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## RESEARCH ARTICLE

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### Key Points:

- Both conventional linear and microbial nonlinear models can capture the pulsed dynamics of heterotrophic respiration
- The moisture-response function combined with model parameterization dominates the modeled uncertainties in heterotrophic respiration
- More observations of nonlinear C phenomena are needed to reduce the simulation uncertainty on soil C cycling in Earth system models

### Supporting Information:

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

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## A Comparison of Linear Conventional and Nonlinear Microbial Models for Simulating Pulse Dynamics of Soil Heterotrophic Respiration in a Semi-Arid Grassland

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**Abstract** As a critical process in regulating terrestrial feedback to climate change, soil heterotrophic respiration is commonly simulated with the first-order kinetics in current Earth system models. Compared with the first-order kinetic models, explicit microbial models are expected to better simulate nonlinear carbon (C)-cycle phenomena, such as the pulse dynamics of soil heterotrophic respiration driven by dry-rewetting cycles in grasslands. However, these two types of models (i.e., linear conventional and nonlinear microbial models) have never been compared based on in situ observations of soil heterotrophic respiration in the semi-arid grassland, which is significantly affected by the dry-rewetting events. Here, based on the field data of soil heterotrophic respiration in a semi-arid grassland in northern China, we first showed that the shift from a conventional linear model to a nonlinear microbial model did not substantially improve the simulation of soil heterotrophic respiration. Then, we quantified the contributions of different moisture-response functions to the uncertainty in simulating the soil C dynamics. The results showed that the selection of moisture-response functions combined with parameterization in the soil C models dominated the modeled uncertainties in soil heterotrophic respiration. These findings suggest that both the conventional linear model and nonlinear microbial model can simulate well the pulse dynamic of soil heterotrophic respiration in grasslands with an improved parameterization of water regulation on soil carbon decomposition. This study also calls for more observations of nonlinear C phenomena for reducing the simulation uncertainty on soil C cycling in Earth system models.

**Plain Language Summary** Soil heterotrophic respiration refers to the process of decomposing soil organic carbon and releasing CO<sub>2</sub> into the atmosphere. Current soil carbon models use the first-order kinetics to represent the decomposition process, but large uncertainties have emerged in simulating soil heterotrophic respiration among these models. Therefore, models incorporating microbial mechanisms are expected to better simulate soil carbon processes than the conventional models, especially in simulating the nonlinear phenomena of soil heterotrophic respiration. To test the ability of these two types of models (i.e., linear conventional and nonlinear microbial models) in simulating the nonlinear soil processes, we evaluate them based on in situ observations of the pulsed dynamics of soil heterotrophic respiration in a semi-arid grassland. We found the microbial-explicit model did not substantially improve the simulation of soil heterotrophic respiration. The moisture-response function combined with parameterization played an important role in reducing the uncertainties in simulating the pulsed dynamics of soil heterotrophic respiration in both types of models.

### 1. Introduction

The dynamic of soil organic carbon (C) under climate change is a key regulator of ecosystem C cycling due to the large C storage capacity in the soil and its high sensitivity to environmental changes (Bradford et al., 2016; Davidson & Janssens, 2006; Doetterl et al., 2015). To improve our understanding of the soil C

dynamics and its interactions with the past and future climate changes, many numerical soil C-cycle models based on the first-order kinetics have been developed. The decomposition of soil organic matters in those models, for example, CENTURY (Parton et al., 1987) and RothC (Jenkinson et al., 1991), is typically represented as multiple pools with first-order decay rates. Although the first-order linear multi pool models have been widely used in Earth system modeling, large uncertainties have emerged in simulating soil C dynamics and soil heterotrophic respiration ( $R_H$ ) among models because of their differences in model structure and parameterization (Bradford et al., 2016; Todd-Brown et al., 2013; Zhou et al., 2021).

One promising approach to reduce the large uncertainties on soil C dynamics in Earth system models is explicitly representing microbial processes with the multi pool models (Luo et al., 2016; Wieder, Allison, et al., 2015). Some recent efforts have been made to develop nonlinear soil C models based on microbial physiological processes (Abramoff et al., 2018; Allison et al., 2010; German et al., 2012; Wang et al., 2013; Wieder et al., 2013; Wieder, Grandy, et al. 2015). In many examples, the microbial process-based models have improved the modeling of the soil C dynamic and its feedbacks to climate change (Wang et al., 2013, 2016; Wieder, Allison, et al., 2015). However, it should be noted that a few other studies also have shown that current microbial models could conversely amplify the uncertainty in predicting soil C responses to climate change due to the complex mechanisms in microbial processes and challenges in model parameterization (Shi et al., 2018; Sulman et al., 2018).

Another important way to improve the accuracy of soil C dynamics in Earth system models is better parameterizations of environmental impacts in the model (Falloon et al., 2011; Sierra et al., 2015; Xia et al., 2013). The environmental response function in current linear or nonlinear soil C models varies significantly among models and hence causes considerable uncertainty in simulating soil C dynamics (Falloon et al., 2011; Sierra et al., 2015). For example, in a grassland ecosystem, Lei et al. (2018) have indicated that different water scalars greatly affected the modeled ecosystem respiration and can result in a large spread of the future projections of the ecosystem C sink.

The above activities of model improvement lead to a new question of how linear conventional and nonlinear microbial models will perform if they are used to simulate the nonlinear C-cycle phenomena, such as the rain-pulse effect in semi-arid grasslands. The rain-pulse effect, often referred to as the “Birch effect,” is a typical microbially driven nonlinear soil process (Birch, 1964; Lawrence et al., 2009; Schimel & Weintraub, 2003). The rain-pulse effect of  $R_H$  is an essential contributor to soil-to-air C (e.g.,  $\text{CO}_2$ ,  $\text{CH}_4$ ) release in semi-arid grasslands (Yan et al., 2014). The pulse C release can be 30-times higher than under normal hydrological conditions and contribute to as much as 40% of ecosystem  $\text{CO}_2$ -efflux in some grasslands (Sponseller, 2007; Yan et al., 2014). Accurate simulation of the rainfall pulse effect is relevant for understanding the soil C dynamics of semi-arid grasslands. However, modeling studies have shown that the rain-pulse effect of  $R_H$  can be captured by some soil microbial models (Salazar et al., 2018; Schimel & Weintraub, 2003; Waring & Powers, 2016) or by some conventional linear models (Waring & Powers, 2016). Therefore, the pulse response of  $R_H$  to rainfall events in semi-arid grasslands provides an ideal case for evaluating the performance of different soil C models.

