**Title**: Global soil carbon loss is predicted to amplify with microbial eco-evolutionary responses to warming

**Authors**: Elsa Abs1,2\*, Scott R. Saleska2, Regis Ferriere1,2,3

**Affiliations**

1 Institut de Biologie (IBENS), Ecole Normale Supérieure, Paris Sciences & Lettres University, CNRS, INSERM, 75005 Paris, France

2 Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

3 International Center for Interdisciplinary Global Environmental Studies (iGLOBES), CNRS, Ecole Normale Supérieure, Paris Sciences & Lettres University, University of Arizona, Tucson, AZ 85721, USA

**\*Corresponding author**: eabs@uci.edu. 321 Steinhaus Hall, CA 92617

# Abstract (150 - max 150 words)

Soil microbes differentially respond to warming climates through variation in functional traits that directly impact global soil carbon emissions from decomposition of soil organic matter. Microbial traits are inherently linked to evolutionary history; yet soil carbon models largely ignore eco-evolutionary dynamics and their implications for responses to warming climates. Here, we applied eco-evolutionary theory to a microbe-enzyme model by incorporating microbial trait optimization with respect to decomposition to calculate future soil carbon projections. Our model predicted that microbes under warming allocated more resources to enzyme production, which led to faster decomposition and soil carbon loss. Specifically, carbon losses were expected to be the most impacted in cold regions. Accordingly, we found significantly greater soil carbon loss by 2100 than predicted under current models. Our model indicated that soil carbon pools will not self-regulate at the ecosystem level, clearly demonstrating the need to incorporate microbial eco-evolution dynamics in global carbon models.

**MAIN TEXT (4,670 - max 15,000 words)**

# Introduction

Soils represent the most understudied component of Earth System Models (ESMs), limiting our ability to accurately predict future soil CO2 emissions. Increasingly, biogeochemical models have integrated explicit parameters to account for microbial community compositional differences that demonstrate soil carbon stocks are sensitive to microbial responses [(William R. Wieder, Bonan, and Allison 2013)](https://paperpile.com/c/jw7igf/Ki3Uu). For example, slight variation in microbial carbon use efficiency (i.e., smaller than 10%) results in drastic shifts in total global soil carbon stocks, from +10 Pg to -300 Pg, under the current 2100 projections. While such changes in microbial traits can occur over long timescales, microbial communities and their underlying function can respond to new climates on annual scales [(Glassman et al. 2018)](https://paperpile.com/c/jw7igf/ibg8A). Therefore, accounting for compositional responses of microbial communities, and considering the underlying traits mediating such responses, will improve our understanding of biogeochemical cycling of soil carbon stocks.

The microbial trait we focused on is extracellular enzyme production. Microbes produce and export enzymes to acquire nutrients by breaking down soil organic matter. Recent microbial field experiments have shown that microbial investment in resource acquisition responds to environmental change at the community level [(Malik et al. 2020)](https://paperpile.com/c/jw7igf/SI9XC). Therefore enzyme production is a key trait for biogeochemical cycling. Furthermore, the more resources microbes allocate to enzyme production, the less they invest in growth [(Sinsabaugh, Antibus, and Linkins 1991)](https://paperpile.com/c/jw7igf/PsBX3). Hence, microbial resource allocation to enzymes is a key trade-off trait, which offers to the modeler an ideal natural evolutionary constraint.

Typically, ecosystem models that incorporate explicit microbial dynamics mask community trait responses and only represent enzyme biochemical responses to abiotic factors (soil temperature, moisture). The few models that integrate microbial trait variation within communities use numerical exploration constrained by stability of the model [(Steven D. Allison, Wallenstein, and Bradford 2010)](https://paperpile.com/c/jw7igf/bsCkn) or data from too short-term (a few days long) lab experiments [(Hagerty et al. 2014; German et al. 2012)](https://paperpile.com/c/jw7igf/lgLC%2B9pW2o). However, the limited availability of lab and field experiments under a range of environmental conditions and timescales hinders our ability to satisfactorily model functional responses.

Multiple co-occurring processes lead to microbial trait variation. They are classically divided into ecological (taxa sorting, dispersal) and evolutionary processes (mutation, horizontal gene transfer, change in allele frequencies) [(Nemergut et al. 2013)](https://paperpile.com/c/jw7igf/i9Xwa). It is yet unknown whether these different processes distinctly affect trait variation, if they peak at different times and in different conditions, and how much of the trait variation is stochastic. Here, as a first step, we looked for the trait variation that would be driven by selection, and we clumped all processes mentioned above under the umbrella “eco-evolutionary processes”. Adaptive dynamics offer a mathematical framework with explicit feedbacks between the ecological and the evolutionary processes. We applied this framework into a consumer-resource type ecological model of microbial soil organic carbon (SOC) decomposition [(Steven D. Allison, Wallenstein, and Bradford 2010)](https://paperpile.com/c/jw7igf/bsCkn).

We hypothesized that the warming-induced faster degradation and uptake enzyme kinetics will benefit enzyme producers and therefore select for higher enzyme production, which should amplify decomposition rate and soil carbon loss. In short, we hypothesized that the inclusion of microbial eco-evolutionary response of enzyme allocation to warming will result in greater loss in total soil carbon stocks.

We compared predictions of soil carbon stocks, over approximately 8,000 1° grid points across continental scales, between two models: one that ignores microbial enzyme allocation optimization and one that incorporates it. The physical driver we focused on is temperature, because it is unequivocally associated with global change [(Intergovernmental Panel on Climate Change. Working Group 1 2007)](https://paperpile.com/c/jw7igf/p32e4) and because the response of enzyme kinetics to temperature is based on fundamental biochemical laws [(van ’t Hoff 1884)](https://paperpile.com/c/jw7igf/u3R67). We used the soil surface temperature projections from a single simulation of the Community Earth System Model (CESM), CCSM4, for the Representative Concentration Pathway 8.5 (RCP8.5).

