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# Microbial dormancy and its impacts on Arctic terrestrial ecosystem carbon budget

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**Abstract**

**A large amount of soil carbon in the Arctic terrestrial ecosystems could be emitted as greenhouse gases in a warming future. However, lacking detailed microbial processes such as microbial dormancy in current biogeochemistry models might have biased the quantification of the regional carbon dynamics. Here the effect of microbial dormancy was incorporated into a biogeochemistry model to improve the quantification for the last and this century. Compared with the previous model without considering the microbial dormancy, the new model estimated the regional soils stored 75.9 Pg more C in the terrestrial ecosystems during the last century, and will store 50.4 Pg and 125.2 Pg more C under the RCP 8.5 and RCP 2.6 scenarios, respectively, in this century. This study highlights the importance of the representation of microbial dormancy in earth system models to adequately quantify the carbon dynamics in the Arctic.**

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## 1. Introduction

The land ecosystems in northern high latitudes (>45° N) occupy 22% of the global surface and store over 40% of the global soil organic carbon (SOC) (McGuire & Hobbie, 1997; Melillo et al., 1993; Tarnocai et al., 2009; Hugelius et al., 2014). During the past decades, a greening accompanying a warming in the region has been documented (Zhou et al., 2001; Lloyd et al., 2002; Stow et al., 2004; Callaghan et al., 2005; Tape et al., 2006). The regional carbon dynamics are expected to loom large in the global carbon cycle and exert large feedbacks to the global climate system (McGuire et al., 2009; Davidson & Janssens, 2006; Bond-Lamberty & Thomson, 2010).

To date, numerous ecosystem models have been developed to project the feedbacks between terrestrial ecosystem carbon cycling and climate (Raich et al., 1991; Zhuang et al., 2001, 2002, 2015; Parton et al., 1993; Knorr et al., 2005; Running & Coughlan, 1988), but they can bias their quantifications due to missing detailed microbial mechanisms in these models (Schmidt et al., 2011; Todd-Brown et al., 2013; Conant et al., 2011; Treseder et al., 2011). Microorganisms play a central role in decomposition of litter and soil organic carbon, which further governs the global carbon cycling and climate change (Xu et al., 2014; Treseder et al., 2011; Wang et al., 2015). An emerging field of research has begun to incorporate microbial ecology into existing process-based models to remedy the inadequate representation of soil decomposition process (Zha & Zhuang, 2018; Schimel & Weintraub, 2003; Allison et al., 2010; German et al., 2012). These microbial-based models tend to better reproduce field and satellite observations than traditional ones that treat soil decomposition as a first-order decay process without considering microbial activities (Treseder et al., 2011; Wieder et al., 2013; Todd-Brown et al., 2011; Lawrence et al., 2009; Moorhead et al., 2006). However, some vital microbial traits

such as microbial dormancy and community shifts are still rarely explicitly considered in large-scale ecosystem models, and this may introduce notable uncertainties (Graham et al., 2014, 2016; Wang et al., 2015; Bouskill et al., 2012; Kaiser et al., 2014).

Dormancy is broadly recognized as a strategy for microorganisms to cope with periodical environmental stresses (Harder & Dijkhuizen, 1983). When environmental conditions are unfavorable for growth, microbes switch to a dormant state, which is a reversible state of low to zero metabolic activity (Stolpovsky et al., 2011; Lennon & Jones, 2011). In this state, biogeochemical processes such as soil decomposition are slow (Blagodatskaya et al., 2013). At any given time, there is only a fraction of number of microbes, likely below 50% of live microbes, in natural soils (Wang et al., 2015; Stolpovsky et al., 2011). Soil decomposition and nutrient cycling mainly depend on these active microbes because only active ones can consume organic matter and replicate themselves (Wang et al., 2015; Blagodatskaya et al., 2014). To date, most existing biogeochemistry models used total microbial biomass as indicator of microbial activities, rather than the active portion of microbial biomass, which could bias the estimates of soil decomposition and ecosystem carbon budget (Hagerty et al., 2014; He et al., 2015). Especially, the Arctic terrestrial ecosystems are nitrogen-limited, neglecting microbial dormancy will lead to incorrect estimates of nitrogen availability through soil decomposition, failing to capture nitrogen feedbacks to carbon dynamics (Wang et al., 2015; Stolpovsky et al., 2011; Thullner et al., 2005). Thus, incorporating dormancy effects will improve model realism and provide a better projection of the Arctic carbon dynamics.

This study incorporated the effects of microbial dormancy trait into an extant process-based biogeochemistry model (MIC-TEM) (Zha & Zhuang, 2018; He et al., 2015). The dormant and active microbial physiology has been considered explicitly in the new version of model

(MIC-TEM-dormancy). The revised model was parameterized, validated, and then applied to evaluate the carbon dynamics during the last and this centuries in the Arctic terrestrial ecosystems (north 45 °N above).

## 2. Methods

### 2.1 Overview

First, we describe how we developed the new model (MIC-TEM-dormancy) by incorporating the microbial dormancy trait into an existing microbial-based biogeochemistry model (MIC-TEM). Second, parameterization and validation of MIC-TEM-dormancy using observed net ecosystem exchange data, and heterotrophic respiration data at representative sites have been shown. Third, we applied the model to northern high latitudes (above 45 °N) for the 20$^{th}$ and 21$^{st}$ centuries, to demonstrate the dormancy effects.

### 2.2 Model description.

A non-dormancy version of biogeochemistry model (MIC-TEM) has been developed by incorporating a microbial module (Allison et al., 2010) into an extant large-scale biogeochemical model (TEM) to explicitly (Zhuang et al., 2001, 2002, 2003) consider the effects of microbial dynamics and enzyme kinetics on carbon dynamics (Zha & Zhuang, 2018). Here we further advanced the MIC-TEM by incorporating algorithms that describe the effects of microbial dormancy dynamics based on He et al. (2015). Different from He et al. (2015), in which microbial module was driven with existing data of carbon stocks and fluxes, our study incorporated the microbial module into an extant MIC-TEM that simulates carbon data dynamically. This coupling enables us to extrapolate our model to whole northern high-latitudes

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region, rather than only for temperate forest region in He et al. (2015). In our new model (MIC-TEM-dormancy), microbial biomass pool was divided into two fractions, including the dormant and active microbial biomass pools. The two microbial biomass pools and the reversible transition between them have been considered explicitly in the new model, which was ignored in MIC-TEM (Figure 1).

In previous MIC-TEM, heterotrophic respiration ($R_H$) is calculated as:

$$R_H = ASSIM*(1-CUE) \quad (1)$$

Where ASSIM and CUE represent microbial assimilation and carbon use efficiency, respectively. For detailed carbon dynamics in MIC-TEM, see Zha & Zhuang (2018).

Here we revised MIC-TEM by incorporating microbial dormancy dynamics according to He et al. (2015). In the new model (MIC-TEM-dormancy), the soil heterotrophic respiration $R_H$ is comprised of three parts: the maintenance respiration from the active and dormant microorganisms and the $CO_2$ production through the process of microbial assimilation (He et al., 2015):

$$R_H = m_R Q_{10mic}^{\frac{temp-15}{10}} B_a + \beta m_R Q_{10mic}^{\frac{temp-15}{10}} B_d + CO_2 \quad (2)$$

where the first two terms are maintenance respiration from the active and dormant microorganisms, respectively. The last term is the $CO_2$ produced during the process of microbial assimilation.

For first two terms, $B_a$ and $B_d$ represents the active and dormant microbial biomass pool, respectively. The parameter $m_R$ denotes the specific maintenance rate at active state ($h^{-1}$), and $\beta$ is the ratio of dormant maintenance rate to active maintenance rate. Thus, $\beta m_R$ denotes the maximum specific maintenance rate at dormant state. Temperature sensitivity was expressed as the $Q_{10}$ function ($Q_{10}^{\frac{temp-15}{10}}$), where temp is soil temperature at top 20 cm (units: °C).

