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

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Abstract

Recent developments in modelling soil organic carbon decomposition include the explicit incorporation of enzyme and microbial dynamics. A characteristic of these models is a positive feedback between substrate and consumers which is absent in traditional first order decay models. Under sufficient large substrate, this new feedback allows an unconstrained growth of microbial biomass. A second phenomenon incorporated in the microbial decomposition models is decreased carbon use efficiency (CUE) with increasing temperature. Here, first we analyse microbial decomposition models by parameterising changes in CUE based on the differentiation between growth and maintenance respiration. We then explore mechanisms that curb unrestricted microbial growth by including finite potential sites where enzymes can bind and by allowing microbial scavenging for enzymes. Finally, we propose a model where enzyme synthesis is associated with a respiratory cost and microbial population adjusts enzyme production in order to optimise their growth.

When applying a step increase in temperature, we find fast responses that reflect adjustments to enzyme dynamics and maintenance respiration, a short-term adjustment in microbial growth, and the long-term change in carbon storage. We find that mechanisms that prevent unrestricted microbial growth lead to a similar response to warming as traditional first order decomposition models.

1 Introduction

Traditional soil organic matter decomposition models are based on first order kinetics, where decomposition scales to the pool size and the scaling factor represents recalcitrance of a specific pool, modified by soil temperature, moisture, and other factors (e.g. van Veen et al., 1984; Parton et al., 1987; Molina et al., 1990; Li, 1996; Chertov and Komarov, 1997). Recent modelling efforts have specifically included catalysis of polymeric soil organic carbon to dissolved organic carbon by extracellular enzymes

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produced by microorganisms in soil, which is thought to be the rate-limiting step in organic matter decomposition process (Schimel and Weintraub, 2003; Fontaine and Barot, 2005). Further, these microbial models explicitly consider carbon use efficiency (CUE) as a function of soil temperature. The resulting prediction of soil carbon dynamics suggests that an increasing temperature attenuates the loss of soil organic matter compared to traditional models (Allison et al., 2010).

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

Further, the response of the microbial decomposition models to warming is very sensitive to microbial carbon use efficiency (Allison et al., 2010; Frey et al., 2013; Kivlin et al., 2013; Schimel, 2013; Tucker et al., 2013; Wang et al., 2013), and turnover (Hagerty et al., 2014). Microbial respiration can be partitioned into a series of carbon expenditures that do not contribute to growth, which include growth respiration, maintenance respiration, expenditures for enzyme production and overflow respiration (Manzoni et al., 2012; Moorhead et al., 2012). Each type of respiratory carbon expenditures differs in their response to temperature. In addition, respiration may be parameterised based on different microbial properties: maintenance respiration is assumed to scale with microbial biomass (Chapman and Gray, 1986; Fontaine and Barot, 2005) while growth respiration may scale to the amount of new tissues built. On the other hand,

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overflow respiration (Russell and Cook, 1995; Franklin et al., 2011) occurs during stoichiometric adjustment (Schimel and Weintraub, 2003; Frost et al., 2005) whereas costs related to enzyme production may be governed by microbial demand and substrate availability and quality, resource diffusion, and microbial diversity (Allison, 2005). This differentiation can have dynamical consequences: for example, maintenance respiration costs would incur even in the absence of carbon uptake, which can lead to a reduction in microbial biomass. In contrast, growth respiration is only due when substrate for growth is available. Inclusion of these microbial models to the coupled climate models by following the framework of Todd-Brown et al. (2012, 2013) may have potential to ultimately reduce uncertainty of climate-carbon feedback in the face of climate change.

Here, we apply a series of simple microbial decomposition models and investigate how different formulations of carbon use efficiency and depolymerisation of soil organic matter affect decomposition.

Our main questions are:

a. how does separating microbial respiration into growth, maintenance, and enzyme production terms affect decomposition dynamics?

b. How do different model implementations of depolymerisation affect the feedback between microbial biomass and soil organic matter, if subjected to warming?

We organise the paper in the following way: first, we introduce a series of microbial decomposition models. Each of which carries single soil organic matter and a single microbial pool. In sequential model modifications, we include differentiation between growth and maintenance respiration, introduction of mechanisms where depolymerisation may be curbed by limited sites of enzyme-substrate reaction or by microbial scavenging for enzymes, and by respiratory costs associated with enzyme production. We then present analytical equilibrium solutions to infer long-term values of carbon use efficiency, soil organic matter, and microbial biomass. For each model, we test its response to a 5 °C warming. Finally, we compare the results against a traditional decomposition model.

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2 Materials and methods

2.1 Model descriptions

We apply five different microbial decomposition models (Fig. 1, Table 1). We start off with a simple microbial-enzyme decomposition model as proposed by Allison et al. (2010) and modified by German et al. (2012). We sequentially alter the model as we make distinction between growth and maintenance respiration (model 2), then different implementations of depolymerisation: we develop a case for diminishing return where increasing enzyme concentrations or microbial biomass result in decreasing marginal depolymerisation (model 3), and provide a model, where the microbial population adjusts enzyme production to optimise growth (model 4). All models describe the dynamics of a single soil organic matter pool and a single microbial pool. However, all models also implicitly take into account interaction between enzymes and substrate, depolymerisation of substrate into a dissolved organic carbon pool on which microbes can feed. Further, both depolymerisation and microbial respiration are temperature dependent, causing increased depolymerisation and reduced microbial carbon use efficiency with warming. We then will evaluate these models under a step increase in temperature.

2.1.1 Model 1: German model

The tendency for soil organic carbon and microbes in the German et al. (2012) model is described with

$$\frac{\mathrm{d}S}{\mathrm{d}t} = I + \lambda_\mathrm{d} \cdot M - D \tag{1}$$

$$\frac{\mathrm{d}M}{\mathrm{d}t} = D \cdot \varepsilon - \lambda_\mathrm{d} \cdot M \tag{2}$$

where S and M are the soil organic matter and the microbial pool, respectively, I the input of fresh litter, λ_d the death-rate of microbes, D the rate of depolymerisation, and

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ε the microbial growth efficiency. Depolymerisation is parameterised as a Michaelis–Menten process with

$$D = \frac{V_{\max 1} \cdot S \cdot M}{K_E + S} \tag{3}$$

where $V_{\max 1}$ is the maximum depolymerisation rate and K_E the half saturation constant for enzymes. Both, $V_{\max 1}$ and K_E are temperature dependent, where

$$V_{\max 1} = V_{\max 1,0} \cdot Q_{10}^{\left(\frac{\Delta T}{10}\right)} \tag{4}$$

$$K_E = K_{E,0} \cdot Q_{10}^{\left(\frac{\Delta T}{10}\right)} \tag{5}$$

where $V_{\max 1,0}$ and $K_{E,0}$ are the maximum rate of depolymerisation and the half saturation constant at reference temperature, respectively, and ΔT is the temperature difference compared to reference temperature.

ε depends linearly on temperature:

$$\varepsilon(\Delta T) = \varepsilon_0 + \Delta T \cdot \varepsilon_{\text{slope}} \tag{6}$$

where ε_0 is the carbon use efficiency at reference temperature, and $\varepsilon_{\text{slope}}$ the change in carbon use efficiency per °C temperature (ΔT) change. Implicit in this model is that microbial enzyme productivity scales to microbial biomass (see also Appendix), and that depolymerised carbon is at steady state with rates of depolymerisation and microbial uptake (German et al., 2012).

