

# Soil microorganisms regulate extracellular enzyme production to maximize their growth rate

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## Key Points:

- Soil microorganisms balance the investment in extracellular enzymes so as to maximize their growth rate
- A mathematical expression for optimal extracellular enzymes production is derived
- Regulation of extracellular enzyme production can strongly affect soil carbon projections

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## Abstract

Soil carbon cycling and ecosystem functioning can strongly depend on how microbial communities regulate their metabolism and adapt to changing environmental conditions to improve their fitness. Investing in extracellular enzymes is an important strategy for the acquisition of resources, but the principle behind the trade-offs between enzyme production and growth is not entirely clear. Here we show that the enzyme production rate per unit biomass may be regulated in order to maximize the biomass specific growth rate. Based on this optimality hypothesis, we derive mathematical expressions for the biomass specific enzyme production rate and the microbial carbon use efficiency, and verify them with experimental observations. As a result of this analysis, we also find that the optimal enzyme production rate decays hyperbolically with the soil organic carbon content. We then show that integrating the optimal extracellular enzyme production into microbial models may change considerably soil carbon projections under global warming, underscoring the need to improve parameterization of microbial processes.

## Plain Language Summary

Understanding how soil microbial communities function and cycle carbon and nutrients is detrimental to accurately project future soil carbon stocks and global warming and to properly manage soils. In order to assimilate carbon and energy, microbial communities produce extracellular enzymes that degrade soil organic matter to then be able to uptake it. However, the enzyme production process requires microbes to invest resources at the expense of their own growth, giving rise to a complex trade-off that has been difficult to predict. Here we leverage a microbial model and recent experimental data on soil microbial communities across the UK to show that soil microbial communities regulate the investment in resource acquisition to maximize their growth rate. This finding provides an underlying principle that describes how soil microbes may regulate physiological trade-offs and results in a mathematical formulation that can be integrated into microbial carbon models to improve predictions of soil carbon cycling.

## 1 Introduction

Soil microbial communities play a major role in the biogeochemical cycles of carbon (C) and nutrients in the biosphere (Falkowski et al., 2008; Paul, 2014; Naylor et al., 2020) and their functioning is essential not only to soil health and fertility (Brady & Weil, 2016), but also to soil carbon sequestration and, in turn, global warming (Singh et al., 2010). Microbially-explicit C models are increasingly being used to account for how microbial processes control soil C decomposition (Allison et al., 2010; J. Schimel, 2001; German et al., 2012; Davidson et al., 2014; Sulman et al., 2018). An important aspect of these models is that through the microbial carbon use efficiency (CUE) —the ratio of C used for growth to C acquired— they account for how microbes are allocating C between anabolism, catabolism, and production of extracellular enzymes (Manzoni et al., 2012; R. L. Sinsabaugh et al., 2013; Geyer et al., 2016; Manzoni et al., 2018). However, how microbes regulate their enzyme production in response to soil environmental conditions is not clear and, as a result, microbial models are formulated assuming that the enzyme production rate is simply proportional to the microbial biomass.

The production of extracellular enzymes is an essential step in the decomposition of soil organic carbon (SOC) (Conant et al., 2011). Soil microorganisms release extracellular enzymes in order to catalyze the depolymerization of complex soil organic matter compounds and produce soluble, low molecular weights compounds that can be readily assimilated (R. Sinsabaugh & Moorhead, 1994). To this end, microbes need to allocate available resources, in the form of carbon and energy, to the synthesis of these enzymes, hence necessarily facing a trade-off (Koch, 1985; Ramin & Allison, 2019; Malik et al., 2019). In fact, while synthesizing extracellular enzymes comes at the expense of

growth and carbon use efficiency, higher extracellular enzyme concentrations result in faster depolymerization and, in turn, potentially higher C assimilation by microbes. Characterizing this trade-off and how it is affected by environmental conditions is crucial to quantify SOC decomposition dynamics, especially in response to perturbations (Sihi et al., 2016; Sulman et al., 2018).

