A Computationally Efficient Method for Parameter Sensitivity Analysis of Microbially Explicit Biogeochemical Models Accounting for Long-Term Behavior

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Abstract Microbial ecological models become increasingly complex owing to the incorporation of many parameters and multiple biotic and abiotic processes. However, little attention has been paid to the variations in the parameter sensitivity during long-term versus short-term simulations. Here, we developed a Multi-Objective Parameter Sensitivity Analysis (MOPSA) method to efficiently identify the important parameters in complex microbial ecological models with multiple response variables of interest in terms of short- and long-term model simulations. We found that MOPSA was more computationally efficient for complex microbial ecological models than Sobol's method because of MOPSA's reliability and low computational sample size. In addition, we address the increased significance of microbial physiology in mediating long-term than short-term soil C-N cycling, indicating that experiment-model integration practices should examine model behaviors beyond the conventional short-term experimental period. The outcomes of this study provide an efficient global sensitivity analysis method for parameterization and the scientific foundation for microbial physiology in mediating long-term microbial ecological processes.

Plain Language Summary Biogeochemical cycles can be effectively characterized by process-based modeling. Microbial ecological models are more intricate and include more parameters in comparison to traditional ecological models. This complexity demands substantial computational resources when using current methods to estimate model sensitivity to different parameters. To address this challenge, we developed an efficient global sensitivity analysis method, known as Multi-Objective Parameter Sensitivity Analysis (MOPSA). Using MOPSA, we successfully conducted sensitivity analyses over both short and long timeframes for the complex microbial model. Our study reveals that microbial physiology becomes more significant in mediating long-term carbon and nitrogen cycling, compared to short-term processes. This highlights the need to pay close attention to the long-term processes when we conduct experiment-model integration practices.

1. Introduction

Increasing attention is being paid to the complex ecosystems and their responses to climate change (Babin, 2020; Halbritter et al., 2020; Rineau et al., 2019). Process-based models have been developed to facilitate the understanding of complex biogeochemical cycles (Gardner et al., 2020). Particularly, the recent development of microbial ecological models has increased model complexity (Kyker-Snowman et al., 2020; Sulman et al., 2017; Tang & Riley, 2015; Trivedi et al., 2016; Wang et al., 2022). Parameterization of such models is a grand challenge and requires a better understanding of the model parameters and their controls on biogeochemical processes (Reimer et al., 2022; Saifuddin et al., 2021). Sensitivity analysis is therefore an indispensable tool to fulfill the purpose of a successful model parameterization and interpretation of the effects of specific parameters on model processes and relevant results (Nossent et al., 2011). However, few sensitivity analyses have been conducted pertaining to microbial ecological models with a variety of soil microbial and carbon-nitrogen (C-N) variables.

The importance order of parameters to the model output may differ between short- and long-term simulations when the model contains time-dependent nonlinear processes (Song et al., 2013). The temporal scale can be very different for different ecological processes (Allison et al., 2010; Jian et al., 2020). In this study, we define a period of less than 5 years as the short term from the perspective of soil organic matter turnover (Georgiou et al., 2017; Klumpp et al., 2007; Lajtha et al., 2005). The concern is whether the small perturbation in the short-term (<5 years) simulations would cause large variation in the long-term (several decades to hundreds of years)

simulations. For microbial ecological models, long-term model behavior at the 100-year scale has not been sufficiently investigated (Jian et al., 2020). Specifically, it is not clear whether microbial physiological parameters significantly influence the simulation of long-term ecological processes. Therefore, it is necessary to explore the differences in parameter sensitivity of microbial ecological models between the short- and long-term time scales, as well as the effects of microbial physiological parameters on ecological processes, especially in the long term.

Global sensitivity analysis is becoming increasingly popular because it provides a comprehensive measure of sensitivity in case of nonlinearities and interactions among parameters (Dai et al., 2019). The representative global sensitivity methods are Sobol's method (Sobol, 1990) and multi-parametric sensitivity analysis (MPSA) (Hornberger & Spear, 1981), which are widely used in model sensitivity analyses (Butler et al., 2014; Liu et al., 2011; Zi et al., 2005). However, there are still problems with the global parameter sensitivity analysis: (a) most of the methods focus on the parameter sensitivity pertaining to a single objective (i.e., response variable), however, accounting for multiple objectives in ecosystem modeling requires to integrate the sensitivity analysis results of each objective; (b) the computational cost increases with the number of parameters (Sarrazin et al., 2016), which appeal for a more efficient sensitivity analysis method, particularly for complex microbial ecological models; and (c) for the methods based on the cumulative distribution of parameters (e.g., MPSA), the division of acceptable and unacceptable parameter clusters lacks objectivity.

The MEND model is one of the microbially explicit biogeochemical models that have been progressively developed in recent years (Sulman et al., 2018; Wieder, Allison, et al., 2015). MEND has been tested in different soils and ecosystem from laboratory to field and global scale (Gao et al., 2020; Jian et al., 2020; Wang, Peng, et al., 2019). We used the MEND model as an example to explore efficient global sensitivity analysis methods accounting for long-term model behavior. In our study, we chose the Dinghushan broadleaf forest ecosystem as a case study. The Dinghushan Biosphere Reserve, where this ecosystem is located, benefits from a distinctive geographical advantage, characterized by intact southern subtropical zonal forests. The Dinghushan Station within the reserve has established numerous permanent sample plots within typical forest ecosystems, providing abundant field measurement data [Zhou et al., 2013].

This study aims to facilitate the understanding of microbial ecological processes in the short- and long-term based on a comprehensive and efficient global sensitivity analysis. To this end, we proposed a new MPSA, namely Multi-Objective Parameter Sensitivity Analysis (MOPSA), to objectively measure the sensitivities of multiple objectives of response variables to varying parameter values. We demonstrate the applicability, repeatability (i.e., reliability), and computational efficiency of the proposed MOPSA, further facilitating efficient model calibration against field experimental data. Then, we compared the sensitivity results between short-term (three-year) and long-term (100-year) model simulations. Finally, we analyze microbial effects on C-N processes over time. We expect to better understand the role of microbes in regulating long-term soil biogeochemical processes by developing and implementing a thorough and efficient global sensitivity analysis.

2. Materials and Methods

2.1. Sensitivity Analysis Methods

Here, we introduce the sensitivity analysis methods (i.e., MOPSA and Sobol's method), the procedures to implement them for a sensitivity analysis, the quantification of the sensitivity index, and the determination of the overall sensitivity scalar of a parameter pertaining to multiple response variables. In this context, a sensitive parameter means that the model outputs (i.e., values of a response variable) are sensitive to a change in this parameter.

2.1.1. Multi-Objective Parameter Sensitivity Analysis (MOPSA) Method

The proposed MOPSA has three important features (Figure 1): (a) it divides the parameter samples into ten equal-sized clusters (see Step (5) and (6) and Equation 3), which has been effectively adopted in other studies (Noacco et al., 2019; Sajid, 2021; Wagener et al., 2001) to avoid arbitrarily specifying a threshold between behavioral and non-behavioral clusters; (b) it quantifies the differences among different parameter clusters based on the non-parametric Wilcoxon Rank Sum Test (Conover, 1998), which does not require known parameter distributions; and (c) it reflects the importance of each parameter to multiple response variables by developing a normalized overall sensitivity scalar (i.e., $SO_k \in (0,1]$, see Step (7) and Equation 4). The proposed MOPSA defines the
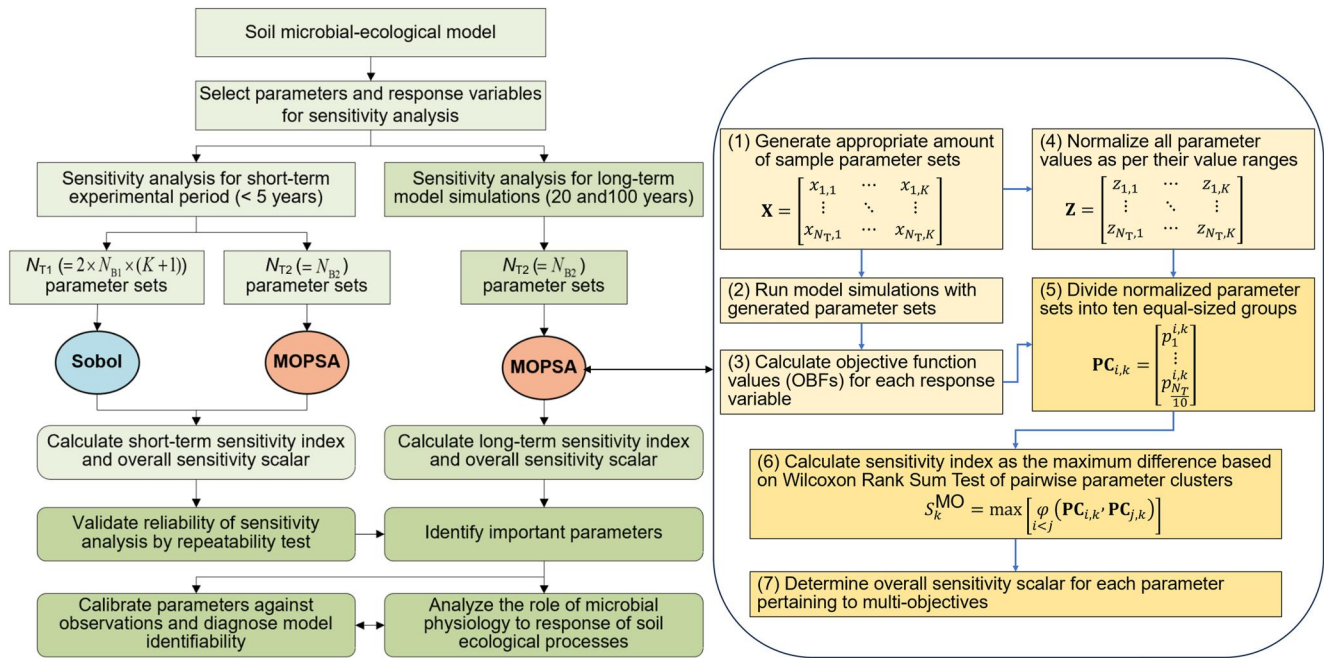
Figure 1. The framework of sensitivity analysis for the short- and long-term model simulations. The short-term covered the 3-year experiments with field observations. The long-term covered 20-year and 100-year long periods (2009–2029 and 2009–2109) including both the three-year experimental period (2009–2012) and the post-experimental period (2013–2109). N_{T1} and N_{T2} are the total sample size for Sobol's method and Multi-Objective Parameter Sensitivity Analysis (MOPSA), respectively; N_{B1} and N_{B2} are the base sample size for Sobol's method and MOPSA, respectively; and K is the number of parameters. The procedure of MOPSA is shown in the box on the right, with detailed descriptions provided in Section 2.1.1.

sensitivity index as the maximum difference in pairwise comparisons of the 10 parameter clusters, where the "between-cluster" difference is defined as the Wilcox "estimate" (R Development Core Team, 2021). The procedure for MOPSA consists of seven main steps (Figure 1 and Figure S1 in Supporting Information S1).

Step (1) Generate sample parameter sets. Obtain an adequate amount of sample parameter sets by random sampling within the defined range for each parameter (see Section of sampling for sensitivity analysis). The nth sample parameter set ($n = 1, 2, \cdots, N_T$) is $\mathbf{X}_n = (x_{n,1}, x_{n,2}, \cdots, x_{n,K})$ including K parameters. Thus, a total of N_T sample parameter sets ($\mathbf{X}$) are generated.

Step (2) Run the model simulations with generated parameter sets.

