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Key Points:

- Slower increase of microbial Carbon/Nitrogen (C/N) ratio compared to soil C/N ratio was modeled, similar as observation
- Dynamic Carbon use efficiency modulated by C/N ratios of substrate and microbes could be revealed by explicitly representing microbial dynamics
- Feedback between soil C pool and climate might be weakened by suppressed microbial biomass growth under warming climate

Supporting Information:

Supporting Information may be found in the online version of this article.

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Global Simulation and Evaluation of Soil Organic Matter and Microbial Carbon and Nitrogen Stocks Using the Microbial Decomposition Model ORCHIMIC v2.0

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Abstract Soils contain the largest amount of land carbon, even a small change of this pool can significantly affect atmospheric CO₂ and climate change. A good representation of soil organic carbon (SOC) dynamics in Earth system models is therefore crucial to predict future climate change. The dynamics of SOC is largely driven by microbial activities and modulated by N cycles. Nevertheless, very few models have explicitly represented soil microorganisms and N cycles integrated at global scale. Here, we present an update of the microbial-mediated ORCHIMIC model and its application to simulate global gridded SOC stocks, microbial biomass, soil C/N ratio, microbial C/N ratio, and heterotrophic respiration. This is a new attempt to model SOC dynamics with an explicit microbial representation with N dynamics applied at global scale. The model shows relatively good performance in reproducing global SOC and microbial biomass C. The spatial distributions of soil and microbial C/N ratios were not well reproduced because they are sensitive to mineral nitrogen availability controlled by plant uptake, which is not explicitly represented in the model. However, similar relationship between C/N ratios of microbes and soil as observation demonstrated the potential of the model to reproduce global C/N ratios for both microbe and soil pools. Dynamic carbon use efficiency modulated by substrate C/N ratio, consistent with observation, were well represented by mechanistic including microbial dynamics. Modeled suppressed microbial biomass growth under warming climate indicating a weaker positive feedback between soil C pool and climate compared to that predicted by traditional Earth system models.

1. Introduction

Soils are the most important organic carbon reservoir on Earth and a key component of global carbon (C) cycle dynamics in response to climate and anthropogenic land use change. Soil organic carbon (SOC) stocks are roughly estimated to 1,500 Pg C excluding permafrost and peatlands (Scharlemann et al., 2014) which is two times what the mass of CO₂ in the atmosphere and three times the amount stored in vegetation biomass (IPCC, 2013). Large uncertainties are nevertheless associated to empirical SOC stocks estimations (Tifafi, Guenet, & Hatté, 2018). Soils carbon modeling receives a particular attention in Earth System Models mainly because a slight modification of the plant inputs or decomposition outputs can have a significant impact on their evolution, with huge consequences for future CO₂ and climate change (Luo et al., 2016; Minasny et al., 2017; Schmidt et al., 2011). This has motivated research studies to evaluate ESMs performances in reproducing global SOC stocks and their dynamics (Hashimoto et al., 2015; He et al., 2016; Koven et al., 2013; Todd-Brown et al., 2013, 2014). The recent generation of ESMs known as the CMIP5 ensemble has low to moderate performances to reproduce global mean SOC stocks as well as heterotrophic respiration fluxes for present day, with clear model outliers (Hashimoto et al., 2015; Todd-Brown et al., 2013). The spatial variability of SOC is generally not well captured (Hararuk et al., 2014; Todd-Brown et al., 2013), suggesting that acceptable performance for the ensemble-mean global stock might be due to bias compensations between individual models. Using 14C data, He et al. (2016) showed that the soil carbon models of ESMs overestimated the soil carbon sequestration potential by 40%. This result is coherent with studies showing that processes absent from the ESMs such as priming (i.e., a modification of the SOC mineralization

rates induces by inputs of labile OC) may reduce carbon storage in models (Wieder et al., 2013; Sulman et al., 2014; Guenet et al., 2018).

Approaches to improve SOC models compatible with ESMs have been proposed in the past (Abramoff et al., 2018; Camino-Serrano et al., 2018; Huang et al., 2018; Koven et al., 2013; Nakhavali et al., 2018; Tifafi, Camino-Serrano, et al., 2018; Wieder et al., 2013), but most of them do not explicitly represent microbial decomposers who are the main actors of the SOC dynamics (Kallenbach et al., 2016). Soil microorganisms are incredibly diverse. In one gram of soil, thousands of species may be encountered (Torsvik & Øvreås, 2002). Representing this complexity at global scale is unachievable with present day knowledge, but modeling explicitly microbial mediated carbon and nutrient fluxes with some simplifications is realizable (Huang et al., 2018; Wieder et al., 2013). Nitrogen (N) and phosphorous (P) are largely recognized as a key driver of SOC decomposition and stabilization (Johnson, 2006; Kattge et al., 2009; Luo et al., 2004; Obersteiner et al., 2013) and efforts have been done by the ESMs modeling community to explicit include the nitrogen and the phosphorous cycle as a constraint on the C cycle (Goll et al., 2014, 2017; Yang et al., 2014; Zaehle & Friend, 2010; Grant, 2013; Zhu et al., 2019). However, most of these works did not represent microbes and enzymes, which are the key drivers for decomposition of soil organic matters. Li et al. (2019) showed that model with microbes represented could improve the prediction of mineral N by 19% compared the model without microbial dynamics, suggesting the necessity of representing microbes in Earth system models to capture nitrogen cycle. Some models considering microbial dynamics and C-N interaction and potentially adapted to Earth system models has been recently developed such as Microbial-ENzyme-mediated Decomposition (MEND) model (K. Wang et al., 2017; G. Wang, 2020) and The Microbial-MIneral Carbon Stabilization (MIMICS) model (Kyker-Snowman et al., 2020; Wieder et al., 2015), but so far not implemented in an Earth system model. Among living organisms, microbial activity is strongly related to stoichiometric constraints (Soong et al., 2018; Xu et al., 2013) and such constraints must be explicitly accounted for into a SOC model aiming at representing explicit microbial dynamics and enzymes-mediated decomposition.

In this study, we present a new attempt to model both the carbon and nitrogen cycles, and different soil microorganisms active in the mineralization of carbon and nitrogen. The tool used is an updated version of the ORCHIMIC model (Huang et al., 2018) which is an ESM compatible scheme for soil carbon and nitrogen dynamics with explicit representation of soil microorganisms, with their affinity to produce enzymes cleaving different pools of organic matter. A particularity of the model is to have a flexible enzyme production depending on the environment, which feedbacks on microbial decomposers populations and activity. Instead of representing the huge diversity of the soil microorganisms, we used a functional community with flexible characteristics (C/N ratio, dormancy, death rates, etc.). We evaluate the performance of the model applied globally against several global products like the total SOC stocks, the C/N of the soil organic matter, the total soil microbial biomass and its C/N ratio as well as heterotrophic respiration fluxes.

