

Quantifying microbial ecophysiological effects on the carbon fluxes of forest ecosystems over the conterminous United States

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Abstract There is a pressing need to develop earth system models (ESMs), in which ecosystem processes are adequately represented, to quantify carbon-climate feedbacks. In particular, explicit representation of the effects of microbial activities on soil organic carbon decomposition has been slow in ESM development. Here we revised an existing Q_{10} -based heterotrophic respiration (R_H) algorithm of a large-scale biogeochemical model, the Terrestrial Ecosystem Model (TEM), by incorporating the algorithms of Dual Arrhenius and Michaelis-Menten kinetics and microbial-enzyme interactions. The microbial physiology enabled model (MIC-TEM) was then applied to quantify historical and future carbon dynamics of forest ecosystems in the conterminous United States. Simulations indicate that warming has a weaker positive effect on R_H than that traditional Q_{10} model has. Our results demonstrate that MIC-TEM is superior to traditional TEM in reproducing historical carbon dynamics. More importantly, the future trend of soil carbon accumulation simulated with MIC-TEM is more reasonable than TEM did and is generally consistent with soil warming experimental studies. The revised model estimates that regional GPP is $2.48 \text{ Pg C year}^{-1}$ (2.02 to $3.03 \text{ Pg C year}^{-1}$) and NEP is $0.10 \text{ Pg C year}^{-1}$ (-0.20 to $0.32 \text{ Pg C year}^{-1}$) during 2000–2005. Both models predict that the conterminous United States forest ecosystems are carbon sinks under two future climate scenarios during the 21st century. This study suggests that terrestrial ecosystem

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models should explicitly consider the microbial ecophysiological effects on soil carbon decomposition to adequately quantify forest ecosystem carbon fluxes at regional scales.

1 Introduction

Over the period 1951–2012, the global land and ocean instrumental temperature records show an increasing trend of 0.12 °C per decade (IPCC 2013). To date, ecosystem models are the primary tools to quantify carbon (C) dynamics (McGuire et al. 1992; Potter et al. 2007; Zhuang et al. 2003; Chen et al. 2011; Wieder et al. 2013; Todd-Brown et al. 2014). However, the response of the terrestrial C dynamics to changing climate remains highly uncertain (Friedlingstein et al. 2006; Wieder et al. 2013). Much of the uncertainty is due to the inadequate representation of ecosystem processes that determine the exchanges of water, energy and C between the land ecosystems and the atmosphere (Wieder et al. 2013). There is a pressing need to improve our understanding of the feedbacks between terrestrial biosphere and the atmosphere, and provide critical information to studying long-term biosphere interactions with other components of the Earth system (Law et al. 2006; IPCC 2007; Potter et al. 2007; Xiao et al. 2011). Given the large amounts of soil carbon and intensifying carbon-climate feedbacks (Davidson et al. 2012), greater attention should be paid on improving the numerical representation of soil biogeochemistry models at multiple scales in Earth System Models (ESMs) (Wieder et al. 2013).

Recently, ecosystem models explicitly incorporated the dynamics of microbial enzyme kinetics are shown to perform well in comparison with observed data (Allison et al. 2010; Wieder et al. 2013). Further, the effects of environmental factors and substrate availability on microbial physiology, in turn, affecting soil carbon decomposition have been well investigated (Xu et al. 2014). While these studies focused on either soil C pool or model performance, they have been slow to incorporate these microbial mechanisms into large-scale ecosystem models to quantify soil respiration under future climatic conditions. Heterotrophic respiration (R_H) is an indispensable component of soil respiration and approximates the rate of soil organic matter (SOM) decomposition (Hanson et al. 2000; Bond-Lamberty and Thomson 2010). Moreover, SOM decomposition process is closely coupled with soil nitrogen (N) mineralization that determines soil N availability and affects gross primary production (GPP). However, these processes have not been adequately incorporated into ESMs to quantify ecosystem C dynamics, especially at large spatial and long temporal scales.