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For the third term, the $CO_2$ produced through microbial assimilation is calculated as in He et al. (2015) and Allison et al. (2010):

$$CO_2=ASSIM*(1-Y_g) \quad (3)$$

Where ASSIM represents the variable of microbial assimilation and the parameter $Y_g$ represents carbon use efficiency. Microbial assimilation (ASSIM) is calculated as in He et al. (2015):

$$ASSIM = \frac{1}{Y_g}\frac{\Phi}{\alpha} m_R Q_{10enz}^{\frac{temp-15}{10}} Ba \left(\frac{CN_{soil}}{CN_{mic}}\right)^{0.6} \quad (4)$$

Here parameter $\alpha$ is called the maintenance weight ($h^{-1}$), $CN_{soil}$ and $CN_{mic}$ denotes the C:N ratio of soil and that of microbial biomass to consider substrate quality. Besides, $\Phi$ is called substrate saturation level and defined as in He et al. (2015) and Wang et al. (2014):

$$\Phi = \frac{S}{K_s+S} \quad (5)$$

Where $K_s$ is the half saturation constant for substrate uptake as indicated by the Michaelis–Menten kinetic, and S is soluble C substrates that are directly accessible for microbial assimilation (Wang et al., 2014). Here we quantified concentration of soluble C substrates that are directly accessible for microbial assimilation by using conceptual framework from Davidson et al. (2012):

$$S = \text{Soluble C} * D_{liq} * \theta^3 \quad (6)$$

The term 'Soluble C' denotes the state variable of soluble carbon pool. $D_{liq}$ is the diffusion coefficient of the substrate in the liquid phase, and is formulated as $D_{liq} = 1/(1\text{-}BD/PD)^3$. BD is the bulk density and PD is the soil particle density. $\theta$ is the volumetric soil moisture.

Different from MIC-TEM, the transitions between active and dormant microbial biomass are included in MIC-TEM-dormancy. We used $B_{a\rightarrow d}$ and $B_{d\rightarrow a}$ denotes the transition from the active to dormant microbe and from the dormant to active microbe, respectively (He et al., 2015; Wang et al., 2014):

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$$B_{a\to d} = (1-\Phi)m_R Q_{10mic}^{\frac{temp-15}{10}} B_a \quad (7)$$

$$B_{d\to a} = \Phi m_R Q_{10mic}^{\frac{temp-15}{10}} B_d \quad (8)$$

Dormancy rate is affected by substrate availability ($B_a$, $B_d$), soil temperature (temp) and soil moisture ($\theta$ in $\Phi$).

The active microbial biomass ($B_a$) is modeled as (He et al., 2015; Wang et al., 2014):

$$\frac{dBa}{dt} = ASSIM * Y_g - m_R Q_{10mic}^{\frac{temp-15}{10}} B_a - B_{a\to d} + B_{d\to a} - DEATH - EPROD \quad (9)$$

Where DEATH and EPROD denotes microbial biomass death and enzyme production, which are modeled as proportional to active microbial biomass with constant rates $r_{death}$ and $r_{EnzProd}$ (Allison et al., 2010):

$$DEATH = r_{death} * Ba \quad (10)$$

$$EPROD = r_{EnzProd} * Ba \quad (11)$$

Where $r_{death}$ and $r_{EnzProd}$ are the rate constants of microbial death and enzyme production, respectively.

The dormant microbial biomass ($B_d$) is modeled as (He et al., 2015; Wang et al., 2014):

$$\frac{dB_d}{dt} = -\beta m_R Q_{10mic}^{\frac{temp-15}{10}} B_d + B_{a\to d} - B_{d\to a} \quad (12)$$

The Soluble C pool is modeled as (He et al., 2015; Allison et al., 2010):

$$\frac{d\ Soluble\ C}{dt} = DECAY - ASSIM + ELOSS + DEATH \quad (13)$$

Where DECAY represents the enzymatic decay of soil organic carbon (SOC), and ELOSS represents the loss of enzyme.

DECAY is regulated by enzyme biomass (ENZ), soil organic carbon (SOC), soil temperature, and substrate quality (He et al., 2015):

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$$DECAY = V_{max} * Q_{10enz}^{\frac{temp-15}{10}} * ENZ * \frac{SOC}{Km_{uptake}+SOC} * (120 - CN_{soil}) \quad (14)$$

Where $V_{max}$ is the maximum SOC decay rate, $Km_{uptake}$ is half saturation constant for enzymatic decay.

ELOSS is modeled as a first-order process (Allison et al., 2010) to represent enzyme turnover:

$$ELOSS = r_{enzloss} * ENZ \quad (15)$$

Where $r_{enzloss}$ is the rate constant of enzyme loss.

The soil organic carbon pool (SOC) is modeled as:

$$\frac{dSOC}{dt} = Litterfall - DECAY \quad (16)$$

Where Litterfall is estimated as a function of vegetation carbon (Zhuang et al., 2010).

Last, enzyme pool (ENZ) is modeled as:

$$\frac{dENZ}{dt} = EPROD - ELOSS \quad (17)$$

With the modification of microbial carbon dynamics by considering microbial life-history trait, soil decomposition is changed since it is controlled by microbes. When microbial dormancy is considered, the number of active microbes that participate in soil decomposition is different. The changes in soil decomposition directly influence the amount of soil respiration, and further influence soil nitrogen (N) mineralization that determines soil N availability for plants, affecting gross primary production (GPP). Since both GPP and soil respiration ($R_H$) can be affected by microbial dormancy, net ecosystem production (NEP) will also be affected.

### 2.3 Model parameterization and validation

The detailed description of parameters that are related to microbial dormancy can be found in He et al. (2015) (Table 1). Here we calibrated the MIC-TEM-dormancy at six representative

sites with gap-filled monthly net ecosystem productivity (NEP, $gCm^{-2}mon^{-1}$) data in northern high latitudes (Table 2). Site-level climatic data and soil texture data were organized for driving model. All sites information can be found on AmeriFlux network (Davidson et al., 2000). The results for model parameterization were presented in Figure 2. We conducted the parameterization using a global optimization algorithm known as SCE-UA (Shuffled complex evolution) method (Duan et al., 1994). An ensemble of 50 independent sets of parameters were performed based on prior ranges from literature (Table 1) to minimize the difference between the monthly simulated and measured NEP at the chosen sites. The cost function of the minimization is:

$$\mathrm{Obj} = \sum_{i=1}^{k}(\mathrm{NEP}_{obs,i} - \mathrm{NEP}_{sim,i})^2 \quad (17)$$

Where $\mathrm{NEP}_{obs,i}$ and $\mathrm{NEP}_{sim,i}$ are the observed and simulated NEP, respectively. k is the number of data pairs for comparison. Except for the parameters of microbial dormancy, other parameters are derived directly from MIC-TEM (Zha & Zhuang, 2018). The optimized parameters were used for model validation and regional simulations.

For model validation, we chose another six sites that containing monthly NEP data from AmeriFlux network (Table 3). Moreover, we also conducted site-level validations with monthly soil respiration data from AmeriFlux network and Fluxnet dataset. The site information was provided in Table 4. For these sites, we assumed 50% of soil respiration was heterotrophic respiration ($R_H$) for forest (Hanson et al., 2000), 60% and 70% of that was $R_H$ for grassland (Wang et al., 2009) and tundra (Billings et al., 1977). Because there is a limited amount of measured data of heterotrophic respiration, we could not conduct a regional validation for all pixels in northern high latitudes. Instead, we extracted 61 sites providing data of average annual heterotrophic respiration from ORNL global Soil Respiration Dataset (https://daac.ornl.gov/SOILS/guides/SRDB_V4.html, Bond-Lamberty et al., 2018) for model

validation. The site-level observed average annual $R_H$ was used to compare with simulated annual $R_H$ by MIC-TEM-dormancy and MIC-TEM. The new model (MIC-TEM-dormancy) was run at monthly time step to keep consistent with the time step of MIC-TEM. Although microbial dynamics occur at fine temporal scales (Tang & Riley, 2014), we can still quantify the cumulative impacts of microbial dynamics on carbon and nitrogen cycling at monthly time by not changing the model structure.

