amplitude of the oscillations dampens over time (Fig. 2). Rates  
22   of respiration oscillate along with microbial biomass, before settling at the initial rate in the  
23   long-term (after ca. 200 years).

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

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

### 15 **3.2 Analytical steady state solutions**

16 The analysis of equilibria helps to understand the model behaviour. We first address the “long  
17 time scale” in Table 2 where we solve for the steady state of the entire system (i.e.  $\frac{dM}{dt} = 0$  and  
18  $\frac{dS}{dt} = 0$ ). In the long-term, the steady state microbial biomass is identical in the FWD and the  
19 REV model and depends on input of fresh organic matter, the microbial CUE, and microbial  
20 turnover (Table 2, right-most column). The same microbial biomass is also realised in the  
21 OPT model under zero cost ( $\mu=0$ ) (see Eq. 15 and Table 2, right-most column). In contrast,  
22 the analytical steady state solutions of S are different among the models: For the REV and the  
23 OPT model, the input of fresh litter is a determining variable for the steady state, but not for

1 the FWD model. In the OPT model the resulting equilibria of S and M end up being complex  
2 expressions, and we did not calculate the long-term equilibria of M, but expressed them  
3 simply as a function of soil organic matter. The OPT model has – under the assumption of  
4 marginal costs ( $\mu \rightarrow 0$ ) the same steady state solution for M as the other models. Further, the  
5 steady states of S are the same in the traditional first order model (FOD) and the OPT model  
6 with zero cost. As expected, the effect of enzyme production cost has a negative impact on  
7 microbial biomass.

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

13 In the FWD model, we find that the quasi-steady state for M requires a perfect balance of  
14 parameters that govern growth- and death rates (Table 2, second column). In absence of such  
15 a balance (referred to as knife-edge equilibrium, see Schimel and Weintraub, 2003), M would  
16 therefore grow or decay indefinitely. It becomes clear that the soil organic matter pool must  
17 respond on a similar time scale as microbes in order to maintain microbial biomass within  
18 acceptable boundaries. In the REV and the OPT models, the short-term equilibria are a  
19 function of soil organic matter (Table 2, second column). In the REV, and the OPT model,  $\bar{M}$   
20 is strongly determined by the rate of depolymerisation at a given S, the CUE and the  
21 microbial death rate. A weaker affinity for the substrate (larger half-saturation constant) and  
22 higher enzyme production cost act to reduce  $\bar{M}$  in these models.

### 23 **3.3 Quasi-Steady State of Microbial Biomass**

1 Given the equilibrium biomass, and the resulting decomposition at quasi-steady state, we set  
2 up a second line of modelling experiment, where depolymerisation rates as well as microbial  
3 respiration and death are calculated based on microbial biomass at quasi-steady state (Table 2,  
4 second and third columns). It follows that a fraction  $(1 - \epsilon)$  of depolymerisation is  
5 immediately recycled back into the soil organic matter pool, yielding the equation  $\frac{dS}{dt} = (1 -$   
6  $\epsilon) * D$ . Depolymerisation is immediately partitioned into respiration and into a returning  
7 carbon flux, which mimics microbial death. In this modelling setup, microbial biomass is thus  
8 no longer a state variable and the models are reduced to single pool setup (Fig. 1b).  $\bar{M}$  is  
9 diagnosed from  $S$  and parameters that determine depolymerisation and microbial turnover  
10 (Table 2, second column). Compared to the base models, the steady state models yield very  
11 similar results for  $S$  and respiration, but they do not reproduce the early adjustment of the  
12 microbial biomass to the temperature step. Instead of a slow adjustment to the sudden  
13 warming,  $\bar{M}$  increases with the instantaneous increase of depolymerisation. However, over a  
14 timescale of  $<1$  year,  $\bar{M}$  and  $R$  converge to the values of the base models in REV and the OPT  
15 model, and therefore the quasi-steady state appears to be an acceptable assumption over  
16 medium to long time scales. Our results further show that the depolymerisation in the OPT  
17 model at quasi-equilibrium and at marginal enzyme production cost ( $\mu \rightarrow 0$ ) yields a  
18 depolymerisation formulation that is functionally the same as a first order decomposition  
19 model, and therefore respiration and the dynamics of  $S$  are the same for the quasi-steady state  
20 OPT model and the traditional first order model.

### 21 **3.4. Partitioning between maintenance and growth respiration**

22 In the third modification of our base models, we partition respiration in our models into a  
23 temperature independent growth respiration and a temperature (and biomass) dependent  
24 maintenance respiration. This affects the transient pattern of the FWD in that it increases the

1 feedback between microbes and substrate (evidenced by higher amplitudes in M, S, and  
2 respiration). This is because part of respiration is now tied to microbial biomass, which lags  
3 depolymerisation. CUE initially decreases less than in the base model, because maintenance  
4 respiration lags the growing microbial biomass. The maintenance term introduces also a mild  
5 oscillation into CUE, as microbial biomass waxes and wanes. Interestingly, including  
6 maintenance respiration decreases oscillation frequency. In the REV and the OPT model,  
7 microbial biomass is slightly higher and respiration is slightly below the values of the base  
8 models shortly after the step increase, however, this difference diminishes over time. The  
9 nuanced consideration of microbial respiration causes CUE to decline in 2 stages. The initial  
10 drop occurs via the immediate increase in maintenance respiration. This drop is followed by  
11 further changes in CUE as M oscillates (FWD model), or as M net growth is diminishing  
12 (REV and OPT). Similar as in the case with equilibrium microbes, differences disappear  
13 within < 1 year after the step warming. We note that in our modelling setup, we adjusted the  
14 temperature sensitivity of the maintenance respiration such that CUE is the same at reference  
15 (15°C) and elevated (20°C) temperature.