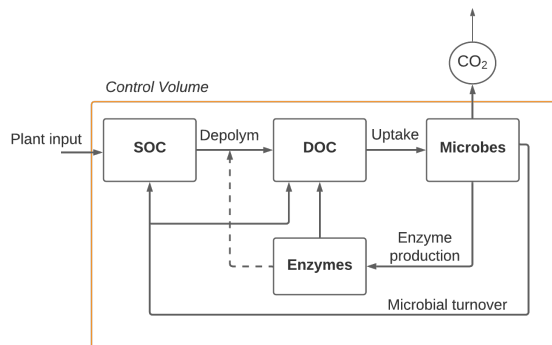
Recent developments in microbial C modeling incorporate extracellular enzyme production and activities (Allison et al., 2010; Allison, 2014; Sihi et al., 2016; Sulman et al., 2018; Abramoff et al., 2018). Contrarily to traditional C models which adopted a constant CUE value or directly estimated C decomposition as a first-order reaction not explicitly controlled by microbial activity (e.g., (Parton et al., 1987; C. Li, 1996; Manzoni et al., 2009)), microbial models with explicit physiology couple C decomposition to microbial and extracellular enzyme activities (R. Sinsabaugh & Moorhead, 1994; J. Schimel, 2001; Allison et al., 2010; Sihi et al., 2016). These new models have the potential to improve the prediction of soil C dynamics by taking into account the microbial response to different biological, physical, chemical conditions across environmental gradients (Wieder et al., 2013, 2015). However, they include more equations, state variables, and parameters that make them difficult to calibrate. In-depth analyses of microbial processes and trade-offs in resource allocation can improve parameterization of such models and contribute to reducing the structural and parameter uncertainty in SOC projections.

Here, we hypothesize that microbial communities regulate the trade-off between growth and production of extra-cellular enzymes in order to maximize the biomass specific growth rate. We provide explicit mathematical expressions for the biomass specific enzyme production rate and for the microbial CUE, and show that the trade-off between growth and enzyme production is controlled by the SOC content. After testing our predictions against experimental observations, we show that including this optimal regulation of enzyme production in microbial models provides a considerably different response to warming, especially in terms SOC content.

## 2 Theory: optimal regulation of extracellular enzymes production

We begin by deriving an expression for the production of extracellular enzymes based on the optimality hypothesis that soil microbes regulate the production of enzymes to maximize the biomass specific growth rate. We will then test our results against experimental observations in Sec. 3.

We leverage the core formulation of microbial carbon models, which reflect our state-of-the-art understanding of microbial processes in soils. Soil microbial processes are generally described considering four carbon pools, as showed in Fig. 1 (Allison et al., 2010; Sihi et al., 2016). The soil organic carbon (SOC), supplied by plant input, is broken down into soluble organic carbon (DOC) via the depolymerization of complex SOC molecules, catalyzed by extracellular enzymes (the enzyme pool,  $E$ ) pro-



**Figure 1.** Schematic representation of carbon pools and their interactions in microbial carbon models.

duced by soil microbes ( $B$ ) (J. P. Schimel & Weintraub, 2003; Allison et al., 2010). The microbial biomass uptakes DOC, partly converting it to  $\text{CO}_2$  to obtain energy (i.e., catabolism) and using the rest for synthesizing new biomass and producing extracellular enzymes (Figure 2A). The soil microbial community is thus treated as a single species with average physiological parameters that are meant to represent the large variability of the soil environment.

These microbial processes lead to the following expression for the biomass growth rate (Manzoni et al., 2012; Hagerty et al., 2018),

$$G = U - P_E - R_U - R_B - R_E, \quad (1)$$

where  $U$  is the DOC uptake rate,  $P_E$  is the production rate of extracellular enzymes, and  $R$ s are the carbon losses via respiration. These include respiration linked to C uptake ( $R_U$ ), to the production of enzymes ( $R_E$ ), and maintenance respiration  $R_B$ . The formulation of  $G$  in Eq. 1 is particularly suitable to variational approaches, as it explicitly distinguishes the terms contributing positively to growth ( $U$ ) from those contributing negatively ( $R$ s and  $P_E$ ). Eq. 1 in fact contains the trade-off between growth and production of extracellular enzymes, as it accounts for the C costs of producing enzymes ( $P_E$  and  $R_E$ ), which necessarily reduce growth by reducing the microbial CUE (Koch, 1985; Ramin & Allison, 2019) (Figure 2).