Step (3) Calculate the objective function values (OBFs). Calculate OBFs of a specific response variable (e.g., C or N pool or flux). The OBF is defined as the mean squared error (MSE) that reflects the deviation of the simulated output values relative to the reference values over time:

$$f_{m,n}^{\text{obj}} = \sum_{t=1}^{T} \left(Y_{m,n,t} - Y_{m,t}^{\text{ref}} \right)^2 \tag{1}$$

where $f_{m,n}^{\text{obj}}$ denotes the OBF of the nth sample parameter set ($n = 1, 2, \cdots, N_T$) as per the mth response variable ($m = 1, 2, \cdots, M$); $Y_{m,n,t}$ is the simulated output value of the nth sample parameter set at time t ($t = 1, 2, \cdots, T$); and $Y_{m,t}^{\text{ref}}$ is the reference value at time t, which specifically refers to the value simulated by the reference parameter set. Usually, the reference parameter set is made up of the median of each parameter range (Choi et al., 1999).

Step (4) Normalize samples of each parameter according to their value ranges with the following formula:

$$z_{n,k} = \frac{x_{n,k} - x_k^{\min}}{x_k^{\max} - x_k^{\min}} \tag{2}$$

where $x_{n,k}$ denotes the original value of the nth sample ($n = 1, 2, \cdots, N_T$) of the kth parameter ($k = 1, 2, \cdots, K$) in the model; $x_k^{\min}$ and $x_k^{\max}$ denote the minimum and maximum value of the kth parameter, respectively; and $z_{n,k}$ denotes the normalized value of $x_{n,k}$. Thus, N_T normalized sample parameter sets ($\mathbf{Z}$) are obtained.

Step (5) Divide $\mathbf{Z}$ into ten equal-sized groups as per the sorted OBFs in ascending order (Naranjo et al., 2012). A given parameter k's values are ordered according to the objective function value of each simulation that the parameter with that value was used in, then divided into 10 clusters.

Step (6) Quantify the sensitivity of a parameter pertaining to a given response variable. Since the probability distribution of a parameter is often unknown, the non-parametric Wilcoxon Rank Sum Test is performed to test the significance of the difference in the cumulative distribution between pairwise parameter clusters. To adequately reflect the parameter sensitivity, we define the sensitivity index as the maximum Wilcox "estimate" of the pairwise differences based on normalized parameter clusters (R Development Core Team, 2021):

$$S_k^{\text{MO}} = \max\left[\underset{i<j}{\varphi}\left(\mathbf{PC}_{i,k}, \mathbf{PC}_{j,k}\right)\right] \tag{3}$$

where S_k^{MO} denotes MOPSA's sensitivity index of the kth parameter ($k = 1, 2, \cdots, K$); $\mathbf{PC}_{i,k}$ denotes ith cluster ($i = 1, 2, \cdots, 9$) of the kth parameter; $\mathbf{PC}_{j,k}$ denotes jth cluster ($j = 2, \cdots, 10$) of the kth parameter; and $\varphi(\mathbf{PC}_{i,k}, \mathbf{PC}_{j,k})$ denotes Wilcox "estimate", that is, the median of the differences between $\mathbf{PC}_{i,k}$ and $\mathbf{PC}_{j,k}$. A greater difference indicates a higher sensitivity of a given response variable to the change in a parameter. In addition, the p-value of the Wilcoxon Rank Sum Test is used to assess whether the sensitivity is statistically significant ($p < 0.05$) or not.

Step (7) Determine the overall sensitivity of a parameter as per M response variables (i.e., multiple objectives). The above analysis (i.e., Step (1) to Step (6)) is for a single objective (i.e., a single response variable) when $M = 1$. If there are multiple response variables for sensitivity analysis, the overall sensitivity of a parameter can be estimated from the rankings of the sensitivity indices for each response variable rather than from the actual values of sensitivity indices, as this is less susceptible to the extreme values (Makler-Pick et al., 2011). The overall sensitivity scalar of a parameter is calculated as:

$$SO_k = \frac{1}{K \times M} \sum_{m=1}^{M} SIR_{k,m} \tag{4}$$

where $SO_k \in (0,1]$ is the overall sensitivity scalar of the kth parameter ($k = 1, 2, \cdots, K$) to all response variables; and $SIR_{k,m}$ is the ranking ($SIR_{k,m} = 1, 2, \cdots, K$) of the kth parameter as per the mth response variable ($m = 1, 2, \cdots, M$). The rankings are based on the values of sensitivity indices in ascending order and a higher ranking means a higher sensitivity index. A higher overall sensitivity scalar (SO_k) indicates that the parameter is more important for all response variables.

2.1.2. Sobol's Method

Sobol's method determines the contribution of each parameter and their interactions to the variance of the output (Sobol, 1990), which can handle nonlinear and nonmonotonic functions and models. The model output is represented as:

$$Y = f(\mathbf{X_s}) = f(x_1, x_2, \cdots, x_K) \tag{5}$$

where Y is the model output (or objective function); and $\mathbf{X_s} = (x_1, x_2, \cdots, x_K)$ is the parameter set including K parameters. In this paper, the objective function of Sobol's method is consistent with that of MOPSA, that is, Equation 1. Assuming that the parameters are mutually orthogonal, the total variance can be decomposed into the following form:

$$V(Y) = \sum_{k=1}^{K} V_k + \sum_{k=1}^{K-1} \sum_{q=k+1}^{K} V_{k,q} + \cdots + V_{1,\ldots,K} \tag{6}$$

The Sobol's sensitivity indices are calculated from the ratio of the partial variance to the total variance:

$$S_k^{\mathrm{F}} = \frac{V_k}{V} \tag{7}$$

$$S_k^{\mathrm{TO}} = S_k + \sum_{q \neq k} S_{k,q} + \cdots \tag{8}$$

where S_k^{F} is the first-order index of the kth parameter; and S_k^{TO} is the total-order index of the kth parameter. The first-order sensitivity index is used as the main effect to measure the partial contribution of a single parameter to the output variance. The total-order sensitivity index considers both first-order, second-order, and higher-order effects.

Due to the complexity of microbial ecological models, Sobol's sensitivity index is solved by Monte Carlo integration (Saltelli et al., 2010). A higher Sobol's sensitivity index implies that the parameter has a greater influence on the model outputs (Nossent et al., 2011). When multiple objectives are considered, the overall sensitivity scalar of a parameter is calculated according to Equation 4 based on the rankings of the total-order sensitivity indices.

2.2. Sampling for Sensitivity Analysis

The quasi-random Sobol sequence is a sampling method with good convergence and determinism (Renardy et al., 2021). We used the Sobol sequence to generate base parameter samples of Sobol's method and MOPSA. In Sobol's method, two independent sample matrices of size $N_{\mathrm{B}1} \times K$ are employed to compute the Monte Carlo integrals, where $N_{\mathrm{B}1}$ represents the number of base samples, and K is the number of parameters. Based on these two matrices, Saltelli (2002) developed a method to estimate the Sobol's sensitivity index, with a total sample size of $N_{\mathrm{T}1} = 2 \times N_{\mathrm{B}1} \times (K + 1)$. The total sample size for MOPSA is $N_{\mathrm{T}2} = N_{\mathrm{B}2}$, which depends only on the number of base samples ($N_{\mathrm{B}2}$) (Choi et al., 1998). For a general model (within 20 parameters), a few hundred parameter samples may suffice to meet the MPSA's calculation requirements [Choi et al., 1998], while for complex models, 2,000 and more parameter samples might be necessary (Zi et al., 2005). MOPSA is less influenced by the complexity of the model compared to Sobol's method.

The base sample sizes ($N_{\mathrm{B}1}$ and $N_{\mathrm{B}2}$) do not necessarily have to be the same for the two methods (Sobol and MOPSA). We conducted individual tests of the base sample sizes for MOPSA and Sobol's method to determine adequate sample sizes. The adequacy of the number of parameter samples is tested by the uncertainty of the sensitivity index (i.e., half of the 95% confidence interval) (Sarrazin et al., 2016). The confidence interval for Sobol's sensitivity index is calculated by the bootstrap resampling method (Efron & Tibshirani, 1993). The confidence interval for the MOPSA's sensitivity index is obtained from Wilcoxon Rank Sum Test (R Development Core Team, 2021). The number of parameter samples is adequate if the uncertainty interval of the highest sensitivity index for a response variable does not exceed 10% of its value, indicating that the sensitivity results are convergent (Zhang et al., 2015).

We calculated short-term (3-year) sensitivity indices using Sobol's method with 109, 2,000, 4,000, 6,000, and 8,000 base samples, resulting in corresponding total sample sizes of 8,066 ($=2 \times 109 \times 37$), 148,000, 296,000, 444,000, and 592,000, respectively. For MOPSA, the total and base sample sizes were consistent, set at 2,000, 4,000, 6,000, and 8,000, respectively. Note that Sobol's sample size of 8,066 was the closest to MOPSA's sample size of 8,000. During the long-term simulations, we calculated 20-year sensitivity indices using Sobol and MOPSA, based on sample sizes of 592,000 and 8,000, respectively. Additionally, we employed MOPSA with 8,000 total samples to derive 100-year sensitivity indices.

2.3. Microbial-ENzyme Decomposition (MEND) Model

Sensitivity analysis was performed on the latest MEND model (Wang et al., 2022). The MEND model describes the transformation processes of soil C and N by explicitly representing the relevant microbial and enzymatic physiology. The C-N processes include soil organic matter (SOM) decomposition, microbial N mineralization and immobilization, nitrification, denitrification, biological N fixation, and plant-microbe competition on inorganic N. Unlike some conventional models using fixed soil C and N stoichiometry (Bonan et al., 2013; Thornton

& Rosenbloom, 2005), the C:N stoichiometry of the SOM and microbial pools of the MEND model varies over time. Microbes respond to resource stoichiometric imbalances, increasing the difficulty to model calibration compared to models with fixed C:N ratios or model calibrations as per C or N individually. We need to consider the C and N stoichiometry, in addition to the C and N pools, within reasonable limits. The structure of the MEND model is shown in Figure S2 in Supporting Information S1, while the governing equations and component fluxes of the MEND model are detailed in Tables S1, S2, and S3 in Supporting Information S1.

We selected 36 model parameters for the sensitivity analysis and set the parameter sampling ranges (Table 1) based on the profile of the study area and previous studies on the MEND model (Wang, Huang, et al., 2019; Wang et al., 2020; Wang et al., 2021). The model outputs included 11 major C-N related response variables (Table 2, the subscript CN denotes the C:N ratio): (a) four soil microbial variables, that is, total microbial biomass C (MB), active microbial biomass C (MBA), and the C:N ratios in these two microbial pools, that is, MB_{CN}, and MBA_{CN}; (b) one enzyme variable (ENZ) representing the total concentration of all C-N related enzymes; (c) soil respiration flux variable (CO_2), (d) two SOM variables (SOM and SOM_{CN}); and (e) three inorganic N variables, that is, NH_4^+, NO_3^-, and N_2O.

2.4. Model Data and Analysis Design

The study area is a subtropical broadleaf forest in the Dinghushan Biosphere Reserve (DBR) in southern China (Zhou et al., 2014). Soils in the DBR are classified as Ultisol according to the United States Department of Agriculture (USDA) soil classification (Wang, Huang, et al., 2019). We drove the model simulations with forcing climatic and environmental data including soil temperature, moisture, pH, litter biomass, and wet and dry N deposition rates (Figure S3 in Supporting Information S1). The field experimental data covered the period from August 2009 to December 2012 (Wang et al., 2020). The time step was hourly in our model simulations.

To examine the sensitivity results as per the model behaviors under short-term (<5 years) and long-term (several decades to hundreds of years) simulations, we designed two strategies with contrasting simulation periods (i.e., the short-term vs. the long-term) to implement the sensitivity analysis of the MEND model. The short-term strategy was limited to the same period as the three-year experiments with field observations, that is, from August 2009 to December 2012. The long-term strategy covered a 100-year period (2009–2109) including both the three-year experimental period (2009–2012) and the post-experimental period (2013–2109). As for the post-experimental period, we used the forcing data during 2009–2012 as cyclic inputs to drive the long-term model simulation (Figure 1).