Terrestrial Ecosystem Model (TEM) is a large-scale biogeochemical model which has been widely used to evaluate the response of terrestrial ecosystem carbon dynamics to climatic changes (Felzer et al. 2004; Tang and Zhuang 2009; Zhuang et al. 2010). However, TEM is lacking the detailed representation of soil microbial physiological effects on R_H . In order to improve the mechanistic robustness of the model, we revised the classic Q_{10} -based R_H algorithms by incorporating the algorithms developed in He et al. (2014) to develop a new version of TEM (MIC-TEM). The new algorithms explicitly consider the direct impacts of soil temperature on biochemical reactions and the indirect effects on R_H affected by substrate availability, enzyme activities, and microbial physiology (Appendix 1). MIC-TEM was then used to estimate the carbon fluxes under changing climates over the conterminous United States. This study aimed to assess the reliability of MIC-TEM and examine the effects of the detailed microbial physiological representation on seasonal and annual carbon dynamics at regional and long-term temporal scales.

2 Method

2.1 Overview

We first revised R_H formula of TEM by incorporating the effects of changing microbial carbon (MIC), enzyme carbon (ENZ), and soluble carbon (SOLC) as well as soil microbial physiology. The model was then calibrated and verified for forest ecosystems with observed net ecosystem exchanges (NEE) and estimated GPP from eddy covariance flux towers. Next, we applied the model to estimate forest carbon fluxes for each $0.5^\circ \times 0.5^\circ$ grid cell across the conterminous US under future climate scenarios of RCP 2.6 and RCP 8.5 for the 21st century.

2.2 The revised terrestrial ecosystem model

TEM is a terrestrial ecosystem model to estimate carbon and nitrogen fluxes and pool sizes of plants and soils using spatially referenced information (Raich et al. 1991; McGuire et al. 1992; Melillo et al. 1993; Zhuang et al. 2003, 2010). A daily version of TEM (Zhu et al. 2013), which has been coupled with a Soil Thermal Model (STM) and a Water Balance Model (WBM) to account for the effects of soil temperature and hydrological dynamics on carbon fluxes, was used. In TEM, R_H is defined as a function of soil organic carbon (SOC), temperature (Q_{10}), soil moisture (MOIST), and the gram-specific decomposition constant K_d :

$$R_H = K_d \times SOC \times Q_{10} \times MOIST \quad (1)$$

More details of R_H algorithms can be found in previous publications (e.g., Zhuang et al. 2003, Chen et al. 2011). The revised R_H algorithm for MIC-TEM was based on a microbial-enzyme model (Allison et al. 2010) and the DAMM model (Davidson et al. 2012), where R_H was directly controlled by either microbial biomass (MIC) or enzyme (ENZ) using a Michaelis-Menten enzyme kinetic function (Table S1) (He et al. 2014):

$$R_H = Vmax_{CO_2} \times \frac{[S_x]}{Km_{S_x} + [S_x]} \times \frac{[O_2]}{km_{O_2} + [O_2]} \times MIC \quad (2)$$

where $Vmax_{CO_2}$ is the maximum reaction rate of heterotrophic respiration ($mg\ S_x\ C\ cm^{-3}$ soil). kM (unit substrate $C\ cm^{-3}$ soil) is the corresponding Michaelis-Menten half-saturation constant. MIC is microbial biomass ($mg\ C\ cm^{-3}$ soil). More details on $Vmax_{CO_2}$, kM , and MIC calculation could be found in Supplementary Material (Appendix 2).

$[S_x]$ is the concentration of dissolved organic substrates, defined as a function of total soluble C (i.e., Soluble C pool), volumetric water content of the soil, and the diffusion coefficient of substrate in liquid phase:

$$[S_x] = [S_{xsoluble}] \times D_{liq} \times \theta^3 \quad (3)$$

where $[S_{xsoluble}]$ is total soluble C, θ is the volumetric water content of the soil, and D_{liq} is a diffusion coefficient of the substrate in liquid phase.

$[O_2]$ is the concentration of O_2 , modeled with a simple function of air-filled porosity and the diffusion coefficient for O_2 in air:

$$[O_2] = D_{gas} \times 0.209 \times \alpha^{4/3} \quad (4)$$

where D_{gas} is the diffusion coefficient. 0.209 is the volume fraction of O_2 in air and α is the air-

filled porosity of the soil. The total porosity is calculated based on bulk density (BD) and particle density (PD).

$$\alpha = 1 - \frac{BD}{PD} - \theta \quad (5)$$

More details of these algorithms could be found in Supplementary Materials (Appendix 2) and a previous study (He et al. 2014).