2.1.2 Model 2: modified German model (include maintenance respiration rate)

While the dynamics of the soil organic matter pool remains the same as in model 1, we partition microbial respiration into growth and maintenance respiration. The dynamics of the microbial pool is then characterised with

$$\frac{\mathrm{d}M}{\mathrm{d}t} = (D - \lambda_{\mathrm{r}} \cdot M)(1 - g) - \lambda_{\mathrm{d}} \cdot M \tag{7}$$

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where g is the growth respiration fraction and λ_r the maintenance respiration rate. The separation of microbial respiration in growth and maintenance terms is motivated by similar formulation in other microbial (Beefting et al., 1990; Van Bodegom, 2007), vegetation growth (Foley et al., 1996; Cannell and Thornley, 2000; Arora, 2002; Thornley, 2011; Pretzsch et al., 2014), and ecosystem-scale (Sistla et al., 2014) models. Growth respiration is applied after requirements for maintenance respirations are met. Maintenance respiration (respiration related to non-growth components) is typically proportional to microbial biomass (Van Bodegom, 2007). Growth respiration is typically much less sensitive to warming than maintenance respiration (Frantz et al., 2004). Hence, we apply a constant growth respiration and parameterise the temperature sensitivity of maintenance respiration with a Q_{10} function:

$$\lambda_r = \lambda_{r,0} \cdot Q_{10}^{\left(\frac{\Delta T}{10}\right)} \tag{8}$$

where $\lambda_{r,0}$ is the maintenance respiration rate at reference temperature.

2.1.3 Model 3: diminishing return model

In the Appendix, we derive two models which show a diminishing increase of depolymerisation as microbial mass increases. These models include (a) a case where microbes are scavenging for free enzymes, and (b) where potential sites of enzyme-substrate reactions are finite. We simplified depolymerisation in these diminishing return models such that it becomes again a Michaelis–Menten type function:

$$D = \frac{V_{max3} \cdot S \cdot M}{K_M + M} \tag{9}$$

where K_M is a half saturation constant that determines the diminishing return function. In the cases developed in the Appendix, K_M incorporates factors indicating the finite sites for enzyme substrate interactions, or the efficiency with which microbes scavenge for free extracellular enzymes. A major difference to models 1 and 2 is that now the

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microbial biomass, instead of the amount of soil organic matter appears in the denominator. Therefore, the depolymerisation per unit biomass decreases as biomass increases (diminishing return).

2.1.4 Model 4: optimised enzyme production model

We further probe a model where microbial enzyme production is optimised for growth. We motivate this by microbial competition (Allison, 2005), which will allow microbes to succeed if microbial enzyme production allows the highest possible return. Optimisation only has meaningful results for the case of limited substrate availability (i.e. a diminishing return, possibly through constraints in potential sites for enzyme-substrate reaction) and if there is a cost associated with microbial enzyme production.

Depolymerisation as a function of enzyme production can be parameterised by

$$D(P) = \frac{P \cdot V_{\max 4} \cdot S}{K_P + P} \tag{10}$$

where P is the microbial enzyme production and K_P a half saturation constant (see the Appendix for full derivation and interpretations of $V_{\max 4}$ and K_P).

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

$$G = (1 - g)(D(P) - P \cdot c - \lambda_r \cdot M) \tag{11}$$

where c is the respiratory cost per unit enzyme produced.

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

$$D = V_{\max 4} \cdot S - \sqrt{K_P \cdot c \cdot V_{\max 4} \cdot S} \tag{12}$$

And the cost per unit carbon depolymerised is then

$$\frac{P \cdot c}{D} = \mu = \sqrt{\frac{K_P \cdot c}{S \cdot V_{\max 4}}} \tag{13}$$

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2.1.5 Model 5: traditional decomposition model

The last model is the traditional decomposition model, with the modification that carbon use efficiency changes with temperature:

$$\frac{dS}{dt} = S \cdot k \cdot Q_{10,k}^{\left(\frac{\Delta T}{10}\right)} \cdot \varepsilon(\Delta T) \tag{14}$$

where k is the first order decomposition constant, and $Q_{10,k}$ is the temperature sensitivity factor of the decomposition rate. Model 5 can also be considered as a special case of model 4, where the cost of enzyme production is zero, and the microbial biomass is at an instantaneous equilibrium with the rate of decomposition. Respiration (R) is then

$$R = S \cdot k \cdot Q_{10,k}^{\left(\frac{\Delta T}{10}\right)} \cdot (1 - \varepsilon) \tag{15}$$

We note, that here – in contrast to traditional models – CUE decreases with temperature.

2.2 Parameterisation and implementation

All models are implemented in STELLA, version 10.0.3. We tune parameters in the five microbial-enzyme models such that all models result in the equal amount of microbial biomass, substrate, and carbon use efficiency, at equilibrium for two temperatures, 15 and 20 °C. We are aware that many of the parameters are largely unknown and there is ample room for parameter adjustment. Here, we seek congruency of the models in their long-term response of 3 crucial variables, namely carbon use efficiency, soil organic matter, and microbial biomass, and evaluate their transient response instead.

We start off with model 1 where we use the parameters as reported in German et al. (2012), however, we report V_{max1} and K_E by including tuning factors and by considering 15 °C as our reference temperature. In other words, V_{max1} and K_E are the product of the reference values in German et al. (2012), their respective tuning parameters and their adjustment to our reference temperature, 15 °C. Further, we have

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converted the exponential temperature sensitivity of V_{max1} and K_E in model 1 to a Q_{10} term.

In model 2, to obtain the same equilibrium values for substrate, microbial biomass, and carbon use efficiency, we adjust g, λ_r, and Q_{10,λ_r}. We first parameterised maintenance respiration, where, the coefficient for maintenance respiration is scaled to microbial turnover (Van Bodegom, 2007). We assume that carbon turnover from maintenance estimation is ca. one-third of microbial death-rate such that:

$$\lambda_{r,0} = 0.334 \cdot \lambda_d \tag{16}$$

this constrains g at reference temperature to

$$g = \frac{\lambda_d - \varepsilon_0 \cdot (\lambda_d + \lambda_{r,0})}{\lambda_d - \varepsilon_0 \cdot \lambda_{r,0}} \tag{17}$$

To obtain the same equilibrium values of CUE, S, and M, at 20 °C as in model 1, we adjust $Q_{10,V_{max2}}$ and Q_{10,λ_r} such that model 2 has the same carbon use efficiency as model 1 (which in turn results into the same microbial biomass and soil organic carbon).

In model 3, we again seek to obtain the same equilibria values for carbon use efficiency, microbial biomass, soil organic matter, and decomposition at 15 and 20 °C. To allow a diminishing return mechanism, we assumed that most of the enzyme decay/loss in a scavenging model is attributed to microbial consumption instead of denaturation. Alternatively, under conditions of limited enzyme-substrate reaction sites, we assumed that there is an excess of free enzymes, and therefore, enzyme concentrations are higher than their corresponding half saturation concentrations. Overall, these assumptions would suggest a K_M that is smaller than M ($K_M < M$). Here, we chose K_M to be 0.37 of M at the reference temperature. Note, that the half saturation constant in this model has different formulations (unit: mg M cm^{-3}) than the previous models (unit: mg S cm^{-3}). V_{max3} and $Q_{10,V_{max3}}$ are tuned to yield equivalent equilibrium values of S.