2. Materials and Methods

2.1. Model Description

ORCHIMIC v2.0 is an updated version of ORCHIMIC v1.0 (Huang et al., 2018), which follows the structure of ORCHIDEE, but includes microbes. In ORCHIMIC v2.0, equations describing several microbial functional types (MFTs) in ORCHIMIC v1.0 were replaced by new ones for a “mega functional group,” meant to represent (implicitly) the adjustment of different communities leading to emerging functional properties such as flexible total microbial biomass C/N ratios and dynamic enzyme production for four kinds of enzymes targeting at extracting C or N from fresh organic matter (FOM) or soil organic matter (SOM), so that this MFT can modify its own characteristics (e.g., biomass C/N ratios and producing the enzymes getting the largest benefit) to better survive in the environment. In ORCHIMIC v2.0, we kept two fresh organic matter pools, structural litter (LS) and metabolic litter (LM), and three soil organic matter pools, active (SA), slow (SS), and passive pool (SS), to remain consistent with the original pools of the ORCHIDEE land surface model. Microbes make C and N available (available pool, Avail) through decomposing substrates by enzymes and grow by taking up C and N from available pool. Equations 1–14 describe the dynamics of each pool showed in Figure 1. The symbols with their meanings and units used in the formulas are listed in Table 1. Updated processes including transformation between active and dormant states and maintenance respiration are described in supporting information (Text S1). Developments related to dynamic C/N ratios

Figure 1. Changes of carbon (C) and nitrogen (N) fluxes when microbes are C ($BACN_t < BCN_{opt}$, red) or N limited ($BACN_t > BCN_{opt}$, blue). Red C+(-) or N+(-) mean the C or N flux would increase (decrease) when $BACN_t < BCN_{opt}$; Blue C+(-) or N+(-) mean the C or N flux would increase (decrease) when $BACN_t > BCN_{opt}$.

are described in Sections 2.2.1 and 2.2.2. For all other processes, details can be found in our earlier work (Huang et al., 2018).

For LM and LS pool, their input is litter from turnover of vegetations, and the output is enzymatic decomposition of themselves:

$$\frac{dLM_x}{dt} = LM_{x,in} - D_{x,LM}, \quad (1)$$

$$\frac{dLS_x}{dt} = LS_{x,in} - D_{x,LS}, \quad (2)$$

For SA pool, its input includes turnover of microbes and enzymes, and the input is enzymatic decomposition of itself:

$$\frac{dSA_x}{dt} = BAd_x \times (1 - s_x) + EFCd_x + EFNd_x + ESCd_x + ESNd_x - D_{x,SA}, \quad (3)$$

For SS pool, there are fluxes from LM, LS (different for lignin and non-lignin fraction) and SA pool when these pools are decomposed, and decomposition of itself is the only output:

$$\frac{dSS_x}{dt} = D_{x,LM} \times LtoSS + D_{x,LS} \times (1 - LLf) \times LtoSS + D_{x,LS} \times LLf \times 0.7 + D_{x,SA} \times SAtoSS - D_{x,SS}, \quad (4)$$

Table 1
List of Symbols Used in This Study and Their Intended Meanings

Symbols	Descriptions	Units
ENZ	Abbreviation for enzyme	/
MIC	Abbreviation for microbe	/
j	Represents substrate j	[LM, LS, SA, SS, SP]
X	Represents C or N element	[C, N]
LM_X	X in litter metabolic pool	$\text{g X (kg soil)}^{-1}$
LS_X	X in litter structural pool	$\text{g X (kg soil)}^{-1}$
SA_X	Soil active organic matter pool	$\text{g X (kg soil)}^{-1}$
SS_X	Soil slow organic matter pool	$\text{g X (kg soil)}^{-1}$
SP_X	Soil passive organic matter pool	$\text{g X (kg soil)}^{-1}$
$Avail_X$	X pool directly available for microbe's uptake	$\text{g X (kg soil)}^{-1}$
$Adsorb_X$	X pool adsorbed on mineral surfaces	$\text{g X (kg soil)}^{-1}$
BA_X	X in active microbial biomass	$\text{g X (kg soil)}^{-1}$
BD_X	X in dormant microbial biomass	$\text{g X (kg soil)}^{-1}$
EFC_X	X in enzyme that extracts C from FOM	$\text{g X (kg soil)}^{-1}$
ESC_X	X in enzyme that extracts C from SOM	$\text{g X (kg soil)}^{-1}$
EFN_X	X in enzyme that extracts N from FOM	$\text{g X (kg soil)}^{-1}$
ESN_X	X in enzyme that extracts N from SOM	$\text{g X (kg soil)}^{-1}$
$D_{X,j}$	Flux of X decomposed from substrate j	$\text{g X (kg soil)}^{-1} dt^{-1}$
$LM_{X,in}$	Input of X for LM	$\text{g X (kg soil)}^{-1} dt^{-1}$
$LS_{X,in}$	Input of X for LS	$\text{g X (kg soil)}^{-1} dt^{-1}$
$EFCd_X$	X in EFC that is deactivated in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$ESCd_X$	X in ESC that is deactivated in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$EFNd_X$	X in EFN that is deactivated in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$ESNd_X$	X in ESN that is deactivated in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$EFCg_X$	X in new EFC produced in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$ESCG_X$	X in new ESC produced in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$EFNg_X$	X in new EFN produced in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$ESNg_X$	X in new ESN produced in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
LLf	Lignin fraction of the LS pool	unitless
$LtoSS$	The fraction of decomposed LM and non-lignin LS that go to SS pool	unitless
$SAtOSS$	The fraction of decomposed SA that go to SS pool	unitless
$SAtOSP$	The fraction of decomposed SA that go to SP pool	unitless
$SStOSP$	The fraction of decomposed SS that go to SP pool	unitless
BAG_X	X in new B produced in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
BAd_X	X in BA that died in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
s_X	Soluble fraction of dead microbial for X	unitless
$Uptake_X$	X taken up by the microbes in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$Adsorb_{Avail,X}$	Adsorbed $Avail_X$ in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$Desorb_{Adsorb,X}$	Desorbed $Adsorb_X$ in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
$leaching_X$	The loss of X due to leaching	$\text{g X (kg soil)}^{-1} dt^{-1}$
$Dloss_{N,j}$	Gaseous N losses during decomposition of substrate j	$\text{g X (kg soil)}^{-1} dt^{-1}$
BAm_X	BA_X lost due to maintenance respiration in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$
BDM_X	BD_X lost due to maintenance respiration in one time step	$\text{g X (kg soil)}^{-1} dt^{-1}$

Table 1
Continued

Symbols	Descriptions	Units
$Veg_{uptake,N}$	N uptake by vegetation	$g\ X\ (kg\ soil)^{-1}\ dt^{-1}$
$B_{AtoD,X}$	X transformed from BA_X to BD_X in one time step	$g\ X\ (kg\ soil)^{-1}\ dt^{-1}$
$B_{DtoA,X}$	X transformed from BD_X to BA_X in one time step	$g\ X\ (kg\ soil)^{-1}\ dt^{-1}$
$Vmax$	Maximum uptake rate, prescribed fixed value	$g\ X\ (g\ MIC\ C)^{-1}\ h^{-1}$
$Vmax_X$	Maximum uptake rate of X	$g\ X\ (g\ MIC\ C)^{-1}\ h^{-1}$
BCN	Microbial C/N mass ratio	Unitless
$BACN$	C/N mass ratio for active microbial biomass	Unitless
BCN_{opt}	The optimal microbial C/N ratio	Unitless
BCN_t	The microbial C/N ratio at current time step t	Unitless
CUE_{eff}	The effective carbon use efficiency	Unitless
NUE_{eff}	The effective nitrogen use efficiency	Unitless
R_g	Growth respiration	$g\ C\ (kg\ soil)^{-1}\ dt^{-1}$
R_e	Respiration due to enzyme production	$g\ C\ (kg\ soil)^{-1}\ dt^{-1}$
$R_{m,a}$	Maintenance respiration of active microbe	$g\ C\ (kg\ soil)^{-1}\ dt^{-1}$
ECN	C/N ratio of enzyme	Unitless
$K_{e,X}$	Enzyme production coefficient for X-extracting enzyme	h^{-1}
$K_{e,X,Sub}$	Enzyme production coefficient for X-extracting enzyme targeting at Sub (Sub can be FOM or SOM)	h^{-1}
$K_{e,X,Sub,t}$	Enzyme production coefficient for X-extracting enzyme targeting at Sub (Sub can be FOM or SOM) after considering the effect of the saturation level of substrate and decomposition of enzymes	h^{-1}
$DE_{X,j}$	Enzymatic decomposition efficiency when extracting X from substrate j, which is defined as the amount of X extracted from substrate j by one unit of enzyme	$g\ X\ (g\ ENZ\ C)^{-1}$