**2.4 Spatial extrapolation**

For historical simulations during the 20$^{th}$ century, two sets of regional simulations using MIC-TEM-dormancy and MIC-TEM at a spatial resolution of 0.5° latitude × 0.5° longitude were conducted. Our model simulation contains two parts: spin-up and transient simulation. A typical spin-up was conducted to get the model to a steady state for each spatial location, which will be used as initial conditions for transient simulations (McGuire et al., 1992). During spin-up procedure, cyclic forcing data was used to force the model run, and repeated continuously until dynamic equilibrium was achieved at which the modeled state variables show a cyclic pattern or become constant. Specifically, this study used the monthly historical climate data from 1900 to 1940 to repeatedly drive the model for the spin-up. Before spin-up procedure, the model was initialized with default built-in carbon stocks (Raich et al., 1991). During transient simulations, the calibrated ecosystem-specific parameters were used for regional simulations. The previous dynamic equilibrium was used as initial value for transient simulation. The historical climatic forcing data, including the monthly air temperature, precipitation, cloudiness, and atmospheric $CO_2$ concentrations, were organized from the Climatic Research Unit (CRU TS3.1) from the University of East Anglia (Harris et al., 2014). Gridded data of soil texture (Zhuang et al., 2003),

elevation (Zhuang et al., 2015), and potential natural vegetation (Melillo et al., 1993) from literatures were also used. In our model, we assumed that soil texture, elevation, and potential natural vegetation data only vary spatially, not vary over time (Zhuang et al., 2015).

In addition, regional simulations over the 21st century were conducted under two Intergovernmental Panel on Climate Change (IPCC) climate scenarios (RCP 2.6 and RCP 8.5). The future climatic forcing data under these two climate change scenarios were derived from the HadGEM2-ESmodel, which is a member of CMIP5project213 (https://esgf-node.llnl.gov/search/cmip5/). Then the regional estimations were obtained by summing up the gridded outputs for our study region. The positive simulated NEP represents a $CO_2$ sink from the atmosphere to terrestrial ecosystems, while a negative value represents a source of $CO_2$ from terrestrial ecosystems to the atmosphere.

## 3. Results

### 3.1 Inversed Model Parameters and model validation

Using SCE-UA ensemble method, 50 independent sets of parameters were converged to minimize the objective function. Then the optimized parameters are calculated as the mean of these 50 sets of inversed parameters. The boxplot of parameter posterior distributions reflects different ecosystem properties at these sites (Figure 3). For instance, carbon use efficiency (CUE) was much higher in tundra types than in forests, meaning microorganisms in environment with higher energy limitation tend to enhance the efficiency of energy transportation. Besides, alpha, the maintenance weight, was also much higher in tundra types than in forests. The opposite can be seen from parameter beta, the ratio of dormant maintenance rate to specific maintenance rate for active

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biomass. Other microbial related parameters did not differentiate much among different vegetation types.

After parameterization, the MIC-TEM-dormancy was validated with monthly NEP data for six representative ecosystems, and the comparisons between monthly observed NEP and simulated NEP were presented in Figure 4. With the optimized parameters, the dormancy-based model was used to reproduce NEP to compare with the measured NEP (Table 5). The statistical analysis shows that $R^2$ ranges from 0.67 for Atqasuk to 0.93 for Bartlett Experimental Forest (Table 5). Generally, our new model performs better for forest ecosystems than for tundra ecosystems. Compared with MIC-TEM, which is no dormancy-based, dormancy model performs better for alpine tundra, temperate coniferous forest, and grassland. For other sites, two models show similar performance (Table 5). Another set of sites with monthly soil respiration data were selected to conduct model validation. The comparisons between monthly observed $R_H$ and simulated $R_H$ from two contrasting models were conductd (Figure 5). MIC-TEM-dormancy has higher $R^2$ and lower RMSE (Table 6). Sixty-one sites with average annual $R_H$ in northern high-latitude region were used to further evaluate the new model performance. The dormancy model has lower intercept and slope with $R^2$ of 0.45, while $R^2$ of MIC-TEM is 0.3 (Figure 6). These analyses indicate that new model is more realistic in representing heterotrophic respiration ($R_H$) by considering microbial dormancy. This difference further affects soil available nitrogen dynamics, influencing nitrogen uptake by plants, the rate of photosynthesis and NPP.

### 3.2 Regional carbon dynamics during the 20$^{th}$ century

Regional extrapolation with both models estimated a regional carbon sink but with different magnitudes (Figure 7c). Here positive values of NEP represent sinks of $CO_2$ into terrestrial

ecosystems, while negative values represent sources of $CO_2$ to the atmosphere. With optimized parameters, MIC-TEM estimated a regional carbon sink of 77.6 Pg with the interannual standard deviation of 0.21 Pg C $yr^{-1}$ during the 20$^{th}$ century. However, MIC-TEM-dormancy nearly doubles the sink at 153.5 Pg with the interannual standard deviation of 0.12 Pg C $yr^{-1}$ during the last century, which estimates 75.9 Pg more carbon sink than MIC-TEM does but with less interannual variation (Figure 7c). At the end of the century, MIC-TEM estimated that NEP reaches 1.0 Pg C $yr^{-1}$ in comparison with MIC-TEM-dormancy estimates of 1.5 Pg C $yr^{-1}$ (Figure 7c). Both models simulated similar trends for regional NPP, $R_H$ and NEP (Figure 7). Generally, they show an increasing trend in the 20th century except a slight decrease during the 1960s (Figure 7). Meanwhile, with optimized parameters, MIC-TEM-dormancy estimated NPP and $R_H$ at 7.94 Pg C $yr^{-1}$ and 6.4 Pg C $yr^{-1}$, which are 5.8% and 16.3% less than the estimations from MIC-TEM, respectively (Figures 7a and 7b). This pronounced difference of NEP between two models comes from the disparity between the simulated NPP and $R_H$ with them. Without considering dormancy, MIC-TEM estimates more active microbial biomass since it assumes the whole microbial biomass pool will participate in soil decomposition. The fact is only active part of microbial biomass can work for soil decomposition, meaning MIC-TEM overestimates $R_H$. On the other hand, Overestimation of $R_H$ can induce higher nitrogen uptake by plants, which will accelerate rate of photosynthesis and further enhance NPP projection. Although MIC-TEM estimates higher NPP and $R_H$ than MIC-TEM-dormancy does, NEP estimated from MIC-TEM is actually lower.

The average annual seasonal patterns of NPP, $R_H$ and NEP during the 1990s were also organized from regional simulations with two models (Figure 8). Temporally, both two models projected higher NPP and $R_H$ in summer than in winter (Figures 8a and 8b) due to higher soil temperature and moisture (McGuire et al., 1992). MIC-TEM produced less $R_H$ in winter but

higher $R_H$ in summer than MIC-TEM-dormancy (Figure 8b), which indicates that without dormancy, model tends to estimate lower soil respiration compared to dormancy model due to ignorance of dormant respiration in winter but estimate higher soil respiration due to higher estimation of active biomass in summer. In the meantime, seasonal cycle of NPP with MIC-TEM-dormancy shows a relative flattening pattern compared with MIC-TEM, which is similar to seasonal cycle of $R_H$ (Figure 8a). This is because higher $R_H$ can cause higher NPP due to the reasons we have mentioned above. Though $R_H$ and NPP show the similar seasonal patterns, NEP can still show different pattern since it's the difference between NPP and $R_H$. Here seasonal cycles of NEP with models are close to each other (Figure 8c), but dormancy model projected slightly higher NEP in summer. Besides, setting the $R_H$ projection from MIC-TEM as baseline, MIC-TEM-dormancy averagely projected 33% less $R_H$ in summer (May to September), and 30% more in winter (other months). This suggested that relative difference of $R_H$ between two models in summer was higher than in winter.