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In model 4, we adjust V_{max4} and $Q_{10,V_{max4}}$ (in a similar manner like model 3) such that the system again yields equilibrium values for S at 15 and at 20 °C as in the other models if c is zero. Higher costs ($c > 0$) therefore will yield different equilibrium result, depending on the cost of enzyme production. Both, the half saturation constant and the cost per enzyme produced are parameters that are hard to come by. Instead, the solution allows us to quantify these based on variable fractions of depolymerisation (see Appendix).

Here, we analyse the model 4 based on different levels of enzyme expenditures and expressed them as enzyme costs per unit carbon depolymerised ($\mu = \frac{P_C}{D}$), where μ is 0, 10, and 50 % of the depolymerisation rate at reference temperature. This yields an expression for the combined cost (c) and the half saturation constant (K_P):

$$K_P \cdot c = \mu^2 \cdot D_{\mathrm{Eq.},\Delta T=0} \cdot Q_{10}^{\left(\frac{\Delta T}{10}\right)} \tag{18}$$

where $D_{\mathrm{Eq.},\Delta T=0}$ is the rate of depolymerisation at 0 enzyme cost and reference temperature. The temperature sensitivity of half saturation constant is the same as to other models.

Finally, in model 5, the traditional decomposition model, we adjust the parameters k, ε_0, and $Q_{10,k}$ to obtain the same S, M, and CUE as in all other models at 15 and at 20 °C. The difference to a traditional formulation of first order decomposition is a variable (i.e. decreasing) carbon use efficiency.

All parameter values are given in Table 2.

2.3 Determination of apparent Q_{10}

We determined an apparent Q_{10}, $Q_{10}(t)$ by relating the changes of the respiration per unit soil organic matter to the changes in temperature (ΔT) at any given time (t):

$$\frac{R(t)}{S(t)} = \frac{R_0}{S_0} \cdot Q_{10}^{\left(\frac{10}{\Delta T}\right)}(t) \tag{19}$$

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where $R(t)$ and $S(t)$ are the instantaneous rates of respiration and soil organic matter, respectively, and R_0 and S_0 the equilibrium respiration rates and equilibrium substrate at reference temperature.

3 Results

We first analyse the equilibrium state of microbial biomass by setting the tendency for the microbial biomass to zero ($\frac{dM}{dT} = 0$), while assuming a constant soil organic matter pool. This is useful since in many cases microbial turnover is much faster than the turnover of bulk soil organic matter (Stark and Hart, 1997; Schmidt et al., 2007). In models 1 and 2 (German and modified German model), the microbial biomass would hold an unstable equilibrium (also termed a knife-edge equilibrium, see Schimel and Weintraub, 2003). The equilibrium solution is independent of M and requires thus a perfect balance of the parameters that govern growth- and death-rates (Table 3). This means, that microbial biomass would thus either grow indefinitely or decay to zero. It becomes clear that the soil organic matter pool must response on a similar time scale as microbes in order to maintain microbial biomass within acceptable boundaries.

Modification of the model to allow a diminishing return with increasing enzyme production or with increasing microbial mass (models 3 and 4), will result into a stable microbial biomass under constant substrate concentration (Table 3, leftmost column). The inclusion of enzyme production costs and optimisation of microbial growth yields an equilibrium biomass where the half saturation constant (K_P) becomes important as it is, next to the direct enzyme expenditure, a central determinant of how much effort is being put into the production of enzyme. The equilibrium biomass under constant substrate allows to gauge the short-term response to a warming: all, catalytic rates, microbial respiration rates, and half saturation constants are temperature sensitive, therefore microbes will benefit from warming as depolymerisation is faster (increased V_{max}), but this benefit is reduced by the concomitant temperature response of λ_r and

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the half saturation constants. As a consequence, microbial biomass in models 3 and 4 can both increase or decrease with warming.

In the long term (Table 3, 3 rightmost columns) soil organic matter will adjust to the short-term microbial changes. Soil organic matter is inversely related to the maximum catalytic rate in all models. Rates of litter input are important determinants of soil organic matter in models 3 to 5. In contrast, in the microbial model based on German et al. (2012) and our derivative with maintenance respiration (models 1 and 2) the soil carbon pool is independent of the rate of new carbon added to the soil and solely a function of microbial parameters. Allowing soil organic matter to adjust to microbial growth and decay allows now a stable microbial biomass in models 1 and 2. Both, the maximum catalytic rate and the half saturation constant have no impact on the long-term microbial biomass in models 1 to 3. Therefore, if carbon use efficiency is set to be equal in these three models, biomass, too converges to the same values. For model 4, the optimised enzyme production model, the resulting equilibria of S, M, and CUE end up being complex expressions, and we did not calculate the long-term equilibria of M and CUE, but expressed them simply as a function of soil organic matter. As expected, the effect of enzyme production cost has a negative impact on carbon use efficiency and microbial biomass and feeds back into the soil organic matter.

3.1 Model simulations

The transient response for the different models to a temperature step from 15 to 20 °C is shown in Fig. 2. We note that all models are forced through the same initial and final values of M, S, and CUE by way of parameter adjustments, and we focus on the models' transient behaviours (see method section). The long-term adjustments to warming are reduction in S, M, and CUE while rates of respiration return to the initial value, equilibrating with the amount of new carbon entering the system.

Model 1 shows oscillations in M and S, as noted earlier (Wang et al., 2014). The warming triggers an increase in depolymerisation, which in turn feeds microbial biomass, causing a higher rate of depolymerisation. This positive feedback experiences

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a break only when the substrate (S) is sufficiently depleted, such that microbial biomass begins to decline. However the positive feedback takes over again, the decreasing microbial biomass results in reduced depolymerisation until microbial biomass is low enough for soil organic matter to recover. The amplitude of the oscillations dampen over time (Fig. 2).

Separating out maintenance and growth respiration in model 2 increases the feedback between microbes and substrate (evidenced by higher amplitudes in M, S, and respiration). This is because part of respiration is now tied to microbial biomass, which lags depolymerisation. Carbon use efficiency initially decreases less than in model 1 (Fig. 2), because maintenance respiration lags the growing microbial biomass. The maintenance term introduces therefore also mild oscillation into the instantaneous carbon use efficiency, as microbial biomass waxes and wanes. Interestingly, including maintenance respiration decreases oscillation frequency.

The transient dynamics in model 3 with a diminishing return as enzyme (or microbial) concentration increases, is smoother compared to models 1 and 2 (Fig. 2). Allowing a finite site for enzyme-substrate reaction or microbial scavenging for enzymes curbs the growth of microbial biomass. In contrast to models 1 and 2, warming in model 3 leads to a decrease of microbial biomass, because the (curbed) carbon gain from the increase in depolymerisation can not balance the warming induces increase in maintenance respiration losses.

Model 4 considers the metabolic cost of enzyme production and allows optimising microbial growth. In absence of costs towards enzyme production (i.e. $\mu = 0$), depolymerisation becomes a first order decomposition process. The transient behaviour of S and M is similar between model 3 and model 4 (without respiratory costs of enzyme production). However, the absence of a half saturation constant in model 4 (Eq. 10) yielded a quicker adjustment of microbial biomass to temperature, a slightly slower degradation of soil organic matter initially, and a much more pronounced initial drop in CUE. Decomposition in model 4 without enzyme costs behaves the same way as decomposition in the traditional linear model (model 5), therefore, values of soil or-

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ganic matter are almost equal with an indistinguishable difference that stems from an immediate return of dead microbial biomass in model 5.