To compare soil carbon predictions of the two models (with and without optimization), we initialized both models with enzyme allocation optimized to the local 2010 temperature (Fig. S1), meaning we assumed that we were at an equilibrium in 2010 and we ignored the last century of warming. Our 2010 soil carbon stock predictions were concordant with prior observations of current soil carbon stocks (Harmonized World Soils Database; [(Fao/Iiasa/Isric/Isscas/Jrc 2012)](https://paperpile.com/c/jw7igf/DEUBc) (Fig. S2). We described both models, parameter values, and robustness analysis of our results in Material and Methods and the Supplementary Materials. We reported here the most robust overall results.

# RESULTS

## Eco-evolutionary optimization amplifies warming-induced global soil carbon loss

When incorporating microbial eco-evolutionary dynamics, we observed a nearly two-fold decrease in global soil C by 2100 in response to warming conditions (Fig. 1). Notably, we observed the largest accentuation of C loss between models in the years of 2040-2060. This corresponds to the strongest episode of predicted warming and provides a direct connection between microbial eco-evolutionary dynamics and the sensitivity of soil carbon pools to temperature. For sensitivity analysis we varied the parameter that captures the local advantage given to enzyme producers (*c0*) because it is the only new parameter other (than enzyme allocation) that we added to Allison et al. 2010’s model (see Methods). For the rest of the analysis, we chose the value of *c0* that maximized change in global soil carbon (*c0* = 1.17). With this value, global soil carbon loss by 2100 reaches 265 Pg with microbial eco-evolutionary optimization compared to 145 Pg without. As a comparison, ESMs predicted a global soil carbon loss to be between 104 and 629 Pg [(Todd-Brown et al. 2014)](https://paperpile.com/c/jw7igf/RIv6Q). We conducted a sensitivity analysis instead of determining an uncertainty area because this study aims to show the consequences of a theory rather than to give quantitative predictions. Assessment of the uncertainty coming from data, structure, forcing, and parameters could be the focus of a future study.



**FIGURE 1. Global projections of soil C stock from 2010 to 2100.** (Left y axis) Temporal change in global total soil carbon without (dashed) and with (plain) microbial eco-evolutionary optimization. (Right y axis, orange) Temporal change in global average surface soil temperature between 2010 and 2100 from the RCP8.5 scenario with the CCSM4 model. Global soil C stock is calculated every decade between 2010 and 2100, as the sum of local soil C stock across all sites. Parameter values are defined in Table S1.

To explain these results, we analytically solved the eco-evolutionary model. We found that the eco-evolutionary equilibrium (optimum) for microbial enzyme allocation is an increasing function of microbial growth efficiency, maximum uptake rate, and intensity of competition between different strains, and a decreasing function of mortality (see equation (12) in Methods). As stated earlier, we removed temperature dependencies coming from numerical exploration and short-term experiments; only the biochemical dependency of enzyme kinetics on temperature was retained (equations 5-8 in Methods). As a consequence, the optimal enzyme allocation we found responds to temperature only through a dependency of maximum uptake rate on temperature. Maximum uptake rate is an increasing function of temperature and optimal enzyme allocation an increasing function of maximal uptake rate, therefore optimal enzyme allocation is an increasing function of temperature.

Finally, we looked at the sensitivity of the steady states of soil carbon decomposition rate and stock with respect to enzyme allocation and temperature. We found that soil carbon decomposition rate is an increasing function, and soil carbon stock a decreasing function, of both enzyme allocation and temperature (Fig. S3). As a consequence, soil carbon sensitivity to temperature at fixed enzyme allocation explains that warming results in soil carbon loss without microbial optimization. And soil carbon response with microbial optimization is the result of the direct effect of temperature on soil carbon and of the indirect effect of temperature on soil carbon through its effect on enzyme allocation. We found earlier that warming selects for higher enzyme allocation, which results in faster decomposition and the higher soil carbon loss observed in Figure 1.

**Effect of microbial eco-evolutionary optimization is stronger in cold regions**

While incorporating eco-evolutionary dynamics into the model drastically decreased the predicted total carbon pool, the magnitude of this predicted decrease varied between geographical regions (Figure 2). The optimization of microbial enzyme allocation has little to no effect in low to intermediate latitudes (central and Northern South America, Africa, SE Asia, Australia), doubles the losses of soil carbon in intermediate to high latitudes like in the continental US, and triples soil carbon losses in the highest latitudes (Scandinavia, NE Canada, South Chile).



**FIGURE 2. Global distribution of the effect of microbial optimization predicted by the eco-evolutionary model.** This map shows the difference between model runs with optimization minus runs without optimization.The effect of optimization is the difference between the model runs (with and without optimization) in their predictions of change in soil carbon between 2010 and 2100. Colors indicate intensity of the effect of optimization: (gray) no effect of optimization, (red) optimization amplifies soil carbon loss, (blue) optimization reduces soil carbon loss. Optimization of microbial enzyme allocation amplifies soil carbon loss everywhere. Its effect is spatially heterogeneous and is stronger in high latitudes.

The first reason for the spatially heterogeneous effect of optimization is the non-linear sensitivity of soil carbon to enzyme allocation coupled with the spatial heterogeneity in initial (2010) enzyme allocation. Soil carbon steady state is a decreasing concave-up function of enzyme allocation, meaning that soil carbon will decrease more with the same increase in enzyme allocation when enzyme allocation is low. And because optimal enzyme allocation is an increasing function of temperature, optimal enzyme allocation in 2010 is lower in high latitudes where temperature is low (Figure 3a). Microbial optimal enzyme allocation is close to 0% of assimilated C in high latitudes and up to 15% in low latitudes.