In this study, we applied eight terrestrial C cycling models by incorporating two different soil C model structures (linear conventional or nonlinear microbial) and four soil water-scalar schemes. Using these models, we conducted numerical experiments to simulate the rain pulse effect on soil C dynamics in a semi-arid grassland. Based on the comparative analysis, this study aimed to evaluate (1) whether the conventional linear model can capture nonlinear soil C process due to the rain-pulse effect as microbial models do, and (2) how the moisture response function affects the model performance in simulating the nonlinear soil C process.

## 2. Materials and Methods

### 2.1. Site Description and Data Sources

The observational soil  $\text{CO}_2$ -efflux data and meteorological forcings for models were obtained during the growing season in 2009 from a continuous field manipulative experiment in a semi-arid grassland in China. The study site is located at Duolun County ( $42^{\circ}27'N$ ,  $116^{\circ}41'E$ ) in northeastern Inner Mongolia, China. The dominant species of this region are *Stipa krylovii*, *Agropyron cristatum*, *Leymus chinensis*, and *Artemisia*

*frigida*. According to the U.S. soil taxonomy classification system (Yuan et al., 2005), the soil at the study site is classified as Calcic-orthic Aridisol. The mean annual air temperature is 3°C, ranging from −30°C in the winter to 34°C in the summer. The mean annual precipitation is 377 mm, nearly 95% (i.e., 358 mm) of which fall in the growing season (May to October).

The  $R_H$  was measured based on the clipping method (Byrne & Kiely, 2006). This method was used to separate the auto- and heterotrophic parts of soil respiration, which assumed that continuous removal of living plants greatly inhibited root growth in the clipped plots and the soil CO<sub>2</sub>-efflux in the plots would mainly come from soil fauna and microbial respiration. Therefore, three 1 × 1 m clipped plots 5–30 m apart were designed in late April 2006. The living plants in these clipped plots and an area of 10 cm around the plots were removed a month before the first measurement. Meanwhile, a PVC collar (20.3 cm in diameter and 8 cm in height) was inserted into the soil at a depth of 3 cm in each plot one month before the first measurement. Soil CO<sub>2</sub> efflux was continuously measured every half an hour during the growing season using an infra-red gas analyzer (LI-840, Li-Cor Inc., Lincoln, NE, USA) with three automatic measurement chambers. Soil CO<sub>2</sub> efflux rate was determined by the time-series of CO<sub>2</sub> concentrations in these chambers, which were recorded by a CR1000 data logger (Campbell Scientific Inc., CSI, USA Utah, Utah) and were processed by LoggerNet 3.1 (CSI, USA). Each measurement lasted 120 s. This measurement lasted from the beginning of May to the end of October during 2009. Most missing data gaps were less than 2 h and were filled by linear interpolation based on the nearby data or the linear relationship between  $R_H$  and soil moisture.

The precipitation and the CO<sub>2</sub> fluxes, including net ecosystem exchange (NEE) and ecosystem respiration (ER), were recorded at a half-hour time step by a nearby eddy covariance flux tower located 4 m above the ground. In this study, NEE represented the net CO<sub>2</sub> exchange between ecosystem and atmosphere, and a positive NEE means ecosystem carbon release while the negative NEE means ecosystem carbon uptake. The gross primary productivity (GPP) was calculated as the difference between NEE and ER. More details of the measurement and calculation method have been described in Zhang et al. (2007). Soil temperatures were measured by soil temperature probes (CSI, USA) with a depth of 10 cm. The volumetric soil moistures were measured by the CS616 soil water probes (CSI, USA) at a depth of 0–10 cm. These probes were placed near the soil CO<sub>2</sub> efflux chambers and the mean values of half-hour soil temperature and moisture were recorded simultaneously in the CR1000 data logger (CSI, USA).

## 2.2. Model Description

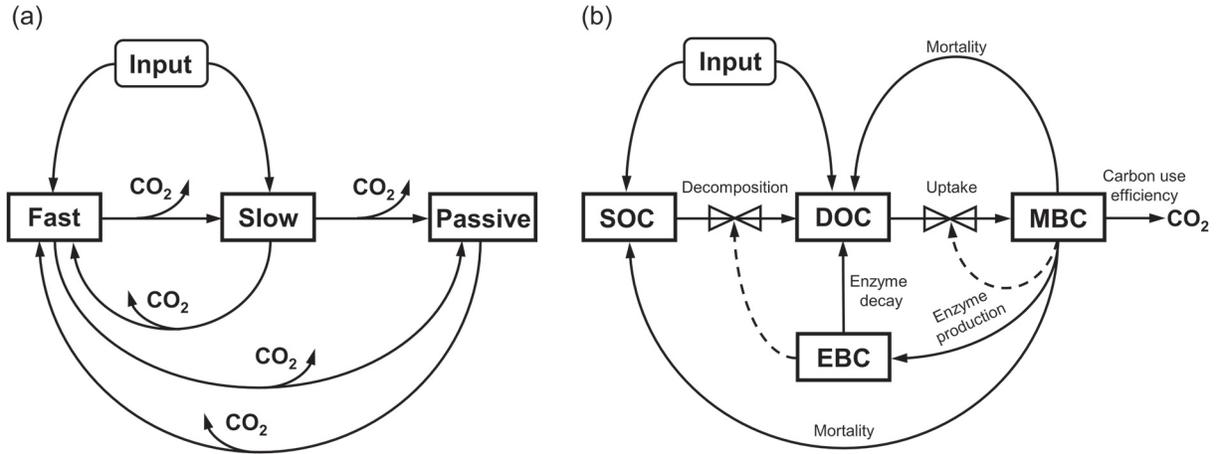
### 2.2.1. Model Structures

To evaluate how well different model structures capture the soil C dynamics in response to the rain events, we incorporated two models (linear conventional vs. nonlinear microbial model) into a terrestrial C cycling model that is a simplified version of the Terrestrial ECOSystem (TECO) model (Weng & Luo, 2008). The conventional linear model is based on Liang et al. (2018), while the nonlinear microbial model is based on Allison et al. (2010), outlined in Figure 1. Both models include the same above ground C allocation process and the input of litterfall. We used the measured GPP as the input of the models.