### 16 **3.5. Enzyme production expenditures**

17 Finally, we analyse how levels of costs associated with enzyme production affects soil carbon  
18 storage and response to temperature (Fig. 4). Because of largely unknown parameters we  
19 express enzyme expenditures as the fraction of respiratory carbon for enzyme production per  
20 unit carbon depolymerised at the reference state (see Eq. 8). We tested 3 levels of enzyme  
21 production cost: 0%, 10%, and 50% of equilibrium depolymerisation at our reference  
22 condition (i.e. 15°C). As expected, increasing enzyme production cost reduced the rate of  
23 depolymerisation, and S is therefore maintained at a higher level. The increasing costs also  
24 resulted into a smaller relative decline of S in response to warming, whereas the absolute loss

1 is larger, indicated by higher rates of respiration. Similarly, the response of CUE to warming  
2 is smaller and the decline of M is less pronounced if enzyme production costs are considered.

3

#### 4 **4 Discussion**

5 Recently developed microbial decomposition models (Schimel and Weintraub, 2003; Allison  
6 et al., 2010; German et al., 2012) highlight the importance of microbial processes and  
7 microbial physiology during decomposition. Their application specifically highlights the role  
8 of extracellular enzymes during decomposition and how these constraints will further affect  
9 the release of soil organic matter as a consequence of warming. While microbial  
10 decomposition models are able to improve prediction of organic carbon stock globally, and  
11 can successfully recreate litter decomposition dynamics, the long-term trajectory of a  
12 warming response needs further evaluation (Wang et al., 2014). In particular, a positive  
13 feedback between depolymerisation and microbes can only be curbed via the longer term  
14 adjustment of soil organic matter and therefore lead to oscillation in both microbial biomass  
15 and soil organic matter (Wang et al., 2014). The oscillation is the consequence of a positive  
16 feedback between depolymerisation and microbial growth, and is evidenced by a knife's edge  
17 or unstable equilibrium under constant substrate condition (Schimel and Weintraub, 2003). A  
18 break in this feedback only occurs via interplay with the reduction of soil organic matter.

19 Such interplay occurs on a longer timescale than that of microbial turnover, causing the  
20 swings in M and S. We note that some attenuation of the oscillation may occur via direct input  
21 into a DOC pool that does not require depolymerisation (Allison et al., 2010), a feature not  
22 considered here.

23 The display of oscillation in the FWD model has been a point of critique as it has not been  
24 observed in laboratory and field incubation studies (Wang et al., 2014). Here, we introduce

1 mechanisms that curb the positive feedback between substrate and microbial biomass. We  
2 portray two scenarios, where each increment in microbial biomass or enzyme concentration  
3 yields a smaller increase in depolymerisation than the previous increment (i.e. diminishing  
4 return). The scenarios we worked out are 1) microbial biomass feeds on active extracellular  
5 enzymes, 2) limited sites for substrate/enzyme reactions (see Appendix B). We derived the  
6 forms of depolymerisation from the original Michaelis-Menten kinetics and the resulting  
7 formulations presented in the method section are simplified and more illustrative versions of  
8 more complex functions. Wang and Post (2013) arrived at the same function for  
9 depolymerisation of the reverse Michaelis-Menten model, where an enzyme only adsorbs to a  
10 fraction of binding sites because of complex substrates. The simplified formulation of  
11 depolymerisation and microbial consumption we arrived at has been dubbed reverse  
12 Michaelis-Menten formulation (Schimel and Weintraub, 2003), because microbial biomass  
13 (or enzyme concentration) instead of the substrate concentration is now occurring in the  
14 denominator of the depolymerisation term, invoking the diminishing return. Our analysis  
15 shows that the positive feedback between decomposition and microbial growth is removed, as  
16 our REV model has now a stable equilibrium.

17 Limited sites may play a role if the substrate has a high volume to surface ratio, or if the  
18 substrate is associated with minerals (Davidson and Janssens, 2006; Gillabel et al., 2010;  
19 Conant et al., 2011; Davidson et al., 2012, 2014; Cotrufo et al., 2013; Wagai et al., 2013;  
20 Benbi et al., 2014; Wieder et al., 2014a; Tang and Riley, 2015). Our implementation of  
21 limited substrate causes a surplus of free enzymes that compete among themselves for binding  
22 to substrates similar to the Langmuir adsorption isotherm theory (Vetter et al., 1998; Schimel  
23 and Weintraub, 2003, Wang and Post, 2013, and see Appendix B, Model with limited  
24 available substrate). Effects of microbial scavenging for enzymes cause a diminishing return  
25 because more microbial biomass will lead to an increased probability of enzymes being

1 consumed before they interact with soil organic matter. Other mechanisms of diminishing  
2 return as enzyme increase may be stabilisation of enzymes into organic matter-humate  
3 complex (Allison, 2006), or sorption to minerals, soil organic matter, or microbes (Tang and  
4 Riley, 2015). Diminishing returns also occur with rate-yield tradeoffs (Allison, 2014).

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

17 The response to temperature in our OPT model closely resembles the traditional first order  
18 decay model (FOD). In the limit of enzyme production cost is zero, depolymerisation occurs  
19 at the maximum rate ( $V_{max} * S$ ), confirming the resemblance to the first order model. This  
20 model shows the strongest response to warming in the long term because the temperature  
21 dependence of depolymerisation is not reduced via a half saturation constants ( $K_E$  in forward,  
22  $K_M$  in OPT, and  $K_P$  in OPT model) as in the FWD or REV model. We note that half saturation  
23 constants in our models combine several parameters such as enzyme productivity relates to  
24 microbial biomass, and turnover of the enzyme pool. In the REV and the OPT model, smaller

1 the half saturation constant is, the closer we arrive at the formulation of decomposition in a  
2 first order model, this occurs via an increase of enzyme concentration by way of higher  
3 production or reduced enzyme turnover. Both, parameter are hard to come by.