The second reason for the spatially heterogeneous effect of optimization is the spatially heterogeneous change in optimal enzyme allocation between 2010 and 2100. This itself is the result of two factors. One, RCP8.5 projections predict a latitudinal gradient for warming intensity, with more intense warming predicted in high latitudes (Fig. S4). Second, optimal enzyme allocation is also a nonlinear function of temperature. The analytical expression for microbial optimal allocation obtained from mathematically solving the system of equations (equation (12) in Methods), showed that since maximum uptake rate is an exponential, and therefore, concave-up function of temperature, optimal enzyme allocation is a concave-down function of temperature. This means that optimal enzyme allocation will increase more under the same warming intensity when initial temperature is low (fig. S5). As a result of both higher warming intensity and higher temperature sensitivity of enzyme allocation in cold regions, the increase in enzyme allocation by 2100 ranges between 0 and 3% between low and high latitudes respectively (Figure 3b). To be more specific, in the model without optimization, faster warming in high latitudes is already responsible for stronger soil carbon loss in high latitudes (Fig. S6). In the model with optimization, the change in enzyme allocation further exacerbates the decrease in soil C driven by faster warming.



**FIGURE 3. Global distribution of the optimal enzyme allocation: (a) in 2010, (b) change between 2010 and 2100.** Optimal allocation to enzymes corresponds to an optimum of microbial fitness calculated by our eco-evolutionary model with explicit resource allocation trade-off. (a) An allocation to enzymes equal to 0.1(orange) means that on average in the community, microbes allocated 10% of the carbon they assimilate to producing enzymes and 90% to growth (minus respiration costs). (b) A change in allocation to enzymes of +0.01 in a location where 2010 enzyme allocation is 0.1 means that 2100 allocation to enzymes is 0.11.

## Effect of microbial trait optimization is robust to parameters and climate scenarios

Finally we showed that the aggravation effect of optimization is generally robust to other assumptions about microbial responses. When we added other estimates of how microbial carbon use efficiency (CUE) or mortality respond to temperature [(Hagerty et al. 2014; Steven D. Allison, Wallenstein, and Bradford 2010)](https://paperpile.com/c/jw7igf/lgLC%2BbsCkn), optimization of enzyme allocation still increased soil carbon losses (Fig. S7). The exception is when mortality is very sensitive to temperature, in which case enzyme allocation decreases with warming, because optimized fitness compensates rapid death with direct investment in growth (equation (12)). Further, we also considered spatial and temporal variability in litter input (projections taken from the same model and scenario as for surface soil temperature). Without enzyme allocation optimization, total soil carbon was predicted to slightly increase by 2100 because the generally higher litter inputs due to elevated CO2 concentrations offset the effect of warming. However with eco-evolutionary optimization, these gains are divided by a factor close to 2 (Fig. S8). Finally, integrating spatial variability in enzyme kinetics based on German et al. (2012)’s measurements increases the effect of optimization (Fig. S9), while integrating both variability in litter and enzyme kinetics, reduces the effect of optimization (Fig. S10). See the Methods for more detail about microbial temperature sensitivity, litter and enzyme data.

# DISCUSSION

Given that microbial communities are expected to respond to new climate conditions through a variety of ecological and evolutionary processes, we investigated the implications of these processes for soil carbon stocks. Using an existing microbial model of decomposition, we found that optimal allocation to enzymes increases with increasing temperature through the microbial maximum uptake rate. This microbial optimization strategy amplifies the effect of the initial biochemical response, which allows for soil carbon turnover to increase with warming. We found that optimizing microbial resource allocation results in 1.8x greater soil carbon losses at the global scale. We also pointed out that the effect of optimization is not homogenous, but rather is expected to be the strongest in colder regions.

To understand why warming increases allocation to enzymes, it is important to note that at the individual scale, microbial life history strategies must balance trade-offs between investment in growth and investment in enzymes. Enzymes that function outside of the cell are a public good, which in an evolutionary model introduces the presence of cheaters (i.e. microbes that produce less or no enzymes but take up carbon monomers produced by other microbes’ enzymes). In order to make enzyme production evolutionarily sustainable, we implicitly represented spatial heterogeneity in the evolutionary model (equation (9) in Methods) to make monomer accessibility proportional to investment in enzymes. By increasing enzyme kinetics, and in particular the uptake kinetics, warming decreases the intensity of cheating and therefore increases the profit of investments in enzymes. As a result, microbes that invest more in enzyme production (and less in direct growth) have long-term a higher net growth rate, which results in the selection of communities with higher allocation to enzymes (K- or A- strategy).

Allocation to resource acquisition is dependent on uptake, as well as microbial mortality, growth efficiency and the intensity of competition between strains. Yet, out of these parameters, resource uptake is the only one sensitive to temperature. In the other scenarios where mortality or growth efficiency also responded to temperature, the response of resource allocation was more complex. For instance, empirical evidence suggests that the response functions are more sensitive to temperature for uptake rates than for mortality and growth efficiency at most temperatures [(Hagerty et al. 2014)](https://paperpile.com/c/jw7igf/lgLC). It is interesting, however, that resource allocation does not depend on other parameters, such as the cost of producing enzymes. This is because production cost does not affect microbial net growth (and therefore fitness) but only the realized enzyme production. We tested also whether the relationship of resource allocation to uptake would be less strong if enzyme production was not solely inducible (function of uptake), but if production were constitutive (function of biomass). Results stay quantitatively the same.