Sobol's method and MOPSA were applied to the short-term (3-year) and long-term (20-year) sensitivity analyses of the MEND model. We validated the reliability of the two methods and determine important parameters based on the short-term sensitivity analysis (Figure 1). According to the identified important parameters, we performed model calibration and identifiability against field experimental observations. MOPSA was also used for long-term (100-year) sensitivity analysis due to its low computational cost. We calculated the sensitivity contribution ratios of the microbial parameters to reflect changes in the relative importance of these parameters over the short-term (3-year) and long-term (100-year) biogeochemical processes. In addition, we simulated the response of C-N variables to individual parameter changes in the short and long term to analyze microbial effects on C-N processes over time.

2.5. Validation Method for Sensitivity Analysis

A reliable sensitivity analysis should be reproducible pertaining to the sensitive parameters of the model through the validation method (Andres, 1997). The repeatability test evaluates the rationality of the classification of sensitive and non-sensitive parameters by analyzing the correlations between the model outputs from three well-designed parameter groups (Tang et al., 2007): (a) Group 1: randomly generate parameter samples using the Latin hypercube sampling (Helton & Davis, 2003) with uniform distribution as per each parameter's value range, and N_R (e.g., 1,000) sample parameter sets are constructed (Nossent et al., 2011); (b) Group 2: replace the sensitive parameters in Group 1 with their apriori values, and non-sensitive parameter values remain the same as Group 1; (c) Group 3: replace the non-sensitive parameters in Group 1 with their apriori values, and sensitive parameter values remain the same as Group 1.

Table 1
Microbial-ENzyme Decomposition (MEND) Model Parameter Ranges and Reference Values

ID	Parameter	Description	Units	Range	Reference value
1	Vd	Maximum specific decomposition rate $Vd_{PO} = Vd_{PH} = Vd_M = Vd$	mg C mg^{-1} C h^{-1}	(0.1, 5)	2.55
2	K_{PO}	Half-saturation constant (HSC) for POM$_O$ decomposition	mg C cm^{-3} soil	(10, 100)	55
3	fK_M	$K_M = K_{PO} \times fK_M$, $K_{PH} = K_{PO}/fK_M K_{PH}$ and K_M are HSC for POM$_H$ and MOM, respectively	–	(2, 20)	11
4	Q_{max}	Maximum sorption capacity	mg C cm^{-3} soil	(0.5, 5.0)	2.75
5	K_{ba}	Binding affinity for DOM, sorption rate $k_{ads} = k_{des} \times K_{ba}$	(mg C cm^{-3} soil)$^{-1}$	(1, 16)	8.5
6	k_{des}	Desorption rate for DOM	mg C cm^{-3} soil h^{-1}	(0.0001, 0.01)	0.0051
7	r_E	Enzyme turnover rate	mg C mg^{-1} C h^{-1}	(0.0001, 0.01)	0.0051
8	p_{EP}	$[V_m \times p_{EP}]$ is the production rate of EP (EPO + EPH), V_m is the specific maintenance rate for active microbial biomass	–	(0.0001, 0.05)	0.00251
9	fp_{EM}	$fp_{EM} = p_{EM}/p_{EP}$, $[V_{mt} \times p_{EM}]$ is the production rate of EM	–	(0.1, 3.0)	1.55
10	f_D	Fraction of decomposed POM$_O$ and POM$_H$ allocated to DOM	–	(0.1, 0.5)	0.3
11	g_D	Fraction of dead active microbial biomass allocated to DOM	–	(0.01, 0.5)	0.255
12	g_{PO}	$(1-g_D) \cdot g_{PO}$ is the fraction of dead active microbial biomass entering POM$_O$	–	(0.1, 1)	0.55
13[a]	V_g	Maximum specific uptake rate of DOM for growth	mg C mg^{-1} C h^{-1}	(0.001, 0.1)	0.0505
14[a]	α	$\alpha = V_m/(V_g + V_m)$, V_m is max specific maintenance rate	–	(0.01, 0.5)	0.255
15	K_D	HSC for microbial uptake of DOM	mg C cm^{-3} soil	(0.001, 0.5)	0.2505
16[a]	$Y_g (T_{ref})$	Intrinsic carbon use efficiency at reference temperature (T_{ref})	–	(0.1, 0.6)	0.35
17	k_{Yg}	Slope for Y_g dependence of temperature	1/°C	(0.001, 0.016)	0.0085
18[a]	γ	Maximum microbial mortality rate = $V_m \times \gamma$	–	(0.01, 10)	5.005
19[a]	β	Ratio of dormant maintenance rate to V_m	–	(0.0005, 0.05)	0.0253
20	$VNim_{MB}$	Maximum specific microbial nitrogen (N) immobilization rate, $VNim_{NH4}=VNim_{MB} \times NH4/(NH4 + NO3)$, $VNim_{NO3}=VNim_{MB} \times NO3/(NH4 + NO3)$	mg N mg^{-1} C h^{-1}	(0.0001, 0.1)	0.0501
21	$KsNH4_{MB}$	HSC for microbial immobilization of NH$_4^+$	mg N cm^{-3} soil	(0.0001, 0.01)	0.0051
22	$KsNO3_{MB}$	HSC for microbial immobilization of NO$_3^-$	mg N cm^{-3} soil	(0.0001, 0.01)	0.0051
23	VN_{nit}	Maximum specific nitrification rate (VN_1)	mg N mg^{-1} C h^{-1}	(0.1, 200)	100.05
24	VN_{denit}	Maximum specific denitrification rate, $VN_j = VN_{denit}$, $j = 2$–5	mg N mg^{-1} C h^{-1}	$(1 \times 10^{-5}, 1)$	0.5
25	VN_{fix}	Maximum specific N fixation rate (VN_6)	mg N mg^{-1} C h^{-1}	(0.0001, 0.1)	0.0501
26	KsN_{nit}	HSC for nitrification	mg N cm^{-3} soil	(0.0001, 0.1)	0.0501
27	KsN_{denit1}	HSC for denitrification of NO$_3^-$ and NO$_2^-$ (KSN_3)	mg N cm^{-3} soil	(0.0001, 0.1)	0.0501
28	KsN_{denit2}	HSC for denitrification of NO and N$_2$O (KSN_5)	mg N cm^{-3} soil	(0.0001, 0.1)	0.0501
29	KsN_{fix}	HSC for N fixation	mg N cm^{-3} soil	(0.0001, 0.1)	0.0501
30	VN_{plant}	Maximum plant N uptake rate; $VN_{plant,NH4} = VN_{plant,NO3} = VN_{plant}$	mg N cm^{-3} h^{-1}	$(1 \times 10^{-6}, 0.0001)$	5.1×10^{-5}
31	$KsNH4_{plant}$	HSC for plant uptake of NH$_4^+$	mg N cm^{-3} soil	(0.0001, 0.01)	0.0051
32	$KsNO3_{plant}$	HSC for plant uptake of NO$_3^-$	mg N cm^{-3} soil	(0.0001, 0.01)	0.0051
33	fp_{ENZN}	Production rate of enzymes for mineral N	mg ENZ/mg MBC/h	(0.1, 2)	1.05
34	$NH4_{max}$	Maximum sorption capacity for NH$_4^+$	mg N cm^{-3} soil	$(1 \times 10^{-5}, 0.01)$	0.0050
35	Kba_{NH4}	Binding affinity for NH$_4^+$	(mg N cm^{-3} soil)$^{-1}$	$(1, 1 \times 10^5)$	5,000
36	r_{leach}	Scaling factor for NO$_3^-$ and NO$_2^-$ leaching	–	(0.001, 1)	0.5005

Note. POM$_O$: particulate organic matter (POM) decomposed by oxidative enzymes; POM$_H$: POM decomposed by hydrolytic enzymes; MOM: mineral-associated organic matter; DOM: dissolved organic matter; EP: POM-degrading enzymes; EP$_O$: POM$_O$-degrading enzymes; EP$_H$: POM$_H$-degrading enzyme; EM: MOM-degrading enzymes. [a]Represent the parameters related to the microbial physiological processes of growth, maintenance, carbon use efficiency, mortality, and dormancy, respectively.

Table 2
Microbial-Enzyme Decomposition (MEND) Model Response Variables for Sensitivity Analysis

ID	Response variables	Units	Description
1	MB	mg C cm^{-3} soil	Total microbial biomass carbon
2	MBA	mg C cm^{-3} soil	Active microbial biomass carbon
3	MB$_{CN}$	mg C mg^{-1} N	C:N ratios of the total microbial biomass
4	MBA$_{CN}$	mg C mg^{-1} N	C:N ratios of the active microbial biomass
5	ENZ	mg C cm^{-3} soil	The total concentration of all C-N related enzymes
6	CO$_2$	mg C cm^{-3} d^{-1}	Soil respiration
7	SOM	mg C cm^{-3} d^{-1}	Soil organic matter
8	SOM$_{CN}$	mg C mg^{-1} N	C:N ratios of soil organic matter
9	NH$_4^+$	mg N cm^{-3} soil	The concentration of NH$_4^+$ in the soil
10	NO$_3^-$	mg N cm^{-3} soil	The concentration of NO$_3^-$ in the soil
11	N$_2$O	mg N cm^{-3} soil	The concentration of N$_2$O in the soil

The above $3 \times N_R$ (e.g., 3,000) sample parameter sets are used to simulate the model outputs (e.g., OBFs in this study, see Equation 1). The relationships between the model outputs of the three parameter groups are represented by Pearson's correlation coefficients. Theoretically, if the classification of sensitive and non-sensitive parameter sets is correct, the correlation coefficient (r_{12}) of the model outputs between Group 1 and Group 2 is close to 0, whereas the correlation coefficient (r_{13}) between Group 1 and Group 3 is close to 1 (Tang et al., 2007).

2.6. Model Calibration and Identifiability

We calibrated the important parameters identified by the sensitivity analysis using observed heterotrophic respiration (R$_h$), MBC, MB$_{CN}$, and NH$_4^+$. Field observations were conducted between August 2009 and December 2012. R$_h$ was assessed by the Li-8100 automated soil CO$_2$ flux system with frequency of 1–2 times per month. The fumigation-extraction method was used to estimate microbial biomass C and N (Wu et al., 1990). Microbial biomass C was measured 12 times from November 2009 to December 2011, while the microbial C:N ratio was measured 7 times from July 2010 to December 2011. NH$_4^+$ was determined with a flow injection analysis automated ion analyzer across seven measurements from February 2010 to October 2012 (Wang et al., 2020). There were 49 and 12 data points for R$_h$ and MBC, respectively, while MB$_{CN}$ and NH$_4^+$ had only 7 data points. The coefficient of determination (R^2) was used to evaluate the goodness-of-fit for R$_h$ and MBC because R^2 is most applicable to evaluate the variables that are frequently measured. The mean absolute relative error (*MARE*) was used to evaluate the modeling performance of MB$_{CN}$ and NH$_4^+$ because *MARE* is suitable to evaluate the variables with only a few measurements, typically no more than 10 points (Wang et al., 2022; Wang, Huang, et al., 2019). The formulas for evaluation criteria were as follows:

$$R^2 = 1 - \frac{\sum_{u=1}^{U} [Y_{sim}(u) - Y_{obs}(u)]^2}{\sum_{u=1}^{U} (Y_{obs}(u) - \overline{Y}_{obs})^2} \tag{9a}$$

$$MARE = \frac{1}{U} \sum_{u=1}^{U} \left| \frac{Y_{sim}(u) - Y_{obs}(u)}{Y_{obs}(u)} \right| \tag{9b}$$

where R^2 denotes the coefficient of determination and higher R^2 is preferred; *MARE* is the mean absolute relative error and lower *MARE* means better simulation; Y_{sim} is the simulated value; Y_{obs} is the observed value; $\overline{Y}_{obs}$ is the mean value for Y_{obs}; and U is the number of data.