2.3 Model sensitivity analysis and parameterization

A sensitivity analysis focusing on R_H dynamics would help identify which processes are important in simulating R_H and was achieved by using a variance-based global sensitivity analysis technique based on the SOBOL sampling method (Pappas et al. 2013). Ten key parameters were selected to conduct the sensitivity analysis (Table 1; He et al. 2014; Chen et al. 2011; Zhu and Zhuang 2013). After that, we parameterized MIC-TEM with a global optimization algorithm (Shuffled complex evolution method developed at the University of Arizona (Duan et al. 1992; Duan et al. 1994) at six selected AmeriFlux sites which represent major forest types across the conterminous US (Table S2, Fig. S1). The parameterization method followed the procedures described in He et al. (2014). The global optimization method was then used to minimize the cost functions:

$$J_1 = \sum_{i=1}^k (NEP_{obs,i} - NEP_{sim,i})^2 \quad (6)$$

$$J_2 = \sum_{i=1}^k (GPP_{obs,i} - GPP_{sim,i})^2 \quad (7)$$

where NEP_{sim} and GPP_{sim} are the simulated NEP and GPP and NEP_{obs} and GPP_{obs} are the observed NEP and GPP, respectively. k is the number of data pairs for comparison. We optimized parameters through minimizing the two cost functions simultaneously (Eqs. (6) and (7)) with a global optimization method (He et al. 2014).

3 Results

3.1 Model performance at AmeriFlux sites

The parameterized MIC-TEM was able to reproduce the annual dynamics of the observed NEP and GPP at each verification site (Table S2), with r^2 mostly larger than 0.6 and root mean square errors (RMSE) around $2 \text{ g C m}^{-2} \text{ day}^{-1}$ for NEP. r^2 was mostly larger than 0.74 and RMSEs were around $4 \text{ g C m}^{-2} \text{ day}^{-1}$ for GPP (Table S2). Specifically, at deciduous forest sites, MIC-TEM better captured the variation of carbon fluxes and had a significant correlation ($r^2 > 0.70$ for NEP and $r^2 > 0.87$ for GPP) when compared to evergreen forest sites ($r^2 > 0.35$ for NEP and $r^2 > 0.74$ for GPP). At the Niwot Ridge site, there was a relatively weak linear relationship between simulated and observed NEP ($r^2 = 0.35$). This discrepancy mainly came

Table 1 Key MIC-TEM Parameters

Parameter	Definition	Unit	Prior Range
Cmax	Maximum rate of photosynthesis C	g C m ⁻² day ⁻¹	[50, 1500]
Kr	Logarithm of plant respiration rate at 0 °C	g g ⁻¹ day ⁻¹	[-9.5, -0.2]
Kc	Half saturation constant for CO ₂ -C uptake by plants	μL L ⁻¹	[20,600]
Raq _{10a0}	Leading coefficient of the Q ₁₀ model for plant respiration	None	[1.35,3.36]
Ea_micup	Soluble and diffused Sx uptake by microbial	J mol ⁻¹	[3.5e4, 7.0e4]
Ea_Sx	Activation energy of microbes assimilating Sx to CO ₂	J mol ⁻¹	[3.5e4, 7.0e4]
Ea_SOC	Activation energy of decomposing SOC to soluble C	J mol ⁻¹	[3.5e4, 7.0e4]
Vmax_CO ₂₀	Maximum microbial respiration rate	mg respired Sx cm ⁻³ soil h ⁻¹	[1.0e6, 1.0e8]
Vmax_uptake ₀	Maximum microbial uptake rate	mg Sx cm ⁻³ soil (mg biomass cm ⁻³ soil) ⁻¹ h ⁻¹	[1.0e6, 1.0e8]
Vmax_SOC ₀	Maximum rate of converting SOC to soluble C	mg decomposed SOC cm ⁻³ soil (mg Enz cm ⁻³ soil) ⁻¹ h ⁻¹	[1.0e6, 1.0e8]

from R_H estimation since the STM only had a crude algorithm for snow dynamics, which was not able to fully capture the magnitude of soil temperature in winter (Zhuang et al. 2002; Hao et al. 2014).