**Implications for projections of global carbon stocks**

Our study is a first step to understanding the role of microbial eco-evolution in the carbon cycle, by replacing the expected ecosystem attenuation responses by mechanistic population-driven trait optimization. One of the most pressing challenges for soil scientists is to improve climate projections while reducing uncertainty in global soil carbon response to warming (Bradford et al 2016). One way to address this is through the use of experimental studies (see Crowther et al (2016)) to directly investigate the consistency of soil carbon sensitivity to warming; however, due to spatial heterogeneity across regions, there still exists a large degree of uncertainty in scaling local observations to global predictions to understand the effects of warming. Adding microbial trait variation with past and present climate will only increase prediction uncertainty given the high sensitivity of carbon variables to microbial parameters (Wieder et al 2013). At the same time, several empirical studies have shown the capacity for microbial communities to rapidly respond, through ecological [(Glassman et al. 2018)](https://paperpile.com/c/jw7igf/ibg8A) and evolutionary mechanisms [(Chase, Weihe, and Martiny 2021)](https://paperpile.com/c/jw7igf/ibjQC), to warming temperatures on short timescales with implications for carbon related traits.

**Implications for ecological and biogeochemical theory**

Although our result of stronger eco-evolutionary response in cold-adapted communities matches experimental findings [(Bradford et al. 2008)](https://paperpile.com/c/jw7igf/cRgse), the direction of its effect does not since we found larger soil carbon losses. Carbon models that have attempted to integrate microbial eco-evolutionary response usually make the assumption that it will lead to an attenuation or a cancellation of the observed initial community trait response to warming, that is generally a smaller to no decrease of microbial CUE [(Steven D. Allison, Wallenstein, and Bradford 2010; William R. Wieder, Bonan, and Allison 2013)](https://paperpile.com/c/jw7igf/bsCkn%2BKi3Uu). With our approach of microbial fitness optimization by modeling the process of selection, we predicted that enzyme allocation increases, and if the carbon use efficiency of enzymes is higher than of biomass [(Burns et al. 2013)](https://paperpile.com/c/jw7igf/0MagA), we then predicted an increase in CUE.

Experimental results on the effect of microbial eco-evolution on soil carbon loss vary depending on the time after warming and on the trait. To our knowledge, the field experiment closest to our simulation experiment (warming only, long-term) is the one of Melillo et al. [(Melillo et al. 2017)](https://paperpile.com/c/jw7igf/xrJfh), where they conducted a 26-year-long warming experiment on soil microbial communities in the Harvard forest. They found four phases of community reorganization associated with different changes in function, such as increased lignase activity or decreased CUE. However two of those phases were associated with accentuated soil carbon loss and the other two with attenuated soil carbon loss. It is probable that the “one microbe / one substrate” assumption is not sufficient to obtain this temporal variability in CUE response, and that our model could predict such variability if we integrated explicit substrate and microbial diversity with the possibility for different traits to vary at different times for the different microbial groups. Another possibility is that there are flow dynamics happening between accessible and inaccessible (mineral-associated) carbon in Melillo et al.’s soil that we could add in our model [(Sulman et al. 2014)](https://paperpile.com/c/jw7igf/cm8CE).

Other modifications in the model could lead to more realistic regional distributions of microbial strategies, starting with taking into account other environmental factors besides temperature [(Malik et al. 2020)](https://paperpile.com/c/jw7igf/SI9XC). For example, resource allocation can be sensitive to moisture and litter quality [(Manzoni 2017)](https://paperpile.com/c/jw7igf/UjsJQ) and we expect that the global distributions of microbial resource allocation strategies will greatly improve with the inclusion of soil characteristics (as done in MIMICS [(W. R. Wieder et al. 2014)](https://paperpile.com/c/jw7igf/CFcKE) or CORPSE [(Sulman et al. 2014)](https://paperpile.com/c/jw7igf/cm8CE)). Along these lines, working at a higher spatial and temporal precision could improve our predictions of microbial optimal strategy, for example in high latitudes where microbial activity might be seasonal due to phases of dormancy [(Zha and Zhuang 2020)](https://paperpile.com/c/jw7igf/TYUDY).

Finally, we would like to test whether explicitly including the processes behind the change in microbial community mean trait value (i.e. sorting of initial functional diversity vs. de novo mutations) would lead to the same predictions as ours with no explicit representation of diversity within a location. The effect of functional diversity has been explored numerically [(Kaiser et al. 2014; S. D. Allison 2012)](https://paperpile.com/c/jw7igf/BEb4y%2BRtk1q) and theoretically [(Loreau 2001)](https://paperpile.com/c/jw7igf/1RdP6) in microbial systems but without evolution. The effect of evolution has been looked at in theoretical models but not in microbial systems, and on assembly rather than function [(de Mazancourt, Johnson, and Barraclough 2008; Johansson 2008)](https://paperpile.com/c/jw7igf/FhAqw%2B3YLff). If the trait trajectory remains unchanged with evolution and explicit representation of microbial diversity, we will conclude that our fitness optimization based techniques are sufficient to predict microbial functional response to environmental changes [(Weng et al. 2019; Sauterey et al. 2015)](https://paperpile.com/c/jw7igf/PfVyZ%2BS8Raf). However we might be able to identify conditions (of initial diversity, of environmental change) under which it matters whether evolution versus community shifts are driving trait variation [(Chase, Weihe, and Martiny 2021)](https://paperpile.com/c/jw7igf/ibjQC).

In summary, this work directly incorporates microbial trait optimization at the global scale with implications for carbon cycling. We validated our hypothesis that warming-induced acceleration of enzyme kinetics benefits enzyme producers, therefore enzyme production increases, as does soil carbon losses, with microbial eco-evolutionary responses to warming. This study does not intend to provide absolute predictions of global soil carbon, but rather highlight the strong effect of microbial trait optimization in a mechanistic model of decomposition. Despite the gaps in our knowledge of which traits are adaptive to warming climates, the inclusion of evolutionary theory provided a mathematical framework to extrapolate analytical predictions and test the robustness of our model to other parameters and scenarios expected under future climate change. Future work should consider regional data on microbial traits under selection, particularly those involved in carbon cycling. Ultimately, our study provides a springboard for understanding the potential for eco-evolution of soil microbes to affect climate projections, and that future research should reconcile evolutionary-based predictions with ecosystem scale observations.