4 The response of decomposition to warming can be viewed as a response occurring on multiple  
5 timescale. For example, enzyme activity produces likely an immediate response, microbial  
6 respiration responses may also be triggered quickly, although longer term acclimation may  
7 occur (Frey et al., 2013). It may take longer for microbial biomass to respond to the changes  
8 (weeks to months). Finally, because the rate of decomposition is slow compared to the overall  
9 abundance of soil organic matter, discernible changes in this pool occur on timescales of  
10 months to years. Based on the distinct rates of adjustments, timescales can – in principle –  
11 be separated by assuming a quasi-steady state of pools that turn over fast.

12 The assumption that both enzyme concentrations and DOC (i.e. the depolymerisation  
13 products) are at quasi-steady state cuts across all models presented here (FWD, REV and  
14 OPT, see Appendix A). When we extend our assumption of steady state to the microbial  
15 timescale (quasi-steady state of microbial biomass), we find that for both the REV and the  
16 OPT model, the short-term response of microbial biomass and respiration is influenced by the  
17 adjustment of microbial dynamics to the warmer temperature. Because microbial biomass  
18 jumps immediately to higher level after the temperature increase in such an equilibrium  
19 assumption, depolymerisation and thus respiration are affected. However, the equilibrium  
20 assumption does not affect the trajectory of the soil carbon pool,  $S$ . At timescales that allow  
21 microbes to turn over a couple of times (several months), the quasi-steady state poses a  
22 suitable approximation to represent respiration and microbial biomass, even after a sharp  
23 perturbation in form of a step change. Perhaps more intriguing is the fact that a traditional first  
24 order model is the special case of the OPT model with microbial quasi-steady state and with

1 marginal enzyme production costs ( $\mu \rightarrow 0$ ). Here, we maintain reduction of CUE under  
2 increasing temperature in the FOD, a feature typically not include in traditional first order  
3 models.

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

17 In the OPT model, we introduce an additional respiration term, namely the cost of enzyme  
18 production, which we allow microbes to adjust in order to optimise growth. It is interesting  
19 that increasing costs lead to a smaller immediate response in respiration and more resilient  
20 soil organic matter pool in the long term, when subject to warming. The early respiration  
21 response in the OPT model is both a product of higher rates of depolymerisation, but also a  
22 higher rate of enzyme production. However, the enhancement relative to the rates at reference  
23 temperature is smaller, the higher the enzyme production cost. In the long term, soil organic  
24 matter decreases much less when enzyme production costs are considered. This yield tradeoff

1 thus act to buffer respiration increases that could be expected from physiological responses  
2 alone ( $V_{\max}$ ), although the effects are smaller and may be well within the uncertainty of the  
3 temperature response of any parameters considered here.

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

20

## 21 **5 Conclusions**

22 Our findings suggest that different formulation of how microbes acquire substrate will have  
23 significant impact on the short vs. long-term consequences of warming. Here, we present  
24 simple, yet feasible mechanisms of microbial dynamics. We show that substrate limitation in

1 the form of decreasing marginal return can create a break in the positive feedback between  
2 microbial biomass and depolymerisation, turning a forward Michaelis-Menten model into a  
3 reverse model. We further separate out 3 types of respiration, that possibly have consequences  
4 on the temporal trend of CUE in response to warming. Although such separation is more  
5 mechanistic, it remains open whether the addition of extra parameters is justified at this point,  
6 given the uncertainty in models, and because much of the effects of this separation diminishes  
7 on timescales longer than the microbial lifespan. Finally, our OPT model is among our suite  
8 of models, the one that most closely resembles the traditional first order decomposition  
9 model, and can be converted to such a model by applying a series of tangible mechanisms and  
10 simplification. These include 1) mechanisms of diminishing returns that breaks the feedback  
11 between substrate and microbes 2) relaxing the proportionality of enzyme production and  
12 microbial biomass, 3) small cost associated with enzyme synthesis, 4) assumption of  
13 microbial quasi-steady state.

14

## 15 **Appendix A**

### 16 **Michaelis-Menten kinetics with enzyme denaturation**

17 The dynamics of the enzyme-substrate complex are

$$18 \frac{d[E]}{dt} = P - K_S[S][E] - \lambda_{E1} * [E] + K_r + K([ES]) \quad (A1)$$

$$19 \frac{d[ES]}{dt} = -(K_{cat} + K_r + \lambda_{E2})[ES] + K_S[S][E] \quad (A2)$$

20 Where P is the microbial production of new enzymes, [S] is the concentration of the substrate,  
21 [E] the concentration of enzymes, [ES] the substrate-enzyme complex,  $K_s$ ,  $K_{cat}$ , and  $K_r$  are  
22 reaction constants that denote substrate-enzyme binding, actual depolymerisation rate, the  
23 reversibility of the enzyme-binding process.  $\lambda_{E1}$  and  $\lambda_{E2}$  are enzyme decay parameters that

1 lead to enzyme denaturation or render enzymes inactive in the free enzyme pool or in the  
 2 enzyme-substrate complex, respectively. In the FWD and REV model, P is proportional to  
 3 microbial biomass. The Michaelis–Menten approximation for depolymerisation assumes that  
 4 the system is in quasi-steady state in which the tendency  $\frac{d[ES]}{dt}$  and  $\frac{d[E]}{dt}$  are zero. This implies  
 5 also that tendency of the total enzyme concentration  $\frac{d[Et]}{dt}$  (with  $[Et] = [ES] + [E]$ ) becomes  
 6 zero.