We implemented multi-objective calibration by the modified Shuffled Complex Evolution (SCE) algorithm (Duan et al., 1992). Multiple objectives were weighted together to minimize the overall objective function (*J*):

$$J = w_1 \times \left(1 - R_{R_h}^2\right) + w_2 \times \left(1 - R_{MBC}^2\right) + w_3 \times MARE_{MB_{CN}} + w_4 \times MARE_{NH_4^+} \tag{10a}$$

$$\sum_{v=1}^{4} w_v = 1, w_v \in [0,1] \tag{10b}$$

where w_v is the weighting factor of the objective function (J_v) and $w_v = 0.25$ in this study; $R_{R_h}^2$ and R_{MBC}^2 are the coefficients of determination for R_h and MBC, respectively; $MARE_{MB_{CN}}$ and $MARE_{NH_4^+}$ are the mean absolute relative error of MB_{CN} and NH_4^+, respectively.

An important part of model evaluation is the identifiability analysis (Villaverde et al., 2016), which can be efficiently determined by singular values of the Hessian matrix (Viallefont et al., 1998). We used the covariance-inverse (CI) method to derive the Hessian matrix based on the parameter sets generated during model calibration (Wang & Chen, 2013). The parameter uncertainty was quantified by the Uncertainty Quantification by Critical Objective Function Index (UQ-COFI) method (Wang & Chen, 2013; Wang et al., 2022; Wang et al., 2015). The structural identifiability was diagnosed by the condition number (η):

$$\eta = \frac{\lambda_{max}}{\lambda_{min}} \tag{11}$$

where λ_{max} and λ_{min} are the maximum and minimum singular values of the Hessian matrix, respectively. $1 \leq \eta \leq 10$ means that the model is identifiable, $10 < \eta \leq 200$ means that the model is weakly identifiable, and $\eta > 200$ means that the model is non-identifiable.

2.7. Analysis of Microbial-Ecological Processes

For comparison of the relative importance of a parameter to a response variable in different simulation periods (i.e., short-term vs. long-term), we calculate the sensitivity contribution ratio (Baki et al., 2022), that is, the ratio of the sensitivity index of a parameter to the sum of the sensitivity indices of all parameters:

$$Cr_k = \frac{S_k}{\sum_{k=1}^{K} S_k} \times 100\% \tag{12}$$

where Cr_k denotes the sensitivity contribution of the kth parameter ($k = 1, 2, \cdots, K$) to a given response variable; and S_k denotes the sensitivity index of the kth parameter. The sum of the sensitivity contributions of the selected parameters is used to express the cumulative contribution of these parameters to a given response variable.

To further analyze microbial effects on C-N processes over time, we simulated the response of C-N variables to individual parameter changes in the short-and long-term based on the one-factor-at-a-time (OAT) method (Borgonovo, 2010). We generated a certain number (e.g., 1,000) of parameter samples by the Latin hypercube sampling (Helton & Davis, 2003), and used the coefficient of variation (CV) to quantify the uncertainty in a response variable due to parameter changes (Fraterrigo & Rusak, 2008).

$$CV_{m,k} = \frac{SD_{m,k}}{\overline{Y_{m,k}}} \tag{13}$$

where $CV_{m,k}$ denotes the coefficient of variation for the simulated values of the mth response variable when the kth parameter changes; $SD_{m,k}$ and $\overline{Y_{m,k}}$ denote standard deviation and mean for the simulated values of the mth response variable when the kth parameter changes, respectively.

We used the ratio of the average CV values (IM) to describe the relative importance of the two groups of parameters (i.e., microbial vs. the other parameters).

$$IM_{ST} = \overline{CV}_{MIC,ST} / \overline{CV}_{OTH,ST} \tag{14a}$$

$$IM_{\text{LT}} = \overline{CV}_{\text{MIC,LT}} / \overline{CV}_{\text{OTH,LT}} \qquad (14b)$$

where IM_{ST} and IM_{LT} denote the relative importance of microbial physiological parameters (See the parameters labeled "a" in Table 1) with respect to other parameters in the short and long term, respectively, and the value greater than one indicates that the microbial physiological parameters have a greater impact compared with the other parameters. $\overline{CV}_{\text{MIC,ST}}$ and $\overline{CV}_{\text{MIC,LT}}$ denote the short- and long-term $\overline{CV}_{\text{MIC}}$, respectively; $\overline{CV}_{\text{OTH,ST}}$ and $\overline{CV}_{\text{OTH,LT}}$ denote the short- and long-term $\overline{CV}_{\text{OTH}}$, respectively.

3. Results

3.1. Sensitivity Analysis

We first tested the convergence of the sensitivity index values based on different samples in short-term simulations (Figure S4 in Supporting Information S1). For Sobol's method, the maximum ratios of the uncertainty interval to the highest total-order sensitivity index surpassed 10% with sample sizes of 8,066, 148,000, 296,000, and 444,000, whereas the ratios for all response variables remained below 10% with a total sample size (N_{T1}) of 592,000, corresponding to a $N_{\text{B1}} = 8,000$. As for MOPSA, the maximum ratios of the uncertainty interval to the highest sensitivity index exceeded 10% with sample sizes of 2,000, 4,000, and 6,000, but the ratios for all response variables did not exceed 10% with a total sample size (N_{T2}) of 8,000. This suggests that a sample size (N_{T1}) of 592,000 was deemed adequate for the Sobol's method, while a sample size (N_{T2}) of 8,000 was sufficient for MOPSA. Based on these samples, we analyzed short-term (3-year) and long-term (20-year and 100-year) sensitivity indices of the 11 response variables (Figure 2 and Figure S5 in Supporting Information S1).

3.1.1. Sensitivity Analysis for Each Response Variable

To simplify the results, we focused on the top five sensitive parameters as per the response variables. A higher value of the sensitivity index means that the parameter is more important for that response variable. The total-order sensitivity index in Sobol's method denotes the total contribution of each parameter and their interactions to the variance of the output. However, the sensitivity index in MOPSA is derived from the median of the difference between normalized parameter clusters. For a direct comparison of the two methods, we provide the rankings of the top 5 sensitivity index values by Sobol (Figure S6 in Supporting Information S1) and MOPSA (Figure S7 in Supporting Information S1) for each response variable.

3.1.1.1. Short-Term (3-year) and Long-Term (20-year) Results by Sobol and MOPSA

For the short-term (3-year) results, the total-order sensitivity indices ranged from 0 to 0.60 by Sobol's method (Figure 2a), and the short-term sensitivity indices by MOPSA ranged from 0.03 to 0.62 (Figure 2b). We first compared short-term sensitivity indices of MOPSA (Figure 2b) with Sobol's total-order sensitivity indices (Figure 2a). Microbial variables (MB, MBA, MB$_{\text{CN}}$, and MBA$_{\text{CN}}$) were most sensitive to the intrinsic CUE (Y_g), the half-saturation constant for microbial uptake of dissolved organic matter (DOM) (K_D), the coefficient associated with the microbial mortality rate (γ), the maximum microbial growth rate (V_g), and enzyme turnover rate (r_E) based on MOPSA, while in the Sobol's method, the factor related to maintenance rate (α) and the maximum specific decomposition rate (Vd) were more important than K_D and γ. Enzyme concentrations (ENZ) were primarily controlled by the factor related to α, r_E, Y_g, the factor related to enzyme production rate for particulate organic matter (POM) (p_{EP}), and V_g using MOPSA; while in the Sobol's method, the factor related to enzyme production rate for mineral-associated organic matter (MOM) (fp_{EM}) was more important than V_g. Soil respiration (CO_2) was strongly influenced by α, Vd, V_g, r_E, and Y_g based on MOPSA; whereas in the Sobol's method, V_g and Y_g were less influential than the half-saturation constant for POM decomposition (K_{PO}) and fp_{EM}. Soil C-N variables (SOM and SOM$_{\text{CN}}$) were greatly regulated by Vd, α, r_E, the factor related to the half-saturation constant for SOM decomposition (fK_M), and K_{PO} using MOPSA; while in the Sobol's method, fp_{EM} was more important than fK_M. Inorganic N variables (NH$_4^+$, NO$_3^-$, and N$_2$O) were mainly controlled by the maximum plant N uptake rate (VN_{plant}), α, the maximum N nitrification rate (VN_{nit}), r_E, and the half-saturation constant for plant uptake of NH$_4^+$ ($KsNH4_{plant}$) based on MOPSA; whereas in the Sobol's method, $KsNH4_{plant}$ was less influential than Y_g.
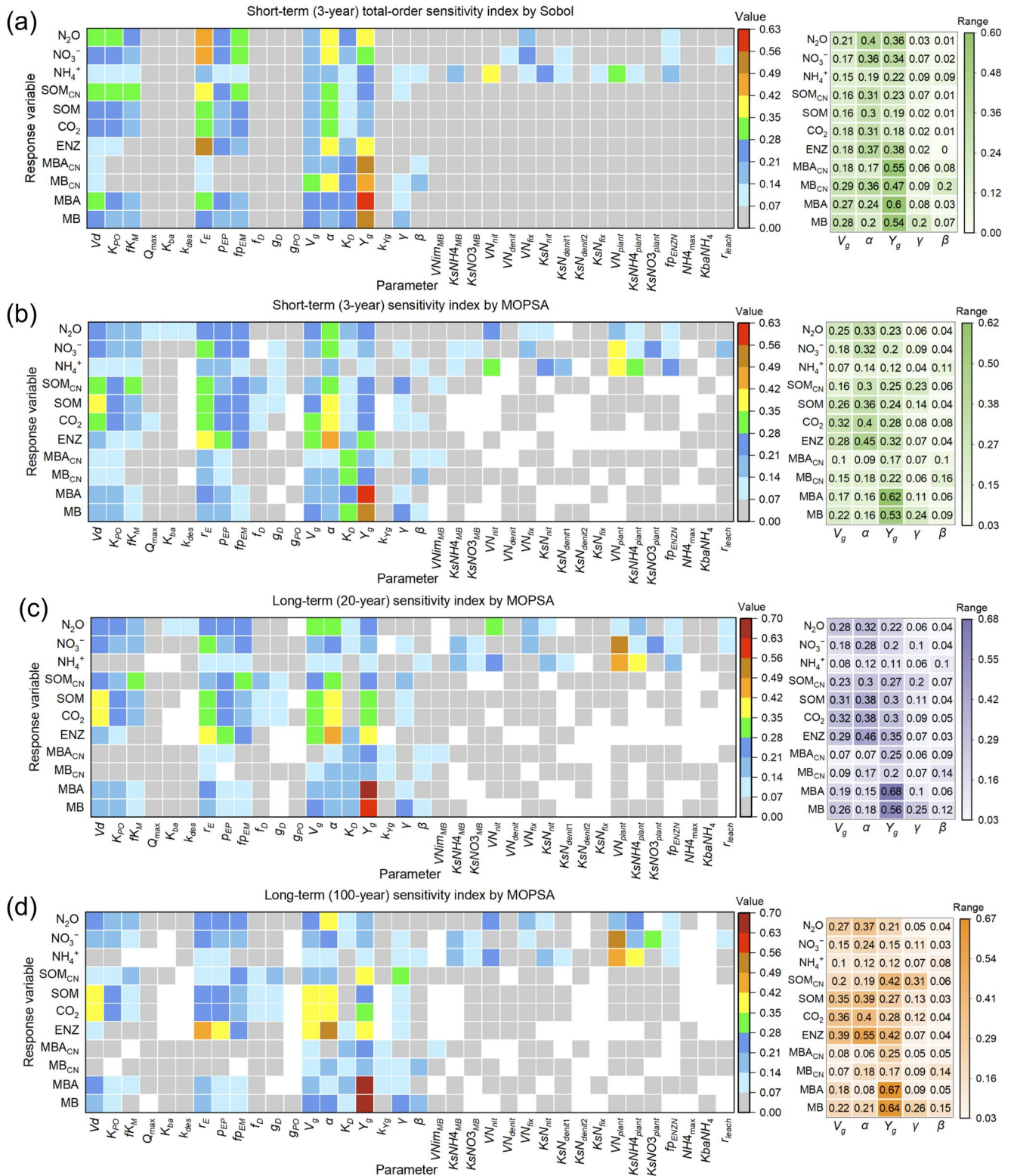
Figure 2. Parameter sensitivity indices with respect to specific response variables. Parameters and response variables are described in Tables 1 and 2, respectively. (a) Short-term (3-year) total-order sensitivity index by Sobol's method. (b) Short-term (3-year) sensitivity index by the Multi-Objective Parameter Sensitivity Analysis (MOPSA) method. (c) Long-term (20-year) sensitivity index by MOPSA. (d) Long-term (100-year) sensitivity index by MOPSA. The white part means that the sensitivity was ignored because the differences in pairwise parameter clusters were not statistically significant ($p > 0.05$).