### 3.3 Regional carbon dynamics during the 21st century

Under the RCP 8.5 scenario, both models estimated the region acts as a carbon sink (Figure 9). The MIC-TEM-dormancy predicted that the sink is 129.9 Pg with the interannual standard deviation of 0.13 Pg C $yr^{-1}$, whereas MIC-TEM estimates the sink is 79.5 Pg with the interannual standard deviation of 0.37 Pg C $yr^{-1}$ during the 21st century (Figure 9). Thus, MIC-TEM-dormancy estimates an increase of 50.4 Pg regional carbon sequestration relative to MIC-TEM but with less interannual variation (Figure 9). Both models predict similar temporal trends for NEP, namely increasing from the 2000s and then decreasing from the 2070s onward (Figure 9). MIC-TEM-dormancy predicts that carbon sink reaches 1.36 Pg C $yr^{-1}$ in the 2090s, which is 0.26 Pg C $yr^{-1}$ more than projection of MIC-TEM. Moreover, MIC-TEM-dormancy estimated

NPP and $R_H$ at 10.2 Pg C $yr^{-1}$ and 8.9 Pg C $yr^{-1}$, which are 1.3 Pg C $yr^{-1}$ and 1.8 Pg C $yr^{-1}$ less than the estimations from MIC-TEM, respectively (Figure 9). Under the RCP 2.6 scenario, the cumulative NEP from two models diverged by 125.2 Pg C by 2100. The trajectory of inter-annual NEP estimated with the two models also diverged. The MIC-TEM predicted the region fluctuates between carbon sinks and sources, and totally acts as a carbon source of 1.6 Pg C with the interannual standard deviation of 0.24 Pg C $yr^{-1}$ during the 21$^{st}$ century. In contrast, MIC-TEM-dormancy projected the region acts as a carbon sink of 123.6 Pg C with the interannual standard deviation of 0.1 Pg C $yr^{-1}$ (Figure 9). MIC-TEM-dormancy estimates NPP and $R_H$ at 9.9 Pg C $yr^{-1}$ and 8.7 Pg C $yr^{-1}$, which are 0.5 Pg C $yr^{-1}$ and 1.7 Pg C $yr^{-1}$ less than the estimations from MIC-TEM, respectively (Figure 9).

The average annual seasonal patterns of NPP, $R_H$ and NEP during the 2990s by two models were also presented (Figure 10). MIC-TEM-dormancy estimated higher $R_H$ in winter, but lower $R_H$ in summer under both future scenarios (Figure 10). Similar seasonal cycle pattern appears for NPP projection. The combined flattening patterns of NPP and $R_H$ result in different patterns for NEP. Under the RCP 2.6 scenario, MIC-TEM-dormancy predicts higher NEP from June to October, but similar NEP in other months to MIC-TEM (Figure 10). Under the RCP 8.5 scenario, MIC-TEM-dormancy predicts higher NEP from June to September, but much lower NEP in other months than MIC-TEM (Figure 10).

## 4. Discussion

Soils are the largest carbon repository in the terrestrial biosphere and hold 2.5 times more carbon than the atmosphere (Frey et al., 2013; Schlesinger & Andrews, 2000). Especially, a significant portion of soil organic carbon currently stored in northern high latitudes region (Tarnocai et al., 2009). Besides, climate over this region has warmed in recent decades (Serreze

& Francis, 2006) and the changing climate is expected to alter the carbon cycle through influencing the activities of microorganisms in controlling soil decomposition (Manzoni et al., 2012; Melillo et al., 2011). Therefore, explicit consideration of microbial traits and functions in large-scale biogeochemistry models is necessary for better quantification of carbon-climate feedbacks (Thullner et al., 2005; Wang et al., 2015). Our regional simulations with two contrasting models (MIC-TEM, MIC-TEM-dormancy) indicate the region was a carbon sink in past decades, which is consistent with results from other process-based models (White et al., 2000; Houghton et al., 2007; McGuire et al., 2009; Schimel, 2013). However, the magnitudes of this sink are quite different in two models. Moreover, MIC-TEM-dormancy predicts the sink will decrease under both RCP 8.5 and RCP 2.6 scenarios during the 21$^{st}$ century, while MIC-TEM projects that the sink will increase under the RCP 8.5 but change to carbon source under the RCP 2.6 scenario. The large difference in two models suggests the importance of incorporating microbial dormancy effects.

The large bias between dormancy and non-dormancy models mainly comes from two parts. First, most important microbial activities such as soil organic carbon decomposition and nutrient cycling largely depend on the active fraction of microbial communities, not total microbial biomass (Wang et al., 2014; Blagodatsky et al., 2000). However, only a small part (about 0.1-2%, seldom exceed 5%) of the total soil microbial biomass is recognized to be active under natural conditions (Blagodatsky et al., 2011; Werf & Verstraete, 1987). Thus, dormancy could be a prominent feature in soil systems (Wang et al., 2014). Without considering dormancy, the "effective" microbial biomass for soil decomposition could be overestimated, resulting in overestimation of heterotrophic respiration (He et al., 2015). Our regional estimate of $R_H$ is 6.4 Pg C yr$^{-1}$ during the 20$^{th}$ century by MIC-TEM-dormancy, while 7.7 Pg C yr$^{-1}$ by MIC-TEM. No

dormancy model simulated 20.3% higher respiration than dormancy model. For future simulations, MIC-TEM-dormancy predicted 8.7 Pg C $yr^{-1}$ and 9.0 Pg C $yr^{-1}$ of $R_H$ under RCP 2.6 and RCP 8.5 scenarios during the 21st century, respectively. Nevertheless, no dormancy model simulated 19.5% and 21.2% higher respiration than dormancy model under RCP 2.6 and RCP 8.5 scenarios, respectively. He et al. (2015) predicted total soil $R_H$ of all temperate forests (25°N-50°N) from the dormancy model amounted to 7.28 Pg C $yr^{-1}$ and 8.83 Pg C $yr^{-1}$ from a no-dormancy model, which is 21.3% higher than the dormancy model. Although their study region and simulation period are different from our study, the results can still be comparable. Both studies indicated that the magnitude of $R_H$ and proportion from no-dormancy model are higher than dormancy models. Second, high soil respiration stimulates N mineralization in soils (Zhuang et al., 2001, 2002), making more nutrients for photosynthesis of plants (Raich et al., 1991; McGuire et al., 1995). Therefore, NPP will be higher due to the N enrichment from higher $R_H$. However, how NEP will change is still unclear. Our regional estimate of NEP during the 20th century by MIC-TEM-dormancy is 1.54 Pg C $yr^{-1}$, and is 0.78 Pg C $yr^{-1}$ by MIC-TEM. Schimel et al. (2001) reported that a range of estimates of the northern extratropical NEP is from 0.6 to 2.3 PgC $yr^{-1}$ in the 1980s. In comparison with our estimates of 1.61 Pg C $yr^{-1}$ with MIC-TEM-dormancy and 0.84 Pg C $yr^{-1}$ with MIC-TEM, our regional estimates of NEP are in reasonable range. Moreover, our predicted trend of NEP is very similar to the finding of White et al. (2000), indicating that NEP increases from the 2000s to the 2070s, and then decreases in the 2090s. Moreover, future simulations under two contrasting climate scenarios (RCP 2.6 and RCP 8.5) exhibit a large difference of 81.1 Pg C of cumulative NEP during the 21st century by MIC-TEM, but only 6.3 Pg C of that by MIC-TEM-dormancy. This difference indicates microbes provide a resistant response to climate change due to dormancy to some extent (Treseder et al., 2011).