For SP pool, there are fluxes from SA and SS pool when these pools are decomposed, and decomposition of itself is the only output:

$$\frac{dSP_X}{dt} = D_{X,SA} \times SAtoSP + D_{X,SS} \times SSstoSP - D_{X,SP}, \quad (5)$$

For available C pool ($Avail_C$), its input includes decomposition of all substrate pools, turnover of microbes and desorption from mineral surface, and the output includes uptake by microbes, adsorption by mineral surface and leaching:

$$\begin{aligned} \frac{dAvail_C}{dt} = & D_{C,LM} \times (1 - LtoSS) + D_{C,LS} \times LLf \times 0.3 + D_{C,LS} \times (1 - LLf) \times (1 - LtoSS) \\ & + D_{C,SA} \times (1 - SAtoSS - SAtoSP) + D_{C,SS} \times (1 - SSstoSP) + D_{C,SP} + BAd_c \times s_C \\ & - Uptake_C + Desorb_{Adsorb,C} - Adsorb_{Avail,C} - leaching_C, \end{aligned} \quad (6)$$

For available N pool ($Avail_N$), its input is same as that of $Avail_C$ pool, but for the output, besides the output of $Avail_C$ pool, it also includes uptake by vegetation and gaseous loss of N:

$$\begin{aligned} \frac{dAvail_N}{dt} = & D_{N,LM} \times (1 - LtoSS) + D_{N,LS} \times LLf \times 0.3 + D_{N,LS} \times (1 - LLf) \times (1 - LtoSS) \\ & + D_{N,SA} \times (1 - SAtoSS - SAtoSP) + D_{N,SS} \times (1 - SSstoSP) + D_{N,SP} - \sum_j Dloss_{N,j} \\ & + BAd_N \times s_N - BAg_N + Desorb_{Adsorb,N} - Desorb_{Avail,N} + BAm_N + BDM_N \\ & - Veg_{uptake,N} - leaching_N, \end{aligned} \quad (7)$$

For Adsorbed pools ($Adsorb_X$), their main dynamics are adsorption and desorption:

$$\frac{d\text{Adsorb}_X}{dt} = \text{Adsorb}_{\text{Avail},X} - \text{Desorb}_{\text{Adsorb},X}, \quad (8)$$

For enzyme (EFC, EFN, ESC, and ESN) pools, their main dynamics are adsorption and desorption:

$$\frac{d\text{EFC}_X}{dt} = \text{EFC}g_X - \text{EFC}d_X, \quad (9)$$

$$\frac{d\text{EFN}_X}{dt} = \text{EFN}g_X - \text{EFN}d_X, \quad (10)$$

$$\frac{d\text{ESC}_X}{dt} = \text{ESC}g_X - \text{ESC}d_X, \quad (11)$$

$$\frac{d\text{ESN}_X}{dt} = \text{ESN}g_X - \text{ESN}d_X, \quad (12)$$

For active microbial biomass pool (BA) pool, the increase of biomass could result from the growth microbes and transform from dormant state, and the loss of biomass could be death, enzyme production, transform to dormant state and maintenance respiration:

$$\frac{d\text{BA}_X}{dt} = \text{BA}g_X + \text{B}_{\text{DtoA},X} - \text{BA}d_X - \text{EFC}g_X - \text{EFN}g_X - \text{ESC}g_X - \text{ESN}g_X - \text{B}_{\text{AtoD},X} - \text{BA}m_X, \quad (13)$$

For dormant microbial biomass pool, its dynamics are controlled by transformation to or from active state and maintenance respiration:

$$\frac{d\text{BD}_X}{dt} = \text{B}_{\text{AtoD},X} - \text{BD}m_X - \text{B}_{\text{DtoA},X}, \quad (14)$$

2.1.1. Uptake and Assimilation of C and N

The microbial biomass C/N ratios are variable across different regions and different vegetation type (Xu et al., 2013) due to different stoichiometries of microbial groups within the microbial community. To develop a model with microbial groups with specific biomass C/N ratio could simulate the mean C/N ratio for all microbes and its variations. However, unlike in the real environment, homogeneous access to available C and N for microbes is assumed here for a model soil unit, and as a result, any advantage or disadvantage of a specific C/N ratio for one MFT could be unlimited magnified, leading to one dominant microbial group in the end for most of cases. We chose instead to define a meta-microbial group with a flexible and optimality-driven stoichiometry to implicitly represent the effect of diverse functional communities into the model. In ORCHIMIC v2.0, the uptake of C or N is modeled using forward Michaelis-Menten kinetics as given by:

$$\text{Uptake}_X = V_{\text{max}_X} \times \text{BA}_C \times \frac{\text{Avail}_X}{K_{M_{U,X}} + \text{Avail}_X} \times dt, \quad (15)$$

We assume that the meta-microbe's capacity of taking up C and N is fixed (V_{max}), but how its capacity allocated to take up C (V_{max_C}) or N (V_{max_N}) mainly depends on the ratio of optimal microbial biomass C/N ratio (BCN_{opt} , prescribed with 7.6 (molar ratio) based on data from Xu et al., 2013) to current active biomass C/N ratio (BACN_t) and its efficient element use efficiencies (Carbon use efficiency [CUE_{eff}] and Nitrogen use efficiency [NUE_{eff}]):

$$V_{\text{max}_X} = V_{\text{max}} \times \frac{F_X}{F_C + F_N}, \quad (16)$$

$$F_C = \text{BCN}_{\text{opt}} / \text{CUE}_{\text{eff}} \times \left(\frac{\text{BCN}_{\text{opt}}}{\text{BACN}_t} \right)^{a_1}, \quad (17)$$

$$F_N = 1 / NUE_{eff} \times \left(\frac{BACN_t}{BCN_{opt}} \right)^{a_1}, \quad (18)$$

In the above equations, dt is the time step (24 h) $Uptake_X$ is the amount of element X taken up by microbes (g X kg⁻¹ soil), $Vmax_X$ is the microbes' maximum uptake rate of X (h⁻¹), $KM_{U,X}$ is a Michaelis-Menten constant, a_1 is a dimensionless parameter, prescribed with the value of 1, $Vmax$ is the maximum uptake capacity of the microbes, CUE_{eff} and NUE_{eff} are respectively defined as:

$$CUE_{eff} = \frac{BA_{g,C}}{BA_{g,C} + EFC_{gC} + ESC_{gC} + EFN_{gC} + ESN_{gC} + R_{m,a} + R_g + R_e}, \quad (19)$$

$$NUE_{eff} = \frac{BA_{g,N}}{BA_{g,N} + \frac{EFC_{gC} + ESC_{gC} + EFN_{gC} + ESN_{gC}}{ECN}}, \quad (20)$$

where $BA_{g,C}$ and $BA_{g,N}$ are respectively the growth of active microbial C and N, EFC_{gC} , ESC_{gC} , EFN_{gC} and ESN_{gC} are the allocation of C to EFC, ESC, EFN and ESN, respectively, $R_{m,a}$ is the maintenance respiration of active microbes, R_g and R_e are growth respiration and the respiration due to enzyme production, respectively, ECN is the C/N ratio of enzymes.