We conducted a comparison between the long-term (20-year) results obtained from MOPSA (Figure 2c) and Sobol (Figure S5 in Supporting Information S1). Both MOPSA and Sobol determined four out of the top five parameters as being the same in terms of microbial variables, soil respiration, and soil C-N variables. For enzyme concentrations, both methods identified the same top five sensitive parameters. Moreover, regarding inorganic N variables, MOPSA and Sobol's method shared agreement on three out of the top five sensitive parameters. Based on sensitivity index values of Sobol and MOPSA, we also calculated ranking differences (Figure S8 in Supporting Information S1). Most of difference values in the sensitivity ranking between the two methods for parameters related to microbial physiology, enzyme turnover and production, and the enzymatic decomposition of SOM were within 6, while larger disparities in rankings were observed for N-related parameters.

3.1.1.2. Comparison of Short- and Long-Term Results by MOPSA

We conducted comparative analyses between the short- and long-term outcomes using MOPSA (Figures 2b–2d). For microbial variables, Vd was more important than K_D in the 20-year compared to the 3-year results, while in the 100-year, α was found to be more crucial than r_E compared to the 20-year results. The top five sensitive parameters remained consistent across all three periods for enzyme concentrations and soil respiration. Concerning soil C-N variables, V_g and fp_{EM} were more influential than fK_M and K_{PO} in the 20-year compared to the 3-year results, whereas in the 100-year, Y_g and γ were more significant than fp_{EM} and r_E compared to the 20-year results. As for inorganic N variables, V_g and fp_{EM} exhibited greater importance than fK_M and K_{PO} in the 20-year compared to the 3-year results, while in the 100-year, the half-saturation constant for plant uptake of NO_3^- ($KsNO3_{plant}$) proved more crucial than VN_{nit} compared to the 20-year results.

We obtained sensitivity ranking differences between short- and long-term analyses based on MOPSA (Figure S9 in Supporting Information S1). Sensitivity rankings for sensitive parameters, including those associated with enzyme turnover and production and microbial physiology, exhibited less variation over the long term compared to the short term. Conversely, sensitivity rankings for relatively less critical parameters, such as those linked to N-related processes, displayed more variability. Regarding time scales, the most significant changes in sensitivity ranking differences were observed between 100 and 3 years.

3.1.2. Overall Sensitivity Scalar (SO_k) Pertaining to all Response Variables

We sorted the parameters in descending order of the overall sensitivity scalar (SO_k) values (Table 3). A higher value of SO_k means that the parameter was more important to the 11 response variables. We focused on the top 12 important parameter changes identified by MOPSA and Sobol.

For the short-term SO_k, both MOPSA and Sobol identified the same top four important parameters: r_E, α, Y_g, and Vd. The parameters ranked fifth to ninth by MOPSA were p_{EP}, V_g, K_{PO}, K_D, and fp_{EM}, while Sobol also recognized these parameters but with different rankings. Both MOPSA and Sobol identified fK_M, and γ as the tenth and eleventh ranked parameters. However, the parameters ranked twelfth by MOPSA and Sobol were β and the fraction of decomposed POM allocated to DOM (f_D), respectively. For the 20-year SO_k, both MOPSA and Sobol determined identical top five parameters (α, Y_g, r_E, V_g, Vd) and the twelfth parameter (the factor related to dormant maintenance rate (β)). The parameters ranked sixth to eleventh by MOPSA were fp_{EM}, p_{EP}, K_D, K_{PO}, γ, and fK_M, while Sobol also identified these parameters but with different rankings.

For the long-term (100-year) SO_k, the top 12 important parameters were α, Y_g, V_g, r_E, Vd, p_{EP}, γ, fp_{EM}, K_D, K_{PO}, β and VN_{plant}. Notably, the parameter α ranked first and four microbial physiological parameters (Y_g, V_g, γ, and β) exhibited higher rankings in the 100-year analysis compared to the other two periods, indicating the increased importance of microbial physiological parameters in the long-term than in the short-term simulations.

3.2. Validation of Sensitivity Analysis and Determination of Important Parameters

We first performed repeatability tests to verify the reliability of Sobol's method and MOPSA. The parameter sets of each response variable for validation should contain the main sensitive parameters. We found that MOPSA and Sobol's method were not significantly different by testing different parameter sets. Here, we present the validation results for the top 12 sensitive parameters based on the short-term sensitivity indices (Figure 3a). For Sobol's method, the correlation coefficient (r) of the objective function values (OBFs) between Group 1 and Group 2 (r_{12}) was 0.08 ± 0.10 (mean ± standard deviation), whereas r between Group 1 and Group 3 (r_{13}) was 0.90 ± 0.14. For

Table 3
*Overall Sensitivity Scalar (SO_k) Pertaining to All Response Variables*

R_k	Sobol Parameter	ST SO_k	MOPSA Parameter	ST SO_k	Sobol Parameter	LT$_{20}$ SO_k	MOPSA Parameter	LT$_{20}$ SO_k	MOPSA Parameter	LT$_{100}$ SO_k
1	r_E	0.94	r_E	0.92	α	0.95	α	0.93	α	0.93
2	α	0.93	α	0.91	Y_g	0.93	Y_g	0.92	Y_g	0.92
3	Y_g	0.93	Y_g	0.89	r_E	0.91	r_E	0.89	V_g	0.89
4	Vd	0.87	Vd	0.88	V_g	0.87	V_g	0.86	r_E	0.84
5	V_g	0.84	p_{EP}	0.84	Vd	0.84	Vd	0.80	Vd	0.81
6	K_{PO}	0.83	V_g	0.83	p_{EP}	0.83	fp_{EM}	0.79	p_{EP}	0.77
7	p_{EP}	0.82	K_{PO}	0.80	K_{PO}	0.80	p_{EP}	0.76	γ	0.76
8	fp_{EM}	0.81	K_D	0.79	fp_{EM}	0.80	K_D	0.71	fp_{EM}	0.72
9	K_D	0.80	fp_{EM}	0.78	K_D	0.78	K_{PO}	0.70	K_D	0.67
10	fK_M	0.75	fK_M	0.73	fK_M	0.73	γ	0.69	K_{PO}	0.66
11	γ	0.70	γ	0.66	γ	0.71	fK_M	0.67	β	0.59
12	f_D	0.57	β	0.61	β	0.66	β	0.61	VN_{plant}	0.58
13	β	0.55	VN_{plant}	0.53	fp_{ENZN}	0.59	VN_{plant}	0.59	f_D	0.56
14	KsN_{nit}	0.54	$KsNH4_{plant}$	0.49	KsN_{nit}	0.55	f_D	0.54	fK_M	0.55
15	KsN_{denit1}	0.53	Q_{max}	0.49	VN_{plant}	0.54	k_{Yg}	0.47	$KsNH4_{plant}$	0.54
16	fp_{ENZN}	0.51	f_D	0.48	f_D	0.48	Q_{max}	0.47	KsN_{nit}	0.52
17	Kba_{NH4}	0.47	$KsNH4_{MB}$	0.47	K_{ba}	0.48	fp_{ENZN}	0.46	VN_{fix}	0.51
18	VN_{fix}	0.46	g_D	0.45	VN_{fix}	0.44	VN_{fix}	0.44	g_D	0.50
19	$KsNH4_{MB}$	0.44	K_{ba}	0.45	r_{leach}	0.42	$VNim_{MB}$	0.43	VN_{nit}	0.47
20	$KsNO3_{plant}$	0.44	k_{Yg}	0.43	g_{PO}	0.41	K_{ba}	0.43	k_{Yg}	0.45
21	$KsNO3_{MB}$	0.42	VN_{fix}	0.41	VN_{denit}	0.40	g_D	0.42	$KsNO3_{MB}$	0.43
22	$VNim_{MB}$	0.41	$VNim_{MB}$	0.41	Kba_{NH4}	0.39	k_{des}	0.41	Q_{max}	0.42
23	VN_{nit}	0.40	KsN_{nit}	0.39	Q_{max}	0.38	$KsNH4_{plant}$	0.41	$KsNH4_{MB}$	0.41
24	VN_{plant}	0.40	r_{leach}	0.39	$KsNH4_{plant}$	0.38	KsN_{nit}	0.41	$KsNO3_{plant}$	0.41
25	k_{Yg}	0.35	$KsNO3_{plant}$	0.38	KsN_{denit1}	0.38	$KsNH4_{MB}$	0.41	$VNim_{MB}$	0.41
26	Q_{max}	0.34	fp_{ENZN}	0.36	$KsNO3_{plant}$	0.37	VN_{nit}	0.41	k_{des}	0.40
27	K_{ba}	0.32	VN_{nit}	0.35	$KsNH4_{MB}$	0.35	$KsNO3_{plant}$	0.40	fp_{ENZN}	0.37
28	KsN_{fix}	0.31	$KsNO3_{MB}$	0.31	$VNim_{MB}$	0.33	$KsNO3_{MB}$	0.40	KsN_{denit1}	0.37
29	r_{leach}	0.31	KsN_{fix}	0.28	$KsNO3_{MB}$	0.33	VN_{denit}	0.35	r_{leach}	0.36
30	VN_{denit}	0.28	Kba_{NH4}	0.28	k_{Yg}	0.30	KsN_{denit1}	0.32	K_{ba}	0.34
31	g_D	0.27	VN_{denit}	0.27	KsN_{fix}	0.28	Kba_{NH4}	0.30	VN_{denit}	0.33
32	g_{PO}	0.25	KsN_{denit1}	0.27	VN_{nit}	0.26	r_{leach}	0.29	KsN_{fix}	0.26
33	k_{des}	0.22	k_{des}	0.26	k_{des}	0.24	g_{PO}	0.23	$NH4_{max}$	0.26
34	$KsNH4_{plant}$	0.22	$NH4_{max}$	0.25	g_D	0.22	KsN_{denit2}	0.23	Kba_{NH4}	0.24
35	$NH4_{max}$	0.18	g_{PO}	0.24	$NH4_{max}$	0.11	$NH4_{max}$	0.17	KsN_{denit2}	0.16
36	KsN_{denit2}	0.07	KsN_{denit2}	0.22	KsN_{denit2}	0.07	KsN_{fix}	0.15	g_{PO}	0.12

Note. R_k: the ranking of the overall sensitivity scalar (SO_k); Sobol: Sobol's method; MOPSA: Multi-Objective Parameter Sensitivity Analysis; ST: short-term (3-year); LT$_{20}$: long-term (20-year); LT$_{100}$: long-term (100-year). Parameters are described in Table 1.