Overall, the performance of MIC-TEM was superior to that of TEM as shown in Table S2 at the six sites. Specifically, statistics of MIC-TEM results had notable higher r^2 and lower RMSE than that of TEM at four validation sites (Table S2), showing that MIC-TEM was better able to capture the observed variations and magnitudes of NEP and GPP fluxes.

3.2 Comparison between MIC-TEM simulations and other studies

To demonstrate the performance of MIC-TEM, we simulated the carbon fluxes from 2000 to 2005, driven with the global climate dataset from the National Centers for Environmental Prediction (NCEP) at a 0.5° spatial resolution (Kistler et al. 2001). Estimated annual GPP, net primary production (NPP), and NEP for the conterminous United States over the period varied from year to year (Table 2), with GPP varying from 2.02 to 3.03 Pg C year⁻¹. Average GPP is 2.48 Pg C year⁻¹ (Table 3). This value was close to 1.68 Pg C year⁻¹ estimated by Xiao et al. (2008) over the period 2001–2006 but lower than 3.93 Pg C year⁻¹ based on MODIS GPP product (Zhao et al. 2005) for the period 2000–2005. Annual NPP ranged from 1.20 to 2.12 Pg C year⁻¹ during the same period, average NPP was higher than that of 1.66 Pg C year⁻¹ from MODIS NPP product over 2000–2005 (Zhao et al. 2005). Our estimated NEP was -0.20 to 0.32 Pg C year⁻¹ with an average of 0.10 Pg C year⁻¹. Overall our estimates of NEP were lower than 0.148 Pg C year⁻¹ from Chen et al. (2011), but were higher than -0.4 Pg C year⁻¹ from Xiao et al. (2011).

Table 2 Comparison of carbon dynamics between estimated and other existing estimates of deciduous and evergreen forest ecosystem in the conterminous United States

Method	Reference	Time Period	Estimated averaged annual GPP (Pg C year ⁻¹)	Estimated averaged annual NPP (Pg C year ⁻¹)	Estimated averaged annual NEP (Pg C year ⁻¹)	Comments
SAT-TEM Ecosystem Model combining satellite observations	Chen et al. (2011);	2000–2005	2.78	1.22	0.148	Estimated in this study
TEM Ecosystem Model	McGuire et al. (1992);	2000–2005		1.17		Estimated in this study
MOD17 Remote Sensing Products	Zhao et al. (2005); Running et al. (2004)	2000–2005	3.93	1.66		Aggregated form MODIS primary production products (MOD17)
EC-MOD Regression tree approach	Xiao et al. (2008); Xiao et al. (2011)	2001–2006	1.68		-0.4	Estimated in this study

Table 3 MIC-TEM estimated annual GPP, NPP, and NEP across the conterminous United States over 2000–2005. The units of the carbon fluxes are Pg C year⁻¹

Year	GPP	NPP	NEP
2000	2.02	1.85	-0.20
2001	2.34	2.06	0.32
2002	3.03	1.81	-0.16
2003	2.44	2.12	0.25
2004	2.98	1.38	0.24
2005	2.12	1.20	0.18
Average	2.48	1.73	0.10

3.3 Sensitivity study

We found that the magnitudes of the first order sensitivity index (Si) followed the order of Ea_Sx>Ea_micup>Ea_SOC>Vmax_SOC₀>Vmax_CO₂₀>Vmax_uptake₀ (Fig. S2). The