Next, we employed different levels of enzyme production costs in model 4. That is, we set cost per enzyme production such that total enzyme expenditure is 0, 10, and 50 % of equilibrium depolymerisation at our reference condition (i.e. 15 °C). As expected, increasing enzyme production cost reduced the rate of depolymerisation, and S is therefore maintained at a higher level. The increasing costs also resulted into a smaller response of soil organic matter to warming. Similarly, the response of CUE to warming is smaller and the decline of M is less pronounced if enzyme production costs are considered. Initial hikes in respiration rates are lowest under the highest costs of enzyme production.

We calculated an apparent Q_{10} by relating respiration per unit soil organic matter to its value at 15 °C. Q_{10} values would converge as the system reaches a new steady state, since we adjusted relevant parameters such that equilibrium values of microbial biomass, S, and CUE are the same across all models and for both temperatures. The initial change of respiration Q_{10} was highest in model 2, followed by model 1. In both models transient Q_{10} oscillates while oscillation amplitude is dampening over time. All models which consider microbial dynamics show higher Q_{10} with a downward adjustment over time. Initial hikes in respiration and apparent Q_{10} occur because of increased growth and associated growth respiration (models 1 and 2). Immediately after warming, the higher than equilibrium microbial biomass causes increased maintenance respiration (models 3 and 4) driving up the apparent Q_{10}. In the enzyme production optimisation model (model 4) Q_{10} decreases under higher enzyme production costs while later attenuation is smaller (Fig. 4). Finally, in the traditional model with no (or implicit) microbial biomass Q_{10} does not change over time.

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4 Discussion

4.1 Key differences between models

Recently developed microbial decomposition models (Schimel and Weintraub, 2003; Allison et al., 2010; German et al., 2012) highlight the importance of microbial processes and microbial physiology during decomposition. The application of these models specifically highlights the role of extracellular enzymes during decomposition and how these constraints will further affect the release of soil organic matter as a consequence of warming. Further, it has been shown that carbon use efficiency and microbial turnover are central parameters in the prediction of soil carbon storage to warming (Hagerty et al., 2014). While microbial decomposition models are able to improve prediction of organic carbon stock globally, and can successfully recreate litter decomposition dynamics, the long-term trajectory of a warming response needs further evaluation (Wang et al., 2014). In particular, a positive feedback between depolymerisation and microbes can only be curbed via the longer term adjustment of soil organic matter and therefore lead to oscillation in both microbial biomass and soil organic matter (Wang et al., 2014). Here, we build on recent advances of microbial decomposition models and ask how nuanced representation of CUE (in the form of maintenance respiration and enzyme production cost), and how mechanisms that constrain the depolymerisation at high enzyme or microbial biomass concentration would affect model behaviour and response to warming.

Models 1 and 2, i.e. the microbial decomposition model as proposed by German et al. (2012) and our variation that includes a partitioning between growth and maintenance respiration show qualitatively similar characteristics. Most importantly, the equilibrium solution under a constant substrate concentration (S) shows a knife's edge or unstable equilibrium (Schimel and Weintraub, 2003). As a consequence, changes in microbial biomass result in a positive feedback between depolymerisation and growth. That is, in the case of a temperature increase, depolymerisation picks up, feeds microbe, which produce more extracellular enzymes causing faster rates of depolymeri-

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sation. A break in this feedback only occurs via reduction of soil organic matter. The positive feedback in conjunction with a break in a slower responding soil carbon pool leads to oscillation in M, S, and respiration. Separating respiration into growth and maintenance terms changes the model behaviour marginally. In fact, the positive feedback between microbial biomass and soil organic matter depolymerisation in model 2 is slightly amplified compared to model 1 because maintenance respiration lags depolymerisation.

While the partitioning between growth and maintenance respiration in the microbial pool is slightly more realistic (Sinsabaugh et al., 2013), the changes between models 1 and 2 are small overall. For example, changes in frequency and amplitude can easily be introduced by other parameter changes (Wang et al., 2014). Although it is more mechanistic to separate growth and maintenance respiration, it remains open whether the addition of extra parameters is justified at this point, particularly since this requires knowledge of climate sensitivity of these different respiration terms.

The oscillatory behaviour arising from the spiraling between microbial growth and depolymerisation in models 1 and 2 has been a point of critique as it has not been observed in laboratory and field incubation studies (Wang et al., 2014). Here, we propose mechanisms that introduce a break in the positive feedback between substrate and microbial biomass. We portray two scenarios, where each increment in microbial biomass or enzyme concentration yields a smaller increase in depolymerisation than the previous increment (i.e. diminishing return). The scenarios we worked out are (1) microbial biomass feeds on active extracellular enzymes, (2) limited sites for substrate/enzyme reactions (see Appendix). We derived the forms of depolymerisation from the original Michaelis–Menten kinetics and the resulting formulations presented in the method section are simplified from more complex mathematical expressions (see Appendix). The simplified formulation of depolymerisation and microbial consumption we arrived at has been dubbed reverse Michaelis–Menten formulation (Schimel and Weintraub, 2003), because microbial biomass (or enzyme concentration) instead of the substrate concentration is now occurring in the denominator of the depolymerisa-

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tion term, invoking diminishing return. Our analysis shows that the positive feedback between decomposition and microbial growth is removed, as model 3 has now a stable equilibrium.

Limited sites may play a role if the substrate has a high volume to surface ratio, or if the substrate is associated with minerals (Davidson and Janssens, 2006; Gillabel et al., 2010; Conant et al., 2011; Davidson et al., 2012, 2014; Cotrufo et al., 2013; Wagai et al., 2013; Benbi et al., 2014; Wieder et al., 2014a; Tang and Riley, 2015). Our implementation of limited substrate causes a surplus free enzymes that compete among themselves for binding to substrates similar to the Langmuir adsorption isotherm theory (Vetter et al., 1998; Schimel and Weintraub, 2003 and see Appendix). Effects of microbial scavenging for enzymes cause a negative feedback because more microbial biomass will lead to an increased probability of enzymes being consumed before they interact with soil organic matter. Other mechanisms of diminishing return as enzyme increase may be stabilisation of enzymes into organic matter-humate complex (Allison, 2006), or sorption to minerals, soil organic matter, or microbes (Tang and Riley, 2015). Diminishing returns also occur with rate-yield tradeoffs (Allison, 2014).

Many microbial decomposition models work under the assumption that enzyme production is proportional to microbial biomass. It is conceivable, that microbes are adjusting production to maximise return or growth (Cooney, 2009; Merchant and Helmann, 2012). We consider such an optimisation of microbial growth under the consideration of an acquisition cost in the form of respiratory expenditures for enzyme synthesis (model 4). While the exact cost of enzyme synthesis is not known, we fixed parameters (the product of K_P and c) that they relate to the fractional expense of carbon depolymerised upon initialization (i.e. at steady state and reference temperature, Eq. 13). Importantly, enzyme optimisation is not possible for some of the models presented here. Higher enzyme production would always lead to further microbial growth in models 1 and 2 and the highest yield would occur infinite enzyme production. Similarly, in the case of microbial scavenging for enzymes, additional investments into enzymes always increases depolymerisation.