# MATERIAL AND METHODS

## Baseline microbe-enzyme model representing explicit resource allocation trade-off

Our baseline microbe-enzyme model (Fig S11) is a second-order model of soil organic carbon (SOC) dynamics that expands upon the model of Allison et al 2010 (AWB) by explicitly representing a microbial trade-off between carbon allocation to growth versus extracellular enzyme production. It includes SOC (C), dissolved organic C (DOC), microbial biomass C (M) and explicit enzyme mass C (Z). SOC increases with litter input (*I*), and declines with leaching (*eC*) and enzyme decomposition, which is assumed to be catalyzed according to Michaelis-Menten kinetics of the enzyme pool as represented by the last term in equation (1):

(1)

DOC receives the product of SOC decomposition, as well as the product from the recycling of dead microbes (*dM*) and inactive enzymes (*dZ*). We did not include litter input to the DOC pool, represented in AWB, because the steady states are not sensitive to it (see sensitivity analysis in Table S2) and it simplifies the analytic solution. DOC decreases with leaching (*eD*) and microbial uptake, where it is assumed that microbial cells have a limited amount of transporters, hence another Michaelis-Menten process represented by the last term in equation (2):

(2)

Microbial biomass turns over with rate *dM*, and grows proportionally to DOC uptake and a growth efficiency term that accounts for the loss to respiration due to the energetic cost of biomass production (*γM*), minus a portion of it allocated to enzyme production (*φ*):

(3)

Finally the enzyme pool grows with microbial uptake and allocation to enzyme production, and declines with enzyme turnover rate:

(4)

The resource allocation trade-off is parameterized with *φ*, with *φ* the fraction of DOC uptake allocated to enzyme production, and (1-*φ*) the fraction allocated to yield. Parameter units and values are detailed in Table S1.

## Steady states

The model (Eqs. 1-4) possesses either one globally stable equilibrium, or three equilibria (one of which is always unstable). There are thresholds *φ*min and *φ*max such that the single globally stable equilibrium exists for *φ* < *φ*min or *φ* > *φ*max and is given by *C* = *I*/*eC*, *D* = 0, *M* = 0, *Z* = 0. Thus, at this equilibrium, the microbial population is absent and no decomposition occurs. For *φ*min < *φ* < *φ*max, the microbial population can either go extinct (then the system stabilizes at the same equilibrium as before) or persists at or around a non-trivial equilibrium, which can be solved analytically (more details on the non-trivial equilibrium, *φ*min and *φ*max in Note S1).

## Temperature dependence

At the molecular and cellular level, the effect of warming on microbial decomposition is mediated by the temperature sensitivity of intra- and extra-cellular enzymatic activity [(Wallenstein, Mcmahon, and Schimel 2009; German et al. 2012; Burns et al. 2013)](https://paperpile.com/c/jw7igf/hFjlV%2B9pW2o%2B0MagA). In the baseline ‘kinetics-only’ scenario, microbial uptake parameters (maximum uptake rate, *vUmax*, half-saturation constant, *KUm*) and exoenzyme kinetics parameters (maximum decomposition rate, *vDmax*, half-saturation constant, *KDm*) increase with temperature [(Hochachka and Somero 2002; Davidson and Janssens 2006)](https://paperpile.com/c/jw7igf/urhdv%2BJiJYW) in an exponential manner:

(5)

(6)

(7)

(8)

## Eco-evolutionary optimization of microbial resource allocation

Assuming heritable variation in the exoenzyme allocation fraction trait, *φ*, we used the framework of adaptive dynamics [(Metz, Nisbet, and Geritz 1992; Geritz et al. 1998)](https://paperpile.com/c/jw7igf/7nr8b%2BFoQuF) to predict the strength and direction of selection on trait *φ* and the evolutionarily stable value, *φ*\*. In this framework, eco-evolution is modeled as a competition process between a ‘resident strategy’ (wild-type) and alternate strategies (‘mutants’) within a set of feasible phenotypes. In a given environment (*e.g.* at a given temperature), an evolutionarily stable strategy (ESS) is a phenotype that, when resident, no mutant can invade. The adaptive dynamics framework provides the mathematical criteria to identify ESSs and check their attractivity, i.e. that they can be reached by a sequence of small evolutionary steps, each step involving the replacement of a resident phenotype by a mutant phenotype. Here the set of feasible phenotypes is the range (*φ*min , *φ*max) at a given temperature, for which the non-trivial ecosystem equilibrium exists.

To model the competition effect of a resident phenotype, *φ*res, on the population growth of a mutant phenotype, *φ*mut, we extended the baseline microbial-enzyme model written for a single type (Eq. 3). To account for the local nature of the interaction between rare mutant and common resident cells, we introduced a function (hereafter denoted by *c*) of the difference between *φ*res and *φ*mut to measure how local decomposition by mutant and resident cells differ from ‘mean field’ (average) decomposition by resident cells. Thus, for given *C*, *D*, *Z*, the growth of the mutant population is governed by:

(9)

where *D*res is the equilibrium *D* predicted by the ecosystem model for the resident phenotype *φ*res. Here function *c* satisfies *c*(0) = 0, *c*(*z*) > 0 if *z* > 0 and *c*(*z*) < 0 if *z* < 0. The underlying assumption is that each microbe has access to DOC partly as a public good and partly as a private good [(Driscoll and Pepper 2010)](https://paperpile.com/c/jw7igf/lxlXA). The public good part results from the diffusion of exoenzymes. The private good part results from local decomposition at the microscopic scale of cells and exoenzymes that they produce themselves. A mutant cell that invests more in exoenzymes has access to more DOC than the average resident cell because the cell’s private good is greater whereas all cells share the same public good. In a spatially implicit model like ours, diffusion is not directly modeled, but its effect on the accessibility of DOC to a mutant strain can be phenomenologically accounted for by a parameterization that puts mutant cells at a competitive advantage for DOC if the mutant phenotype invests more in exoenzyme production than the resident phenotype, or at a competitive disadvantage if the mutant phenotype invests less. This parameterization is achieved with the function *c* in Eq. 9, where *c* < 1 when *φ*mut < *φ*res and *c* > 1 when *φ*mut > *φ*res. This phenomenological approach is consistent with the mathematical construction and numerical analysis of a spatially explicit model of resident-mutant local interaction that accounts for soil diffusion [(Abs, Leman, and Ferrière 2020)](https://paperpile.com/c/jw7igf/mMv6B).