The C taken up by microbes from the available C pool (Figure 1) first meets the need for maintenance respiration and enzyme production, and the amount of C left can be potentially used in microbial biomass growth. The N taken up will first meet the need for enzyme production and the rest of N can be potentially used in microbial biomass growth. If the ratio of the amount of C and N available for growth is between a minimum (BCN_{min}) and maximum values (BCN_{max}) for C/N ratios for microbial biomass, all C and N will be assimilated. If this ratio is larger than BCN_{max} , the excess C will be respired through overflow respiration (R_o) and if it is smaller than BCN_{min} , the excess N will be released back into the available mineral N pool (Figure 1).

2.1.2. Enzyme Production

In ORCHIMIC v1.0, each microbial pool produced two kinds of enzymes that extracted C from FOM and SOM, respectively, and the extraction of N followed the C/N ratio of different substrates. In reality, soil organic matters compose of various components targeted by various enzymes, making the ratio of extracted C to N might be different from the overall C/N ratio of soil organic matters. Moorhead et al. (2012) developed a microbial model with two kinds of enzyme decomposing two substrates with different C/N ratios. In their model, though the total enzymes production is fixed, the microbes can adjust the production of each kind of enzyme to make the C/N ratio of the available C pool maximize microbial growth. Inspired by this idea, we consider two types of enzymes, C-extracting and N-extracting ones, for both FOM and SOM, in this new version. The C/N ratios for all types of enzymes considered was set to 3 (Allison et al., 2014). We assume that the diverse microbial functional groups implicitly contained in our meta-microbial pool have a fixed capacity to produce enzymes, but they produce more C-extracting or N-extracting enzymes depends on whether it is C or N limited (Figure 2). Microbes can also produce more FOM-decomposing or more SOM-decomposing enzymes, depending on which one is more efficient (Figure 2). When the modeled C/N ratio of active microbes ($BACN_t$) is larger (or smaller) than BCN_{opt} , the microbes become N (or C) limited and will tend to increase N-extracting ($K_{e,N}$) (or C-extracting, $K_{e,C}$) enzymes, by increasing this specific enzyme production coefficient. The capacity ($K_{e,X}$) allocated to produce X-extracting enzymes is defined as function of f_C and f_N (Equation 21), both of which are function of optimal and current microbial biomass C/N ratios (Equation 22 and 23):

$$K_{e,X} = \begin{cases} 0.25, & \text{if } \frac{f_X}{f_C + f_N} < 0.25 \\ \frac{f_X}{f_C + f_N}, & \text{if } 0.25 < \frac{f_X}{f_C + f_N} < 0.75 \\ 0.75, & \text{if } \frac{f_X}{f_C + f_N} > 0.75 \end{cases} \quad (21)$$

Figure 2. Diagram of strategies of the meta-microbial pool to adjust among the production of 4 kinds of enzymes extracting C or N from fresh (FOM) or soil (SOM) organic matter. The red (blue) show that microbes will decrease (increase) C-extracting enzymes and increase (decrease) N-extracting enzymes when $BACN_t > BCN_{opt}$ ($BACN_t < BCN_{opt}$). The purple (green) show that microbes will increase FOM decomposing enzymes and decrease SOM decomposing enzymes when $DE_{X,FOM} > DE_{X,SOM}$ ($DE_{X,FOM} < DE_{X,SOM}$), where X represented C or N.

$$f_C = \left(\frac{BCN_{opt}}{BACN_t} \right)^{a_1} \quad (22)$$

$$f_N = \left(\frac{BACN_t}{BCN_{opt}} \right)^{a_1} \quad (23)$$

The enzyme element extraction efficiency or enzyme decomposition efficiency ($DE_{X,Sub}$), defined as amount of element X extracted by one unit of corresponding enzyme, is the major controller determining the enzyme production capacity ($K_{e,X,Sub}$) allocated to decompose FOM or SOM:

$$K_{e,X,Sub} = \begin{cases} 0.25, & \text{if } \frac{DE_{X,Sub}^{a_2}}{DE_{X,FOM}^{a_2} + DE_{X,SOM}^{a_2}} < 0.25 \\ \frac{DE_{X,Sub}^{a_2}}{DE_{X,FOM}^{a_2} + DE_{X,SOM}^{a_2}}, & \text{if } 0.25 < \frac{DE_{X,Sub}^{a_2}}{DE_{X,FOM}^{a_2} + DE_{X,SOM}^{a_2}} < 0.75 \\ 0.75, & \text{if } \frac{DE_{X,Sub}^{a_2}}{DE_{X,FOM}^{a_2} + DE_{X,SOM}^{a_2}} > 0.75 \end{cases} \quad (24)$$

As in ORCHIMIC v1.0, the effects of substrate and available pool on enzyme production are still considered:

$$K_{1,Sub,X} = \frac{DE_{X,Sub}}{KM_E + DE_{X,Sub}} \quad (25)$$

$$K_{2,X} = 1 - Sat_X \quad (26)$$

The final production coefficient ($K_{e,X,Sub,t}$) for enzymes that extracts X (C or N) from different substrates (FOM or SOM) is given by:

$$K_{e,X,Sub,t} = K_e \times K_{e,X} \times K_{e,X,Sub} \times K_{1,Sub,X} \times K_{2,X} \quad (27)$$

In Equations 21, 22 and 24, a_1 and a_2 are parameters with prescribed value of 1 but might be optimized, KM_E is a Michaelis-Menten constant with a prescribed value of 1 g X (enzyme-C)⁻¹. The subscript Sub represents FOM or SOM substrate. K_e is the total enzyme production coefficient. The final production of a specific enzyme are production of the corresponding coefficient and active microbial biomass.

2.2. Model Forcings

ORCHIMIC is a module that can be integrated into a full land surface model or run offline to calculate litter and soil carbon stocks C and N. In the offline mode, the forcings needed for ORCHIMIC are litter C input, litter lignin content, soil relative moisture, soil temperature, litter C/N ratio, N deposition, plant N uptake and leaching. All these forcings are variables typically simulated by global CN land surface models. To obtain the forcings that are not N related, we run the land surface model ORCHIDEE-MICT (Guimberteau et al., 2018) based on ORCHIDEE with no N cycle (Krinner et al., 2005) to equilibrium, with re-gridded 5° spatial resolution climate data CRUNCEP v7 (see Guimberteau et al. (2018) for more details) and plant functional types (PFTs) maps from Peng et al. (2017) for years 1901–1910. The litter C input and lignin content were directly taken from ORCHIDEE-MICT. Because the soil is divided into 32 layers with a maximum depth of 38 m in ORCHIDEE-MICT, and ORCHIMIC v2.0 is not designed to model microbial biomass and SOC below 1 m soil e.g., as it is not coupled with processes such as bioturbation and oxygen limitations in deeper soil layers, only the top 1 m depth integrated soil relative moisture and soil temperature were used. These two soil climate forcings were prescribed from ORCHIDEE-MICT output with a daily time step. The litter C/N ratio data were derived from GOLUM-CNP data-driven model (Y. Wang et al., 2018) to assign the N content of C input fluxes from ORCHIDEE-MICT, and the annual N deposition data were from R. Wang et al. (2017). An annual 5% loss of available C and N as leaching was assumed (Y.-P. Wang et al., 2007). As plant N uptake is not explicitly represented in ORCHIMIC, we assumed a annual flux that was equal to the N input from litter with annual change following NPP, being removed by plants from the soil mineral N available pool of ORCHIMIC (Figure 1). To avoid a crash of microbes biomass because of a very strong competition for N with plants, we assumed that the plant N uptake cannot be larger than 1% or 5% of available N.