The uptake rate  $U$  is expressed as a function of the dissolved organic carbon (DOC) and microbial biomass ( $B$ ), according to the Michaelis-Menten expression

$$U = U_{max} B \frac{\text{DOC}}{\text{DOC} + K_U}, \quad (2)$$

where  $U_{max}$  is the biomass specific uptake rate under non-limiting DOC concentrations and  $K_U$  is the half-saturation constant. We assume that the concentration of DOC is proportional to product of SOC and enzyme concentration  $E$ . Under quasi-steady state conditions for the enzyme pool, the enzyme concentration  $E = P_E/\delta_E$ , so that  $\text{DOC} = \beta \text{SOC} \cdot P_E/\delta_E$  ( $\beta$  being a proportionality coefficient) and the uptake rate

$$U = U_{max} B \frac{\text{SOC} \cdot P_E}{\text{SOC} \cdot P_E + K'_U}, \quad (3)$$

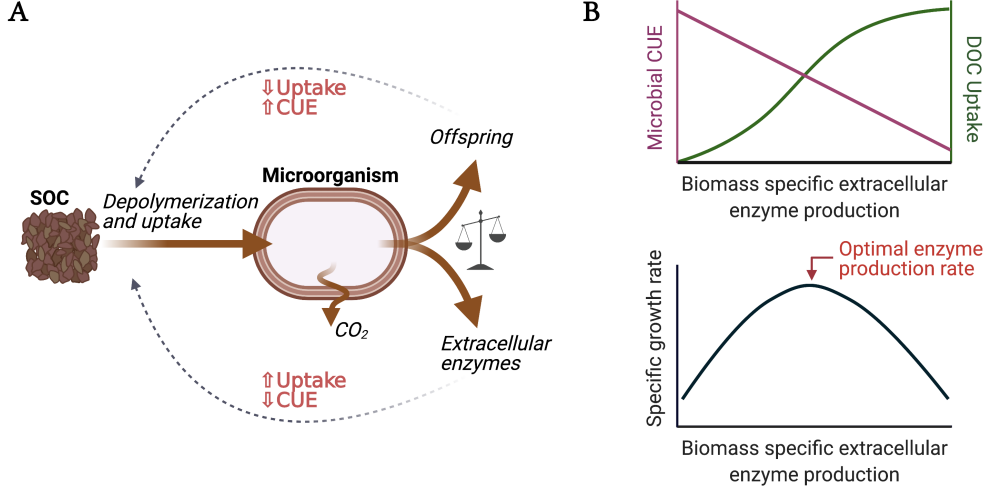
where  $K'_U = \delta_E \cdot K_U/\beta$ ,  $P_E$  is the enzymes production rate, and  $\delta_E$  is the enzymes turnover rate. Expressing, as in microbial models, the respiration fluxes as  $R_U = r_U \cdot U$ ,  $R_B = r_B \cdot B$ ,  $R_E = r_E \cdot P_E$  (where  $r$ s are respiration coefficients) and the production of enzymes as  $P_E = k_E \cdot B$ , ( $k_E$  is the biomass specific enzyme production rate) the biomass specific growth rate ( $\mu = G/B$ ) can be written as

$$\mu = U_{max} \frac{\text{SOC} \cdot k_E \cdot B}{\text{SOC} \cdot k_E \cdot B + K'_U} (1 - r_U) - r_B - k_E (1 + r_E). \quad (4)$$