The conventional model includes three soil pools divided based on their decomposition rates: a fast soil C, a slow soil C, and a passive soil C (Figure 1a). Each pool in the conventional model has a constant turnover rate, and CO<sub>2</sub> is released from each pool through C decomposition, and a fraction of C in one pool is transferred to another. Parameters describing fractions between the three soil C pools are shown in Table S1. The decomposition of each C pool is represented by the following equation (Lawrence et al., 2009):

$$\frac{dC_i}{dt} = k_i C_i M_s T_s \quad (1)$$

where  $C_i$  is the pool size (g C m<sup>−2</sup>) and  $k_i$  is the turnover rate in each specific pool (day<sup>−1</sup>).  $T_s$  and  $M_s$  are scalar schemes of temperature response function and moisture response function (MRF) respectively to modify the C decomposition rate depending on the abiotic environment. The temperature response function ( $T_s$ ) in all models of this study was expressed as follows (Lei et al., 2018):



**Figure 1.** The diagram of the two carbon cycle models in this study, (a) with conventional structure (from TECO model) and (b) microbial structure (Allison et al., 2010) in the part of the soil, respectively (Fast soil carbon pool, Fast; Slow soil carbon pool, Slow; Passive soil carbon pool, Passive; Soil organic carbon, SOC; Dissolve organic carbon, DOC; Microbial biomass carbon, MBC; Enzyme biomass carbon, EBC). TECO, Terrestrial ECOSystem.

$$T_s = Q_{10}^{\frac{T_{\text{soil}} - T_{\text{ref}}}{T_{\text{ref}}}} \quad (2)$$

where the  $T_{\text{soil}}$  represents the soil temperature ( $^{\circ}\text{C}$ ).  $Q_{10}$  and  $T_{\text{ref}}$  are set to 2 and 10 ( $^{\circ}\text{C}$ ), respectively (Friedlingstein et al., 2006).

The microbial soil C cycling model used in this study incorporates four pools: a microbial biomass carbon (MBC), a dissolved organic carbon (DOC), a soil enzyme biomass carbon (EBC), and a soil organic carbon (SOC) (Figure 1b). The two processes of the decomposition of SOC and the assimilation of MBC from the DOC pool are represented as the Michaelis-Menten function (Allison et al., 2010):

$$F_s = V_{\text{max}} \times \text{EBC} \times \frac{\text{SOC}}{\text{Km} + \text{SOC}} \quad (3)$$

$$F_U = V_{\text{max uptake}} \times \text{MBC} \times \frac{\text{DOC}}{\text{Km}_{\text{uptake}} + \text{DOC}} \quad (4)$$

where  $F_s$  is the fraction of SOC decomposition.  $F_U$  is the fraction of MBC uptaking from DOC.  $V_{\text{max}}$  and  $V_{\text{max uptake}}$  indicate the maximal decomposition rate ( $\text{day}^{-1}$ ), which is calculated by the Arrhenius equation.  $\text{Km}$  and  $\text{Km}_{\text{uptake}}$  ( $\text{g C m}^{-2}$ ) is the half-saturation of the MBC or EBC on the substrate. Microbial death and enzyme production are modeled as a constant fraction of MBC. The enzyme turnover is a first-order process with a constant rate. More details about the parameters and processes are described in Allison et al. (2010).

Heterotrophic CO<sub>2</sub> ( $R_H$ ) is the fraction of DOC assimilated by microbes that is not allocated to biomass production:

$$R_H = V_{\text{max uptake}} \times \text{MBC} \times \frac{\text{DOC}}{\text{Km}_{\text{uptake}} + \text{DOC}} (1 - \text{CUE}) \quad (5)$$

where  $V_{\text{max uptake}}$  represents the maximum decomposition rate of DOC assimilated by microbes. MBC is the microbial biomass carbon.  $\text{Km}_{\text{uptake}}$  is the half-saturation of the substrate. CUE is the carbon use efficiency.

More descriptions of parameters for the microbial model are shown in Table S2. More details of the microbial model can be found in Allison et al. (2010), such as the changes of MBC and EBC.

Considering the effects of environmental factors (e.g., temperature and moisture), we added the temperature and water responses into the Michaelis-Menten function:

**Table 1**  
Moisture Response Function (MRF) Parameterizations on Soil Carbon Decomposition From Four Different Terrestrial Biosphere Models

	Provenance	Moisture response function
MRF <sub>1</sub>	CABLE	$\left(\frac{1.7 - W_C}{1.15}\right)^{6.6481} \left(\frac{W_C + 0.007}{0.557}\right)^{3.22}$
MRF <sub>2</sub>	IBIS	$\frac{-(W_C - 0.6)^2}{e^{0.08}}$
MRF <sub>3</sub>	LPJ-DGVM	$0.25 + 0.75W_C$
MRF <sub>4</sub>	TECO	$\begin{cases} 5 \times W_C & (W_C < 0.2) \\ 1 & (W_C \geq 0.2) \end{cases}$

Note. WC: soil water content (v/v%).

Abbreviation: TECO, Terrestrial ECOSystem.

$$\frac{dC_i}{dt} = V_{\max} \times C_i \times \frac{S}{K + S} M_s T_s \quad (6)$$

where the  $M_s$  and the  $T_s$  are the scalar schemes as used in the linear soil C model.

### 2.2.2. Soil Water Response Parameterizations

To assess and compare the contribution of different MRF schemes (i.e.,  $M_s$ ) to the uncertainty in the soil C dynamics modeling, we incorporated four soil MRF schemes in the TECO model and re-parameterized them (Table 1). These MRFs are all derived from terrestrial C cycle models. The scheme MRF<sub>1</sub> from the CABLE model (Wang et al., 2010) and the MRF<sub>2</sub> from IBIS model (Kucharik et al., 2000) are nonlinear functions of soil moisture, while the MRF<sub>3</sub> from LPJ-DGVM model (Sitch et al., 2003) and the MRF<sub>4</sub> from TECO model (Weng & Luo, 2008) are linear functions of soil moisture. Their response curves to soil moisture are shown in Figure S1. The moisture-response functions MRF<sub>1</sub> and MRF<sub>2</sub> start from 0

and grow to unit 1 when the soil water content exceeds 50%. While the linear response function MRF<sub>3</sub> changes from 0.25 to 0.6 with soil water content from 0% to 50%. The linear response function MRF<sub>4</sub> has the maximum growth rate with a range from 0 to 1 when the soil water content increases from 0% to 20%.

### 2.3. Data Assimilation for Improving Model Parameterization

In this study, we combined two C-cycle structures (conventional and microbial) models with four MRF schemes, which then produce eight model variants. All of them had parameter optimizations via a data assimilation method before their comparisons. To optimize the parameters of models, the conditional Bayesian inversion was used to assimilate data in this study (Du et al., 2017; Jiang et al., 2018; Li et al., 2016; Ma et al., 2017). The Bayes' theorem can be expressed as follow:

$$p(\theta | Z) \propto p(Z | \theta)P(\theta) \quad (7)$$

where  $P(\theta)$  represents the prior knowledge of the parameters in the models, referring to the previous studies (Allison et al., 2010; Shi et al., 2018). The detailed description of the parameters is shown in Tables S1 and S2. Additionally, the likelihood function  $p(Z | \theta)$  was calculated based on the assumption that the errors (with mean biases removed) between each observation data and model simulation results followed a Gaussian distribution with a zero mean. It can be expressed as follows:

$$p(Z | \theta) \propto \exp \left\{ - \sum_{t \in Z} \frac{[Z(t) - X(t)]^2}{2\sigma^2(t)} \right\} \quad (8)$$

where  $Z(t)$  is the observation stream at time  $t$ ,  $X(t)$  is the corresponding simulated variable, and  $\sigma(t)$  is the standard deviation of the observation set.