2.3. Model Setup

The ORCHIMIC was run at daily time step for 20,000 years. The initial SOC concentration was set to 10 g C kg⁻¹ soil with C/N ratios of 12, and initial fractions of SOC of 5%, 45%, and 55% based on those simulated by ORCHIDEE-MICT assumed to be active, slow, and passive, respectively. The initial litter concentration was set to 1 g C kg⁻¹ soil with half being metabolic and the other half being structural. The initial active and dormant microbial biomass concentrations were both set to 1.10⁻⁵ g C kg⁻¹ soil with C/N ratios prescribed to an optimal value at 7.6. The initial size of all other pools were all set to 0 g C kg⁻¹ soil. It has to been noted that the initial values had very small effects on sizes of each pool as long as the spinup simulation is long enough (20,000 years as in our case) as we run the model to near equilibrium states in each 5° grid cell.

2.4. Data Used to Evaluate the Model

The processes, like bio- and cryo-turbation that bury carbon to deep soil layers, especially to soil deeper than 1 m, are not included in ORCHIMIC v2.0, so only the data for top 1 m soil were used to evaluate our model. Global microbial biomass C and microbial biomass C/N ratio for the top 1 m soil were compared with the product from Xu et al. (2013) using multiple linear regression models based on 3,422 observations. The simulated fractions of microbial biomass carbon in SOC were evaluated against data from Serna-Chavez et al. (2013) obtained from multivariate linear models based on 414 observations. To evaluate the soil carbon modeled by ORCHIMIC v2.0, we used the soil carbon data for the top 1 m soil from World Inventory of Soil Emission Potentials (WISE) (Batjes, 2015) and gridded Global Soil Data set for use in Earth System Models (GSDE) (Wei et al., 2014). Model outputs from boreal regions were also compared with Northern Circumpolar Soil Carbon Database version 2 (NCSCD v2) (Hugelius et al., 2013), a data set of SOC storage in the

Figure 3. Global distribution of microbial biomass carbon from ORCHIMIC (a) and Xu et al. (2013) (b) and comparison between them for each plant functional type (PFT) with the circles are PFT averaged values and error bars show the standard deviations (c).

northern circumpolar permafrost region. The soil C/N ratios (defined as ratio of SOC to total nitrogen) from GSDE was used to evaluate the modeled soil C/N ratios by ORCHIMIC. Last, modeled annual heterotrophic respiration was compared to maps from Hashimoto et al. (2015) estimated by up-scaling site data from a global database (Bond-Lamberty & Thomson, 2010) using fitted functions of monthly air temperature and precipitation. All evaluation data set were re-gridded to $5^\circ \times 5^\circ$ and vegetation-types weighted averaged values (except for NCSCD v2) were calculated over grids with 50% of area was occupied by given vegetation type (Figure S1) and compared to those from ORCHIMIC. For NCSCD v2, SOC data at $5^\circ \times 5^\circ$ were directly compared with the output from ORCHIMIC. Our model results represented the average states from year 1901–1910, while the data used to evaluate the model represents the states for more modern time. Based on our previous simulation (Burke et al., 2017), the change of global total soil carbon between 1900 and 2000, one of the key state variables we trying to evaluate, is smaller than the differences among different data set used for evaluation. Thus, the data mentioned above should be able to be used as benchmark data to evaluate the model ORCHIMIC v2.0.

3. Results

3.1. Microbial Biomass Carbon

The global total soil microbial biomass predicted by ORCHIMIC was 20 Pg C, which is between the 14 Pg C estimated by Serna-Chavez et al. (2013) and the 24 Pg C found by Xu et al. (2013). The change of active biomass fraction generally followed that of ratio of microbial growth to death but with lag (Figure S1). The modeled microbial biomass was sensitive to the plant N-uptake flux we imposed, with a larger microbial biomass when the maximum allowed plant N uptake is smaller (Figure S2). The spatial pattern of microbial biomass carbon is similar to the empirical data of Xu et al. (2013) with a 3–4 times higher microbial biomass carbon in northern high latitudes than in the tropics. The spatial correlation coefficient at 5° resolution between model and data is 0.496 ($p = 2.0 \times 10^{-49}$). Area weighted averaged microbial biomass for 13 vegetation types (PFT) used in ORCHIDEE-MICT (Table S1) calculated based on the PFT map from Peng et al. (2017) are compared with empirical data in Figure 3c. The modeled PFT averaged microbial biomass were com-

Figure 4. Global distribution of microbial biomass C/N ratio from ORCHIMIC (a) and Xu et al. (2013) (b) and comparison between them for each plant functional type (PFT) with the circles are PFT averaged values and error bars show the standard deviations (c).

Figure 5. Global distribution of fraction of microbial biomass carbon in soil organic carbon in % from ORCHIMIC (a) and Serna-Chavez et al. (2013) (b) and comparison between them for each plant functional type (PFT) with the circles are PFT averaged values and error bars show the standard deviations (c).

parable (within one standard deviation) and positively correlated ($R = 0.826$, $p = 5.1 \times 10^{-4}$) to aggregated data from Xu et al. (2013).

3.2. Microbial Biomass C/N Ratio

The modeled microbial biomass C/N ratio is shown in Figure 4 and compared with the one estimated by Xu et al. (2013). The spatial pattern of observations was captured for South America and South Africa but not for the northern high latitudes where the model generally underestimated microbial C/N ratios. Though modeled microbial biomass C/N ratios were generally higher than those estimated by Xu et al. (2013) by 27%, they were correlated with the data ($R = 0.46$, $p = 0.11$) at PFT level and model outputs were within the range of one standard deviation of the Xu et al. (2013) observations. It should be noted that the predicted microbial C/N ratios are sensitive to the plant N uptake with generally lower C/N ratio where the maximum allowed plant N uptake is smaller (Figure S4). Despite the discrepancy, the relationship between microbial biomass C/N ratio and substrate C/N ratio modeled by ORCHIMIC v2.0 was similar to that observed based on data from Manzoni et al. (2017) (Figure S5). The increases of microbial biomass C/N ratio with one unit of increase for substrate C/N ratio were 0.20 and 0.16 from ORCHIMIC and data from Manzoni et al. (2017), respectively.