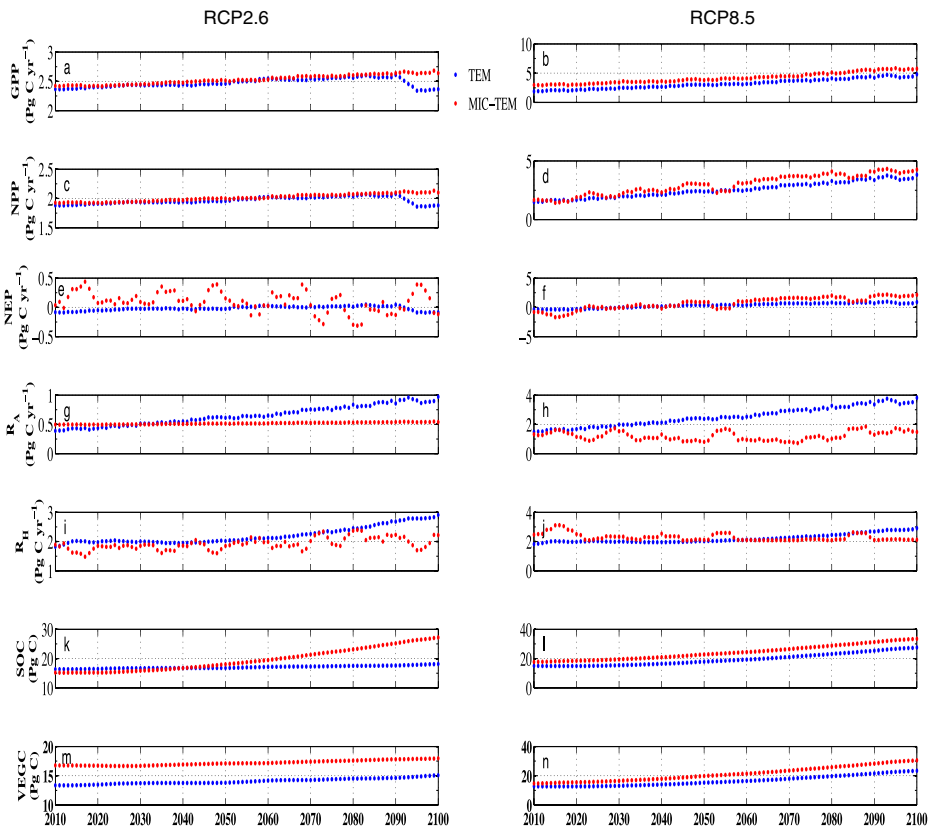


Fig. 1 Projected dynamics of carbon fluxes and stocks projected by TEM and MIC-TEM under the RCP 2.6 and 8.5 scenarios for the conterminous United States from 2006 to 2100. Left panels are the simulations under the RCP2.6 scenario while right panels under RCP8.5. GPP represents gross primary production, NPP represents net primary production, NEP represents net ecosystem production, R_A represents autotrophic respiration, R_H represents heterotrophic respiration, SOC represents soil organic carbon, VEGC represents vegetation carbon. Positive NEP values represent carbon sinks while negative values represent carbon sources to the atmosphere

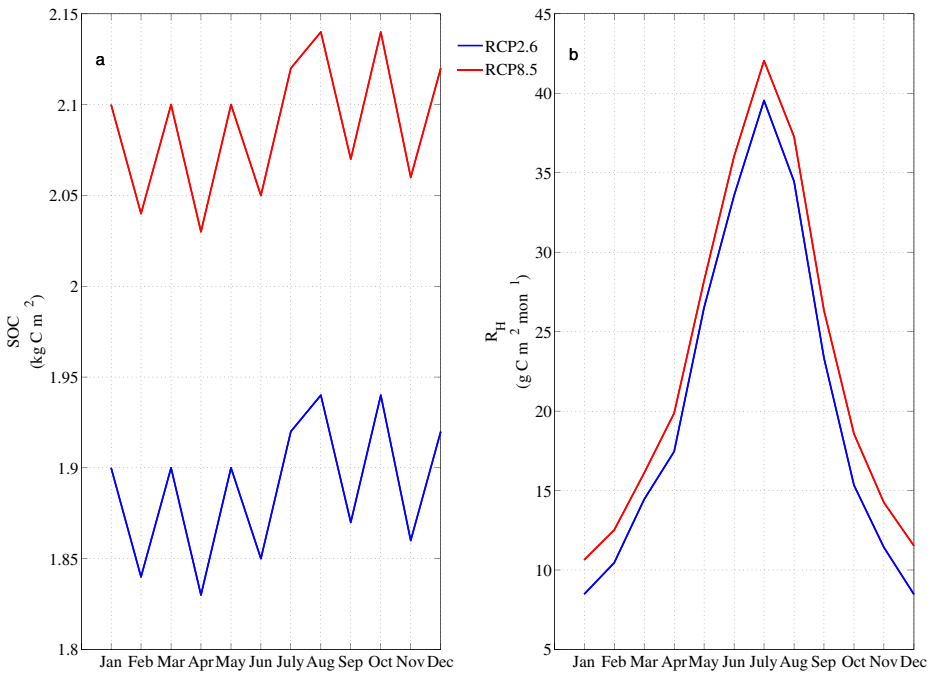


Fig. 2 Seasonal variations in mean soil organic carbon (SOC) and heterotrophic respiration (R_H) simulated with TEM under RCP 2.6 and 8.5 scenarios