The posterior probability distribution of parameters was obtained by the Markov chain Monte Carlo (MCMC) technique with adaptive Metropolis-Hastings (M-H) algorithm (Hastings, 1970; Metropolis et al., 1953). The new proposal parameters were generated by:

$$C^{\text{new}} = C^{k-1} + r(\theta_{\max} - \theta_{\min}) \quad (9)$$

where  $\theta_{\max}$  and  $\theta_{\min}$  are the maximum and minimum values of the given parameter space, respectively (shown in Tables S1 and S2),  $C^{k-1}$  means the parameter set of the previous step, and  $r$  is a random variable

between  $-0.5$  and  $0.5$  with a uniform distribution. The initial samples (approximately 5,000 for each run) were discarded after the running means, and standard deviations (SDs) were stabilized (regarded as the burn-in period) (Du et al., 2017). All the accepted samples without the burn-in periods were used for posterior analysis. In total, there are 50,000 accepted samples from five parallel chains to construct the posterior distribution.

The initial values of total soil C used in the models were obtained from measurements (Liu et al., 2013). The optimized values of the ratio of each C pool to the measured total soil C in the conventional model are used as the initial stable state of the model. The upper ranges of the initial values of MBC, EBC, and DOC in the microbial model for data assimilation were set  $\sim 1\%$  of total C carbon (Wieder et al., 2013). To equilibrate the models under different parameter sets, we set each step of data assimilation to run 7,300 time-steps before the start of the simulations used to examine if the new parameter set should be accepted or rejected. The detailed information on the initial state variables in the models is shown in Table S3.

#### 2.4. Model Evaluation

To evaluate the ability of models to simulate the soil C dynamics, we compared the modeled  $R_H$  with experimental data by deviance information criterion (DIC) (Liang et al., 2018; Spiegelhalter et al., 2002). In our study, half of the observation data were randomly selected for parameter optimization by data assimilation and the other half for verification. For each model, DIC was calculated by

$$\text{DIC} = \bar{D} + p_D \quad (10)$$

where

$$\bar{D} = \frac{1}{n} \sum_{i=1}^n \left( -2 \log \left( p(Z | \theta^i) \right) \right) \quad (11)$$

and

$$p_D = \bar{D} + 2 \log \left( p(Z | \bar{\theta}) \right) \quad (12)$$

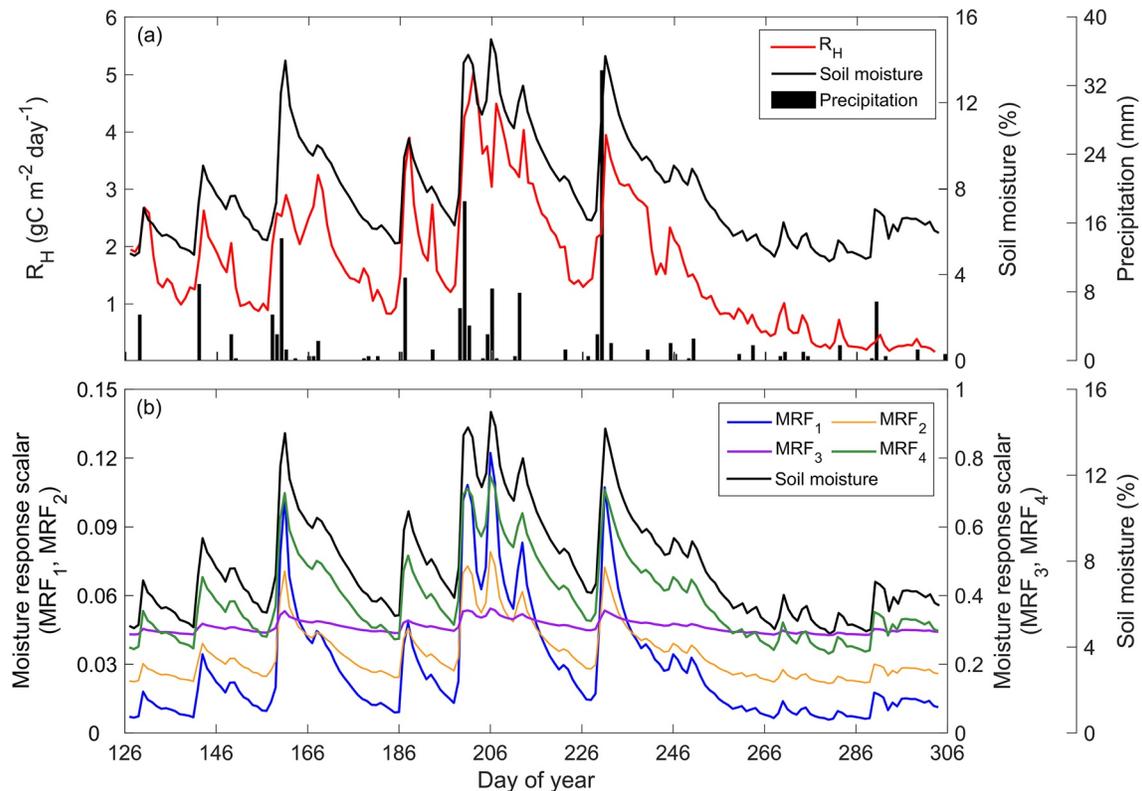
where  $n$  is the number of the generated parameter sets, and  $\bar{\theta}$  is the mean of the generated parameter sets. A smaller DIC for a model means a better simulation against observational data.

We randomly selected 1,000 parameter sets from the posterior probability distribution formed by data assimilation in each model from the eight model combinations. We further obtained the DICs of the simulations from these parameter sets. The DIC results were used to evaluate the performance of these models. Comparing the DIC results of conventional and microbial models, we analyzed which of these model structures can better capture the rain pulse.