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The model with no-cost enzyme production closely resembles the traditional first order decay model with the variation of an explicit microbial pool and variable carbon use efficiency. In this model, depolymerisation occurs at the maximum reaction rate (V_{max}). Fixing the steady state values of S, M, and CUE of the no-cost model 4 to the respective values of Model 1 required us to choose Q_{10} for V_{max4} close to 1, indicating no change in maximum depolymerisation with warming, which confirms the lower climate sensitivity found in microbial decomposition model (Allison et al., 2010). Therefore, the response to warming for the no-cost model 4 (Fig. 2) mainly stems from the increase in maintenance respiration and the associated decline in carbon use efficiency.

Perhaps the most intriguing feature of the optimised enzyme production model is that increasing costs lead to a smaller immediate response in respiration and more resilient soil organic matter pool in the long term, when subject to warming. The immediate respiration response can be attributed to the higher microbial biomass that can be maintained if enzyme expenditures are low. A warming then increases maintenance respiration much more in the low-cost scenario. In the long term soil organic matter decreases much less when enzyme production costs are considered. The decrease in the soil organic matter pool in the high cost scenario ($\mu = 0.5$) is a mere 3 % under a 5 °C warming, compared to 12.5 % if costs are negligible.

Model 4 (at low cost) is among our suite of models, the one that most closely resembles the traditional first order decomposition model. Here, we modified a traditional model by a variable carbon use efficiency and we obtain a qualitatively similar result as in model 4. The nuances are small and mainly caused by the lag of carbon returned, as it passes through the microbial biomass. Even if the enzyme production costs are higher, the functional form of the response to warming can easily be captured by a first order decomposition model.

4.2 Short-term and long-term response to temperature

Because many of the parameters in these models are hard to come by, we chose the strategy to start off with a previously used set and adjust the different models such

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that their equilibrium values of microbial biomass, soil carbon storage, and carbon use efficiency are the same at the reference temperature (15 °C) and at the warmed temperature (20 °C). We obtained this mainly by adjusting first V_{max} (maximum depolymerisation), and λ_r (per M maintenance respiration rate) to obtain a match at the reference temperature, followed by tuning temperature sensitivity (Q_{10}) for V_{max} and λ_r to obtain identical values across models for M, S, and CUE at the warmed equilibrium. The tuning of V_{max} and the Q_{10} of V_{max} and λ_r yield different values across the models.

We investigate the consequence of this tuning by analysing the transient changes in the "apparent" Q_{10}. We define apparent Q_{10} as the Q_{10} response of the relative respiration (respiration per unit substrate, see method section). While the apparent Q_{10} converges over time, the differences in physiological temperature responses (Q_{10} for V_{max} and λ_r) have different impact in the short term. These differences in physiological responses are evident immediately after the temperature increase, as they are displaying very disparate responses in respiration, and consequently in the apparent Q_{10} (Fig. 4). Models 1 and 2 show the strongest initial response before the apparent Q_{10} adjusts to its long-term value. In the models with diminishing return (models 3 to 5) the long-term temperature response is much closer to the short-term (physiological) response. But also the models with diminishing return show considerable differences. The major difference in the model structure between model 3 and model 4 (assuming where costs of enzyme synthesis are 0) is a non-negligible half saturation constant (K_M = 0.37 of microbial biomass at reference temperature). The respiration in model 3 increases much more dramatically than in model 4, causing Q_{10} to increase to a higher level, before slowly adjusting down. A sizeable cost for enzyme synthesis with optimisation of microbial growth, further reduces a long-term adjustment of the temperature sensitivity. Similar to the first order decomposition model, the initial response to a temperature increase is quasi-locked in and does not change much over time.

The difference in the apparent Q_{10} critically shows, that understanding the mechanisms, how microbial biomass acquires its building blocks, insights in what limits this

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acquisition, and also how the microbial community responses to limitation are central to our understanding of how soil organic matter responds to warming.

We acknowledge that we used a simplified set-up of our model suite. For example, we assumed that depolymerised carbon in soil solution (dissolved organic carbon) is always at steady state with the microbial biomass. We justified this simplification by assuming fast and efficient scavenging for microbes. We further did not include nutrient requirements of microbes. Considering the stoichiometric requirements can in particular change the allocation of resources to optimise enzyme synthesis. Nevertheless, our suite of models show the importance of how the depolymerisation step is formulated in mathematical models when evaluating the response of decomposition under warming.

5 Conclusions

Our findings suggest that different formulation of how microbes acquire substrate will have significant impact on the short vs. long-term consequences of warming. Here, we present simple, yet feasible mechanisms of microbial dynamics. We show that substrate limitation in the form of decreasing marginal return can create a break in the positive feedback between microbial biomass and depolymerisation, but also opens the possibility of microbes to optimise carbon uptake. We find that decreasing marginal return leads to apparent temperature responses that are closer to the physiological responses, even more so when microbes adjust enzyme production to optimise growth. Carefully designed long-term experiments, can therefore, provide insights and can further help with the interpretation of short-term incubations.

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Appendix A:

A1 Michaelis–Menten kinetics with enzyme denaturation

The dynamics of the enzyme-substrate complex is

$$\frac{\mathrm{d}[E]}{\mathrm{d}t} = P - K_S[S][E] - \lambda_{E1} \cdot [E] \quad \text{(A1)}$$

$$\frac{\mathrm{d}[\mathrm{ES}]}{\mathrm{d}t} = -(K_{\mathrm{cat}} + K_{\mathrm{r}} + \lambda_{E2})[\mathrm{ES}] + K_S[S][E] \quad \text{(A2)}$$

where P is the production of new enzymes, $[S]$ are the concentration of free sites available for enzyme substrate complexation, $[E]$ 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.

We are mostly interested in total enzyme concentration

$$[E_t] = [\mathrm{ES}] + [E] \quad \text{(A3)}$$

The Michaelis–Menten approximation for depolymerisation assumes that the system is in quasi steady state in which the total enzyme concentration $[E_t]$. Here we include also that the total available sites do not change (S is constant) within the timescale of enzyme reactions. This implies that Eq. (A2) becomes zero as the different reactants will approach a steady state

And thus

$$[E] = \frac{[E_t]K_E}{([S] + K_E)} \quad \text{(A4)}$$

$$[\mathrm{ES}] = \frac{[E_t][S]}{([S] + K_E)} \quad \text{(A5)}$$

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And the rate of depolymerisation

$$D = \frac{[E_t] \cdot V_{\max} \cdot [S]}{([S] + K_E)} \tag{A6}$$

where D is the familiar Michaelis–Menten equation with $K_E = \frac{K_{\text{cat}} + K_r + \lambda_{E2}}{K_S}$ and $V_{\max}$ is equivalentto K_{cat}.

A2 DOC and enzyme dynamics

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

Similarly, we estimate the equilibrium total enzyme concentration by setting its tendency to zero:

$$\frac{\mathrm{d}E_t}{\mathrm{d}t} = P - \lambda_{E2}[\mathrm{ES}] - \lambda_{E1}[E] = 0 \tag{A7}$$

where P is the production of enzymes. Substituting Eqs. (A4) and (A5) for E and ES yields

$$E_t = \frac{P([S] + K_E)}{\lambda_{E1} K_E + \lambda_{E2}[S]} \tag{A8}$$

And the overall depolymerisation yields

$$D = \frac{P \cdot K_{\text{cat}} \cdot [S]}{\lambda_{E1} K_E + \lambda_{E2}[S]} \tag{A9}$$

We note, that previous models (Allison et al., 2010; German et al., 2012) assumed a general decay of the total enzyme pool, where

$$\frac{\mathrm{d}E_t}{\mathrm{d}t} = P - \lambda_E \cdot E_t \tag{A10}$$

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This is the special case of $\lambda_{E1} = \lambda_{E2} = \lambda_E$. This case leads to an equilibrium concentration of

$$E_t = \frac{P}{\lambda_E} \tag{A11}$$

And depolymerisation as:

$$D = \frac{\frac{P}{\lambda_E} \cdot K_{\text{cat}} \cdot [S]}{[S] + K_E} \tag{A12}$$

Finally, microbial decomposition models assume that enzyme production is proportional to the microbial biomass: $P = b \cdot M$, hence, in the special case of a general decay of enzymes

$$D = \frac{V_{\max} \cdot M \cdot [S]}{[S] + K_E} \tag{A13}$$

With $V_{\max} = \frac{b \cdot K_{\text{cat}}}{\lambda_E}$.