3.3. Fraction of Microbial Biomass Carbon in Soil Organic Carbon

The modeled fraction (f_{MBC}) of microbial biomass carbon in total SOC was close to the one estimated by Serna-Chavez et al. (2013) for global average. The modeled spatial patterns were also similar to those from Serna-Chavez et al. (2013) for South America, North America, Europe and Africa (Figure 5). However, it seems that the modeled f_{MBC} was generally underestimated for Asia and overestimated for Oceania. The modeled PFT averaged f_{MBC} were comparable to those estimated by Serna-Chavez et al. (2013) for most of the PFTs ($R = 0.455$, $p = 0.12$). The model underestimated f_{MBC} for Tropical Broadleaf Evergreen forest (TrBrEv) ($1.5\% \pm 0.3\%$ vs. $3.1\% \pm 1.5\%$) but still within the range of one standard deviation. If the maximum allowed plant N uptake is decreased to 1%, the modeled f_{MBC} are increased and f_{MBC} for the TrBrEV vegetation could reach $2.5\% \pm 0.5\%$ (Figure S6).

3.4. SOC

The spatial distribution of SOC modeled by ORCHIMIC is showed in Figure 6d and compared with those from WISE, GSDE, NCSCD v2 and ORCHIDEE-MICT simulation (Figure 6). The modeled global SOC (1,318 Pg C) and SOC in northern region (384 Pg C) were slightly lower than those from WISE (1,524 Pg C), GSDE (1,455 Pg C) and NCSCD v2 for northern regions (448 Pg C), respectively. The spatial pattern of SOC was captured by ORCHIMIC with high SOC stocks in northern high latitude. When the stocks were averaged per PFT, the correlation between modeled SOC from ORCHIMIC and from WISE or GSDE is high ($R = 0.982$ and 0.889 , respectively) (Figures 6g and 6h). For NCSCD region, that does not cover all the PFTs, we calculated a 5° spatial correlation of 0.39 ($p = 2.4 \times 10^{-11}$) (Figure 6f), not as good as between

Figure 6. Global distribution of soil organic carbon from World Inventory of Soil Emission Potentials (WISE) (a), Global Soil Data set for use in Earth System Models (GSDE) (b), ORCHIDEE-MICT (c), ORCHIMIC (d) and NCSCD v2 (e) and comparison of ORCHIMIC to NCSCD v2 (f, the circles are values for the $5^\circ \times 5^\circ$ grids), WISE (g, the circles are plant functional type [PFT] averaged values and error bars show the standard deviations), GSDE (h, the circles are PFT averaged values and error bars show the standard deviations) and ORCHIDEE-MICT (i, the circles are PFT averaged values and error bars show the standard deviations).

averaged PFT values at global scale. The ORCHIMIC underestimated SOC for grids with high SOC values typical from northern regions, but more than 76% of the modeled values still fall between the 2:1 line and 1:2 line. The modeled PFT averaged SOC were also highly correlated ($R = 0.99$, $p = 0.0$) to those from ORCHIDEE-MICT because the forcing of ORCHIMIC including FOM input, soil temperature and soil moisture were all from ORCHIDEE-MICT, but regression between ORCHIMIC and ORCHIDEE-MICT deviated from the 1:1 line due to the different decomposition processes in ORCHIMIC. As previously, the modeled SOC stocks were sensitive to the plant N uptake we imposed with lower SOC by 17.8% when the maximum allowed plant N uptake is reduced (Figure S7).

Figure 7. Global distribution of soil C/N ratio from ORCHIMIC (a) and GSDE (b) comparison between them for each plant functional type (PFT) with the circles are PFT averaged values and error bars show the standard deviations (c).

Figure 8. Global distribution of soil heterotrophic respiration from ORCHIMIC (a), ORCHIDEE-MICT (b), and Hashimoto et al. (c), and comparison between them for each plant functional type (PFT) ((d)–(f), the circles are PFT averaged values and error bars show the standard deviations).

3.5. Soil C/N Ratio

The modeled soil C/N ratios are showed in Figure 7a. The spatial patterns in South America, Africa and tropical Asia were captured by ORCHIMIC compared to those from GSDE (Wei et al., 2014) though overestimated, but not for the northern high latitudes. The modeled soil C/N ratios were smaller when the maximum allowed plant N uptake was reduced in a test from 5% to 1% (Figure S8). The modeled PFT averaged soil C/N ratios positively correlated with the GSDE data but with a low $R = 0.0250$ ($p = 0.94$), possibly due to the poor representation of plant N uptake as a model forcing. Spatial R at 5° resolution is lower, 0.087 ($p = 0.01$). Nevertheless, the global average of soil C/N ratio was comparable to the empirical upscaling from GSDE, which is also prone to extrapolation errors (12 ± 5 and 11 ± 5 , respectively).

3.6. Soil Heterotrophic Respiration

The global total soil heterotrophic respiration from ORCHIMIC, ORCHIDEE-MICT and Hashimoto et al. (2015) were very similar (all equal to 51 Pg C/yr). The spatial patterns were captured by ORCHIMIC and ORCHIDEE-MICT well, even though both tend to overestimate soil heterotrophic respiration in tropical regions (Figure 8). When heterotrophic respiration was averaged per PFTs, both models also correlated well with the Hashimoto et al. (2015) upscaling with R of 0.89 for both models. Finally, heterotrophic respiration from ORCHIMIC and ORCHIDEE-MICT were also highly correlated with each other ($R = 0.989$, $p = 0.0$ at 5° resolution). This is not surprising since we are comparing model at equilibrium where inputs are similar to outputs (heterotrophic respiration in this case) and we used FOM inputs from ORCHIDEE-MICT as boundary condition for ORCHIMIC. However, the seasonal cycle of total soil heterotrophic respiration was different between ORCHIMIC and ORCHIDEE-MICT (Figure S9). The seasonal cycles modeled by ORCHIMIC,

Figure 9. Relationship between carbon use efficiency (CUE) and ratio of substrate C/N to microbe C/N. The data from Manzoni et al. were download from <http://bolin.su.se/data/Manzoni-2017>. The data showed for ORCHIMIC were from the global simulation conducted in this study when maximum allowed plant N uptake was set to 1%.

ORCHIDEE-MICT and observed from data by Hashimoto et al. (2015) were similar, but the peak of soil heterotrophic respiration modeled by ORCHIMIC lagged for some PFTs.

3.7. Carbon Use Efficiency

CUE, defined as C uptake allocated to microbial biomass C growth, varies with substrate C/N ratio. CUE might be different for microbes with different C/N ratio. Thus, the relationship between CUE and substrate C/N to microbe C/N ratio, instead of that between CUE and C/N ratio of substrate or microbe, was investigated and compared with that observed by Manzoni et al. (2017) (Figure 9). CUE is generally close to the prescribed maximum value of 0.6 when ratio of substrate C/N to microbe C/N is smaller than a value around 1.7. CUE will decrease fast when ratio of substrate C/N to microbe C/N continues to increase. This is consistent with the observation from Manzoni et al. (2017) even though the range of the model ratio of substrate C/N to microbe C/N is higher than in the observations.