MRF can affect the decomposition of different soil C pools and thus affect the performances of models in simulating  $R_H$ . In our study, the relationships between  $R_H$  and the changes of different soil C pools are measured by the partial correlation that is conducted by the software of Matlab (R2019a). Meanwhile, different moisture-response functions can change the sensitivity of simulating  $R_H$  to the parameters in the model. The sensitivity of parameters in our study is determined by the sensitivity index (I) defined as (Lenhart et al., 2002):

$$I = \frac{|(y_2 - y_1)| / y_0}{2\Delta x / x_0} \quad (13)$$

Where  $y_0$  is the model output ( $R_H$ ) with the initial parameter set  $x_0$ . The model outputs from initial parameters varied by  $\pm \Delta x$  are variable  $y_2$  and  $y_1$ .  $\Delta x$  was set at 0.25 times of initial values. Details of the sensitivity index are available in Lenhart et al. (2002).



**Figure 2.** Time-series of observed  $R_H$  (red line), soil moisture (black line), precipitation (black rectangle) (a), and the scalar ability of four different moisture response functions (MRF) under the conditions of observed soil moisture (b).

### 3. Results

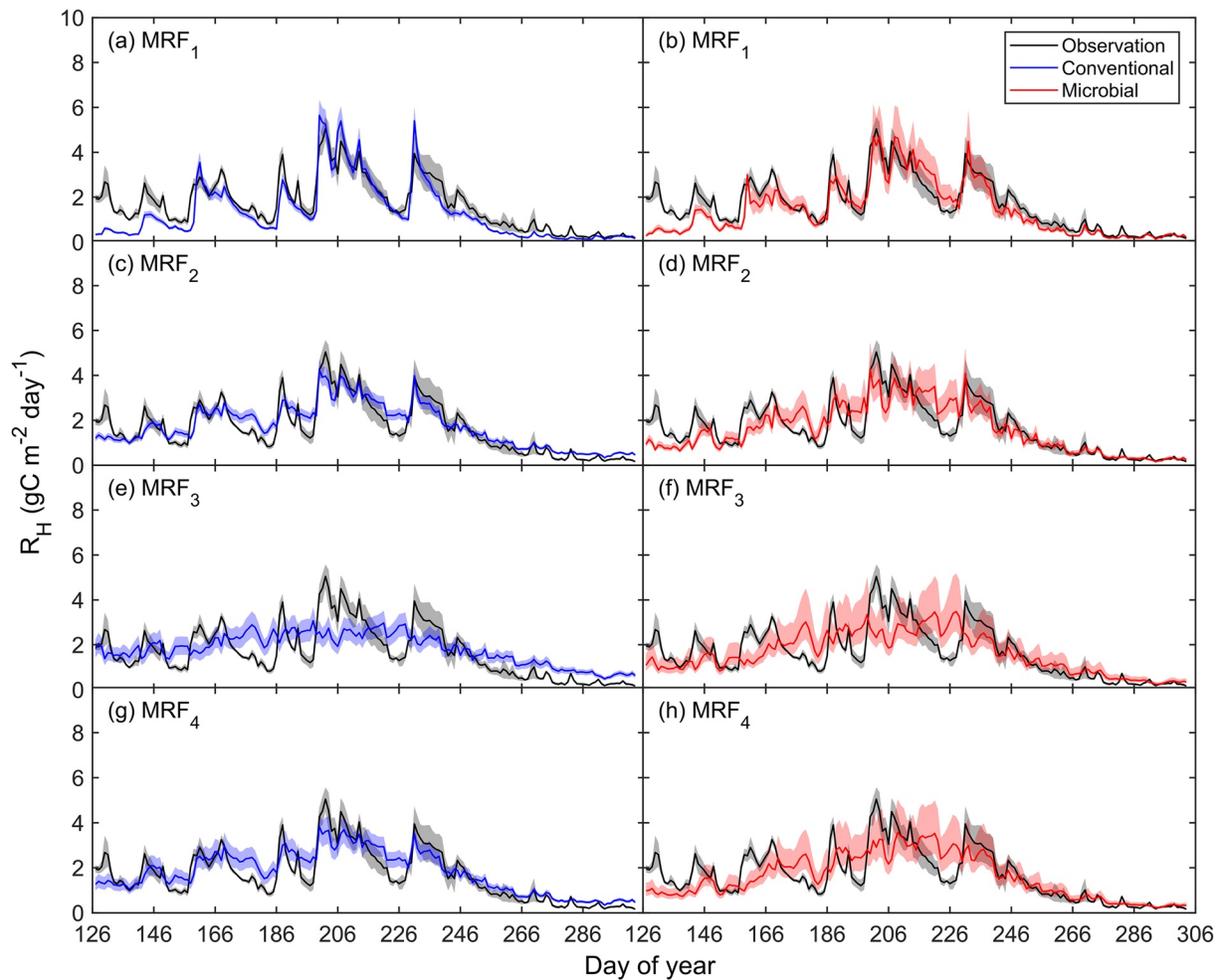
#### 3.1. Observed Rain Pulse in a Grassland

From the observation-based analysis, we show that the patterns of soil moisture and  $R_H$  were significantly affected by the rainfall events during the growing season (Figure 2a). Generally, rainfall events varied from 0.3 to 33.8 mm, and the observed soil moisture increased by 0.4%–132% accompanied by rainfall events. The observed  $R_H$  also showed obvious variations and increased by 4.4%–369.2% in 1–2 days after the rainfall events. After reaching its peak,  $R_H$  gradually returned to pre-rainfall levels in 2–5 weeks (Figure 2a). Additionally, MRFs used in our study showed different regulation abilities under the measured soil moisture conditions. As shown in Figure 2b, during the growing season, the water response scalar of MRF<sub>1</sub> and MRF<sub>2</sub> changed from 0.0058 to 0.12 and 0.022 to 0.079, respectively, while MRF<sub>3</sub> and MRF<sub>4</sub> ranged from 0.28 to 0.36 and 0.23 to 0.75, respectively (Figure 2b).