We used Eq. (A13) in models 1 and 2.

More generally (with specific decay rates for free enzyme and enzymes associated with the substrate)

$$D = \frac{V_{\max} \cdot M \cdot [S]}{[S] + K_S} \tag{A14}$$

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

A3 Microbial consumption of Enzymes

Microbes feeding on free enzymes can be represented as:

$$F = \lambda_{E,M} \cdot [E] \cdot M \tag{A15}$$

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

$$[E] \cdot \lambda_{E1} = [E](\lambda_{E1,0} + \lambda_{E,M} \cdot M) \tag{A16}$$

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

Substituting the new enzyme decay formulation into the depolymerisation (Eq. A9) yields

$$D = \frac{P \cdot K_{\text{cat}} \cdot [S]}{\lambda_{E2} \cdot [S] + \lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \tag{A17}$$

Assuming that enzymes associated with substrate do not undergo denaturation ($\lambda_{E2} = 0$)

$$D = \frac{P \cdot K_{\text{cat}} \cdot [S]}{\lambda_{E1,0} \cdot K_E + \lambda_{E,M} \cdot M \cdot K_E} \tag{A18}$$

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

$$D = \frac{M \cdot V_{\max} \cdot [S]}{K_M + M} \tag{A19}$$

where $V_{\max} = \frac{b \cdot K_{\text{cat}}}{\lambda_{E,M} \cdot K_E}$ and $K_M = \frac{\lambda_{E1,0}}{\lambda_{E,M}}$

A4 Model with limited available substrate

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

$$S = \theta \cdot ([S_f] + [\text{ES}]) \tag{A20}$$

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where S_f are the available sites for enzyme reaction, θ a scalar relating the total amount of substrate to the total potentially free sites (e.g. a surface to mass conversion), and [ES] represents the sites with enzyme-substrate complexes.

Substituting [ES] from Eq. (A5), but knowing that S has now become S_f, we obtain:

$$[S_f] = \frac{S}{\theta} - \frac{[S_f][E_t]}{K_E + [S_f]} \tag{A21}$$

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

$$[S_f] = \frac{1}{2}\left\{ -\left([E_t] + K_E - \frac{S}{\theta}\right) \pm \sqrt{\left(E_t + K_E - \frac{S}{\theta}\right)^2 + 4 \cdot \frac{S}{\theta} \cdot K_E} \right\} \tag{A22}$$

As we assume there are limited reaction sites ($\frac{S}{\theta}$), we simplify this function using a Taylor expansion around ($\frac{S}{\theta} = 0$)

$$S_f = \frac{S}{\theta} \cdot \left(\frac{k_E}{E_t + k_E}\right) + O\left[\left(\frac{S}{\theta}\right)^2\right] \tag{A23}$$

Plugging this into the depolymerisation

$$D = \frac{K_{\text{cat}} \cdot E_t \cdot \frac{S}{\theta}}{E_t + K_E + \frac{S}{\theta}} \cong \frac{K_{\text{cat}} \cdot E_t \cdot \frac{S}{\theta}}{E_t + K_E} \tag{A24}$$

which has a Michaelis–Menten form with a saturating enzyme concentration.

We can also include Equations for enzyme turnover (Eq. A7) to calculate E_t: however, we need to substitute $[S]$ in this Equation with $[S_f]$, thus

$$\frac{\mathrm{d}E_t}{\mathrm{d}t} = P - \frac{\lambda_{E2} \cdot [E_t] \cdot \frac{S}{\theta}}{[E_t] + K_E + \frac{S}{\theta}} - \frac{\lambda_{E1} \cdot [E_t] \cdot [E_t + K_E]}{[E_t] + K_E + \frac{S}{\theta}} \tag{A25}$$

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

$$\frac{dE_t}{dt} \cong P - \frac{\lambda_{E2} \cdot [E_t] \cdot \frac{S}{\theta}}{[E_t] + K_E} - \lambda_{E1} \cdot [E_t] \quad \text{(A26)}$$

The equilibrium solution ($\frac{dE_t}{dt} = 0$) yields a quadratic expression for E_t, however, we can evaluate end member:

a. suppose $\frac{\lambda_{E2} \cdot [E_t] \cdot \frac{S}{\theta}}{E_t + K_E} \gg \lambda_{E1} \cdot [E_t]$, this assumes that enzyme decay occurs mainly when bound to the substrate. Setting $\frac{dE_t}{dt} = 0$, we obtain

$$E_t = \frac{K_E \cdot P}{\lambda_{E2} \cdot \frac{S}{\theta} - P} \quad \text{(A27)}$$

and with P proportional to microbial biomass (M)

$$D = \frac{K_{\text{cat}} \cdot P}{\lambda_{E2}} = V_{\text{max}} \cdot M \quad \text{(A28)}$$

where $V_{\text{max}} = \frac{K_{\text{cat}} \cdot b}{\lambda_{E2}}$.

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 $\frac{\lambda_{E2} \cdot [E_t] \cdot \frac{S}{\theta}}{[E_t] + K_E} \ll \lambda_{E1} \cdot [E_t]$.

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

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

and

$$D = \frac{K_{\text{cat}} \cdot P \cdot \frac{S}{\theta}}{P + \lambda_{E1} \cdot K_E}. \quad \text{(A29)}$$

with $P = b \cdot M$, we have

$$D = \frac{V_{\max} \cdot S}{K_M + M}. \quad \text{(A30)}$$

where $V_{\max} = \frac{K_{\text{cat}}}{\theta}$, and $K_M = \frac{\lambda_{E1} \cdot K_E}{b}$.

A5 Optimising depolymerisation

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

$$D(P) = \frac{P \cdot V_{\max} \cdot S}{K_P + P}. \quad \text{(A31)}$$

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

Microbial growth (G) will be

$$G = (1 - g) \cdot (D - Pc - \lambda_{\text{r}} \cdot M). \quad \text{(A32)}$$

where g is the growth respiration factor, c the respiratory cost per unit enzyme production, and λ_{r} the maintenance respiration factor.

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Enzyme production (P) can be optimised by substituting Eq. (A31) into Eq. (A32) and setting $\frac{dG}{dP} = 0$. This yields:

$$Pc = -K_P c + \sqrt{V_{max} \cdot S \cdot K_P c}. \quad \text{(A33)}$$

The proportion of carbon expended for enzyme production relative to depolymerisation (μ) is

$$\mu = \frac{Pc}{D} = \sqrt{\frac{K_P c}{S V_{max}}}. \quad \text{(A34)}$$

Instead of specifying c, we used Eq. (A34) to express overall microbial carbon expenditure for enzyme production. After assigning a value to μ, we calculate c based on equilibrium S at reference temperature.