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

$$8 \quad [E] = \frac{[Et] K_E}{([S] + K_E)} \quad (A3)$$

$$9 \quad [ES] = \frac{[Et] [S]}{([S] + K_E)} \quad (A4)$$

10 And the rate of depolymerisation

$$11 \quad D = \frac{[Et] * V_{max} * [S]}{([S] + K_E)} \quad (A5)$$

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

#### 14 **DOC and enzyme dynamics**

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

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

$$21 \quad \frac{d[Et]}{dt} = P - \lambda_E * [Et] \quad (A6)$$

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

$$3 \quad [E_t] = \frac{P}{\lambda_E} \quad (A7)$$

4 And depolymerisation as:

$$5 \quad D = \frac{\frac{P}{\lambda_E} * K_{cat} * [S]}{[S] + K_E} \quad (A8)$$

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

$$8 \quad D = \frac{V_{max} * M * [S]}{[S] + K_E} \quad (A9)$$

$$9 \quad \text{With } V_{max} = \frac{b * K_{cat}}{\lambda_E}$$

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

$$12 \quad \frac{d[E_t]}{dt} = P - \lambda_{E2}[ES] - \lambda_{E1}[E] \quad (A10)$$

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

$$15 \quad [E_t] = \frac{P([S] + K_E)}{\lambda_{E1}K_E + \lambda_{E2}[S]} \quad (A11)$$

16 And the overall depolymerisation is thus

$$17 \quad D = \frac{P * K_{cat} * [S]}{\lambda_{E1}K_E + \lambda_{E2}[S]} \quad (A12)$$

18 Which can be converted into a Michaelis-Menten form

$$19 \quad D = \frac{V_{max} * M * [S]}{[S] + K_S} \quad (A13)$$

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

## 2 **Appendix B**

### 3 **Microbial consumption of enzymes**

4 Microbes feeding on free enzymes can be represented as:

$$5 \quad F = \lambda_{E,M} \cdot [E] \cdot M \quad (\text{B1})$$

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

$$8 \quad [E] \cdot \lambda_{E1} = [E] (\lambda_{E1,0} + \lambda_{E,M} \cdot M) \quad (\text{B2})$$

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

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

$$11 \quad D = \frac{P \cdot K_{\text{cat}} \cdot [S]}{\lambda_{E2} \cdot [S] + \lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \quad (\text{B3})$$

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

$$14 \quad D = \frac{P \cdot K_{\text{cat}} \cdot [S]}{\lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \quad (\text{B4})$$

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

$$16 \quad D = \frac{M \cdot V_{\max} \cdot [S]}{K_M + M} \quad (\text{B5})$$

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

### 18 **Model with limited available substrate**

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

$$4 \quad [S] = \theta * ([S_f] + [ES]) \quad (B6)$$

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

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

$$10 \quad [S_f] = \frac{[S]}{\theta} - \frac{[S_f][E_t]}{K_E + [S_f]} \quad (B7)$$

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

$$12 \quad [S_f] = \frac{1}{2} \left\{ - \left( [E_t] + K_E - \frac{[S]}{\theta} \right) \pm \sqrt{\left( [E_t] + K_E - \frac{[S]}{\theta} \right)^2 + 4 * \frac{[S]}{\theta} * K_E} \right\} \quad (B8)$$

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

$$15 \quad [S_f] = \frac{[S]}{\theta} * \left( \frac{K_E}{[E_t] + K_E} \right) + O\left[\left(\frac{[S]}{\theta}\right)^2\right] \quad (B9)$$

16 Plugging this into the depolymerisation

$$17 \quad D = \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E + \frac{[S]}{\theta}} \cong \frac{K_{cat} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E} \quad (B10)$$

18 which has a Michaelis-Menten form with a saturating enzyme concentration. This particular  
 19 solution is for a small amount of binding sites, and enzymes compete for free sites. Thus

1  $[E_t] \gg \frac{[S]}{\theta}$ , and it can be dropped from within the denominator. On a side note: we obtain the  
 2 same expression if we approximate from Eq. B7:

$$3 \quad [S_f] = \frac{[S]}{\theta} - [S_f] \frac{[E_t]}{[S_f] + K_E} \quad (B11)$$

$$4 \quad [S_f] \cong \frac{[S]}{\theta} - \frac{[S_f][E_t]}{K_E} \quad (B12)$$

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

$$6 \quad [S_f] = \frac{[S]}{\theta} \frac{K_E}{[E_t] + K_E} \quad (B13)$$

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

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

$$9 \quad \frac{d[E_t]}{dt} = P - \frac{\lambda_{E2} * [E_t] * \frac{[S]}{\theta}}{[E_t] + K_E + \frac{[S]}{\theta}} - \frac{\lambda_{E1} * [E_t] * ([E_t] + K_E)}{[E_t] + K_E + \frac{[S]}{\theta}} \quad (B14)$$

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

$$11 \quad \frac{d[E_t]}{dt} \cong P - \frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_E} - \lambda_{E1} * [E_t] \quad (B15)$$

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

14 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  
 15 bound to the substrate.