Mutant relative fitness *s*(*φmut* - *φres*) is given by the mutant population growth rate per unit biomass:

(10)

The selection gradient is then obtained by taking the first order derivative of the invasion fitness with respect to the mutant trait:

(11)

where *c*0 = *c’*(0) measures the local competitive advantage to stronger exoenzyme producers, that we call ‘competition asymmetry’. Note that by definition of function *c*, we always have *c*0 > 0. Variation in *c*0 may be caused by different soil diffusion properties, due to *e.g.* physical texture or moisture.

Trait values that nullify the selection gradient are called ‘evolutionary singularities’. An evolutionary singularity can be attractive or repelling, and invadable or non-invadable. Evolutionary singularities that are attractive and non-invadable represent potential end-points of eco-evolution. Evolutionary singularities that are attractive and invadable can lead to evolutionary branching [(Geritz et al. 1998)](https://paperpile.com/c/jw7igf/FoQuF). In a given environment (fixed parameters, constant temperature) there is at most one evolutionary singularity given by defining *φ*\* as the value of *φ* that makes = 0:

(12)

Existence of *φ*\* > 0requires and . Thus, the (cooperative) trait *φ* can evolve above zero only if the local competition advantage to stronger enzyme producers is large enough. The condition for *φ*\* to be evolutionarily stable is *c’’*(0) < 2 c02 and no other condition than existence is required for *φ*\* to be always convergent. Here we assumed that function *c* is such that *φ*\* is evolutionarily stable and attractive.

## Calculations at the global scale

We obtained global projections of soil carbon stocks by calculating the steady states on a grid of 1° × 1° across terrestrial continents. Projected soil temperature was obtained from a single simulation of the Community Earth System Model (CESM), CCSM4, for the Representative Concentration Pathway 8.5 (RCP8.5) from 2005 to 2100 (publically available online at <http://www.cesm.ucar.edu/experiments/cesm1.0/>). It provides daily predictions across 192 points of latitude and 288 points of longitude. We averaged those projections over one year each decade to calculate the local steady states used in all figures. For all sites where the microbial activity is positive, the soil C stock is estimated as the sum of the steady states of SOC and microbial biomass (in units of carbon mass per m2 per centimeter of soil depth). To calculate the effect of optimization, we calculated the sum of changes in soil C stock of every decade between 2010 and 2100. For the predictions obtained with alternative scenarios of microbial temperature sensitivity, we used equations and parameters from Allison et al. [(Steven D. Allison, Wallenstein, and Bradford 2010)](https://paperpile.com/c/jw7igf/bsCkn) and Hagerty et al. [(Hagerty et al. 2014)](https://paperpile.com/c/jw7igf/lgLC) (see equations in Note S2). For the predictions obtained with spatially and temporally variability in litter input, we used the litter projections from the same source as for temperature, and averaged them as well over a year each decade in each site. Finally for the predictions obtained with spatially variable temperature sensitivity of enzyme kinetics, we used the 5 sets of sensitivity parameters obtained by German et al. [(German et al. 2012)](https://paperpile.com/c/jw7igf/9pW2o). We divided continents into 5 clusters based on temperature and moisture (Fig. S12), to which one of the 5 sets of enzyme temperature sensitivity parameters was attributed (Table S3).

**REFERENCES (31 - max 80)**

[Abs, Elsa, Hélène Leman, and Régis Ferrière. 2020. “A Multi-Scale Eco-Evolutionary Model of Cooperation Reveals How Microbial Adaptation Influences Soil Decomposition.” *Communications Biology* 3 (1): 520.](http://paperpile.com/b/jw7igf/mMv6B)

[Allison, S. D. 2012. “A Trait-Based Approach for Modelling Microbial Litter Decomposition.” *Ecology Letters* 15 (9): 1058–70.](http://paperpile.com/b/jw7igf/Rtk1q)

[Allison, Steven D., Matthew D. Wallenstein, and Mark A. Bradford. 2010. “Soil-Carbon Response to Warming Dependent on Microbial Physiology.” *Nature Geoscience* 3 (5): 336–40.](http://paperpile.com/b/jw7igf/bsCkn)

[Bradford, Mark A., Christian A. Davies, Serita D. Frey, Thomas R. Maddox, Jerry M. Melillo, Jacqueline E. Mohan, James F. Reynolds, Kathleen K. Treseder, and Matthew D. Wallenstein. 2008. “Thermal Adaptation of Soil Microbial Respiration to Elevated Temperature.” *Ecology Letters* 11 (12): 1316–27.](http://paperpile.com/b/jw7igf/cRgse)

[Burns, Richard G., Jared L. DeForest, Jürgen Marxsen, Robert L. Sinsabaugh, Mary E. Stromberger, Matthew D. Wallenstein, Michael N. Weintraub, and Annamaria Zoppini. 2013. “Soil Enzymes in a Changing Environment: Current Knowledge and Future Directions.” *Soil Biology & Biochemistry* 58 (March): 216–34.](http://paperpile.com/b/jw7igf/0MagA)