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

$$D = \frac{P \cdot V_{max3} \cdot S}{(K_M + M) \cdot \lambda_E}. \quad \text{(A35)}$$

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

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

Model	Description
Model 1	German et al. (2012)
Model 2	As model 1 but microbial respiration is partitioned into temperature insensitive growth and temperature sensitive maintenance respiration terms.
Model 3	Depolymerisation and uptake relative to microbial biomass decreases with increasing M (diminishing return mechanism).
Model 4	Optimisation of microbial enzyme production to maximise microbial growth, and consideration of carbon costs associated with enzyme synthesis.
Model 5	First order decomposition model, modified to account for temperature sensitive carbon use efficiency.

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Table 2. Parameters used in the five microbial decomposition models (in models 2 to 5, we provide only those parameters where modifications have been made).

Model	Parameter	Unit	Value	Description	Source
Model 1	I	$mg\,cm^{-3}\,h^{-1}$	0.001	Input of fresh litter	German et al. (2012)
	λ_d	h^{-1}	0.0005	Death rate of microbes	
	$V_{max1,0}$	$mg\,cm^{-3}\,h^{-1}$	0.0049	Maximum catalytic rate @ 15 °C	
	$Q_{10,V_{max1}}$	–	1.9	Q_{10} of maximum catalytic rate	
	$K_{E,0}$	$mg\,S\,cm^{-3}$	270	Half-saturation constant @ 15 °C	
	Q_{10,K_E}	–	1.07	Q_{10} of half-saturation constant	
	ε_0	–	0.39	Microbial growth efficiency @ 15 °C	
	ε_{slope}	$°C^{-1}$	−0.016	Microbial growth efficiency temperature slope	
Model 2	$V_{max2,0}$	$mg^{-1}\,M\,cm^{-3}\,h^{-1}$	0.0049	Maximum catalytic rate @ 15 °C	This study
	$Q_{10,V_{max2}}$	–	1.9	Q_{10} of maximum catalytic rate	
	$\lambda_{r,0}$	h^{-1}	0.00017	Maintenance respiration @ 15 °C	
	Q_{10,λ_r}	–	8	Q_{10} of maintenance respiration	
	g	–	0.55	Growth respiration coefficient	
Model 3	$V_{max3,0}$	$mg^{-1}\,M\,cm^{-3}\,h^{-1}$	2.61×10^{-5}	Maximum catalytic rate @ 15 °C	This study
	$Q_{10,V_{max3}}$	–	1.33	Q_{10} of maximum catalytic rate	
	$K_{M,0}$	$mg\,M\,cm^{-3}$	0.68	Half-saturation constant @ 15 °C	
Model 4	$V_{max4,0}$	$mg^{-1}\,M\,cm^{-3}\,h^{-1}$	1.71×10^{-5}	Maximum catalytic rate @ 15 °C	This study
	$Q_{10,V_{max4}}$	–	1.0	Q_{10} of maximum catalytic rate	
	$\frac{P_C}{D}$	–	0, 0.1, 0.5	Enz production cost (as % of decomposition)	
Model 5	k	h^{-1}	1.71×10^{-5}	First order decay constant @ 15 °C	This study
	$Q_{10,k}$	–	1.0	Q_{10} of k	

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Table 3. Equilibrium solutions for microbial biomass, soil organic carbon, and CUE at short/fast time scale (if, S = Eq. S) and long time scale (if, S = Eq. S).

Model	Short/Fast time scale	Long time scale		
	M	S	M	CUE
Model 1	no solution [a]	$\frac{\lambda_d K_E}{V_{max1}\varepsilon-\lambda_d}$	$\frac{I\varepsilon}{(1-\varepsilon)\lambda_d}$	$\varepsilon(T)$
Model 2	no solution [b]	$\frac{K_E b}{V_{max2}(1-g)-b}$	$\frac{I(1-g)}{b-\lambda_d(1-g)}$	$\frac{\lambda_d(1-g)}{b}$
Model 3	$\frac{V_{max3}S(1-g)-K_M b}{b}$	$\frac{b[I(1-g)+K_M\{b-\lambda_d(1-g)\}]}{V_{max3}(1-g)\{b-\lambda_d(1-g)\}}$	$\frac{I(1-g)}{b-\lambda_d(1-g)}$	$\frac{\lambda_d(1-g)}{b}$
Model 4	$\frac{(1-g)(X-Y)^2}{b}$	$\frac{1}{2V_{max4}(1-\eta)^2}[-Y(2\eta-1)\sqrt{4IY(1-\eta)+Y^2}+(1-\eta)(2I-2\eta Y^2)+Y^2]$	$\frac{(1-g)(X-Y)^2}{b}$	$\frac{(1-g)(X-Y)\lambda_d}{bX}$

$X=\sqrt{SV_{max4}}$, $Y=\sqrt{K_P c}$, $b=[(1-g)\lambda_r+\lambda_d]$, $\eta=\frac{(1-g)\lambda_d}{b}$

[a] requires $\lambda_d=\frac{V_{max1}S\varepsilon}{S+K_E}$,

[b] requires $\lambda_d=(1-g)(\frac{V_{max2}S}{S+K_E}-\lambda_r)$.

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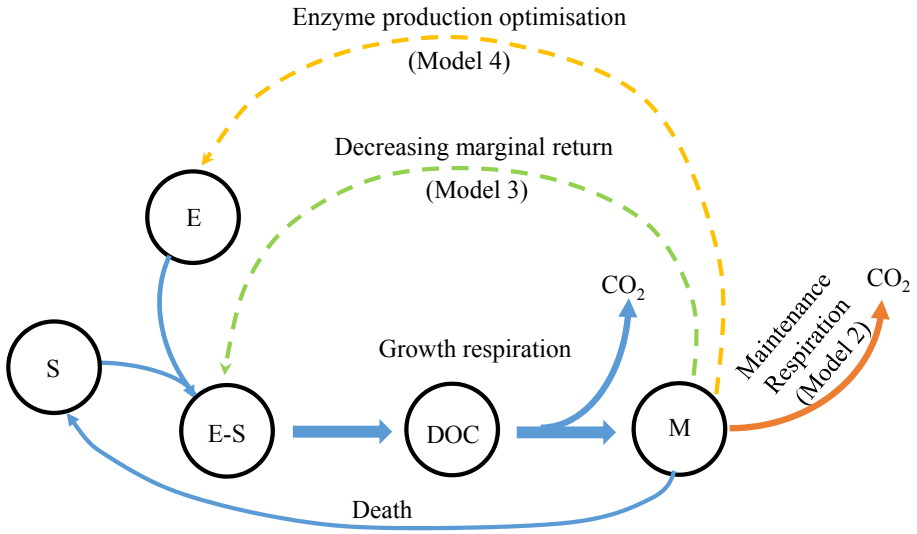

Figure 1. Conceptual diagrams for the microbial-enzyme models used in this study. Solid lines represent material flow (in models 1 and 2) and dashed lines represent information flow (in models 3 and 4). *E*, *S*, E-S, DOC, *M* represent enzyme, substrate, enzyme-substrate complex, dissolved organic carbon, and microbial biomass carbon, respectively.