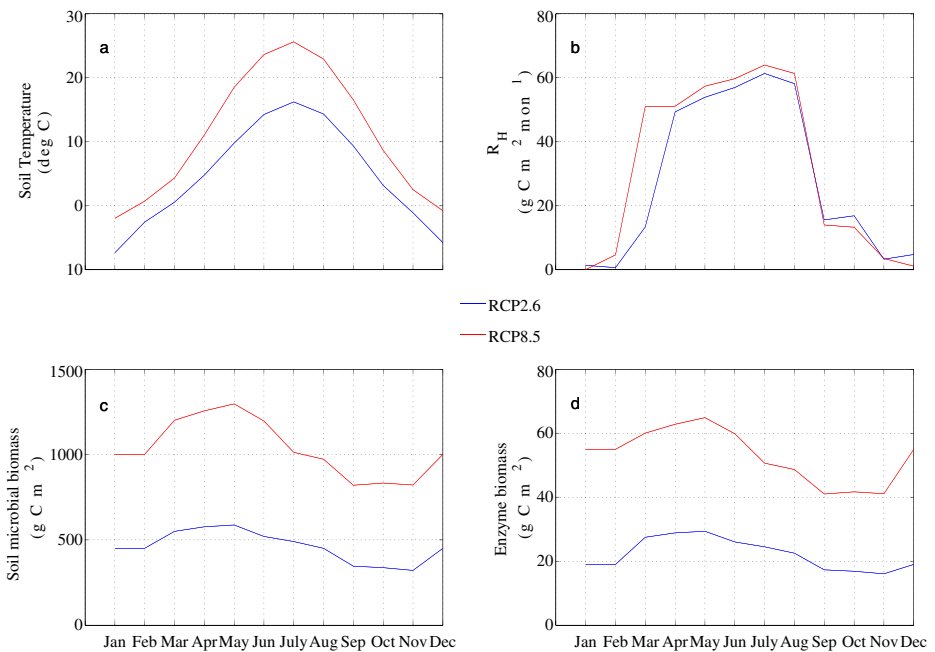


Fig. 3 Seasonal variations in mean soil temperature, heterotrophic respiration (R_H), soil microbial biomass, enzyme biomass simulated with MIC-TEM under RCP 2.6 and 8.5 scenarios

first three high-sensitivity parameters were Ea_{Sx} , Ea_{micup} and Ea_{SOC} , and the last three were $Vmax_{SOC_0}$, $Vmax_{CO_{20}}$ and $Vmax_{uptake_0}$. Herein, the activation energy and the maximum reaction rate were the most and secondary sensitive parameters in MIC-TEM. Microbial assimilation and enzyme decay processes, with which the six parameters are associated, determined the magnitudes of SOLC (Sx). Thereby R_H dynamics might be controlled by substrate availability. $Vmax$ also played an important role in R_H affected by soil temperature (Appendix 2).

To quantify the impact of changes in temperature, MIC-TEM simulations were conducted by varying air temperature at an evergreen and a deciduous forest, respectively (Fig. S3). For these forests, air temperature had a positive effect on R_H and SOLC, but a negative effect on MIC. Two ecosystems were comparably sensitive to air temperature. In the evergreen forest, SOLC was most sensitive to air temperature, where a 10 % air temperature increase caused a 25 % increase of SOLC and a 16 % decrease of MIC. R_H was least sensitive to air temperature, only 7 % R_H changed due to a 10 % air temperature change. In the deciduous forest, SOLC was still most sensitive to air temperature, and a 10 % temperature change caused a 24 % SOLC change.

3.4 Projected carbon fluxes

TEM simulated GPP and NPP increased slowly at first but decreased sharply after the 2090s due to decreasing air temperature (data not shown) in the RCP 2.6 experiment (Fig. 1a), while NEP had a similar trend (Fig. 1e), but slightly decreased after the 2090s. In the RCP 8.5 experiment, GPP, NPP and NEP all showed an increasing trend (Fig. 1b, d and f). Overall, R_H in both experiments showed an increasing trend. Moreover, autotrophic respiration (R_A) and R_H are both significantly correlated to the air temperature trends (Fig. 1g, h, i and j) ($r=0.85$, $p<0.05$, $n=94$).