[Chase, Alexander B., Claudia Weihe, and Jennifer B. H. Martiny. 2021. “Adaptive Differentiation and Rapid Evolution of a Soil Bacterium along a Climate Gradient.” *Proceedings of the National Academy of Sciences of the United States of America* 118 (18). https://doi.org/](http://paperpile.com/b/jw7igf/ibjQC)[10.1073/pnas.2101254118](http://dx.doi.org/10.1073/pnas.2101254118)[.](http://paperpile.com/b/jw7igf/ibjQC)

[Davidson, Eric A., and Ivan A. Janssens. 2006. “Temperature Sensitivity of Soil Carbon Decomposition and Feedbacks to Climate Change.” *Nature* 440 (7081): 165–73.](http://paperpile.com/b/jw7igf/JiJYW)

[Driscoll, William W., and John W. Pepper. 2010. “Theory for the Evolution of Diffusible External Goods.” *Evolution; International Journal of Organic Evolution* 64 (9): 2682–87.](http://paperpile.com/b/jw7igf/lxlXA)

[Fao/Iiasa/Isric/Isscas/Jrc. 2012. “Harmonized World Soil Database (version 1.2).” *FAO, Rome, Italy and IIASA, Laxenburg, Austria*.](http://paperpile.com/b/jw7igf/DEUBc)

[Geritz, S. A. H., E´ Kisdi, G. Mesze´NA, and J. A. J. Metz. 1998. “Evolutionarily Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree.” *Evolutionary Ecology* 12 (1): 35–57.](http://paperpile.com/b/jw7igf/FoQuF)

[German, Donovan P., Kathleen R. B. Marcelo, Madeleine M. Stone, and Steven D. Allison. 2012. “The Michaelis-Menten Kinetics of Soil Extracellular Enzymes in Response to Temperature: A Cross-Latitudinal Study.” *Global Change Biology* 18 (4): 1468–79.](http://paperpile.com/b/jw7igf/9pW2o)

[Glassman, Sydney I., Claudia Weihe, Junhui Li, Michaeline B. N. Albright, Caitlin I. Looby, Adam C. Martiny, Kathleen K. Treseder, Steven D. Allison, and Jennifer B. H. Martiny. 2018. “Decomposition Responses to Climate Depend on Microbial Community Composition.” *Proceedings of the National Academy of Sciences of the United States of America* 115 (47): 11994–99.](http://paperpile.com/b/jw7igf/ibg8A)

[Hagerty, Shannon B., Kees Jan van Groenigen, Steven D. Allison, Bruce A. Hungate, Egbert Schwartz, George W. Koch, Randall K. Kolka, and Paul Dijkstra. 2014. “Accelerated Microbial Turnover but Constant Growth Efficiency with Warming in Soil.” *Nature Climate Change* 4 (10): 903–6.](http://paperpile.com/b/jw7igf/lgLC)

[Hochachka, Peter W., and George N. Somero. 2002. *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford University Press.](http://paperpile.com/b/jw7igf/urhdv)

[Hoff, J. H. van ’t. 1884. *Études de dynamique chimique*. Muller.](http://paperpile.com/b/jw7igf/u3R67)

[Intergovernmental Panel on Climate Change. Working Group 1. 2007. *Climate Change 2007: The Physical Science Basis : Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change : Summary for Policymakers and Technical Summary and Frequently Asked Questions*.](http://paperpile.com/b/jw7igf/p32e4)

[Johansson, Jacob. 2008. “Evolutionary Responses to Environmental Changes: How Does Competition Affect Adaptation?” *Evolution; International Journal of Organic Evolution* 62 (2): 421–35.](http://paperpile.com/b/jw7igf/3YLff)

[Kaiser, Christina, Oskar Franklin, Ulf Dieckmann, and Andreas Richter. 2014. “Microbial Community Dynamics Alleviate Stoichiometric Constraints during Litter Decay.” *Ecology Letters* 17 (6): 680–90.](http://paperpile.com/b/jw7igf/BEb4y)

[Loreau, Michel. 2001. “Microbial Diversity, Producer–decomposer Interactions and Ecosystem Processes: A Theoretical Model.” *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268 (1464): 303–9.](http://paperpile.com/b/jw7igf/1RdP6)

[Malik, Ashish A., Jennifer B. H. Martiny, Eoin L. Brodie, Adam C. Martiny, Kathleen K. Treseder, and Steven D. Allison. 2020. “Defining Trait-Based Microbial Strategies with Consequences for Soil Carbon Cycling under Climate Change.” *The ISME Journal* 14 (1): 1–9.](http://paperpile.com/b/jw7igf/SI9XC)

[Manzoni, Stefano. 2017. “Flexible Carbon-Use Efficiency across Litter Types and during Decomposition Partly Compensates Nutrient Imbalances—Results from Analytical Stoichiometric Models.” *Frontiers in Microbiology*. https://doi.org/](http://paperpile.com/b/jw7igf/UjsJQ)[10.3389/fmicb.2017.00661](http://dx.doi.org/10.3389/fmicb.2017.00661)[.](http://paperpile.com/b/jw7igf/UjsJQ)

[Mazancourt, C. de, E. Johnson, and T. G. Barraclough. 2008. “Biodiversity Inhibits Species’ Evolutionary Responses to Changing Environments.” *Ecology Letters* 11 (4): 380–88.](http://paperpile.com/b/jw7igf/FhAqw)

[Melillo, J. M., S. D. Frey, K. M. DeAngelis, W. J. Werner, M. J. Bernard, F. P. Bowles, G. Pold, M. A. Knorr, and A. S. Grandy. 2017. “Long-Term Pattern and Magnitude of Soil Carbon Feedback to the Climate System in a Warming World.” *Science* 358 (6359): 101–5.](http://paperpile.com/b/jw7igf/xrJfh)

[Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. “How Should We Define ‘fitness’ for General Ecological Scenarios?” *Trends in Ecology & Evolution* 7 (6): 198–202.](http://paperpile.com/b/jw7igf/7nr8b)

[Nemergut, Diana R., Steven K. Schmidt, Tadashi Fukami, Sean P. O’Neill, Teresa M. Bilinski, Lee F. Stanish, Joseph E. Knelman, et al. 2013. “Patterns and Processes of Microbial Community Assembly.” *Microbiology and Molecular Biology Reviews: MMBR* 77 (3): 342–56.](http://paperpile.com/b/jw7igf/i9Xwa)

[Sauterey, Boris, Ben A. Ward, Michael J. Follows, Chris Bowler, and David Claessen. 2015. “When Everything Is Not Everywhere but Species Evolve: An Alternative Method to Model Adaptive Properties of Marine Ecosystems.” *Journal of Plankton Research* 37 (1): 28–47.](http://paperpile.com/b/jw7igf/S8Raf)

[Sinsabaugh, Robert L., Robert K. Antibus, and Arthur E. Linkins. 1991. “An Enzymic Approach to the Analysis of Microbial Activity during Plant Litter Decomposition.” *Agriculture, Ecosystems & Environment* 34 (1): 43–54.](http://paperpile.com/b/jw7igf/PsBX3)

[Sulman, Benjamin N., Richard P. Phillips, A. Christopher Oishi, Elena Shevliakova, and Stephen W. Pacala. 2014. “Microbe-Driven Turnover Offsets Mineral-Mediated Storage of Soil Carbon under Elevated CO2.” *Nature Climate Change* 4 (12): 1099–1102.](http://paperpile.com/b/jw7igf/cm8CE)

[Todd-Brown, K. E. O., J. T. Randerson, F. Hopkins, V. Arora, T. Hajima, C. Jones, E. Shevliakova, et al. 2014. “Changes in Soil Organic Carbon Storage Predicted by Earth System Models during the 21st Century.” *Biogeosciences*. https://doi.org/](http://paperpile.com/b/jw7igf/RIv6Q)[10.5194/bg-11-2341-2014](http://dx.doi.org/10.5194/bg-11-2341-2014)[.](http://paperpile.com/b/jw7igf/RIv6Q)

[Wallenstein, Matthew D., Shawna K. Mcmahon, and Joshua P. Schimel. 2009. “Seasonal Variation in Enzyme Activities and Temperature Sensitivities in Arctic Tundra Soils.” *Global Change Biology* 15 (7): 1631–39.](http://paperpile.com/b/jw7igf/hFjlV)

[Weng, Ensheng, Ray Dybzinski, Caroline E. Farrior, and Stephen W. Pacala. 2019. “Competition Alters Predicted Forest Carbon Cycle Responses to Nitrogen Availability and Elevated CO 2: Simulations Using an Explicitly Competitive, Game-Theoretic Vegetation Demographic Model.” *Biogeosciences*  16 (23): 4577–99.](http://paperpile.com/b/jw7igf/PfVyZ)

[Wieder, William R., Gordon B. Bonan, and Steven D. Allison. 2013. “Global Soil Carbon Projections Are Improved by Modelling Microbial Processes.” *Nature Climate Change* 3 (10): 909–12.](http://paperpile.com/b/jw7igf/Ki3Uu)

[Wieder, W. R., A. S. Grandy, C. M. Kallenbach, and G. B. Bonan. 2014. “Integrating Microbial Physiology and Physio-Chemical Principles in Soils with the MIcrobial-MIneral Carbon Stabilization (MIMICS) Model.” *Biogeosciences*. https://doi.org/](http://paperpile.com/b/jw7igf/CFcKE)[10.5194/bg-11-3899-2014](http://dx.doi.org/10.5194/bg-11-3899-2014)[.](http://paperpile.com/b/jw7igf/CFcKE)

[Zha, Junrong, and Qianla Zhuang. 2020. “Microbial Dormancy and Its Impacts on Northern Temperate and Boreal Terrestrial Ecosystem Carbon Budget.” *Biogeosciences*  17 (18): 4591–4610.](http://paperpile.com/b/jw7igf/TYUDY)

**Acknowledgements**: **General:** We thank Pierre-Henri Gouyon, Rachel Gallery, Moira Hough, Hélène Leman, Laura Meredith, Mitch Pavao-Zuckerman, William Smith, Abigail Swann for discussion, Steve Allison, Alex Chase, Philippe Ciais and Jennifer Martiny for friendly review, and Heather Maugha for editing. **Funding:** For the project leading to this application, E.A. has received funding from Ecole Doctorale Frontières du Vivant and MemoLife Laboratory of Excellence (PIA-10-LBX-54), from a grant from the Genomic Science Program of the United States Department of Energy (DOE) (DE-SC0020382), and from the European Union’s Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 891576. S.R.S. was supported by a grant from the Genomic Science Program of the United States DOE (DE-SC0016440) and the University of Arizona’s Agnese Nelms Haury Program in Environment and Social Justice. R.F. acknowledges support from FACE Partner University Fund, CNRS Mission pour l’Interdisciplinarité, PSL University (IRIS OCAV and PSL-University of Arizona Mobility Program), and a grant from the Dimensions of Biodiversity program of the United States National Science Foundation (DEB-1831493). **Author contributions:** E.A. and R.F. conceived the research. All authors developed the model. E.A. wrote the code and performed the analysis. E.A. wrote the first version of the manuscript. All authors finalized the paper. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. **Code availability:** The sensitivity analysis and figures that support the findings of this study were coded with Mathematica. The global projections were coded on R. The code files have been deposited in “MicFigCode”, <https://github.com/elsaabs/MicFigCode/tree/master>. **Supplementary materials:** are available for this paper at https://doi.org/xxx.