Although our dormancy model can project reasonable carbon fluxes and indicate the importance of incorporating microbial dormancy when compared with no dormancy model (MIC-TEM; Zha & Zhuang et al., 2018), there are some other microbial traits have not yet been considered in our model. For instance, one vital common evolutionary trait of microbe is the community shift (Wang et al., 2015) with changing environment, including warming, N fertilization and precipitation (Treseder et al., 2011; Frey et al., 2013; Allison et al., 2009; Evans & Wallenstein, 2011). Community shift will influence microbial physiology, temperature sensitivity and growth rates (Classen et al., 2015), which will further affect the rate of soil decomposition and other carbon dynamics (Treseder et al., 2011; Schimel & Schaeffer, 2012; Todd-Brown et al., 2011). Moreover, microbial acclimation is another important trait to affect soil decomposition. Recent studies have found the capacity of the microbial community to maintain the warming-induced elevated respiration could decrease over time because of acclimation (Melillo et al. 1993; Todd-Brown et al., 2011). This mechanism of adaption to a new temperature regime shall be factored into future soil decomposition analysis. Besides, microbial community composition was ignored in our model. We didn't separate among functional microbial groups, but gather microbes into one "box". However, microbial community composition could influence ecosystem functioning, and their variance in responses to environmental conditions could alter the prediction of the rates of decomposition of organic material (Balser et al. 2002; Fierer et al. 2007). Especially, some narrowly-distributed functions can be more sensitive to microbial community composition, and these might benefit most from explicit consideration of distinguishing functional groups in ecosystem models (McGuire & Treseder, 2010; Schimel 1995). Thus, functional dissimilarity in microbial communities can be considered in next step for model development (Strickland et al., 2009; Moorhead et al., 2006).

Except for above model limitations, additional uncertainties may come from inadequate model parameterization and model assumptions. For example, a critical microbial parameter, carbon use efficiency (CUE), is a primary control to soil $CO_2$ efflux. Higher CUE indicates more microbial growth and more carbon uptake by plants, while lower CUE indicates higher soil decomposition (Manzoni et al., 2012). Theoretical and empirical studies have suggested that CUE depends on both temperature and substrate quality (Frey et al., 2013) and decreases as temperature increases and nutrient availability decreases (Manzoni et al., 2012). Our study considered the CUE sensitivity to temperature, but not nutrient availability. On the other hand, some model assumptions can also cause uncertainties. For example, we assumed that vegetation will not change during the transient simulation. However, over the past few decades in northern high latitudes, temperature increases have led to vegetation shift from one type to another (Hansen et al., 2006; White et al., 2000). The vegetation changes will affect carbon cycling in these ecosystems.

## 5. Conclusions

This study incorporated microbial dormancy into a detailed microbial-based soil decomposition biogeochemistry model to examine the fate of large Arctic soil carbon under changing climate conditions. Regional simulations using MIC-TEM-dormancy indicated that, over the 20$^{th}$ century, the region is a carbon sink of 153.5 Pg. This sink could decrease to 129.9 Pg under the RCP 8.5 scenario or 123.6 Pg under the RCP 2.6 scenario during the 21$^{st}$ century. Whether considering microbial dormancy or not can cause large differences in soil decomposition estimation between two models. Meanwhile, due to available nitrogen affected by soil decomposition, net primary production is consequently influenced in these two centuries.

The combined changes in soil decomposition and net primary production led to large differences in carbon budget estimation between two models. Compared with MIC-TEM, MIC-TEM-dormancy projected 75.9 Pg more C stored in the terrestrial ecosystems over the last century, 50.4 Pg and 125.2 Pg more C under the RCP 8.5 and RCP 2.6 scenarios, respectively. This study highlights the importance of the representation of microbial dormancy in earth system models in order to adequately quantify the carbon dynamics in northern high latitudes.

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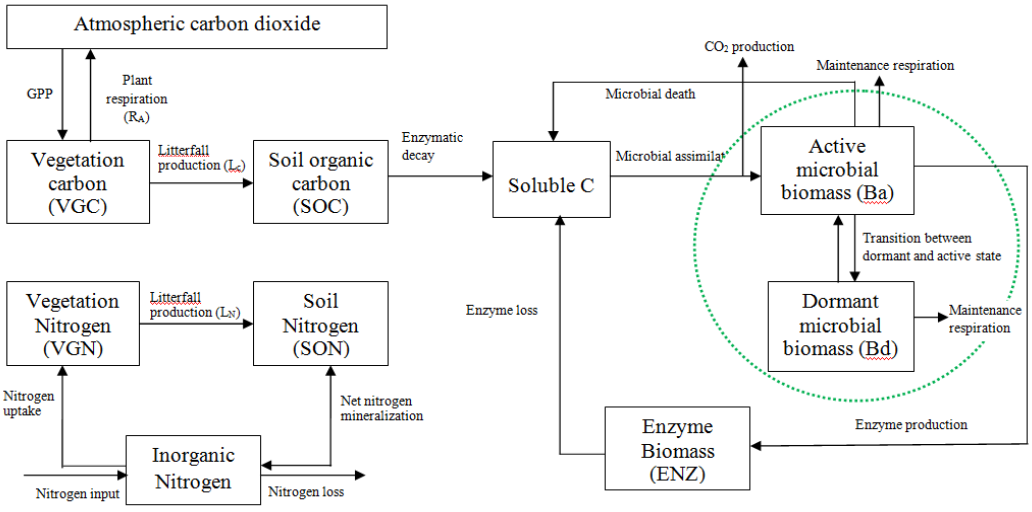


Figure 1. Framework of the dormancy model: microbial biomass is split into two parts, active microbial biomass and dormant microbial biomass (shown in the green dashed circle). Maintenance respiration from these two parts, and the $CO_2$ production through microbial assimilation contributes to heterotrophic respiration. The model was revised based on Zha & Zhuang (2018).

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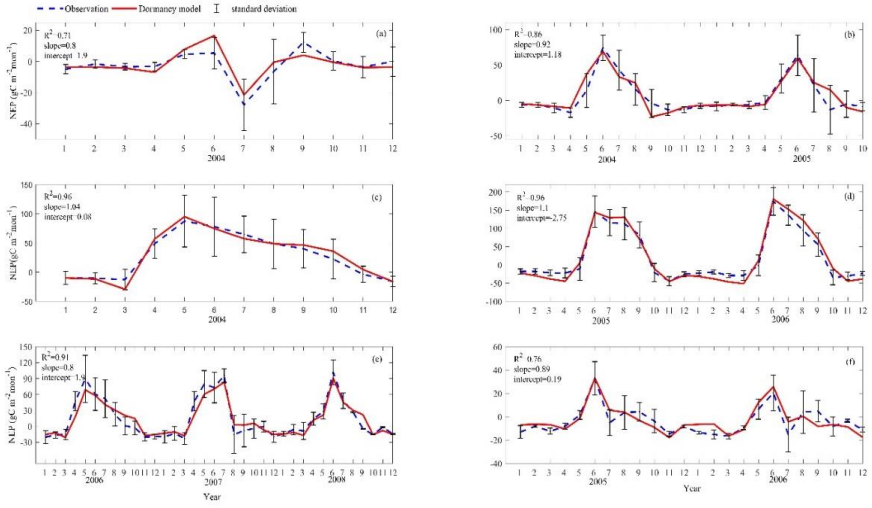


Figure 2. Comparison between observed and simulated NEP (gC $m^{-2}mon^{-1}$) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Univ. of Mich. Biological Station (Temperate deciduous forest), (e) KUOM Turfgrass Field (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different. Error bars represent standard errors among daily measure data in one month.