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

$$17 \quad [E_t] = \frac{K_E * P}{\lambda_{E2} * \frac{S}{\theta} - P} \quad (B16)$$

18 and with  $P$  proportional to microbial biomass ( $M$ )

$$1 \quad D = \frac{K_{cat} * P}{\lambda_{E2}} = V_{max} * M \quad (B17)$$

$$2 \quad \text{Where } V_{max} = \frac{K_{cat} * b}{\lambda_{E2}}$$

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

$$6 \quad \text{b) suppose } \frac{\lambda_{E2} * [E_t] * \frac{S}{\theta}}{[E_t] + K_E} \ll \lambda_{E1} * [E_t]$$

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

$$11 \quad \text{We then obtain: } [E_t] = \frac{P}{\lambda_{E1}}$$

12 And

$$13 \quad D = \frac{K_{cat} * P * \frac{S}{\theta}}{P + \lambda_{E1} * K_E} \quad (B18)$$

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

$$15 \quad D = \frac{M * V_{max} * S}{K_M + M} \quad (B19)$$

$$16 \quad \text{Where } V_{max} = \frac{K_{cat}}{\theta}, \text{ and } K_M = \frac{\lambda_{E1} * K_E}{b}$$

## 17 **Appendix C**

### 18 **Optimising depolymerisation**

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

$$4 \quad D(P) = \frac{P \cdot V_{\max} \cdot [S]}{K_P + P} \quad (C1)$$

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

7 Microbial growth (G) will be

$$8 \quad G = (1-g) \cdot (D - Pc - \lambda_r \cdot M) \quad (C2)$$

9 Where g is the growth respiration factor, c the respiratory cost per unit enzyme production,  
 10 and  $\lambda_r$  the maintenance respiration factor.

11 Enzyme production (P) can be optimised by substituting Eq. C1 into Eq. C2 and setting

12  $\frac{dG}{dP} = 0$ . This yields:

$$13 \quad Pc = -K_P c + \sqrt{V_{\max} \cdot [S] \cdot K_P c} \quad (C3)$$

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

$$15 \quad \frac{Pc}{D} = \sqrt{\frac{K_P c}{[S] V_{\max}}} \quad (C4)$$

16 Instead of specifying c, we used Eq. C4 to express overall microbial carbon expenditure for  
 17 enzyme production. After assigning a value to  $\mu$ , we calculate c based on equilibrium S at  
 18 reference temperature.

19 In contrast, the microbial scavenging scenario does not provide an optimum enzyme  
 20 production. In this case depolymerisation is

1 
$$D = \frac{P \cdot V_{\max 3} \cdot [S]}{(K_M + M) \cdot \lambda_E} \quad (C5)$$

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

3

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16 *Model Dev.*, 8:1789-1808, 2015b.

1 Table 1. Key features of the microbial decomposition models.

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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.

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2

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

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

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

5 \* 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, we provide
- 2 only those parameters where modifications have been made.)

Parameter	Unit	Value	Description	Source
<b>FWD Model</b>				
I	mg cm <sup>-3</sup> hr <sup>-1</sup>	0.001	Input of fresh litter	
$\lambda_d$	hr <sup>-1</sup>	0.0005	Death rate of microbes	
$V_{max, FWD,0}$	mg cm <sup>-3</sup> hr <sup>-1</sup>	0.0049	Maximum catalytic rate @ 15°C	
$Q_{10, V_{max, FWD}}$	-	1.9	$Q_{10}$ of maximum catalytic rate	
$K_E$	mg S cm <sup>-3</sup>	270	Half-saturation constant @ 15°C	German et al., 2012
$\epsilon_0$	-	0.39	Microbial growth efficiency @ 15°C	
$\epsilon_{slope}$	°C <sup>-1</sup>	-0.016	Microbial growth efficiency temperature slope	
<b>FWD Model with maintenance respiration</b>				
$\lambda_{r,0}$	hr <sup>-1</sup>	0.0006	Maintenance respiration @ 15°C	
$Q_{10, \lambda_r}$	-	2.2	$Q_{10}$ of maintenance respiration	This study
g	-	0.24	Growth respiration coefficient	
<b>REV Model</b>				
$V_{max, REV}$	mg <sup>-1</sup> M cm <sup>-3</sup> hr <sup>-1</sup>	2.61*10 <sup>-5</sup>	Maximum catalytic rate @ 15°C	
$K_M$	mg M cm <sup>-3</sup>	0.68	Half-saturation constant @ 15°C	This study
<b>OPT Model</b>				
$V_{max, OPT}$	mg <sup>-1</sup> M cm <sup>-3</sup> hr <sup>-1</sup>	1.71*10 <sup>-5</sup>	Maximum catalytic rate @ 15°C	
$\mu$		0, 0.1, 0.5	Enz production cost ( as % of decomposition @ 15°C steady state)	This study
$K_P * c$	mg M cm <sup>-3</sup>	0, 1.64*10 <sup>-5</sup> 0.0004	combined cost and the half saturation constant	This study
<b>FOD Model</b>				
$k^*$	hr <sup>-1</sup>	1.71*10 <sup>-5</sup>	First order decay constant @ 15°C	This study

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

1 Figure Captions

2 Figure 1. Conceptual diagrams for the microbial-enzyme models applied. Solid lines represent  
3 material flow (in FWD and FWD model with maintenance respiration) and dashed lines  
4 represent information flow (in Rev and OPT models). E, S, E-S, D, DOC, M represent enzyme,  
5 substrate, enzyme-substrate complex, depolymerisation, dissolved organic carbon, and microbial  
6 biomass carbon, respectively. We analyse the different models in three ways: a) Base models of  
7 forward vs reverse formulation of depolymerisation. In the forward version, depolymerisation  
8 scales microbial biomass via enzyme production. In the reverse formulation the decreasing  
9 marginal return curbs rates of depolymerisation. This decreasing marginal return can partly be  
10 overcome by enzyme production optimisation. b) For all models we introduce partitioning  
11 between maintenance and growth respiration. c) Microbes are instantaneously in steady with  
12 substrate delivery (reverse models only).