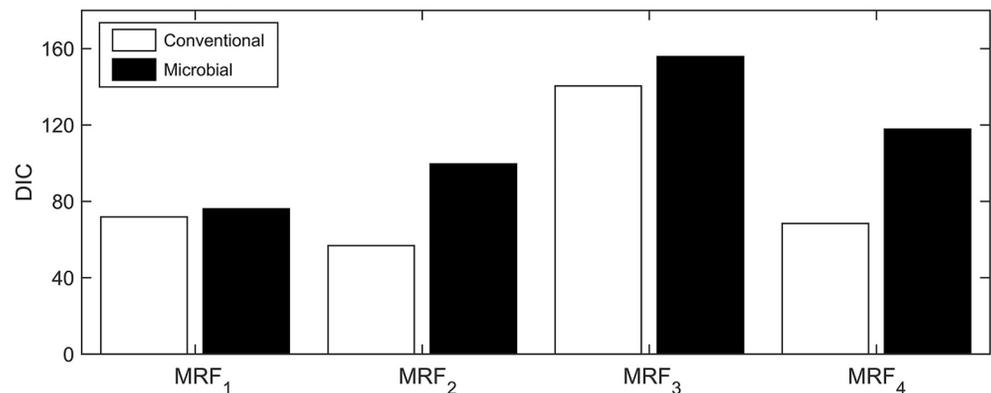
#### 3.2. Model Validation and Comparison

The data assimilation method could effectively constrain most of the targeted parameters in all models (Figure S2). After optimizing the parameters by conditional Bayesian method (see Tables S1 and S2 for optimized parameters in conventional and microbial models, respectively), the modeled daily  $R_H$  from May to October in 2009 matched more closely to the observed values both on timing and magnitude, with differences among models (Figure 3). Most models exhibited similar bias in simulating  $R_H$  during the growing season, which showed an underestimation during the rewetting periods and an overestimation during the dry periods, while models with the MRF<sub>1</sub> scheme showed that a slight overestimation during rewetting periods and an underestimation during dry periods (Figure 3).

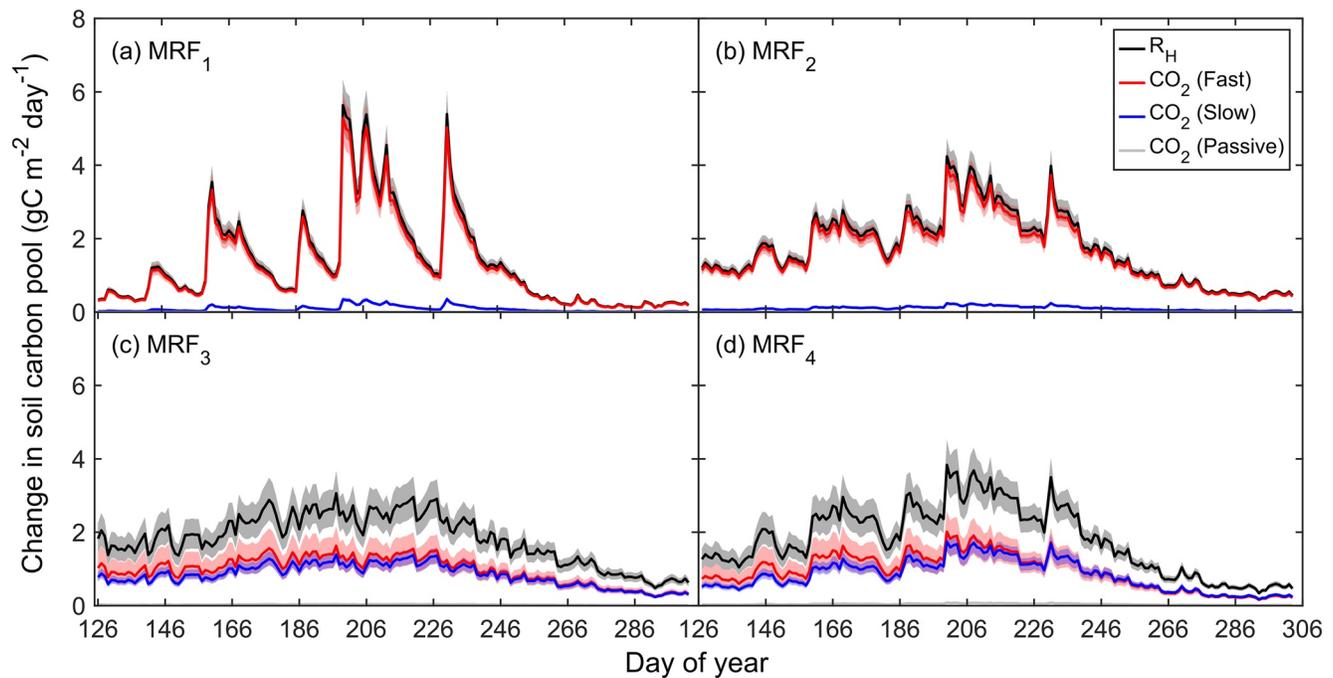
We further evaluated the performance of the eight models. The values of DIC varied greatly among different MRFs in each model structure (Figure 4). Generally, the  $R_H$  from microbial models showed higher DICs



**Figure 3.** Time-series of observed and simulated daily  $R_H$  in Inner Mongolia grassland from May to October in 2009. MRF<sub>1</sub>-MRF<sub>4</sub> represent moisture response function from CABLE, IBIS, LPJ, and TECO, respectively. (a, c, e, and g) represent conventional models with four different moisture response functions, respectively. (b, d, f, and h) represent microbial models with four moisture response functions, respectively (Blue and red range for simulation from conventional and microbial models with posterior parameter sets and solid line for models with parameters of maximum likelihood. Block line and range are observations). TECO, Terrestrial ECOSystem.



**Figure 4.** The results of deviance information criterion (DIC) indicate the comparison of overall model agreement with observations. A smaller DIC represents the model performs better. MRF<sub>1</sub>-MRF<sub>4</sub> represent moisture response functions from four different models (CABLE, IBIS, LPJ, and TECO, respectively). TECO, Terrestrial ECOSystem.



**Figure 5.** Time-series of the contributions of different soil carbon pools to soil heterotrophic respiration ( $R_H$ ) in conventional models (MRF<sub>1</sub>-MRF<sub>4</sub> are moisture response functions from the model of CABLE, IBIS, LPJ, and TECO, respectively). TECO, Terrestrial ECOSystem.