4. Discussion

ORCHIMIC is a new attempt for the explicit microbial biomass representation with nitrogen interactions at global scale with input data compatible with an ESM scheme. Variable microbial biomass C/N ratios were widely observed (Manzoni et al., 2017) and could theoretically modeled by including several microbial function groups with different C/N ratios. However, in homogeneous environment like a grid cell from a global scale model, competition would lead to one single microbial function group with just a little advantage over others at the end, unless some limitations were set. The case is similar for cheaters (microbes do not produce enzymes). For potential grid cells dominated by cheaters, there would be no SOM decomposition in long term and drop in the microbial biomass because cheaters do not produce exoenzymes. This is unrealistic, therefore, in ORCHIMIC v2.0, only one mega microbial functional group was applied, and much less parameters were needed compared to models with several microbial function groups. Various kinds of microbial function groups (e.g., SOM specialists, FOM specialists and cheater) were implicitly included, providing the possibility to implicitly model change microbial community. With these features, ORCHIMIC v2.0 reproduced a reasonable soil carbon stock with slower turnover but more consistent with observation compared to ESMs, and also showed lag in soil heterotrophic respiration peak within a year compared with that from ORCHIDEE-MICT and Hashimoto et al. (2015), suppressed microbial biomass growth under climate warming, varying microbial C/N ratio with changing substrate C/N ratio and dynamic CUE modified by substrate stoichiometry. With different maximum allowed plant N uptake, the effect of plant N uptake could also be roughly investigated.

4.1. Soil Carbon Stock and Its Turnover Time

The total soil carbon stock was well represented. Nevertheless, the improvement compared to the ORCHIDEE-MICT model with a soil module based on CENTURY model (Parton et al., 1987) was not very impressive. When compared to observation-based products, we observed an overestimation of the stock for ORCHIDEE-MICT and an underestimation for ORCHIMIC. The total soil carbon stocks in the top 1 m soil obtained with ORCHIMIC (1,318 Pg C) was lower than the that predicted by ORCHIDEE-MICT (1,918 Pg C), while the GSDE and WISE data gave an estimation between 1,455 and 1,524 Pg C, respectively. Since both models have similar inputs fluxes only a different average turnover time can explain such differences. At equilibrium, turnover time can be estimated by dividing the stock by the input or respiration. In that case we obtained a global estimation of 25.8 years for ORCHIMIC lower than 37.6 years for ORCHIDEE-MICT whereas Raich and Schlesinger (1992) and Amundson (2001) estimated global average turnover times between 18.5 and 32 years based on observations. ESMs tends to overestimate turnovers (He et al., 2016; Shi et al., 2020), ORCHIMIC in this case performed better than ORCHIDEE-MICT. However, the turnover time was less sensitive to temperature in ORCHIMIC than in ORCHIDEE, especially in cold regions (Figure S11). Koven et al. (2017) showed high turnover sensitivity to temperature in cold regions than in warm regions while this pattern was only captured by an Earth system models with explicitly resolving of vertical gradients in soil climate and carbon turnover and by a simplified model with soil freeze-thaw

state processed included. The top 1 m soil was regarded as a single bulk vertically integrated soil pool in ORCHIMIC, while it was discretized into 10 layers in ORCHIDEE-MICT. Also, freeze-thaw processes were included in ORCHIDEE-MICT but not in ORCHIMIC. These might explain the poor representation of soil C turnover sensitivity to temperature. Thus, coupling ORCHIMIC into an ESM with discretized soil layers and freeze-thaw processes is very necessary to accurately project future carbon-climate feedbacks.

4.2. Change of Soil Heterotrophic Respiration Temporal Dynamics

The litter input used in ORCHIMIC was obtained from ORCHIDEE-MICT and the heterotrophic respiration should be equal to litter input at equilibrium, leading to similar spatial distribution of heterotrophic respiration from the two models (Figures 8a and 8b). The concurrence of peaks for heterotrophic respiration and litter input was observed in ORCHIDEE-MICT and the study by Hashimoto et al. (2015), but not in ORCHIMIC. This change in soil heterotrophic respiration temporal dynamics might have influences on the timing and magnitude of net terrestrial CO₂ exchange with the atmosphere (Basile et al., 2020). Both in ORCHIDEE-MICT and the study by Hashimoto et al. (2015), soil respiration was function of soil temperature and the substrate concentration. When the effect of the substrate concentration was smaller than that of soil temperature, the peak of respiration would concur with that of soil temperature (for most of PFTs in Figure S9). However, the peak of respiration might appear earlier than that of soil temperature when the substrate concentration decreased significantly before the peak of soil temperature (PFT 7 and 9 in Figure S9). The delay of respiration peak modeled by ORCHIMIC could be partly explained by the delay of microbial growth (the growth respiration showed in Figure S9). Besides, the seasonal cycle of plant N uptake followed the NPP and plant N fixation was missed in ORCHIMIC, making soil N limited for microbes when NPP was high and the time after. Consequently, the ratio of C and N taken up by microbes might be larger than the upper limit of prescribed microbial biomass C/N ratio range, then overflow respiration would happen, leading to lag of respiration peak. Considering that N fixation rate increases with litterfall (Jurgensen et al., 1992; Grant, 2013), the intensity of overflow respiration in reality might be weaker (or say microbes are less N limited) during this period. Though the ability of ORCHIMIC v2.0 to reproduce temporal variation of soil respiration was not fully evaluated in this study due to unrealistic representation of plant N uptake and lack of N fixation in the model. However, our previous work has showed that the ORCHIMIC v1.0 effectively captured the temporal dynamics of respiratory fluxes and even the magnitude of priming effect from an incubation experiment without N limitation, while the traditional CENTURY model and even the PRIM model aimed to include priming effect not (Huang et al., 2018).

4.3. Temperature Modulated Microbial Pool

The modeled total microbial biomass was within the range of two global scale estimations by Serna-Chavez et al. (2013) and by Xu et al. (2013). Dormancy is an important feature of microbes. Distinction between active and dormant microbes is essential to reproduce the microbial biomass and to explain variation in SOM decomposition (G. Wang et al., 2015). Although ORCHIMIC makes the distinction between active and dormant microbial biomass (Text S1.1), and microbial enzymatic production and respiration fluxes are mainly due to active microorganisms (Lennon & Jones, 2011), most of the soil microbial biomass measurements were done based on fumigation extraction techniques (Vance et al., 1987) which only measure the total biomass including dormant and active microbes. This makes the evaluation of the model would be rather complicated since very few data measure only active microorganisms. Indeed, such measurements are based on several techniques with their pros and cons (e.g., plate count, cell staining or with molecular approaches, see Blagodatskaya and Kuzyakov (2013) for review) but estimation of active microorganisms at global scale is still unavailable. Moreover, the fractions of dormant and active microorganisms depend on the environmental conditions and is therefore time-dependent (De Nobili et al., 2001). Therefore, only total soil microbial biomass products are available at global scale to evaluate such kind of models (Serna-Chavez et al., 2013; Xu et al., 2013). Although the growth rate of microbes (see growth respiration in Figure S9) was larger in summer than in other seasons due to fast decomposing under high temperature, the microbial biomass in summer was smaller than in other seasons due to high maintenance respiration cost and death rate. Higher microbial biomass in spring, autumn and winter than in summer was also previously reported by Xu et al. (2018) and Díaz-Raviña et al. (1995). Thus, increasing SOM decomposition rate with increasing tem-

perature might not last if acclimation of microbes is not fast enough, suggesting a non-linear response of SOM decomposition to climate warming, which differs from that simulated by SOM decomposition models with first order kinetics. With first order kinetics, SOM decomposition would increase with temperature and release large amount of C into atmosphere accelerating global warming and resulting in a positive feedback between climate and soil C pool. However, our model results indicated that this positive feedback might be weakened or even disappear as the result of suppressed growth of microbe due to high maintenance respiration cost and death rate under warming climate. To our knowledge, experiments testing this idea are not available but if our model feature is supported by observations this may deeply modified the soil response to climate change predict by Earth system models that are all based on first order kinetics.