Based on the observation that  $B = \alpha \text{SOC}$ , where  $\alpha$  is a constant (see Fig. 2D in (Malik et al., 2018)), Eq. 4 can be re-expressed as

$$\mu = U_{max} \frac{k_E}{k_E + K_U^*} (1 - r_U) - r_B - k_E (1 + r_E), \quad (5)$$

where  $k_U^* = K'_U/(\alpha \text{SOC}^2)$ . Eq. 5 expresses the growth rate as a function of only SOC (which is inside  $k_U^*$ ) and the biomass specific rate of extracellular enzyme production,  $k_E$ . Note also that  $k_E$  appears both in the uptake rate, a term which positively affect  $\mu$ , and in last term ( $k_E(1+r_E)$ ), which negatively affects  $\mu$ . In fact, under given resource availability, higher  $k_e$  result in faster depolymerization of SOC and in turn higher C uptake, but carries higher C costs, hence reducing the CUE (see Figure 2A). On the contrary, for lower  $k_e$  microorganisms can invest more in growth and increase their CUE,



**Figure 2.** **A** Schematic representation of C flow through a microorganism facing a trade-off in C allocation between growth and production of extracellular enzymes. **B** Conceptual plot showing the effect of enzyme production rate on microbial CUE, DOC uptake rate, and specific growth rate. For given resource availability, higher enzyme production rates promote depolymerization and uptake, but the C costs increase, causing the microbial CUE to decrease. As a result the growth rate ( $\mu = \text{CUE} \cdot U/B$ ) has a maximum at an intermediate (“optimal”) enzyme production rate.

but this results in lower resource acquisition (uptake). In this trade-off, there is an ideal balance between CUE and production of enzymes that maximizes  $\mu$  (Figure 2B).

To obtain the expression for the value of  $k_E$  that satisfies our optimality hypothesis, we compute the derivative of Eq. 5 with respect to  $k_E$ ,

$$\frac{d\mu}{dk_E} = \frac{U^* \cdot k_U^*}{(k_U^* + k_E)^2} - (1 + k_E), \quad (6)$$

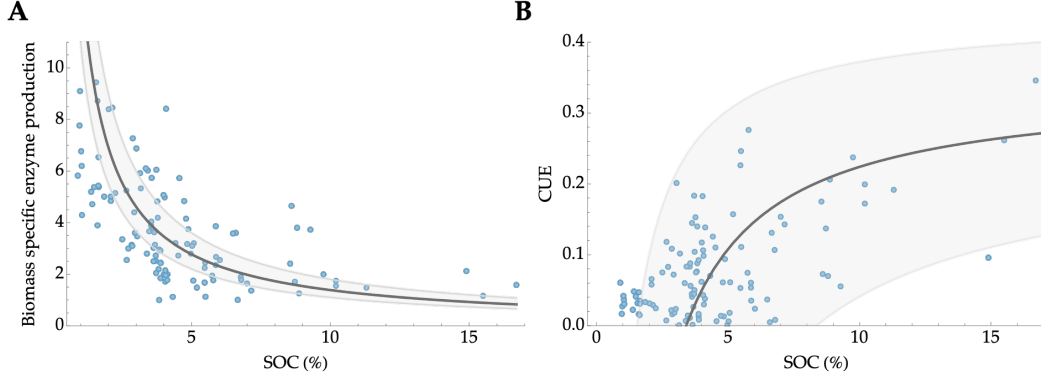
where  $U^* = U_{max}(1 - r_U)$  was introduced for conciseness. Setting  $d\mu/dk_E = 0$  and solving for  $k_E$  then yields the “optimal” value of  $k_E$  that maximises  $\mu$ ,

$$k_E^{opt} = \sqrt{\frac{U^* k_U^*}{1 + r_E}} - k_U^* \approx \sqrt{\frac{U^* k_U^*}{1 + r_E}}, \quad (7)$$

where the last equality derives from the fact that  $k_U^*$  is very small ( $k_U^* \ll 1$ ) and it is negligible compared to the first term where it is inside the square root. Lastly, we can group all the constants—which encode key information on microbial physiology—to obtain a relation between the optimal biomass specific production of enzymes and SOC,

$$k_E^{opt} = \gamma \cdot \frac{1}{\text{SOC}}, \quad (8)$$

where  $\gamma = \sqrt{U^* K'_U / (\alpha + \alpha r_E)}$ . According to Eq. 8, which is a mathematical formulation of the optimality hypothesis,  $k_E^{opt}$  is not a constant, but a function of the SOC content, an important indicator of resources availability. Soil microorganisms thus adjust their biomass specific enzyme production rate  $k_E^{opt}$  to maximize the growth rate  $\mu$  by “sensing” the availability of resources (i.e., “SOC”) in their environment. From this optimality hypothesis, we can also predict how the microbial CUE and the growth rate change