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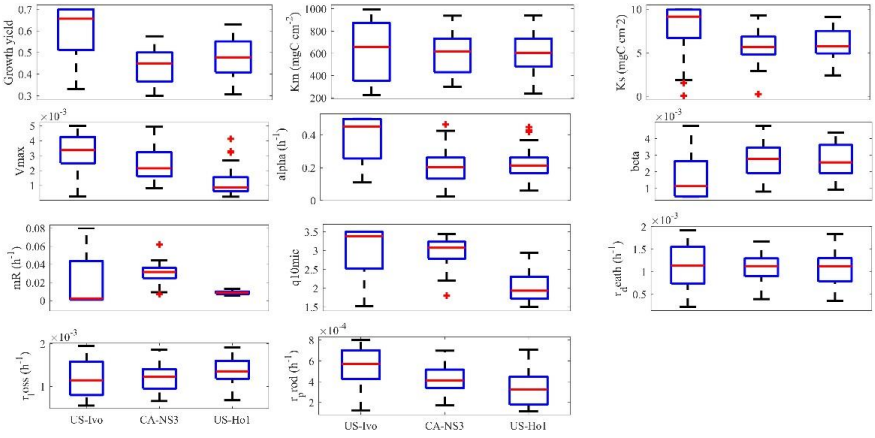


Figure 3. Boxplot of parameter posterior distribution that are obtained after ensemble inverse modeling for MIC-TEM-dormancy all six sites: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-1964 burn site (boreal forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB: Univ. of Mich. Biological Station (temperate deciduous forest), US-KUT: KUOM Turfgrass Field (grassland), US-Atq: Atqasuk (wet tundra).

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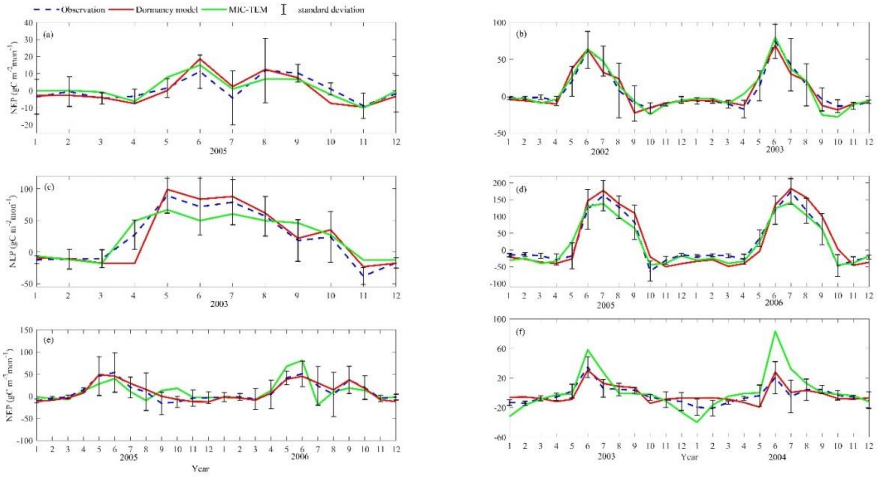


Figure 4. Comparison between observed and simulated NEP (gC $m^{-2}mon^{-1}$) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Bartlett Experimental Forest (Temperate deciduous forest), (e) Brookings (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different.

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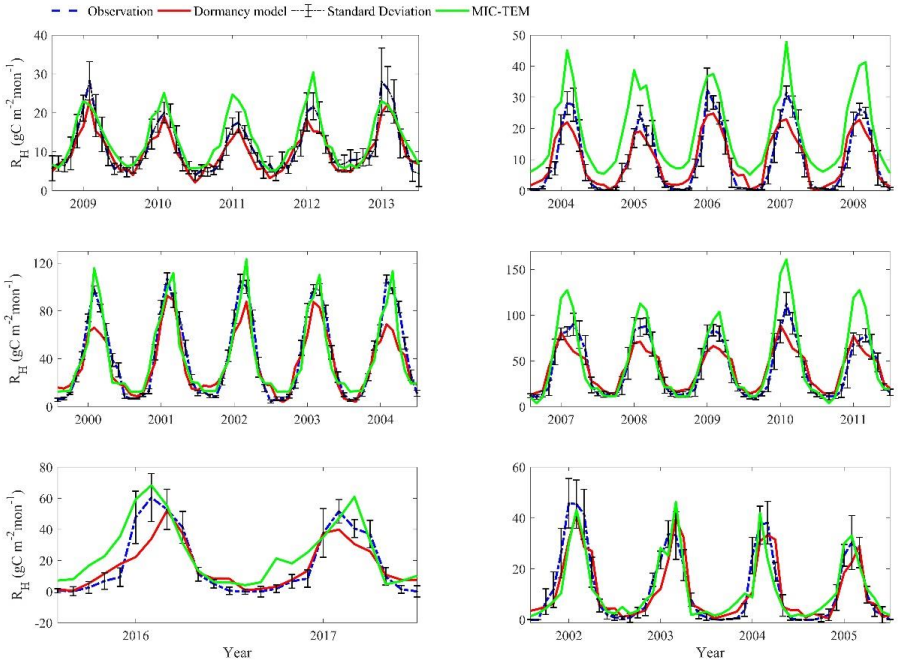


Figure 5. Comparison between observed and simulated $R_H$ (gC m$^{-2}$mon$^{-1}$) at: (a) US-EML (alpine tundra), (b) CA-SJ2 (boreal forest), (c) US-Ho2 (temperate coniferous forest), (d) US-UMB (Temperate deciduous forest), (e) US-Ro4 (Grassland), and (f) RU-Che (Wet tundra). Note: scales are different.

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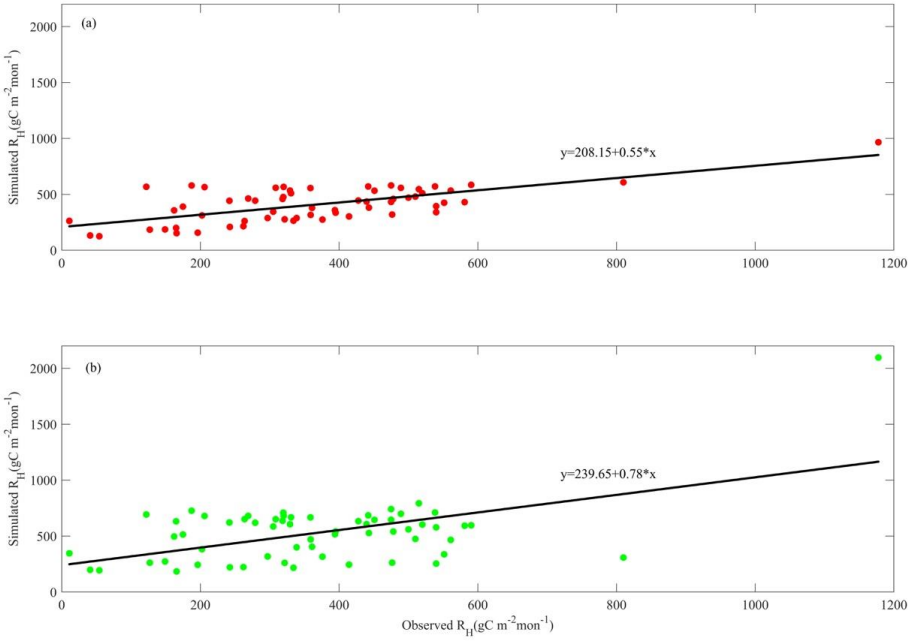


Figure 6. Linear regression between simulated and observed annual $R_H$ (gC $m^{-2}yr^{-1}$) for: (a) MIC-TEM-dormancy, and (b) MIC-TEM.