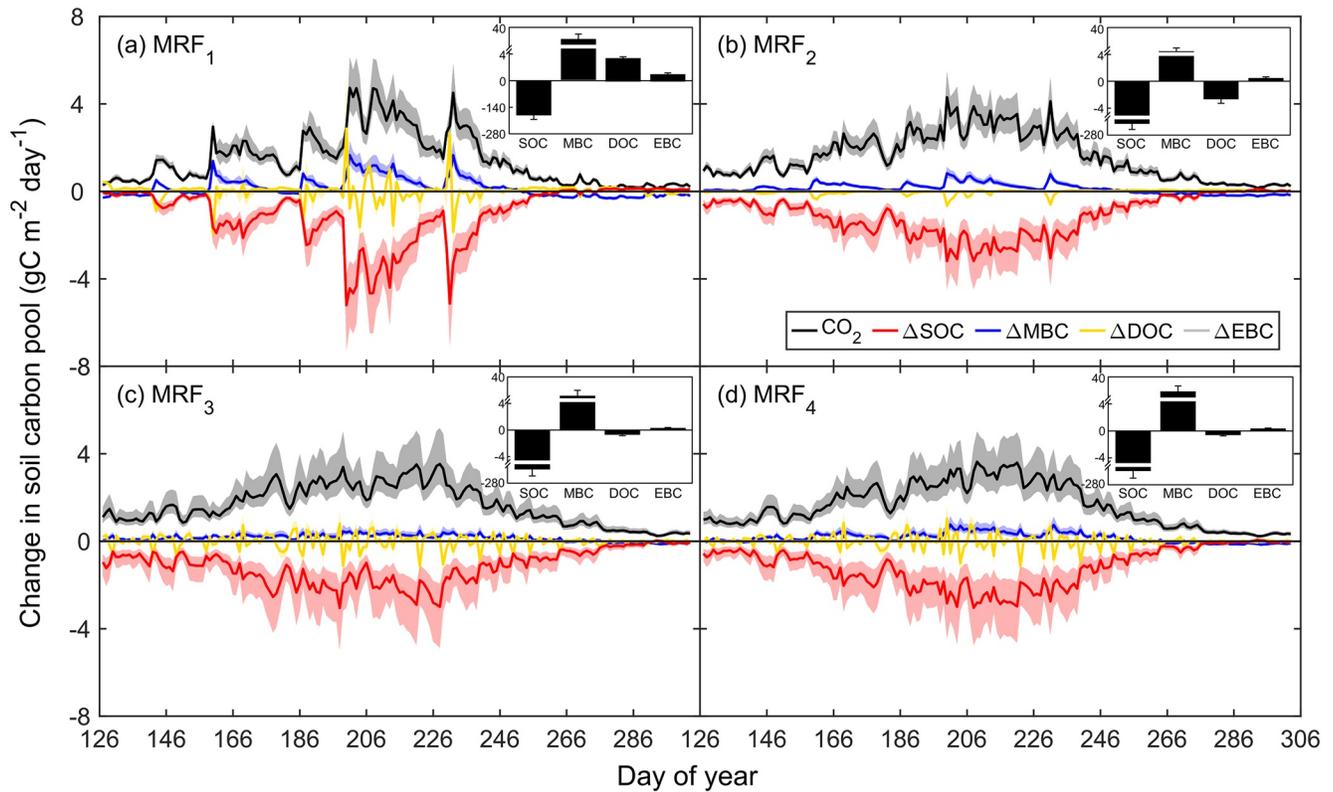
(ranged from 76 to 156) and larger variances than those in conventional models (ranged from 57 to 140) when using the same water scheme (Figure 4). Specifically, the differences between the DIC values for conventional and microbial models were the largest using MRF<sub>2</sub> or MRF<sub>4</sub> schemes. This result indicated that the conventional models show better performance than the microbial models using the same MRF schemes. The conventional model using the MRF<sub>2</sub> scheme (the water response function from IBIS) had the lowest DIC score, showing the best performance among all models (Figure 4).

### 3.3. Impact of the Moisture Response Function

The moisture-response function mainly regulated the decomposition rate of soil C pools in the model. We found that in conventional models with MRF<sub>1</sub> or MRF<sub>2</sub>, the  $R_H$  mainly came from the decomposition of fast soil C, contributing more than 95% of  $R_H$ , while for MRF<sub>3</sub> and MRF<sub>4</sub>, the fast and slow soil C pools contribute almost equally to the release of CO<sub>2</sub> efflux as  $R_H$  from the soil C (Figure 5). The passive C pool in all conventional models contributed negligibly at the seasonal time scale in 2009 (Figure 5).

In the microbial models, the CO<sub>2</sub> production from soil C was directly from the process of microbial absorbing C from DOC and indirectly affected by SOC and EBC that affected the size of MBC and DOC. The cumulative changes in SOC, MBC, DOC, and EBC during the whole growing season were about  $-200 \pm 29.5$ ,  $27 \pm 3.8$ ,  $-0.1 \pm 0.3$ , and  $0.6 \pm 0.1$  g C m<sup>-2</sup> (Figure 6), indicating that most of the CO<sub>2</sub> release or  $R_H$  and the increase in MBC came from the decomposition of the SOC in microbial models. The partial correlation analyses further showed a significant correlation between  $R_H$  and  $\Delta$ MBC ( $R = 0.81$ ,  $P < 0.01$ ) in the model with MRF<sub>3</sub>, and the changes of EBC in models with MRF<sub>2</sub> or MRF<sub>3</sub> were also positively correlated with  $R_H$  ( $R = 0.45$ ,  $P < 0.01$  and  $0.48$ ,  $P < 0.01$  respectively).

The water response function also influenced the contribution of different soil C pools to  $R_H$  (Figures 5 and 6) through changing the model parameters. In conventional models, the most sensitive parameters were the decomposition rate of fast and slow C pools and the fractions of transfer between the two pools. Among these parameters, the decomposition rate of fast pools ( $k_f$ ) and the fraction of C transferred from fast to slow pools ( $f_{fs}$ ), and the initial value of fast pool size ( $f_f$ ) in models with MRF<sub>1</sub> or MRF<sub>2</sub> scheme was higher than models with MRF<sub>3</sub> or MRF<sub>4</sub> scheme (Figure S3a). While the sensitivities for a fraction of C in slow C



**Figure 6.** The changes of soil heterotrophic respiration ( $R_H$ ) and four different carbon pools in the microbial model (soil organic carbon, SOC; microbial biomass, MBC; dissolved organic carbon, DOC; enzyme biomass, EBC). The drawings at the top right show cumulative changes in different carbon pools (MRF<sub>1</sub>-MRF<sub>4</sub> are moisture response functions from the model of CABLE, IBIS, LPJ, and TECO, respectively). TECO, Terrestrial ECOsystem.

pool transferring to fast C pool ( $f_{sf}$ ), the decomposition rate of slow C pool ( $k_s$ ) and the initial value of slow C pool size ( $f_s$ ) in models with MRF<sub>3</sub> or MRF<sub>4</sub> were higher than models with MRF<sub>1</sub> or MRF<sub>2</sub> (Figure S3a). In microbial models, further analysis showed that the parameter of carbon use efficiency ( $CUE_0$ ) is the most sensitive in all microbial models with MRF<sub>1</sub> to MRF<sub>4</sub> schemes, followed by parameters of the initial sizes of MBC, EBC, and DOC (Figure S3b). Besides, MRF affected the sensitivity of the loss rate of the enzyme ( $r_{EL}$ ), maximum catalytic rate of SOC to DOC ( $V_{max0}$ ), and the size of MBC and EBC ( $f_M$  and  $f_E$ ) in microbial models (Figure S3b).