MIC-TEM simulated GPP and NPP continuously increased during the 95-years period (2006–2100) in both experiments (Fig. 1a, b, c and d). In the RCP 2.6 experiment, NEP showed a fluctuating trend (Fig. 1e). Compared to the fluctuating trend of NEP in the RCP 2.6 experiment, NEP decreased sharply in the middle of the 2010s, but slightly increased after the 2020s, which is similar to NPP in the RCP 8.5 experiment (Fig. 2d). In both experiments, R_H trends did not change with air temperature increasing, but R_H in MIC-TEM fluctuated comparing to a R_H steady change in TEM (Fig. 1i and j), which might be due to oversensitivity of R_H in MIC-TEM to high air temperature.

The magnitudes of the estimated carbon fluxes were different between TEM and MIC-TEM models. In the RCP 8.5 experiment, MIC-TEM estimated that GPP, NPP and NEP were 0.98 (0.2 %), 0.42 (0.1 %) and 0.34 (0.5 %) Pg C year⁻¹ higher than those estimated by TEM, respectively (Appendix 2). MIC-TEM estimated that R_H was 0.07 Pg C year⁻¹ (0.03 %) higher than that estimated with TEM. In the RCP 2.6 experiment, the differences were similar to that in the RCP 8.5 experiment, except MIC-TEM simulated R_H was 0.05 Pg C year⁻¹ (0.02 %) lower than that estimated by TEM. The cumulative difference between simulations with two models during the 95-years period was 17.1 Pg C. Under both future climate scenarios, both models predicted that the conterminous United States forest ecosystems acted as a carbon sink during the study period.

TEM R_H was directly controlled by both SOC and soil temperature, while MIC-TEM R_H was directly controlled by SOLC and indirectly by soil temperature. TEM R_H was modeled as a function of Q_{10} and SOC (Eq. (1)). The seasonal TEM R_H had a similar trend with soil

temperature (Figs. 2b and 3a). Specifically, the seasonal TEM R_H slowly increased and started to decline from July. TEM R_H in the RCP 8.5 experiment was higher than that in the RCP 2.6 experiment (Figs. 2a and 3a). Some modeling studies suggested that there is no significant relationship between R_H and soil temperature when soil temperature ranged from -5 to 0 °C (Zhou et al. 2010). But our results showed that there was still a high correlation between soil temperature and R_H in TEM ($r=0.65$; $p<0.05$, $n=470$). MIC-TEM R_H showed the same trend in both future climate scenario experiments (Fig. 3b) and there was a significant correlation between SOLC and R_H ($r=0.73$; $p<0.05$, $n=18$).

3.5 Interactive effects of warming and soil microbial physiology on seasonal R_H

Soil microbial biomass varies seasonally, leading to different correlations between R_H and soil temperature (Bradford et al. 2010; Davidson et al. 2012). MIC-TEM simulations showed that both soil microbial biomass and R_H varied seasonally. In both future climate scenario experiments, the simulated R_H is high from June to August and low in fall and increases from March to May due to increasing ENZ ($r=0.67$) (Fig. 3b). Field studies have also showed that increasing enzyme activity due to rising soil temperature can stimulate CO_2 effluxes (Ostroumov and Siebert 1996; Hanson et al. 2003; Hubbard et al. 2005; Hopkins et al. 2014) (Fig. 3d). R_H and soil temperature has a similar trend, reaching a peak in July (Fig. 3a and b). R_H and soil microbial biomass has a similar trend, sharply decreasing from July to August (Fig. 3b). From May to June, R_H and soil temperature show an increasing trend, while soil microbial biomass and enzyme biomass have a decreasing trend. Warm summer temperature leads to higher microbial R_H but lower soil microbial biomass (Fig. 3b and c), which is consistent with the findings from field studies (Bradford et al. 2008; Frey et al. 2008; Rousk et al. 2012; Weedon et al. 2012). The seasonality of the simulated soil microbial biomass is high in early spring and low in fall, which is consistent with the findings of Xu et al. (2014) (Fig. 3c).