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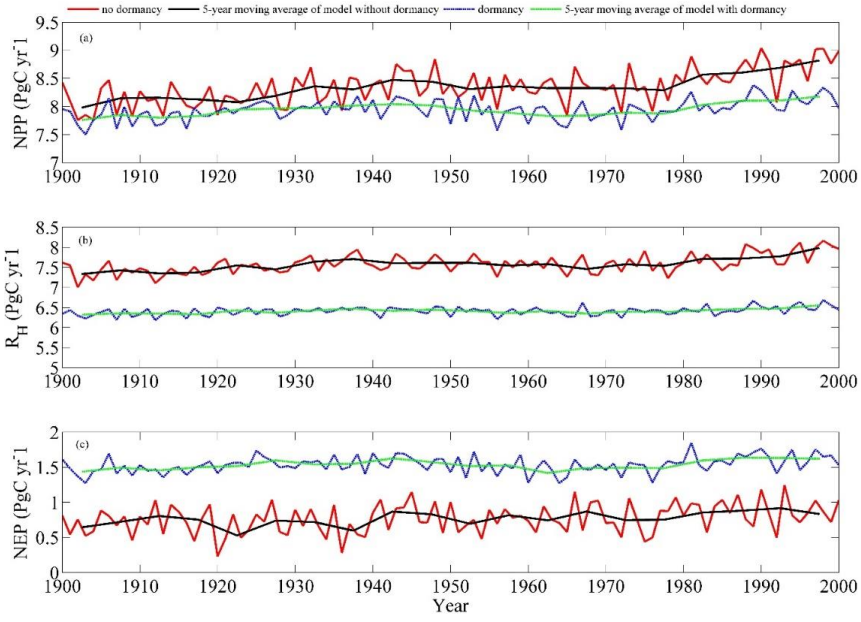


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863 Figure 7. Simulated annual net primary production (NPP, top panel), heterotrophic respiration ($R_H$,
864 center panel) and net ecosystem production (NEP, bottom panel) during the 20$^{th}$ century by
865 dormancy model and MIC-TEM, respectively.

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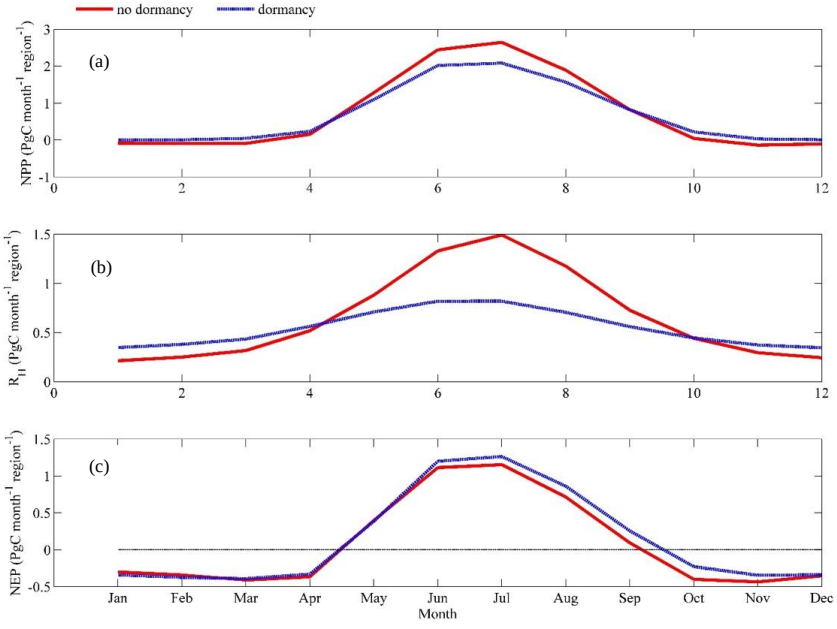


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867 Figure 8. Annual seasonal pattern of simulated (a) net primary production (NPP, top panel), (b)
868 heterotrophic respiration ($R_H$, center panel) and (c) net ecosystem production (NEP, bottom
869 panel) during the 1990s from dormancy model and MIC-TEM.

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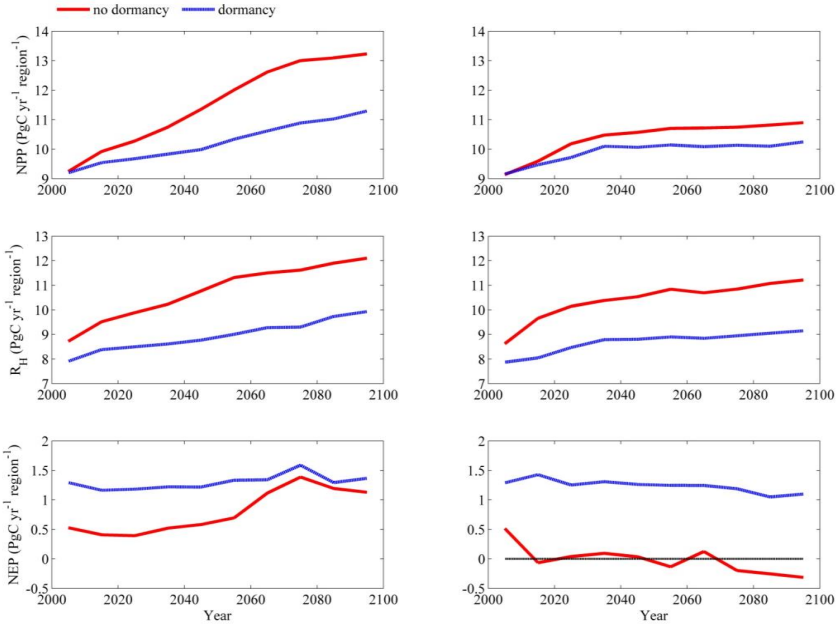


Figure 9. Predicted changes in carbon fluxes: (i) NPP, (ii) $R_H$, and (iii) NEP for all land areas north of 45 °N in response to transient climate change under the RCP 8.5 scenario (left panel) and RCP 2.6 scenario (right panel) with dormancy model and MIC-TEM, respectively. The decadal running mean is applied.

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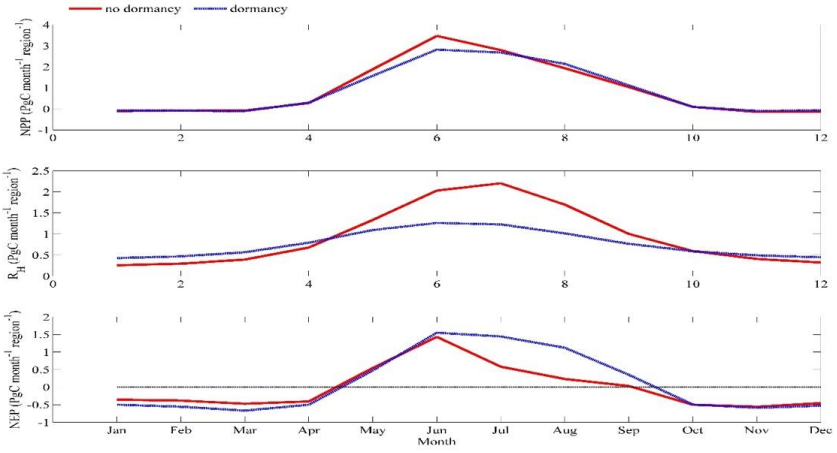
886 (a)