MOPSA, r_{12} was 0.05 ± 0.06 and r_{13} was 0.90 ± 0.12. Since r_{12} was close to 0 and r_{13} was close to 1 for both Sobol's method and MOPSA, the sensitivity classifications could be regarded as accurate for the targeted response variables. Wilcoxon Rank Sum Tests show no significant difference ($p > 0.05$) in the correlation coefficients between
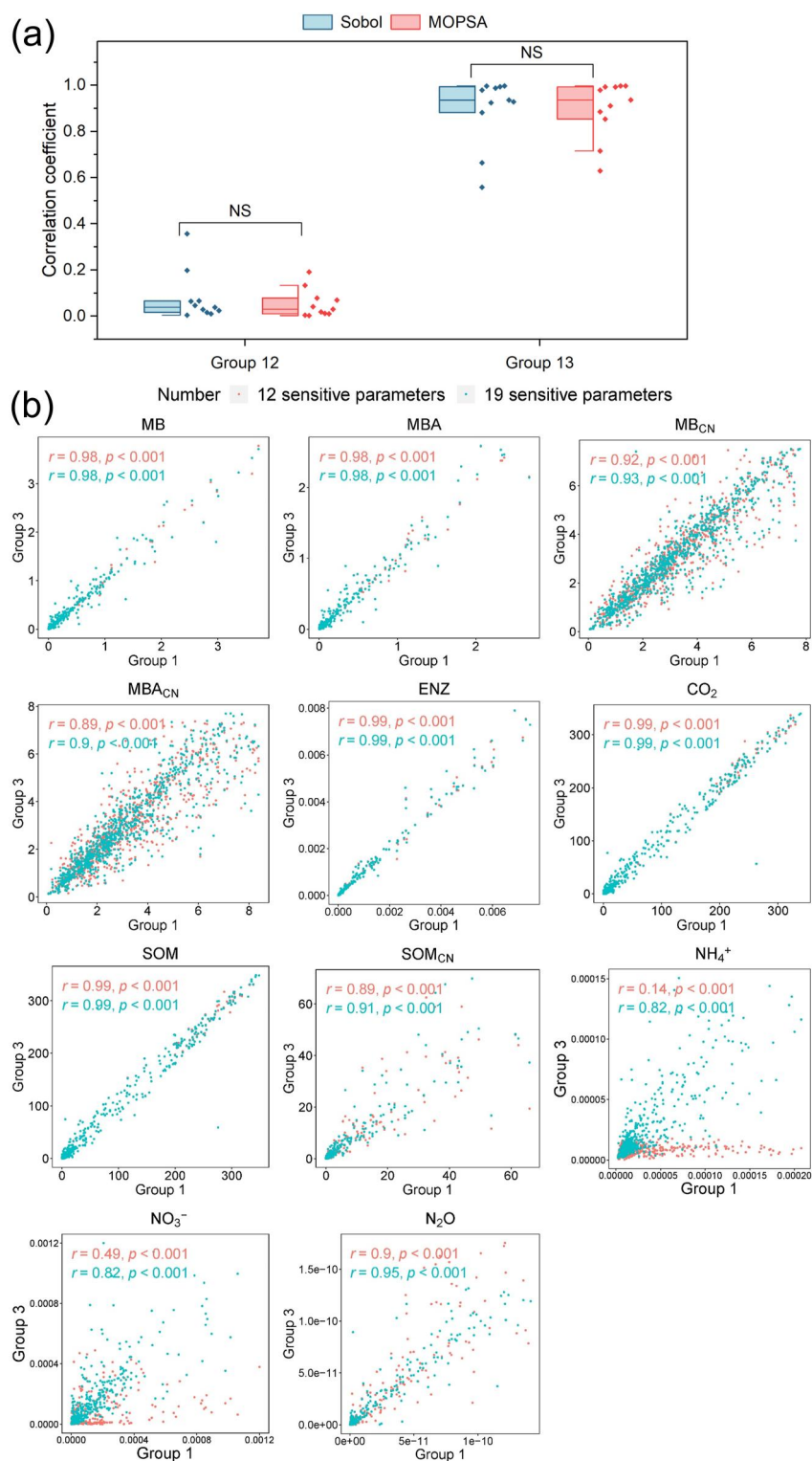
Figure 3. Validation of sensitivity analysis and determination of important parameters by repeatability tests. (a) Reliability validation of Sobol's method and Multi-Objective Parameter Sensitivity Analysis (MOPSA); Group 12: testing parameter sets of Group 1 and Group 2; Group 13: testing parameter sets of Group 1 and Group 3. Group 12 and Group 13 are based on the top 12 sensitive parameters for each response variable. "NS" means no significant difference ($p > 0.05$). (b) Repeatability tests of different sensitive parameter sets for 11 response variables (See Table 2). A correlation coefficient of 0 between the model outputs (e.g., OBFs, see Equation 1) obtained by the parameter Group 1 and Group 2 and the correlation coefficient of

Sobol's method and MOPSA. However, Sobol's method required 592,000 ($=2 \times N_{\text{base}} \times (K + 1) = 2 \times 8,000 \times 37$) sample parameter sets, whereas MOPSA achieved equivalent outcomes with only 8,000 base samples, showing that the efficiency of MOPSA is about 70 times higher than that of Sobol's method.

We used repeatability tests to see if additional parameters were necessary for the response variables based on the rankings of the overall sensitivity indices. By testing different numbers of parameters, we find that if these 12 sensitive parameters (α, r_E, Y_g, Vd, V_g, p_{EP}, K_D, K_{PO}, fp_{EM}, fK_M, γ, and β) were considered, all response variables performed well in the repeatability tests, except for NH_4^+ and NO_3^- (Figure 3b and Figure S10 in Supporting Information S1). This suggested that calibrating these 12 parameters would allow good simulations for most C-N response variables (except for NH_4^+ and NO_3^-). We added parameters related to N processes according to the ranking of the sensitivity indices of NH_4^+ and NO_3^- to improve simulation performances. We found that N-process modeling performance enhanced when these seven parameters were included: the maximum plant N uptake rate (VN_{plant}), the maximum N nitrification rate (VN_{nit}), the half-saturation constant for nitrification (KsN_{nit}), the maximum N fixation rate (VN_{fix}), the production rate of enzymes for inorganic N transformations (fp_{ENZN}), the half-saturation constant for microbial immobilization of NH_4^+ ($KsNH4_{MB}$), and the factor for nitrate N leaching (r_{leach}) (Figure 3b and Figure S10 in Supporting Information S1).

3.3. Calibration of Important Parameters and Diagnosis of Model Identifiability

As per the important parameters identified via sensitivity analysis, we performed two model calibrations using the observed data of R_h, MBC, MB_{CN}, and NH_4^+ (Figure 4). We first calibrated 12 important parameters, which were α, r_E, Y_g, Vd, V_g, p_{EP}, K_D, K_{PO}, fp_{EM}, fK_M, γ and β (see Table 1 for a description of model parameters); and seven N-related parameters (i.e., VN_{plant}, VN_{nit}, KsN_{nit}, VN_{fix}, fp_{ENZN}, $KsNH4_{MB}$, and r_{leach}) were further included. R_h and MBC were simulated well with $R_{R_h}^2 = 0.70$, $R_{MBC}^2 = 0.67$ in the two calibrations (Figures 4a and 4b). The simulations of MB_{CN} performed well with $MARE_{MB_{CN}} = 0.33$ and 0.29 in the first- and second-round calibrations (Figure 4c). Simulated NH_4^+ was not satisfactory until the N-related parameters were considered, with a lower $MARE_{NH_4^+} = 0.28$, compared to $MARE_{NH_4^+} = 0.49$ in the first-round calibrations (Figure 4d). Our model evaluation during the post-calibration period showed a 2.1% ± 1.3% change of SOC compared to the calibration period (Figure S11 in Supporting Information S1), indicating that the calibrated model can produce realistic and reasonable SOC pool sizes in the long run without disturbance.

We obtained 60,365 parameter sets through model calibration of the top 12 sensitive parameters. Based on the CI method, we estimated the singular values of the Hessian matrix (Figure S12 in Supporting Information S1). The condition number (η) was equal to 105, implying that the model parameters were weakly identifiable, which is acceptable for complex microbial ecological modeling with a lot of noise in the observed data.

3.4. Analysis of Short- and Long-Term Microbial-Ecological Processes

We calculated the sensitivity contribution ratio of these five microbial physiological parameters (α, Y_g, V_g, γ, and β) to each response variable (Figure 5). If we use 5% as a threshold for the relative difference between the long-term (100-year) and short-term (3-year) sensitivity contributions, there are five variables (SOM_{CN}, MB, MBA_{CN}, SOM, and ENZ) with relative differences higher than 5% and six variables with smaller differences (Figure 5a). However, it's important to note that five microbial physiological parameters (α, Y_g, V_g, γ, and β) contributed 27.5% and 31.5% to the sensitivity in the short and long term, respectively. For multiple response variables, the contribution ratios of microbial physiological parameters were significantly higher in the long-term than in the short-term simulations ($p = 0.01$) (Figure 5b).

We compared C-N processes simulated by varying five microbial physiological parameters (V_g, α, Y_g, γ, and β) versus those simulated by varying seven other parameters (Vd, K_{PO}, fK_M, r_E, p_{EP}, fp_{EM}, and K_D) based on the OAT method. Short-term (3-year) and long-term (100-year) simulations were obtained for the five C-N variables (MB, MBA_{CN}, ENZ, SOM, and SOM_{CN}) by varying each parameter individually (Figure 6).

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1 between Group 1 and Group 3 mean perfect repeatability. The 12 sensitive parameters are α, r_E, Y_g, Vd, V_g, p_{EP}, K_D, K_{PO}, fp_{EM}, fK_M, γ, and β; the 19 sensitive parameters consist of the aforementioned 12 plus seven N-related parameters: VN_{plant}, VN_{nit}, KsN_{nit}, VN_{fix}, fp_{ENZN}, $KsNH4_{MB}$, and r_{leach}. See Table 1 for a full description of these model parameters.
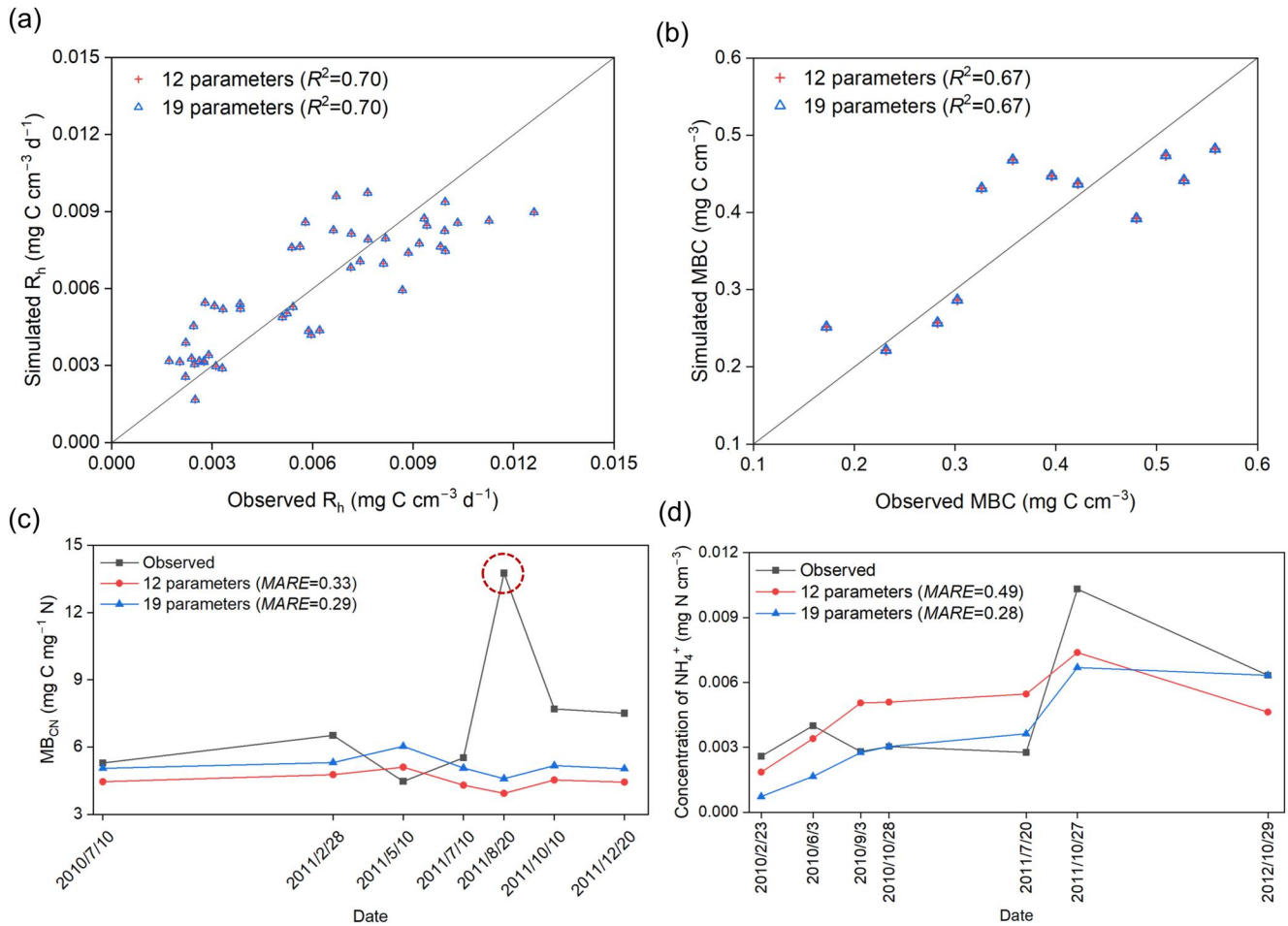
Figure 4. Model simulation results against field experimental data. (a) Heterotrophic respiration flux (R_h); (b) Microbial biomass carbon (MBC); (c) C:N ratios of the total microbial biomass (MB_{CN}), and the data point (in August 2011) marked with a circle is significantly higher than the other observations, which is likely to have a large measurement error (Wang et al., 2020); (d) Concentrations of soil NH_4^+. R^2 is the coefficient of determination and *MARE* is the mean absolute relative error. The 12 parameters in the first calibration are α, r_E, Y_g, Vd, V_g, p_{EP}, K_D, K_{PO}, fp_{EM}, fK_M, γ, and β; the 19 parameters for the second calibration consist of the aforementioned 12 plus seven N-related parameters: VN_{plant}, VN_{nit}, KsN_{nit}, VN_{fix}, fp_{ENZN}, $KsNH4_{MB}$, and r_{leach}. See Table 1 for a full description of these model parameters.