4 Discussion

4.1 The effect of soil temperature on R_H

In Q_{10} based models, raising soil temperature would increase R_H (Eliasson et al. 2005; Davidson and Janssens 2006). For example, TEM R_H in the RCP 8.5 experiment is higher due to higher soil temperature in comparison with the RCP 2.6 experiment. In microbial physiology models, soil temperature indirectly affects soil respiration via the effects on substrate supply (Davidson and Janssens 2006). This indirect effect may explain why SOLC is more sensitive than R_H to raising air temperature (Fig. S3). Recently, laboratory experiments have showed that the temperature sensitivity of microbial community varies with temperature changes (Wei et al. 2014). Thus, future models shall include the effects of soil temperature on microbial community, to adequately quantify microbial biomass, thereby R_H .

In microbial physiological models, microbial carbon use efficiency (CUE) is an important parameter of carbon decomposition process (Tang and Riely 2014). However, to reduce model uncertainties, our study did not consider CUE. Instead, we only assessed the R_H considering the effects of soil microbial biomass and activity (Shi et al. 2006). Further, our model did not

simulate winter R_H because of microbial dormancy in winter (Davidson et al. 2012). However, snow cover insulates the soil surface from cold air temperature and allows heterotrophic respiration to continue through much of the winter (Raich et al. 1991). Therefore, the winter microbial physiology shall be represented in MIC-TEM to improve future model predictions.

4.2 Evaluation of MIC-TEM and its uncertainties

The performance of MIC-TEM was better than that of TEM in simulating carbon fluxes at six AmeriFlux sites (Table S2). Both models are calibrated using the same data and optimization method. Therefore, we could attribute the MIC-TEM performance superiority to its model structure that explicitly considers soil microbial physiology. Meanwhile, compared to previous studies for the same region and similar period, the incorporation of soil microbial processes into TEM shall provide more convincing estimation of carbon fluxes. The models having not explicitly considered the impacts of microbial activities might have provided good estimates. However those seemingly reasonable results might have been due to an inadequate representation of mechanistic processes of terrestrial ecosystems in those models.

The interannual variability of MIC-TEM R_H differs significantly from TEM R_H because R_H in MIC-TEM is controlled by MIC, SOLC and ENZ that changed significantly with time. These differences in R_H may explain the differences in NEP between two models (Appendix 1).

MIC-TEM development is an important step forward to considering the effects of microbial biomass and activities on soil decomposition. However the shift in microbial community structures could also alter the temperature sensitivity of R_H (Bradford et al. 2008, 2010). The microbial community composition changes induced by warming, fire, and soil freeze-thaw processes could also affect soil decomposition (Billings and Ballantyne 2013). These complex feedbacks were not yet included in MIC-TEM. In addition, the NCEP data used to drive MIC-TEM could be another uncertainty source for our estimation. As indicated by Zhao et al. (2005), the NCEP reanalysis data overestimated solar radiation and underestimated temperature. The errors in temperature might introduce errors in carbon fluxes because of the nonlinear relationship between temperature and ecosystem respiration (Chen et al. 2011).

A number of recent studies concluded that better understanding of the temperature response of the processes that control substrate availability, depolymerization, microbial carbon use efficiency, and enzyme production is important to predicting the fate of soil carbon stocks in a warmer world (Eliasson et al. 2005; Allison et al. 2010; Wieder et al. 2013; Hopkins et al. 2014). Thus, future development of MIC-TEM shall incorporate these processes to adequately quantify ecosystem carbon dynamics.

5 Conclusions

We incorporated a number of microbial physiological processes into a process-based biogeochemistry model TEM to more adequately quantify ecosystem carbon fluxes during the 21st century for the conterminous United States. Multiple eddy flux tower data were used to parameterize and verify our models. Ensemble simulations with posterior parameters were conducted at both site and regional levels. The site-level comparisons indicated that the revised TEM performs better. The regional extrapolation of new model across the conterminous United States for the 21st century shows

that the seasonal trends of R_H are dominated by the changes of soil microbial biomass and enzyme biomass other than soil temperature. Our study suggests that quantifying the future net carbon exchange should explicitly consider soil microbial physiological effects. To improve the microbial physiologically-based soil decomposition models, developing more observational data of soil respiration, soil microbial biomass, and enzyme biomass of terrestrial ecosystems should be a research priority.

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