**Figure 3.** **A** Relationship between biomass specific enzyme production and SOC. The continuous line is computed from Eq. 8, fitted by means of a Major Axis Regression ( $p < 0.001$ ). **B** Relationship between microbial CUE and SOC. The continuous line is computed from Eq. 9, also fitted by means of a Major Axis Regression ( $p < 0.01$ ). Gray shaded areas indicate the confidence bands. The experimental observations of biomass specific enzyme production rate, SOC, and CUE are from Malik et al. (2019).

with respect to SOC. Substituting Eq. 8 in Eq. 5 and dividing by  $U/B$  yields a relationship of the form

$$\text{CUE} = \text{CUE}_0 - \frac{b}{\text{SOC}}, \quad (9)$$

where  $\text{CUE}_0 = 1 - r_u - r_B/(U_{\max}\eta)$ ,  $b = (\gamma\sqrt{U^*(1+r_E)})/(U_{\max}\eta)$ , and  $\eta = \gamma/(\gamma + k'_U/\alpha)$ . Combining Eqs. 8 and 9 then yields the relationship between CUE and  $k_E^{\text{opt}}$ ,

$$\text{CUE} = \text{CUE}_0 - \frac{b}{\gamma} k_E^{\text{opt}}, \quad (10)$$

Finally, from Eq. 8 and the fact that  $\text{CUE} = B\mu/U$ , the specific growth rate  $\mu = U_{\max}\eta\text{CUE}$ .

### 3 Experimental verification

To test if soil microorganisms regulate their investment in extracellular enzymes so as to maximize their specific growth rate, we checked whether the observations of  $k_E$  and CUE vary with SOC as predicted by Eqs. 8 and 9, respectively. To this regard, we retrieved experimental data from Malik et al. (2019), which measured biomass specific enzyme production and carbon use efficiency in circumneutral pH soils from 38 sites across the United Kingdom. Sites have variable land uses, including pristine and intensive grasslands and arable soils. Soils also had different SOC content, allowing us to specifically test our expressions. We refer to Malik et al. (2018) and Malik et al. (2019) for more details on soil sampling and analyses. The measurements do not provide directly  $k_E$ , but a proxy for it. Therefore, here we focused on how  $k_E$  decays with the SOC content and not on the specific values of  $\gamma$  or the coefficient relating  $k_E$  to its proxy. We then simply fitted the value of  $\gamma$  through a standard least squares method and tested whether Eqs. 8, 9, and 10 match the observations. By doing so, we also avoided introducing uncertainty in the choice of physiological parameter values.

Figure 3A readily shows that Eq. 7 matches the observations throughout the entire range of measured SOC, lending support to our hypothesis that microorganisms optimize their biomass specific production of enzymes to maximize the specific growth rate,  $\mu$ , for given SOC content. Our theory thus provides a principle according to which soil