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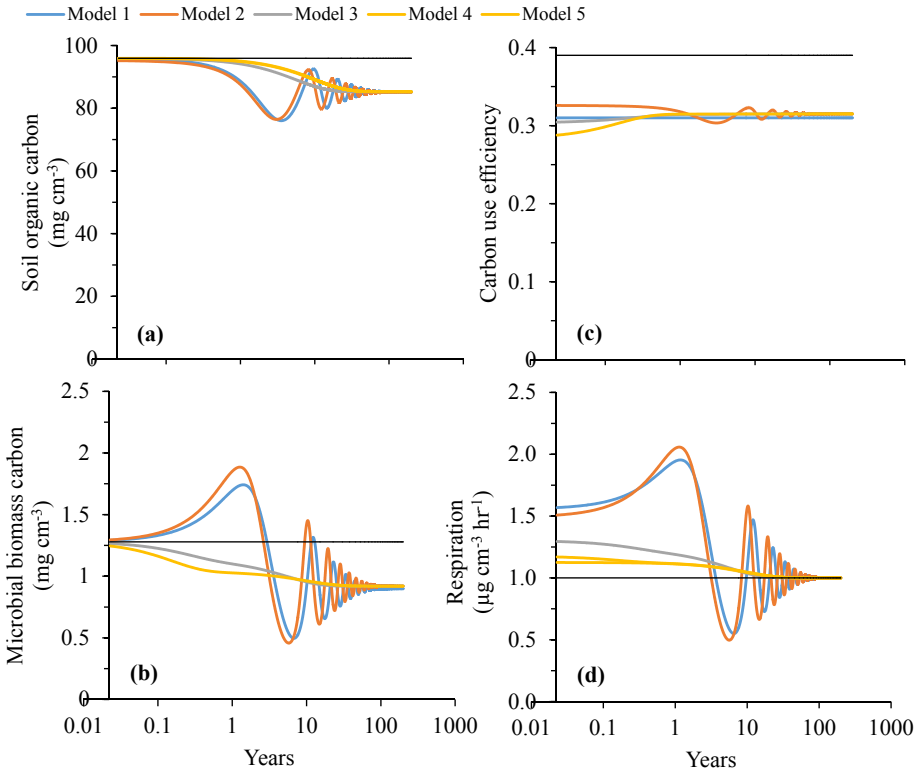

Figure 2. Responses of **(a)** soil organic carbon, **(b)** microbial biomass carbon, **(c)** CUE, and **(d)** respiration to a 5 °C warming for all models. Black line represent initial values, where equilibria @ 15 °C. (Note: simulated soil organic carbon and respiration by model 4 are superimposed with the model 5 results. For model 4, simulations are carried out at zero enzyme production cost, i.e. $\mu = 0$).

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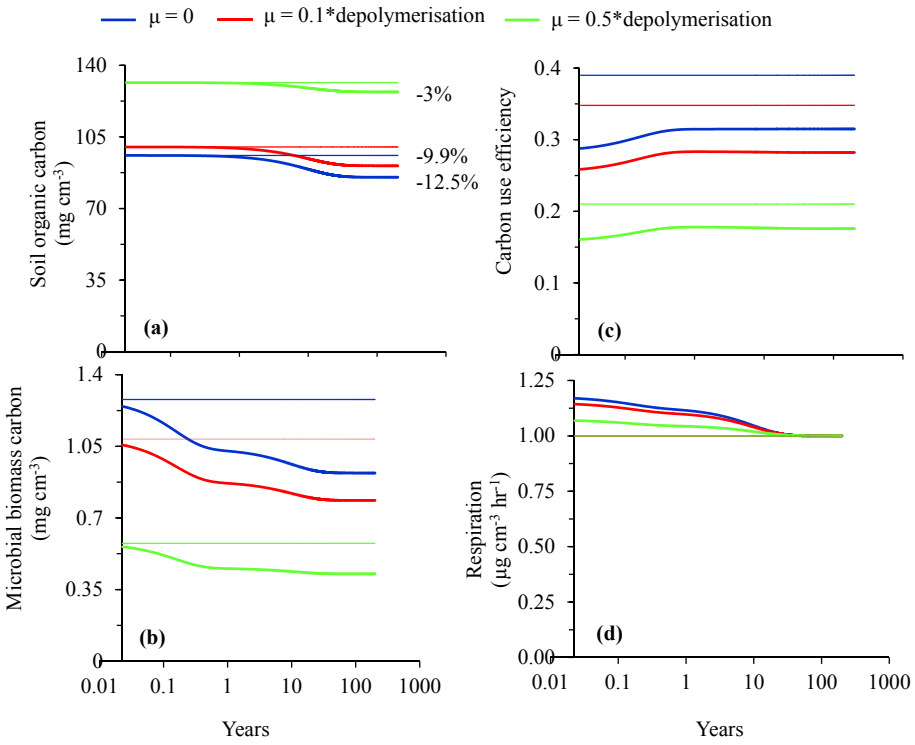

Figure 3. Long-term responses of optimized enzyme production model to a 5˚C warming in **(a)** soil organic carbon, **(b)** microbial biomass carbon, **(c)** CUE, and **(d)** respiration operating at different relative enzyme production costs (μ), see Eq. (13). Thick lines represent warming response and thin lines represent corresponding equilibrium at reference temperature.

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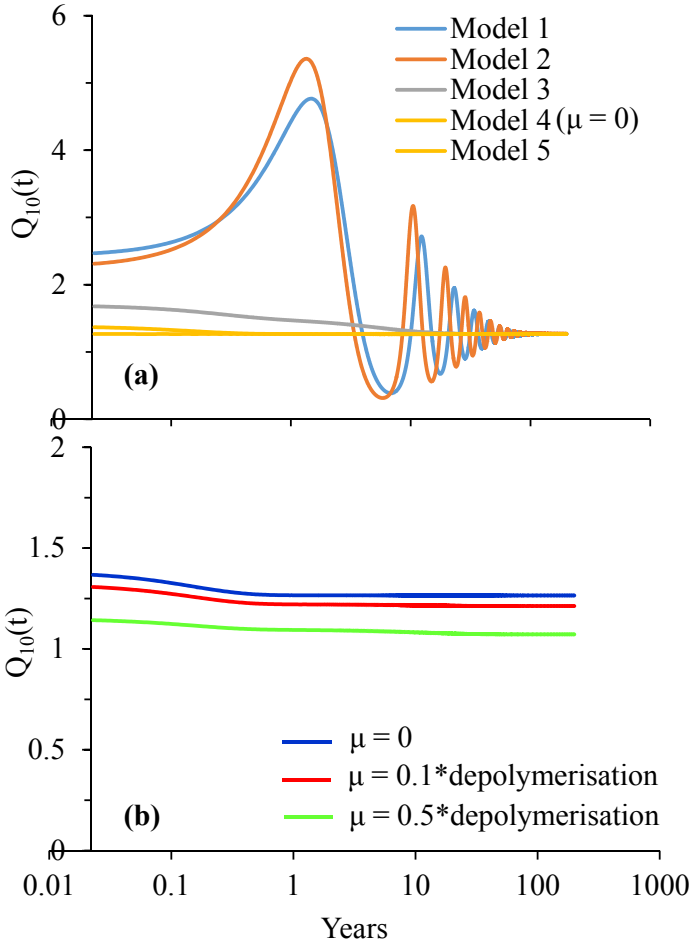

Figure 4. Apparent Q_{10} of respiration over time, $Q_{10}(t)$ **(a)** in our five microbial decomposition models, and **(b)** under different levels of enzyme expenditure cost in model 4.

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