In most cases, the simulated microbial and enzyme variables (MB, MBA$_{CN}$, and ENZ) had higher uncertainty in the short term compared with the long term (Figures 6a–6c). The IM_{ST} and IM_{LT} for MB were 0.95 and 2.42, respectively, indicating that the other parameters had a greater effect on MB in the short term, while the microbial physiological parameters had a greater effect in the long term. For MBA$_{CN}$, the IM_{ST} and IM_{LT} were 2.49 and 2.37, respectively, showing that microbial physiological parameters dominated the variation of MBA$_{CN}$ in both short- and long-term, and the microbial importance increased further in the long run. The IM_{ST} and IM_{LT} of ENZ were 0.90 and 1.25, respectively, which indicated that the other parameters had a significant effect on ENZ in the short term, while the microbial physiological parameters had a greater effect in the long term.

In most cases, the simulated soil C-N variables (SOM and SOM$_{CN}$) had higher uncertainty in the long term compared with the short term (Figures 6d–6f). The IM_{ST} and IM_{LT} of SOM were 0.56 and 0.89, respectively, suggesting that the other parameters had a greater impact on SOM in the short and long term, whereas the importance of microbial physiological parameters was higher in the long term than in the short term. SOM$_{CN}$ exhibited larger uncertainty in the long-term simulations and the IM_{ST} and IM_{LT} of SOM$_{CN}$ were 0.58 and 2.47, respectively, which indicated that the other parameters had a greater effect on SOM$_{CN}$ in the short term, but microbial physiological parameters had a greater effect in the long term.

Using the OAT method, we compared inorganic N variables (NH_4^+, NO_3^-, and N_2O) simulated by varying five microbial physiological parameters (V_g, α, Y_g, γ, and β) versus varying seven N-related parameters (i.e., VN_{plant},
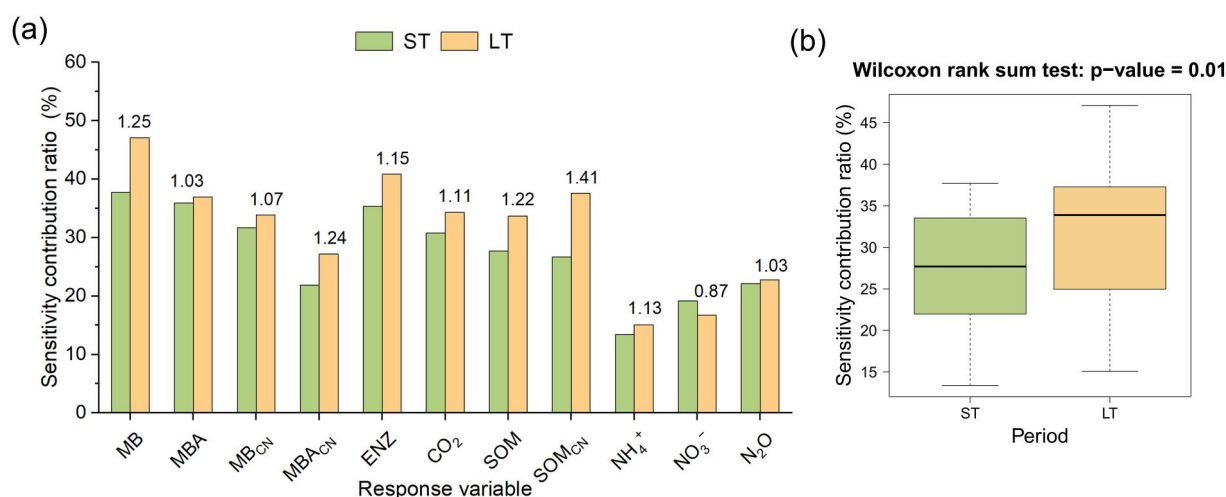
Figure 5. Sensitivity contribution ratio of microbial physiology in the short-term (3-year) and long-term (100-year) model simulations. (a) The sensitivity contribution ratio as per each response variable in the short term (ST) and long term (LT). Response variables are described in Table 2. The contribution ratio refers to the sum of the sensitivity indices of key microbial physiological parameters (α, Y_g, V_g, γ, and β) divided by the sum of the sensitivity indices of all parameters with regard to a specific response variable. The number on the bar is the ratio of the long-term sensitivity contribution rate to the short-term one. (b) Overall comparison between the short- and long-term. The difference between the ST and the LT is considered statistically significant at $p < 0.05$.

VN_{nit}, KsN_{nit}, VN_{fix}, fp_{ENZN}, $KsNH4_{MB}$, and r_{leach}) (Figure S13 in Supporting Information S1). For NH_4^+, N-related parameters were more important than microbial parameters in both short- and long-term, but the effect of microbial physiological parameters increased slightly in the long term (Figure S13a in Supporting Information S1). As for NO_3^-, microbial physiological parameters were more essential in the short term, while N-related parameters were more important in the long term (Figure S13b in Supporting Information S1). For N_2O, microbial physiological parameters had a greater influence in the short and long term compared to N-related parameters (Figure S13c in Supporting Information S1).

4. Discussion

4.1. Comparison of the Two Sensitivity Analysis Methods: MOPSA Versus Sobol

Our results show that the proposed MOPSA was more computationally efficient than Sobol for the sensitivity analysis of complex microbial ecological models. MOPSA was reliable and had much higher computational efficiency than Sobol because far less parameter samples (about 1% of Sobol's samples) were required to conduct reliable sensitivity analysis via MOPSA.

We verified the reliability of MOPSA and Sobol in the complex microbial ecological model by repeatability tests. In this study, although MOPSA and Sobol did not exactly identify the same sensitive parameter sets, there was no significant difference in the repeatability tests between the two sensitivity analysis methods (Figure 3a). This indicated that the sensitive parameter sets determined by MOPSA and Sobol had equivalent effects on the outputs, primarily due to the equifinality of the model parameters (Marschmann et al., 2019; Wang & Chen, 2013). In addition, MOPSA and Sobol determined the identical 12 parameters that were important for soil C-N processes concerning multiple response variables. The model calibrations further confirmed that soil C processes could be well simulated by accounting for the 12 important microbial-enzymatic parameters, while seven N-related parameters were required for better simulations of inorganic N processes (Figure 4).

However, MOPSA had much higher computational efficiency than Sobol. If there is no significant difference in the reliability of the sensitivity analysis results, the simulation time for a sample parameter set and the number of total parameter samples are key factors in applying the sensitivity analysis method (Song et al., 2015). In our study, using parallel computing to run the MEND model on a supercomputing platform with 128 CPU cores, it took about 0.7 hr to execute 8,000 short-term (3-year) simulations and about 10 hr to execute 8,000 long-term (100-year) simulations. Based on the 8,000 sample parameter sets, we successfully conducted the short- and long-term sensitivity analysis using MOPSA. However, the implementation of Sobol's method required 592,000
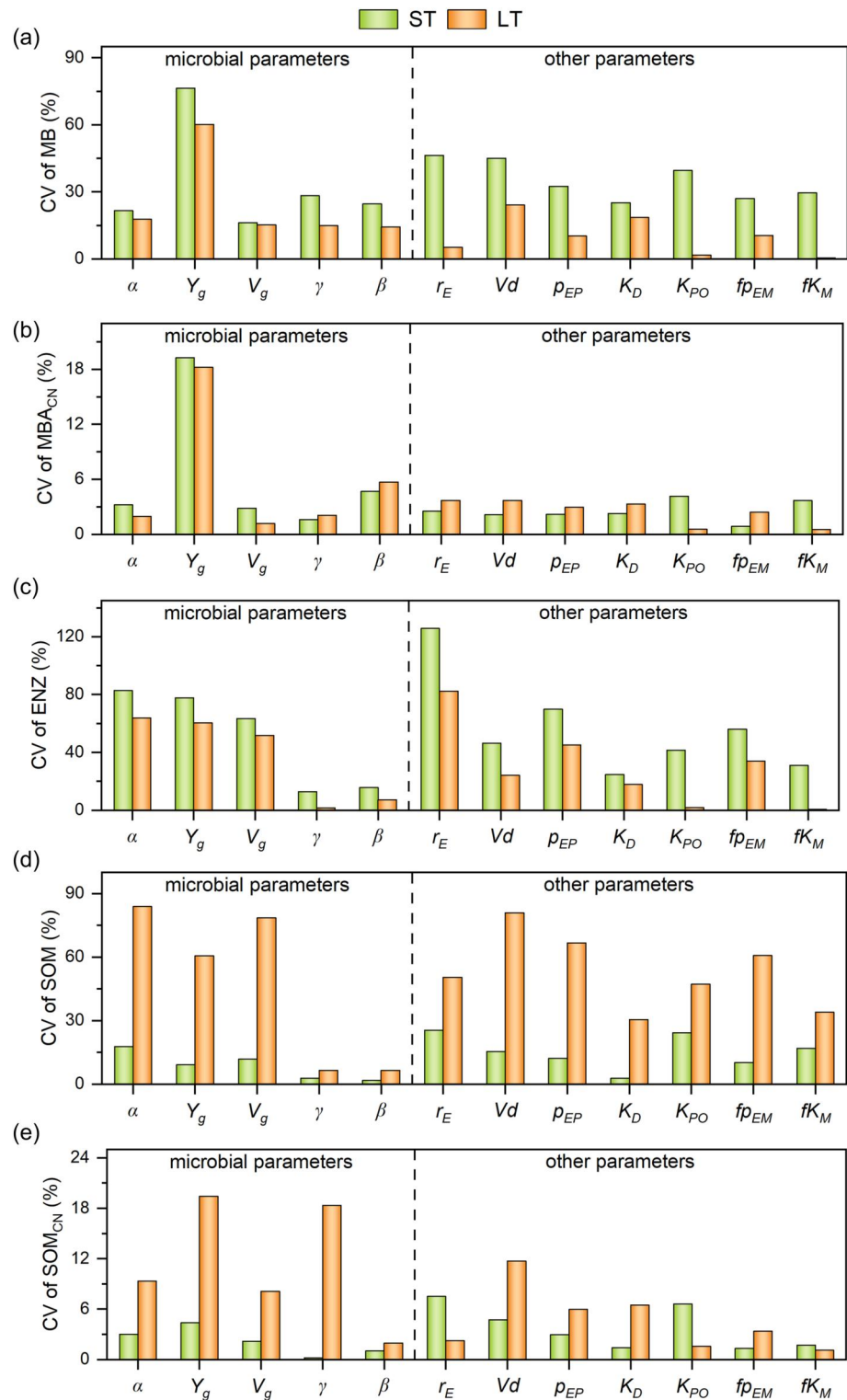
Figure 6. The simulated response of microbial-ecological processes to the changes in microbial physiological parameters versus the other parameters in the short term (ST) and long term (LT). CV denotes the coefficient of variation of the response variable simulated by 1,000 parameter samples. The statistical period for the short-term CV values was the 3-year field experimental period, and the one for the long-term CV values was the last 20 years of the 100-year simulations. See Tables 1 and 2 for a full description of the 12 model parameters and five response variables.