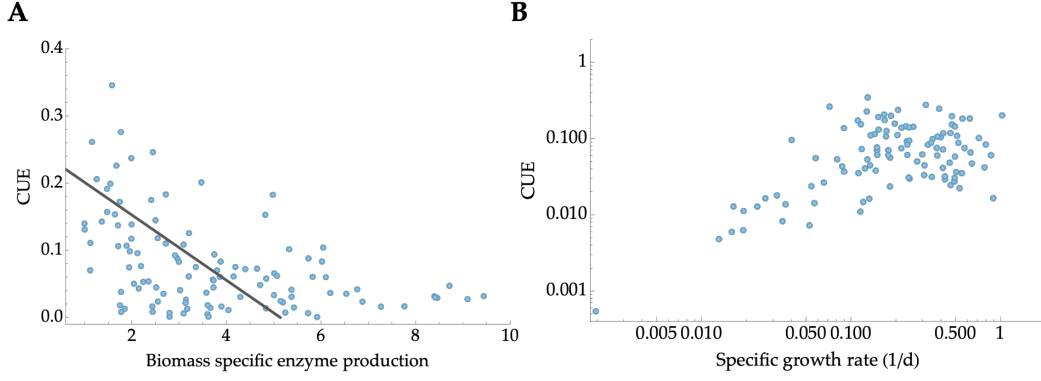
microorganisms regulate the extracellular enzymes-growth trade-off. At low SOC contents microorganisms find it convenient (or are forced) to invest highly in enzymes so as to accelerate the depolymerization of the available SOC content, even if this is low, and obtain enough DOC to uptake. On the contrary, at high SOC contents depolymerization can proceed at high rates even with lower enzyme concentrations. Accordingly, rather than producing excess enzymes with limited benefits, microbes can “afford it” to invest more heavily in the biosynthesis of new biomass. The scatter around the predicted curve is expected, as these measurements include soils with different land use and land cover, soil pH, and microbial diversity (Malik et al., 2018), in addition of course to possible measurement error and uncertainty.

Figure 3B shows that our predictions also match the relationship between CUE and SOC, independently supporting our optimality hypothesis. Eq. 9 provides a mathematical formulation for microbial regulation of the community CUE under optimal regulation of C allocation between growth and production of extracellular enzymes. As we have seen above, at low SOC soil microorganisms need to produce more enzymes to obtain sufficient labile substrate, and as a result the CUE (fraction of C allocated to biosynthesis of new biomass) declines. As the SOC increases, microbes invest less in enzyme production and more into growth, hence increasing their CUE up to their physiological maximum,  $CUE_0$ . This trade-off becomes clearly evident in the negative relationship between CUE and  $k_E^{opt}$  expressed by Eq. 10 (Figure 4A).

## 4 Discussion and implication

Soil microorganisms are biological machines able to evolve and adapt to local environmental conditions to improve their fitness (von Stockar, 2013; Falkowski et al., 2008; Roach et al., 2018; Noda-Garcia et al., 2018; Naylor et al., 2020). To provide a more physical foundation to the concepts of evolution and adaptation, there have been a number of studies trying to identify quantitative measures of fitness for microbial communities, such as the growth rate (Westerhoff et al., 1983; Manzoni et al., 2017), the growth yield (Bachmann et al., 2013), or the energy efficiency (Maitra & Dill, 2015), from which a variety of optimality principles were formulated. According to which one of these principles microorganisms evolve remains an open question, whose answer may depend on the environmental conditions (Lipson, 2015) and the timescale of observation (Roach et al., 2018), but also on the specific independent variables that are being explored, those that are being kept fixed, and what is included as mathematical constraints (Martyushev & Seleznev, 2006). Here we hypothesized that soil microorganisms regulate the production of extracellular enzymes in order to maximize the biomass specific growth rate, while all other physiological parameters (e.g., maximum uptake rate  $U_{max}$ , biomass specific maintenance rate  $r_B$ ) are considered constant, or better that they do not vary with  $k_E$ . The hypothesis is supported for circumneutral pH soils by experimental observations.

To better understand this optimal regulation of enzyme production from a physical point of view, we can further analyze Eq. 7, focusing in particular on  $k_U^*$  ( $= (K_U \cdot \delta_E)/(\alpha \text{ SOC}^2)$ ). As a half-saturation constant for the functional response of microbial uptake to  $k_E$  (see Eq. 5),  $k_U^*$  measures how effective an increase in  $k_E$  would be in increasing microbial C uptake. A high value of  $k_U^*$  indicates that external conditions are not favorable to the action of enzymes and the formation of DOC (i.e., lower SOC) and that there is a relatively low number microorganisms available to produce enzymes. In turn, when  $k_U^*$  is high a microorganism needs to invest more in enzymes to catalyze the formation DOC and uptake it. By contrast, a low value of  $k_U^*$  is indicative of favorable environmental conditions and higher microbial biomass, such that a microorganism can reallocate more resources to growth. Interestingly, inside the square root,  $k_U^*$  is then multiplied by the C gains (in terms of growth,  $U^* = U_{max}(1 - r_U)$ ) and divided by the C costs ( $1 + r_E$ ) of producing more enzymes. This emphasizes the fact that microorgan-