13 Figure 2. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d)  
14 respiration to a 5°C warming in base models (forward vs reverse). The black line represent initial  
15 values, which are model equilibria at 15°C. We chose logarithmic axis to better highlight the  
16 differences in short-term responses. (Note: Differences in simulated soil organic carbon and  
17 respiration by OPT and the FOD are almost equal, and therefore not discernible. In the OPT  
18 model, simulations are carried out at zero enzyme production cost, i.e.  $\mu = 0$ ).

19 Figure 3. Responses of a) soil organic carbon, b) microbial biomass carbon, c) CUE, and d)  
20 respiration to a 5°C warming for all models, if separation of maintenance and growth respiration  
21 are considered, and if microbial biomass is assumed to be at quasi-steady state. Black thin line  
22 represent initial values, where equilibria @ 15°C. Colored thin lines represent base models.

1 Dashed lines (growth and maintenance) and dotted lines (quasi-steady state) represent  
2 modifications for REV and OPT models respectively. (In the OPT model, simulations are carried  
3 out at zero enzyme production cost, i.e.  $\mu = 0$ ).

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

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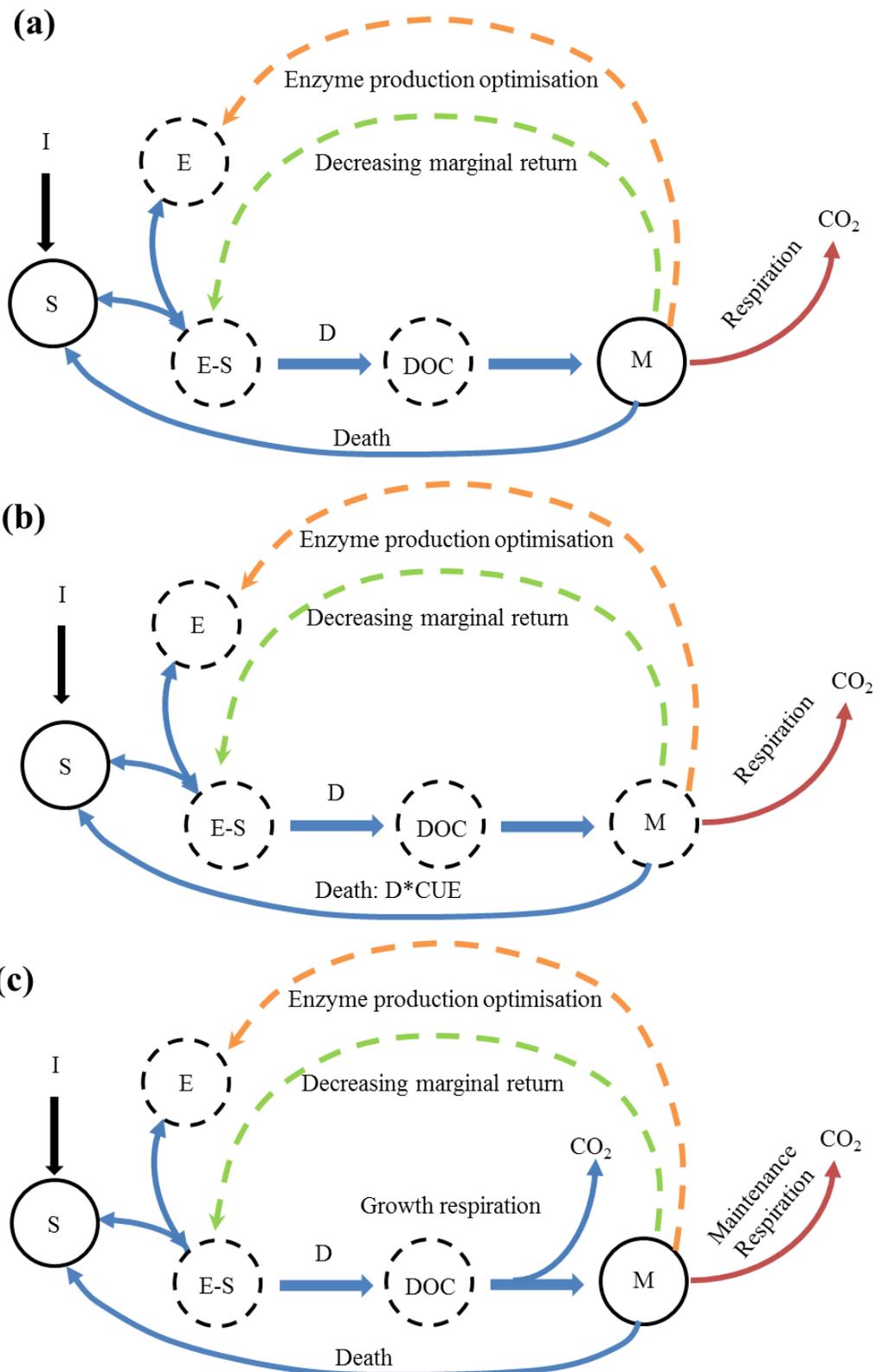
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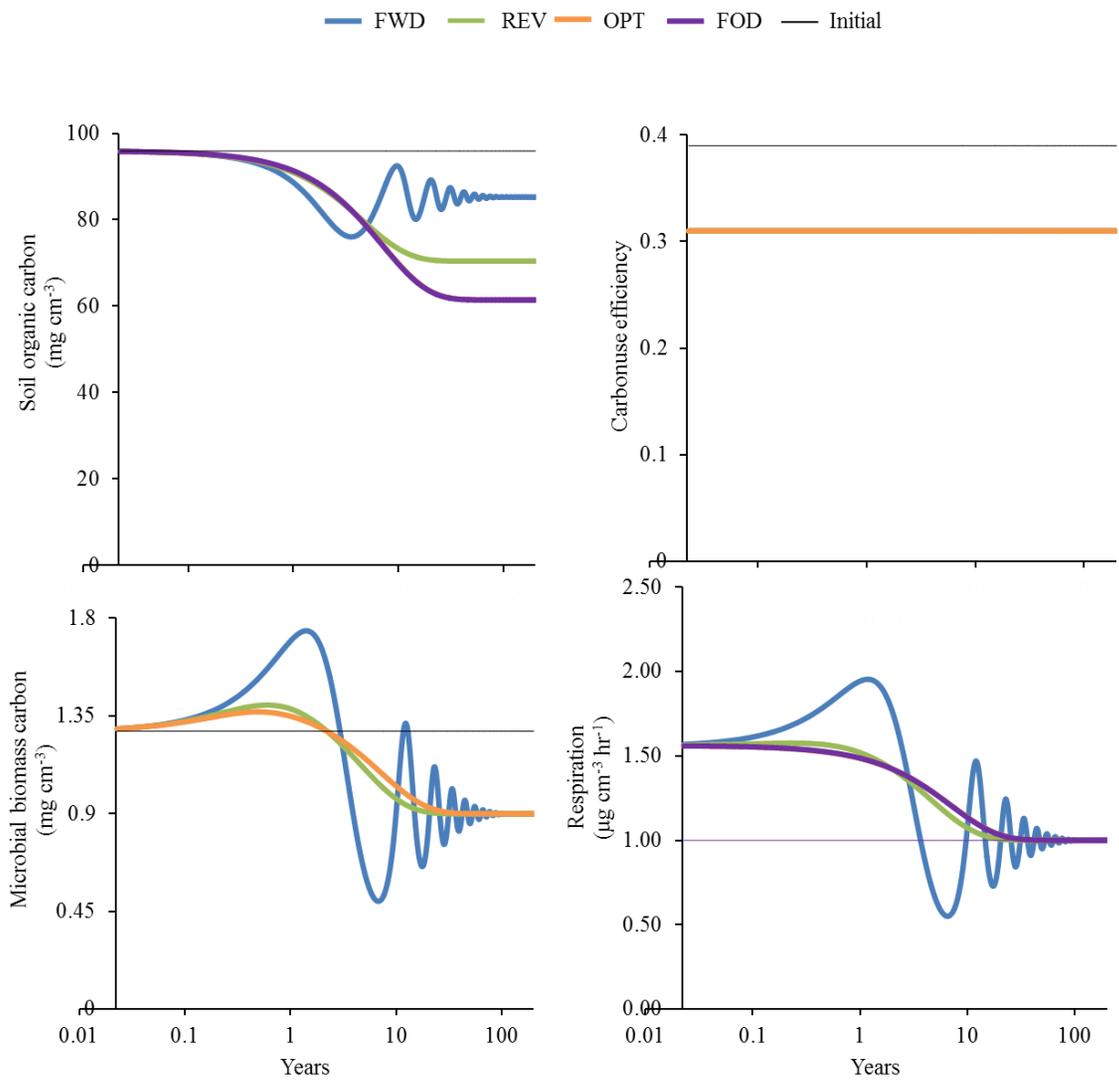
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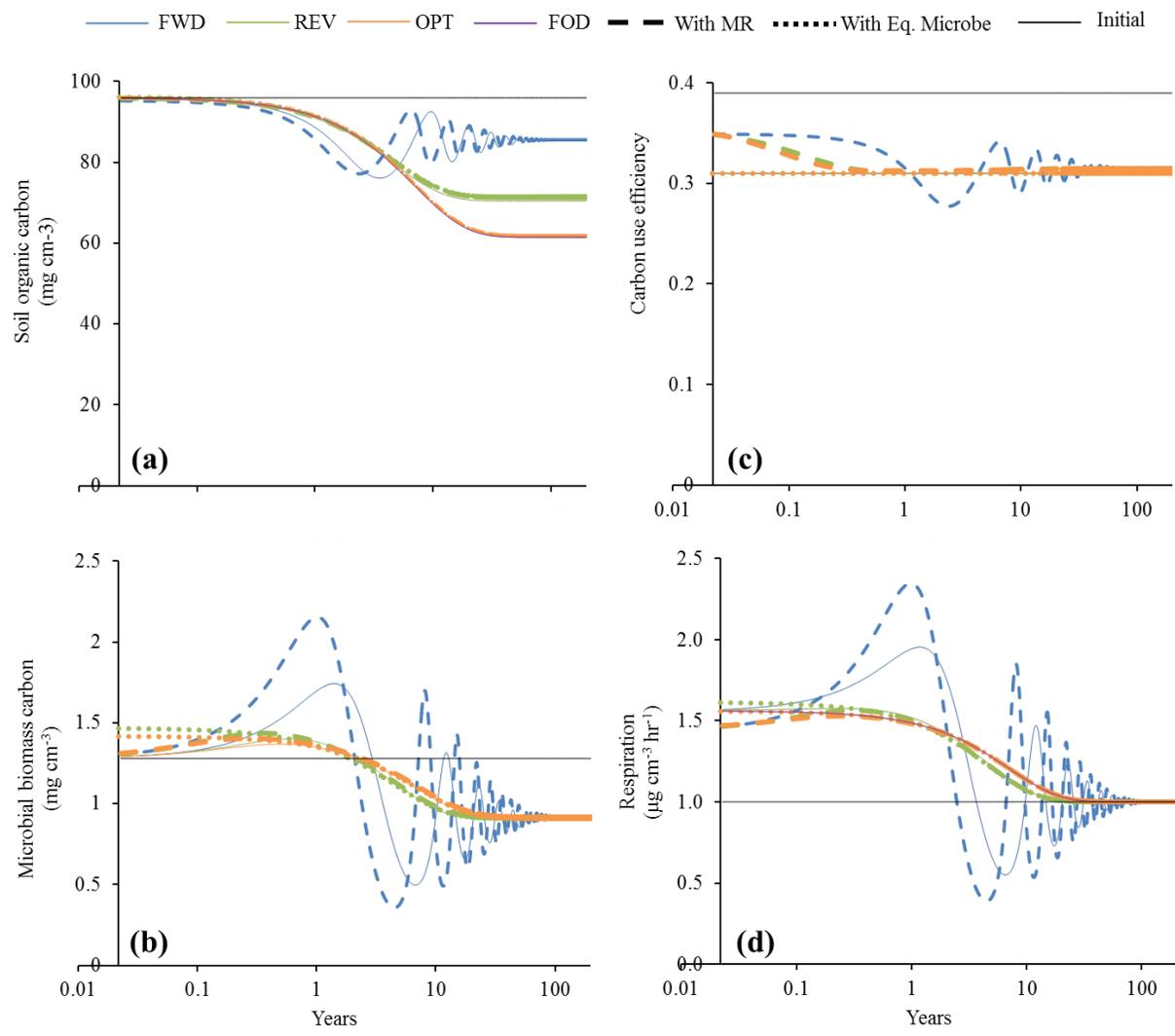
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2 Fig. 1