(=$2 \times N_{base} \times (K + 1) = 2 \times 8{,}000 \times 37$) sample parameter sets, therefore taking ca. 740 hours to complete the long-term simulations for Sobol's sensitivity analysis.

The proposed MOPSA quantifies sensitivity indices more objectively compared to MPSA because MOPSA does not require the artificial classification of parameter clusters. The MPSA method divides the parameter samples into two clusters by a fixed threshold, while different thresholds (e.g., 33%, 50%, or 67% percentile of the objective function values) may lead to different sensitivity results (Song et al., 2015; Yang, 2011). Additionally, the sensitivity indices calculated by MOPSA were close to Sobol's total-order rather than first-order sensitivity indices, indicating that MOPSA well represented the parameter interactions.

Overall, we demonstrated the effectiveness of the proposed MOPSA for the sensitivity analysis of complex models. The appropriate method should be selected according to the purpose of the study. Sobol's method can differentiate the first-order from higher-order sensitivity indices, but the computational cost increases dramatically with the number of parameters (Makler-Pick et al., 2011). Although MOPSA cannot reflect higher-order sensitivities compared to Sobol's method, MOPSA is a more efficient tool in selecting important parameters for model calibration, particularly when the separation of the first-order from the high-order sensitivities is not the focus.

4.2. Scientific Foundation for Microbial Physiology in Mediating Long-Term Soil Microbial Processes

We identified and validated important parameters for multiple C-N response variables. Our results suggest that microbial physiological parameters play an important role in simulating soil C-N processes. The incorporation of microbial physiology into an Earth system model made the simulated global soil C pools more consistent with observations (Wieder et al., 2013) and could reduce uncertainty in the prediction of soil biogeochemical responses to climate change (Garcia-Palacios & Chen, 2022). Furthermore, to extend the general application of our study, we summarized the microbial ecological models with the important parameters (i.e., Y_g, α, V_g, γ, β, Vd, r_E, VN_{plant}, VN_{nit}) (or other equivalent parameters that are informed by them) derived from our results (Table 4). major parameters were shared among around 20 microbial ecological models, although the structures of these models may not be the same.

We acknowledge that the sensitivity of same parameters may vary among models with different specific structure. Here, we expect to emphasize the microbial ecological processes associated with these crucial parameters, highlighting similar biogeochemical implications across different models. The model structure represents various assumptions related to microbial control of SOC decomposition and stabilization through interactions with mineral particles (Dwivedi et al., 2017; Salazar et al., 2018; Tang & Riley, 2015). Differences in model structure reflect varying perspectives on soil biogeochemical processes, such as the adsorption of minerals by organic matter, microbial dormancy, enzymatic decomposition, and the interactions between these processes (Sulman et al., 2017, 2018). Therefore, additional effort should be devoted to scrutinize the model uncertainty arising from varying model structures (Shi et al., 2018), even when using the same biogeochemical parameters.

We stress that microbes have a significant impact on the long-term behavior of soil biogeochemical processes. We found that microbial physiological parameters (α, Y_g, V_g, γ, and β) were more important in long-term simulations based on the increased contribution of microbial sensitivity (Figure 5). Long-term importance covered two main aspects: (a) long-term changes in microbial biomass and enzyme activity were strongly controlled by microbial physiological parameters; and (b) microbial physiological parameters increased their influence on SOM and played a dominant role in the variation of SOM_{CN} in the long run (Figure 6). The response of microbial biomass to parameter changes explained the increased contribution of microbial parameters to soil C-N processes in the long term (Blagodatsky et al., 2010), and the cumulative effect allowed the microbial influence to be further aggregated in the long run (Kallenbach et al., 2016). Active microbial biomass directly affected enzyme production and activity and thus altered SOM decomposition rates (Phillips et al., 2011; Steinweg et al., 2013). Although decomposition rates may not cause significant changes in the SOM pool immediately, small microbe-induced perturbations would cause pronounced cumulative changes over a long period of time (Liang et al., 2017; Melillo et al., 2017). Our study demonstrates that the MEND model captures the important role of microbial physiology in long-term ecological processes. It is necessary to explicitly consider microbial physiological characteristics and microbial enzyme functional groups in ecological modeling (Wang et al., 2022; Wang et al., 2015).

Table 4
Model Parameters Shared by Microbial Ecological Models

Parameter	Description	Models
Y_g	Microbial carbon use efficiency	• Allison's model (Allison et al., 2010) • Carbon, Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE) (Sulman et al., 2017; Sulman et al., 2014) • REaction-network-based model of Soil Organic Matter and microbes (RESOM) (Tang & Riley, 2015) • MIcrobial-MIneral Carbon Stabilization (MIMICS) (Kyker-Snowman et al., 2020; Wieder, Grandy, et al., 2015) • Ecological version of a Soil Microbial Model to Account for Responses To Stress (EcoSMMARTS) (Brangari et al., 2020) • ORCHIMIC (Huang et al., 2021) • German's model (German et al., 2012) • Jena Soil Model (JSM) (Yu et al., 2020) • Soil Enzyme Allocation Model (SEAM) (Wutzler et al., 2017) • Dual Arrhenius Michaelis-Menten-Microbial Carbon and Nitrogen Physiology (DAMM-MCNiP) (Abramoff et al., 2017)
α	Related to microbial maintenance rate	• Schimel's model (Schimel & Weintraub, 2003) • INDividual DIScrete SIMulations SOM (INDISIM-SOM) (Ginovart et al., 2005) • Manzoni's model (Manzoni et al., 2014) • SEAM (Wutzler et al., 2017) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021)
V_g	Specific microbial growth rate	• Schimel's model (Schimel & Weintraub, 2003) • Allison's model (Allison et al., 2010) • MIMICS (Kyker-Snowman et al., 2020; Wieder et al., 2014; Wieder, Grandy, et al., 2015) • Manzoni's model (Manzoni et al., 2014) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021) • JSM (Yu et al., 2020)
γ	Related to microbial mortality rate	• Schimel's model (Schimel & Weintraub, 2003) • INDISIM-SOM (Ginovart et al., 2005) • CORPSE (Sulman et al., 2017; Sulman et al., 2014) • MIMICS (Kyker-Snowman et al., 2020; Wieder et al., 2014; Wieder, Grandy, et al., 2015) • Manzoni's model (Manzoni et al., 2014) • SEAM (Wutzler et al., 2017) • DAMM-MCNiP (Abramoff et al., 2017) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021) • Germain's model (German et al., 2012) • JSM (Yu et al., 2020) • Microbial Carbon and Nitrogen Turnover in soils (MiCNiT) (Blagodatsky et al., 2011)
β	Related to maintenance rate of dormant microbes	• ORCHIMIC (Huang et al., 2021) • Manzoni's model (Manzoni et al., 2014) • EcoSMMARTS (Brangari et al., 2020)
Vd	Maximum specific decomposition rate	• Allison's model (Allison et al., 2010) • CORPSE (Sulman et al., 2017; Sulman et al., 2014) • MIMICS (Kyker-Snowman et al., 2020; Wieder et al., 2014; Wieder, Grandy, et al., 2015) • Manzoni's model (Manzoni et al., 2014) • SEAM (Wutzler et al., 2017) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021) • German's model (German et al., 2012) • JSM (Yu et al., 2020) • MiCNiT (Blagodatsky et al., 2011)
r_E	Enzyme turnover rate	• Schimel's model (Schimel & Weintraub, 2003) • Allison's model (Allison et al., 2010) • Manzoni's model (Manzoni et al., 2014) • SEAM (Wutzler et al., 2017) • DAMM-MCNiP (Abramoff et al., 2017) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021)
p_{EP}	Enzyme production rate	• Schimel's model (Schimel & Weintraub, 2003)

Table 4
Continued

Parameter	Description	Models
VN_{plant}	Plant nitrogen uptake rate	• Allison's model (Allison et al., 2010) • Manzoni's model (Manzoni et al., 2014) • SEAM (Wutzler et al., 2017) • DAMM-MCNiP (Abramoff et al., 2017) • ORCHIMIC (Huang et al., 2018; Huang et al., 2021) • Plant/soil model with two microbial functional types (SYMPHONY) (Perveen et al., 2014) • JSM (Yu et al., 2020) • ORCHIMIC (Huang et al., 2021)
VN_{nit}	Nitrification rate	• INDISIM-SOM (Ginovart et al., 2005) • Microbial community trait-based model (MicroTrait-N) (Bouskill et al., 2012) • MiCNiT (Blagodatsky et al., 2011)

Given the short- and long-term differences in microbial regulation of C-N processes, we argue to pay attention to the long-term C-N dynamics when calibrating microbial ecological models. A previous work demonstrated that estimates of key microbial physiological parameters could differ significantly when model calibration was performed using data sets with different time scales (Jian et al., 2020). The incubation experiments of different time duration suggested that microbial growth rate (V_g) may be overestimated in short-term incubations, as higher substrate availability may stimulate microbial uptake and growth rates in the short term (Schnecker et al., 2019; Sinsabaugh et al., 2013). Our study extends the simulation period from the short-term (<5 years) to the long-term (100 years) and elucidates the necessity of examining model behaviors beyond the conventional experimental period.

5. Conclusions

We developed a comprehensive and efficient global sensitivity analysis method (i.e., MOPSA) to identify important parameters in complex microbial ecological models with multiple response variables in the short- and long-term simulations. The proposed MOPSA can be generalized to complex models owing to its high efficiency and no requirement for the probability distribution of parameters. We proved that for models with less than 40 undetermined parameters, MOPSA achieved convergent sensitivity outcomes with just 8,000 total samples, whereas Sobol's method required 592,000 total samples. Notably, the important parameters identified by the two methods exhibited similarity and no significant differences. It is evident that MOPSA was more computationally efficient than Sobol's method for sensitivity analysis of complex models. Our study demonstrates that microbial physiology may become more significant in mediating long-term than short-term C-N cycling, which, to our knowledge, has not been revealed in previous studies. We acknowledge that this conclusion needs to be further validated against long-term experimental results if available. Nevertheless, we stress that microbial physiology could have important implications for long-term soil C-N processes and that experiment-model integration practices should examine model behaviors beyond the conventional short-term experimental period. The outcomes of sensitivity analysis herein not only provide technical support for parameterization and mechanistic understanding of the MEND model, but also have general implications for other microbial ecological models (Table 4).

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data and code for this study are accessible at Zenodo via https://doi.org/10.5281/zenodo.10875440 (Li et al., 2023) and https://doi.org/10.5281/zenodo.8363781 (Wang et al., 2023).

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A Computationally Efficient Method for Parameter Sensitivity Analysis of Microbially Explicit Biogeochemical Models Accounting for Long-Term Behavior

Li, Wanyu; Wang, Gangsheng; Xiang, Daifeng

01	mingxi zhang	Page 2
	31/10/2024 6:36	
02	mingxi zhang	Page 2
	31/10/2024 6:37	
03	mingxi zhang	Page 2
	31/10/2024 6:39	
04	mingxi zhang	Page 2
	31/10/2024 6:39	
05	mingxi zhang	Page 19
	31/10/2024 6:59	
06	mingxi zhang	Page 19
	31/10/2024 6:59	
07	mingxi zhang	Page 19
	31/10/2024 6:59	