**Figure 4.** **A** Trade-off relationship between CUE and biomass specific enzyme production. The continuous line is computed from Eq. 8. **B** Derived relationship between microbial CUE and specific growth rate, reflecting a resource acquisition strategy (Lipson, 2015). The experimental observations of biomass specific enzyme production rate and CUE are from (Malik et al., 2019).

isms both evaluate whether producing more enzymes is actually necessary to increase uptake (through  $k_U^*$ ) and weigh C benefits and costs (through the ratio  $U^*/(1+r_E)$ ).

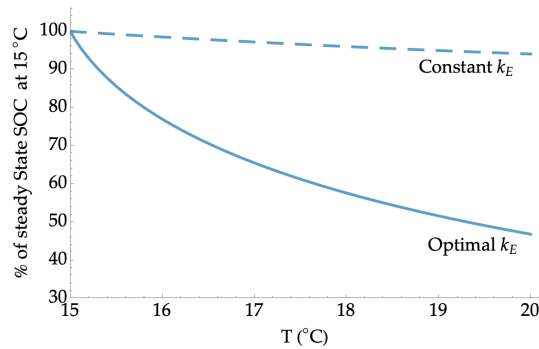
Resource allocation strategies have the potential to greatly impact SOC sequestration and ecosystem functioning, for instance by affecting the relation between growth rate and yield (here CUE) (Lipson, 2015; Ferenci, 2016). Interestingly, our optimality hypothesis (investment in extracellular enzymes to maximize the growth) leads to a positive relationship between the CUE and the specific growth rate (i.e.,  $\mu = U_{max}\eta\text{CUE}$ ), in agreement with what hypothesised by Lipson (2015) for a resource acquisition strategy. This is also in line with what was observed in these soils through metaproteomics (Malik et al., 2018), which indicated higher investment in growth and in resource acquisition in higher SOC and lower SOC soils, respectively. The observations follow the predicted trend (Figure 4B), at least up to a growth rate of  $\approx 0.3 \text{ (d}^{-1}\text{)}$ , after which the CUE tends to decrease. However, the regulation of enzyme production is only one of the multiple factors determining the CUE vs. growth rate relationship. Across the sampled soils, there might be multiple strategies occurring simultaneously and, while resource acquisition may be more important at lower growth rates and CUE (i.e., the increasing branch of the curve in Fig. 4B), fast and energy-wasting growth might affect the CUE at higher growth rates (i.e., the decreasing branch of the curve). Nevertheless, observations span a variety of soils with their own specific properties (e.g., microbial diversity, carbon sources, etc.) and each measurement averages out multiple microbial species and their different strategies within a given soil sample. These factors make it difficult to fully interpret the relationship between CUE and growth rate shown in Figure 4B.

Due to the nonlinear, intertwined interactions between microbial processes and SOC dynamics, the effects of microbial regulation of extracellular enzymes production can also propagate in scale and impact the long-term SOC dynamics (Wieder et al., 2015). Indeed, microbial carbon models have been developed to account for the importance of microbial extracellular enzyme production and depolymerization of SOC, a possible rate-limiting step in SOC decomposition (Bengtson & Bengtsson, 2007; Conant et al., 2011), and improve SOC projections in response to global warming (Allison et al., 2010; Wieder et al., 2015). Here we explored whether improving the representation of enzyme production using our optimality hypothesis gives rise to a different response to warming. To this end, we considered the temperature dependence of the depolymerization and uptake rates, the maintenance respiration, and the half-saturation constants, and analyzed

the steady state SOC content as a function of a temperature increase. The results readily show that the SOC depletion upon warming is substantially more pronounced when using  $k_E^{opt}$  than with a constant  $k_E$  (see Figure 5), suggesting that the representation of enzyme production can considerably alter SOC projections. The optimality hypothesis in fact introduces a positive feedback on SOC depletion. As the SOC content decreases, microbial communities produce more extracellular enzymes and accelerate the depolymerization, further enhancing SOC depletion.