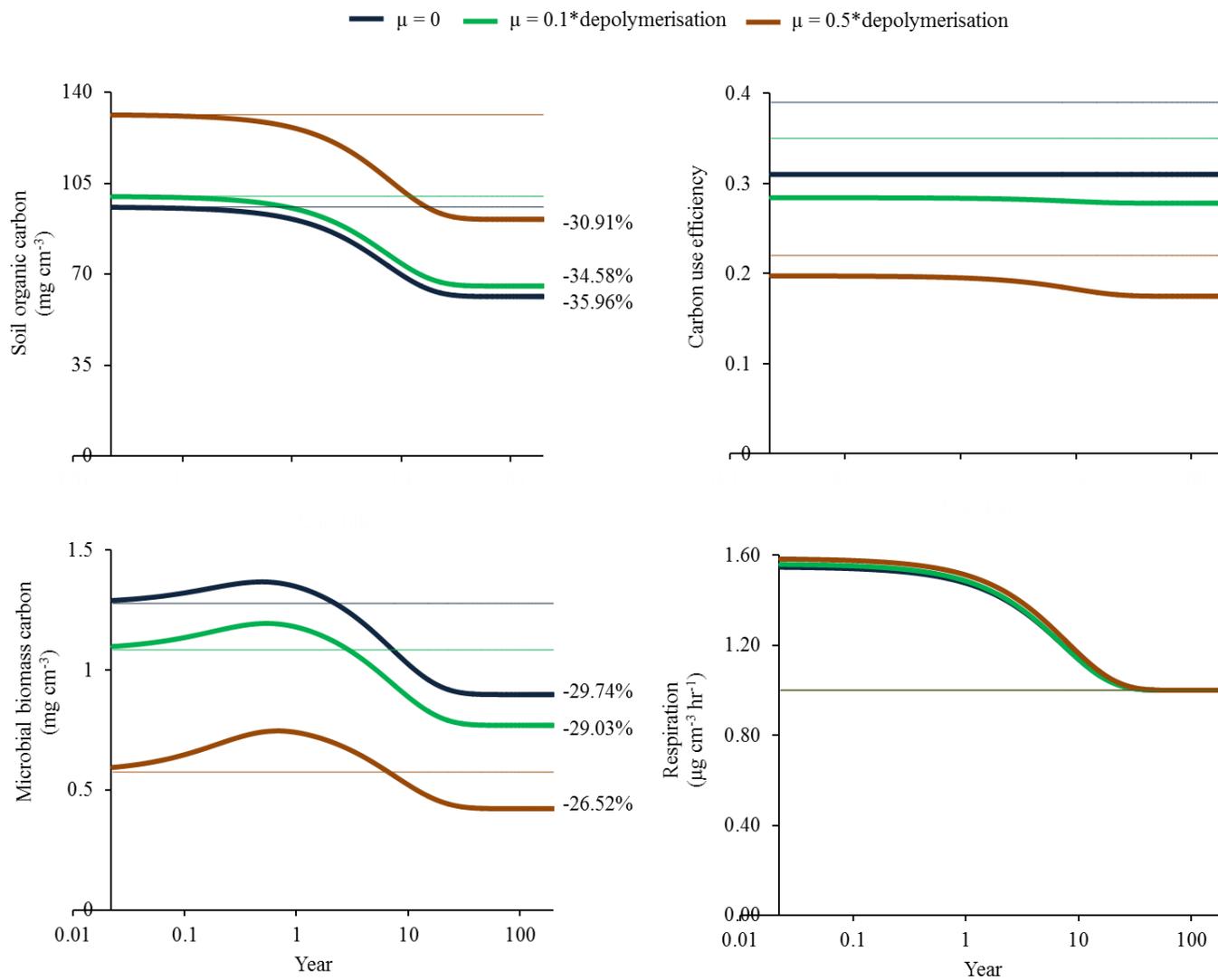
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2 Fig. 2



1

2 Fig. 3



1

2 Fig. 4