The modeled active biomass fraction was in the range of 4%–49% previously reported (Blagodatskaya et al., 2014; He et al., 2015; Van De Werf & Verstraete, 1987). Relatively high active microbial biomass fraction was found in warm regions (Figure S11). However, low active biomass fraction was observed in warm season (Figures S2 and S11), due to high maintenance respiration cost and N limitation caused by strong plant N uptake in warm season in our model, implicating that N availability might be a controlling factor on dormancy, which is consistent with that found by He et al. (2015).

4.4. Increasing Microbial C/N Ratio With Increasing Soil C/N Ratio

The soil C/N ratio predicted by ORCHIMIC was close to observations as global average, but the spatial distribution was not well captured by the model, mainly because plant N uptake was not explicitly represented, and N fixation was missing. However, similar relationship between microbial biomass C/N ratio and substrate C/N ratio as revealed by Manzoni et al. (2017) was also reproduced by ORCHIMIC (Figure S5), suggesting that the model might be able to reproduce global spatial distribution of C/N ratios for both soil and microbe if plant N uptake and N fixation were well represented. The increase of microbial biomass C/N ratio was much slower compared to substrate C/N ratio, which could be partly explained by the dynamic enzyme production scheme introduced in ORCHIMIC v2.0. Under high substrate C/N condition, microbes will assimilate more C leading to increase of C/N ratio of microbial biomass, but with the dynamic enzyme production scheme, microbes would try to exploit more N from substrate, which will contribute to slower increase of microbial biomass C/N ratio.

4.5. Mechanistic Representation of Dynamic Carbon Use Efficiency

CUE is one of the key variables controlling soil C dynamic (Manzoni et al., 2008; Sinsabaugh et al., 2008). It determines the split of C assimilated by a given community between the respiration flux going back to the atmosphere and the growth flux to create biomass. CUE is fixed in classical ESMS, whereas varied CUE controlled by environmental factors like N availability, temperature, etc. was observed (Sinsabaugh et al., 2013; Manzoni et al., 2017). Thus, models aiming at working at global scale should focus more on their ability to reproduce such fundamental variables dynamic like CUE. We previously showed that ORCHIMIC reproduced well some CUE dynamic impacting the respiration fluxes (Huang et al., 2018). Zhang et al. (2018) presented a simple alternative approach that could also reproduce the observed heterotrophic respiration fluxes modified by CUE changes with less parameters, representing perhaps a less risky alternative. Nevertheless, complex and finely detailed mechanistic models are still important to understand the mechanisms behind some emerging properties of ecosystems. As showed in Figure 9, relationship between CUE and ratio of substrate C/N ratio to microbial C/N ratio observed in ORCHIMIC is consistent with that found by Manzoni et al. (2017) based on observation, indicating a reasonable representation of CUE related processes in ORCHIMIC. In ORCHIMIC, only a maximum CUE value of 0.6 supported by thermodynamic calculations (Sinsabaugh et al., 2013) was set, and dynamic CUE was represented in a mechanistic way without introducing extra parameters. The C/N ratio of uptake flux by microbes was generally around that of substrate. When the ratio of substrate C/N to microbe C/N is smaller than a threshold, all C, except those consumed through maintenance respiration, growth respiration and enzyme production, would contribute to microbial biomass C growth, and thus CUE would close to 0.6. The threshold should theoretically be around 1.67 (equal to $1/0.6$). It should be noted that the C uptake is used for maintenance respiration and enzyme production first and microbial C/N ratio is also variable in ORCHIMIC. Thus, the threshold should be a value larger than 1.67 (around 1.7 in Figure 9). CUE would decrease fast after exceeding

this threshold, characterized with the occurrence of overflow respiration. When the amount of C uptake is small, resulting in that the C used for maintenance respiration and enzyme production could be comparable to that could be used for growth, CUE should be smaller than that expected. The C/N ratio of microbes could be variable as modeled in ORCHIMIC might be another explanation of scattered CUE under given ratio of substrate C/N ratio to microbial C/N ratio.4.7 Limitations

In ORCHIMIC, both decomposition of soil organic matter and uptake of C and N by microbes followed the forward Michaelis-Menten kinetics instead of the equilibrium chemistry approximation (ECA) kinetics suggested by Tang and Riley (2013). With diffusion limitations, size contrast between microbes and monomer substrates, and that between enzymes and polymer particles considered, Tang and Riley (2019) showed that microbial uptake and enzymatic depolymerization closely followed the forward Michaelis-Menten kinetics and the reverse Michaelis-Menten kinetics, respectively, while both of them could be well represented by ECA kinetics. The ECA kinetics were demonstrated as a better option in representing microbial and enzymatic dynamics (Tang & Riley, 2019; B. Wang & Allison, 2019), especially when competition among plants, microbes, and mineral surfaces were included (Zhu et al., 2016). Thus, ECA kinetics should be included in future model development, especially in modeling decomposition of FOM and SOM substrates.

Although a “trade off” mechanism was included when modeling microbial uptake for C and N, that one molar C trade with one molar N in optimal condition during the uptake of C and N is remain to be discussed, thus, more researches are needed to fill this gap. As showed in Figures 4 and 7, the modeled microbial C/N ratio and soil C/N ratio differed from those reported, possibly because plant N uptake and N fixation were not explicitly represented in the model, and feedbacks of plant N uptake were also not included. We noted that the model behavior was also affected by the assumption that plant N uptake could not exceed 1% or 5% of available N. If there was no such limit, microbes could be more N limited and might result in more overflow respiration when NPP was high. In meantime, N fixation might compensate the N taken by plants and thus increase the N availability for microbes. Thus, large uncertainties could be expected due to the rough assumption for plant N uptake and miss of N fixation. Efforts to couple plant N uptake and other N related processes into the model are rather necessary to rightly represent the microbial and soil dynamics and then carbon-climate feedback.

Explicit representation of N in large scale models is becoming more common (Tian et al., 2018) and long term trends of primary production are controlled by N availability in such models, in particular in boreal regions (Guenet et al., 2013; Thomas et al., 2013). The modeled microbial biomass and C/N ratio, soil organic matter and C/N ratio by ORCHIMIC varied with the plant N uptake flux imposed (Figures 3–7 and their paired items in supporting information), even though the feedback between the latter and litter input was not included. Such high sensitivities of microbial related parameters to plant N uptake may induce large instability once ORCHIMIC is fully coupled with a plant module. This highlights the difficulty of explicit representation of soil microorganisms in an ESM where several feedbacks between soil, plant and climate are represented and suggests that some necessary simplifications are needed to make the model stable.

5. Conclusions

We applied here a soil model with explicit representation of microbial biomass with flexible C/N ratio at global scale and were able to capture most of the observations for the model outputs considered. Our approach also has a representation of the N cycle and we showed that microbial C/N ratio used here as a surrogate for community structure was very sensitive to plant N uptake with important impact on the soil C dynamic in the long term. The consistent relationship between microbial C/N ratio and substrate C/N ratio with observation demonstrated that the ability of our model to reproduce global C/N ratios of microbe and soil pool if with plant N uptake and N fixation included. Similar dynamic CUE with changing ratio of substrate C/N ratio to microbe C/N ratio as observation could also be modeled by explicitly representing microbial dynamics.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the analysis and conclusions could be found via DOI: [10.5281/zenodo.4050604](https://doi.org/10.5281/zenodo.4050604).

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