## 4. Discussions

### 4.1. Simulated Pulse Dynamics of Soil Heterotrophic Respiration by Different Models

Previous modeling studies have shown that there is controversy about the performance of linear conventional or nonlinear microbial models in simulating nonlinear soil C processes (Lawrence et al., 2009; Shi et al., 2018; Wieder et al., 2013). This study, however, shows that both the conventional and microbial models can capture a typical nonlinear C process (i.e., the  $R_H$  in response to rain pulse effect) in a semi-arid grassland (Figure 3). The simulations of the conventional model are even closer to the observed data than the microbial models in our study based on the results of the deviance information criterion (Figure 4).

Some laboratory-based experiments have suggested that the response of soil C to drying-rewetting events could be better explained by microbial models because they represented more realistic mechanisms of soil C-cycle processes (Manzoni et al., 2014, 2016; Salazar et al., 2018). There are great differences between laboratory experiments and field experiments (Poorter et al., 2016; Xu et al., 2019). Meanwhile, the development of microbial models must link micro-scale mechanisms to macro-scale models, which has to face several challenges compared to linear models, such as parameterization (Luo & Schurr, 2020; Wieder, Allison, et al., 2015). In our study, the microbial nonlinear model utilizes the enzyme biomass to modify available

substrate (DOC), and the microbial biomass and Michaelis-Menten kinetic to adjust the decomposition rate of soil C to match the nonlinear pulsed response in  $R_H$  (Figures 1 and 3). Although this type of microbial model characterizes nonlinear soil C processes more realistically than the conventional linear model, the latter has prevailed in simulations of linear or nonlinear soil C processes on regional or global scales over long periods due to the simpler C pool structure (Lawrence et al., 2009; Waring & Powers, 2016; Wieder, Allison, et al., 2015). The conventional linear model based on the CENTURY-like C pool structure (Jenkinson et al., 1991; Parton et al., 1987) describes the observed nonlinear response of soil C-released  $CO_2$  well by incorporating appropriate environmental response parametrization schemes (e.g., soil moisture-response functions in this study) with optimized decomposition rate parameters (Figures 3 and 5). Other studies have also shown the conventional models performed well in simulating the nonlinear soil C processes. For example, Waring and Powers (2016) have reported that the modified linear model could reproduce the pulsed dynamics of  $R_H$  based on the field experiments in a tropical dry forest.

The development of microbial models is ongoing, and whether the linear conventional model can capture the nonlinear soil C processes as well as the microbial model remains debatable. We argue that these two types of models can both be improved to simulate nonlinear phenomena of soil C processes. Different model structures could be beneficial for unraveling the mechanisms underlying the different nonlinear soil C processes.

#### 4.2. The Role of Moisture-Response Parameterization

In our study, we found that differences among the schemes of moisture-response function dominated the uncertainties of models in simulating the rain-pulsed dynamics of  $R_H$  (Figures 3 and 4). However, the empirical moisture-response functions vary widely among models (Lei et al., 2018; Sierra et al., 2015), and their values used to modify the decomposition processes are greatly different within the same variation range of soil moisture (Figure S1). This study highlights the importance of the moisture-response function in conventional or microbial models to better simulate the nonlinear soil C processes. The moisture-response function in conventional models affects the decomposition rates of different soil C pools and their response to environmental changes (Moyano et al., 2013), while in microbial models, the moisture-response function is generally considered to modify the function of Michaelis-Menten kinetics when microbial mechanisms are embedded in models (Abramoff et al., 2018; Wieder et al., 2013). Other factors can also affect the mechanistic relationship between the  $R_H$  and soil moisture, such as soil properties in pore-scale models (Moyano et al., 2012, 2013), microbial dormancy (Salazar et al., 2018), and soil water transfer processes (Manzoni et al., 2014, 2016; Sánchez-García, Doerr, et al., 2020; Sánchez-García, Oliveira, et al., 2020). Yan et al. (2018) have also considered primary physicochemical and biological processes to develop a novel moisture function of  $R_H$ .

This study further shows different moisture-response functions lead to great variability in the estimated values of some parameters among models (e.g.,  $k_f$  in conventional models and  $CUE_0$  in microbial models) (Figure S2). Such different parameters further cause different contributions of multiple C pools to  $R_H$  among models (Figures 5–6). As a result, the variation in predicting soil C dynamics is further increased among different models. Thus, it is crucial to use the data assimilation approach to constrain the parameters for different models. Meanwhile, more informative datasets should be used to improve model parameterization in simulating the soil C dynamics in response to environmental changes (Luo & Schurr, 2020; Shi et al., 2018; Wang et al., 2009; Xia et al., 2020).

#### 4.3. The Implications for the Development of Soil Carbon Models

This study indicates that conventional linear models with optimized parameterizations (e.g., moisture-response functions) could reproduce non-linear response processes of soil C dynamics (e.g., pulse dynamic of  $R_H$  in grasslands) as well as microbial non-linear models do. This finding implies that parameterization schemes representing the mechanisms of soil C response to environmental factors are still very important for the development of both conventional linear or microbial models. According to previous studies, the uncertainty due to parameterizations of environmental response functions is comparable to that from external climate changes and biogeochemical nutrient limitation (Exbrayat et al., 2013; Moyano et al., 2013; Nishina

et al., 2014). Microbial models, which reflect more realistic non-linear soil C processes than conventional models, are one of the promising future developments in Earth system models (Luo et al., 2016; Manzoni et al., 2016; Schimel & Weintraub, 2003; Shi et al., 2018; Wieder et al., 2013). In this study, we highlight the importance of environmental response functions (e.g., moisture-response functions) in determining the uncertainty of soil C dynamics (Figure 4).

## 5. Conclusions

Our results show that linear conventional models can capture the pulse dynamics of soil heterotrophic respiration in a semi-arid grassland as well as nonlinear microbial models do. Parameterization with a suitable moisture-response function dominates the performances of these two types of models. This study implies that the capability of the current Earth system models in simulating nonlinear soil C phenomena can be improved by not only the incorporation of soil microbial dynamics but also by more accurate parameterizations of environmental impacts. In grassland ecosystems, as shown in this study, an improved parameterization of soil moisture functions is important in reducing the model uncertainty on soil C cycling. Thus, we recommend more in situ observations of nonlinear C phenomena for improving parameter estimates under alternative carbon-cycle model structures.

## Data Availability Statement

We have archived the observational data in Figshare ([doi.org/10.6084/m9.figshare.13114637](https://doi.org/10.6084/m9.figshare.13114637)).

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