While these results highlight the importance of integrating microbial regulation of extracellular enzyme production in microbial models, Figure 5 should still be interpreted with caution since additional processes affect SOC projections. First, the interaction between biomass (e.g., necromass) and mineral surfaces may contribute to SOC stabilization and regulate its depletion under higher temperatures. This may be particularly important in situations (e.g., regeneration of degraded soils) in which microbial communities can switch strategy and start investing more in growth (higher CUE), which will eventually lead to more production of microbial necromass that can be stabilized on mineral surfaces. Second, while temperature does not affect how  $k_E^{opt}$  decays with SOC, it may affect the coefficient  $\gamma$ , which here was calibrated so as to obtain the same steady state SOC as “traditional” microbial models with constant  $k_E$  at 15 °C. This assumption may thus have affected the depletion in SOC content at higher temperatures. There are other possible mechanisms –often not taken into account– that can alter the response to warming, such as the fact that there might be a limited number of SOC-enzymes reaction sites or that microbial communities may feed on free enzymes (Sihi et al., 2016). Microbial communities may also adapt to changes in temperature and regulate their CUE (Allison, 2014), a strategy that may have an impact on resource acquisition investments such as on extracellular enzymes production. Experiments on the effects of soil warming on microbial traits (CUE,  $k_E$ ,  $\mu$ ) (J. Li et al., 2019; Nottingham et al., 2020) and microbes-mineral interactions (Kleber et al., 2021) may provide additional clues to understand the impact of warming on microbial processes more holistically.

Lastly, integrating resource allocation strategies in microbial carbon models (such as Eqs. 8 and 9) may improve their prediction of SOC dynamics, not only in response to warming but also when soils experience temporal variability in resources, such as agricultural ecosystems (Wei et al., 2014; Smith et al., 2016; Sanderman et al., 2017). In these systems the continuous regulation of extracellular enzyme production as resource availability vary might not be captured by a constant  $k_E$  value, likely introducing uncertainty. Improving the parameterization of microbial processes in these cases might help better understand the effect of regeneration practices as well as design suitable agricultural practices for preserving soil health (Kallenbach et al., 2019).



**Figure 5.** Depletion in steady state soil SOC pool as a function of temperature, highlighting the important role that enzyme production regulation plays in SOC projections. We used default parameters provided by (Hagerty et al., 2018),  $Q_{10}$  values from (Sihi et al., 2016), and temperature dependence of half-saturation constants from (Allison et al., 2010).

## 5 Conclusions

There are still large uncertainties in the representation of microbial processes in microbial models, causing them to diverge in their C projections under warming (e.g., (Sihi et al., 2016; Sulman et al., 2018)). Here we focused on the production of extracellular enzymes for the depolymerization of SOC and showed, by interpreting experimental observations, that soil microbes regulate enzyme production so as to maximize their specific growth rate for given SOC content. While microbes invest largely in resource acquisition (i.e., extracellular enzymes) at low SOC contents, they adjust their resource allocation to invest more on biosynthesis of new biomass at higher SOC contents, leading to higher microbial CUE. Our analysis also provided a mathematical expressions for including the regulation of extracellular enzyme production into microbial models and showed that this optimal regulation may result in considerably different SOC projections under warming from those of models assuming a constant biomass specific production rate. Future investigations will explore how to improve parameterization of extracellular enzyme production in state-of-the-art soil microbial and ecosystem models, especially considering mineral-microbes interactions.

## Data Availability Statement

The original data used in this paper can be found in Malik et al. (2018) and Malik et al. (2019). Processed data and the Mathematica code used to draw the Figures is available at 10.4211/hs.7ada4439903f4156be3143e36a9693c7 under a Creative Common Attribution CC-BY.

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