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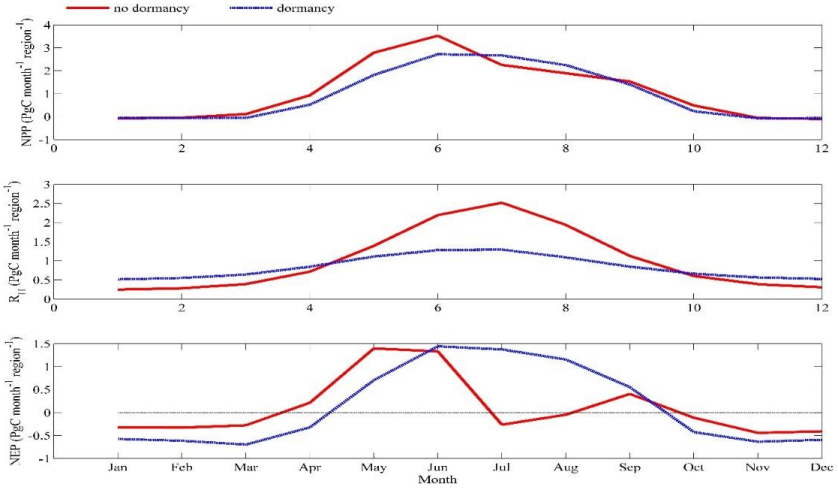
888 (b)




889

890 Figure 10. Annual seasonal pattern of simulated net primary production (NPP, top panel),
891 heterotrophic respiration ($R_H$, center panel) and net ecosystem production (NEP, bottom panel)
892 during the 2090s from dormancy model and MIC-TEM under: (a) RCP 2.6 scenario (top panel)
893 and (b) RCP 8.5 scenario (bottom panel).
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**Table 1. Parameters associated with detailed microbial dormancy in MIC-TEM-dormancy**

| parameter | unit | description | Parameter range | references |
|---|---|---|---|---|
| $m_R$ | $h^{-1}$ | Specific maintenance rate at active state | [0.001, 0.08] | Wang et al. (2014) |
| $Q_{10mic}$ | - | Temperature effects on microbial metabolic activity (rate change per 10 °C increase in temperature). Based on 0.65 eV activation energy for soils | [1.5, 3.5] | He et al. (2015) |
| $Q_{10enz}$ | - | Temperature effects on enzyme activity (rate change per 10 °C increase in temperature). Based on 6% rate increase per degree Celsius | 1.79 | He et al. (2015) |
| $\alpha$ | - | the ratio of $m_R$ to the sum of maximum specific growth rate | [0.01, 0.5] | Wang et al. (2014) |
| $\beta$ | - | Ratio of dormant microbial maintenance rate to $m_R$ | [0.0005, 0.005] | Wang et al. (2014) |
| $Y_g$ | - | carbon use efficiency | [0.3, 0.7] | He et al. (2015) |
| $K_s$ | mgC $cm^{-2}$ | Half-saturation constant for directly accessible substrate | [0.01, 10] | Wang et al. (2014) |
| $Km_{uptake}$ | mgC $cm^{-2}$ | Half-saturation constant for enzymatic decay of SOC | [200, 1000] | He et al. (2015) |
| $r_{death}$ | $h^{-1}$ | Potential rate of microbial death | [$2e^{-4}$, $2e^{-3}$] | Allison et al. (2010) |
| $r_{EnzProd}$ | $h^{-1}$ | Enzyme production rate of microbe | [$1e^{-4}$, $8e^{-4}$] | He et al. (2015) |
| $r_{enzloss}$ | $h^{-1}$ | Enzyme loss rate | [0.0005, 0.002] | Allison et al. (2010) |
| $V_{max}$ | mgC $cm^{-2}$ $h^{-1}$ | Maximum SOC decay rate | [$1e^{-4}$, $5e^{-3}$] | He et al. (2015) |

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**Table 2. Site description and measured NEP data used to calibrate MIC-TEM-dormancy**

| Site Name | Location (Longitude (degrees) /Latitude (degrees)) | Elevation (m) | Vegetation type | Description | Data range | Citations |
|---|---|---|---|---|---|---|
| Univ. of Mich. Biological Station | 84.71W 45.56 N | 234 | Temperate deciduous forest | Located within a protected forest owned by the University of Michigan. Mean annual temperature is 5.83°C with mean annual precipitation of 803mm | 01/2005-12/2006 | Gough et al. (2013) |
| Howland Forest (main tower) | 68.74W 45.20N | 60 | Temperate coniferous forest | Closed coniferous forest, minimal disturbance. | 01/2004-12/2004 | Davidson et al. (2006) |
| UCI-1964 burn site | 98.38W 55.91N | 260 | Boreal forest | Located in a continental boreal forest, dominated by black spruce trees, within the BOREAS northern study area in central Manitoba, Canada. | 01/2004-10/2005 | Goulden et al. (2006) |
| KUOM Turfgrass Field | 93.19W 45.0N | 301 | Grassland | A low-maintenance lawn consisting of cool-season turfgrasses. | 01/2006-12/2008 | Hiller et al. (2011) |
| Atqasuk | 157.41W 70.47N | 15 | Wet tundra | 100 km south of Barrow, Alaska. Variety of moist-wet coastal sedge tundra, and moist-tussock tundra surfaces in the more well-drained upland. | 01/2005-12/2006 | Oechel et al. (2014); |
| Ivotuk | 155.75W 68.49N | 568 | Alpine tundra | 300 km south of Barrow and is located at the foothill of the Brooks Range and is classified as tussock sedge, dwarf-shrub, moss tundra. | 01/2004-12/2004 | McEwing et al. (2015) |

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906 **Table 3. Site description and measured NEP data used to validate MIC-TEM-dormancy**
907

| Site Name | Location (Longitude (degrees) /Latitude (degrees)) | Elevation (m) | Vegetation type | Description | Data range | Citations |
|---|---|---|---|---|---|---|
| Bartlett Experimental Forest | 71.29W/ 44.06N | 272 | Temperate deciduous forest | Located within the White Mountains National Forest in north-central New Hampshire, USA, with mean annual temperature of 5.61 °C and mean annual precipitation of 1246mm. | 01/2005-12/2006 | Jenkins et al. (2007); Richardson et al. (2007); |
| Howland Forest (main tower) | 68.74W/ 45.20N | 60 | Temperate coniferous forest | Closed coniferous forest, minimal disturbance. | 01/2003-12/2003 | Davidson et al. (2006) |
| UCI-1964 burn site | 98.38W/ 55.91N | 260 | Boreal forest | Located in a continental boreal forest, dominated by black spruce trees, within the BOREAS northern study area in central Manitoba, Canada. | 01/2002-12/2003 | Goulden et al. (2006) |
| Brookings | 96.84W/ 44.35N | 510 | Grassland | Located in a private pasture, belonging to the Northern Great Plains Rangelands, the grassland is representative of many in the north central United States, with seasonal winter conditions and a wet growing season. | 01/2005-12/2006 | Gilmanov et al. (2005) |
| Atqasuk | 157.41W/ 70.47N | 15 | Wet tundra | 100 km south of Barrow, Alaska. Variety of moist-wet coastal sedge tundra, and moist-tussock tundra surfaces in the more well-drained upland. | 01/2003-12/2004 | Oechel et al. (2014); |
| Ivotuk | 155.75W/ 68.49N | 568 | Alpine tundra | 300 km south of Barrow and is located at the foothill of the Brooks Range and is classified as tussock sedge, dwarf-shrub, moss tundra. | 01/2005-12/2005 | McEwing et al. (2015) |

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**Table 4. Site description and measured $R_H$ data used to validate MIC-TEM-dormancy model**

| Site | Location (Longitude (degrees) /Latitude (degrees)) | Elevation (m) | Vegetation type | Data range | Citations |
|---|---|---|---|---|---|
| US-EML | 149.25W/ 63.88N | 700 | Alpine tundra | 01/2009-12/2013 | Belshe et al. (2012) |
| CA-SJ2 | 104.65W/ 53.95N | 580 | Boreal forest | 01/2004-12/2008 | Coursolle et al. (2006) |
| US-Ho2 | 68.75W/ 45.21N | 91 | Temperate coniferous forest | 01/2000-12/2004 | Davidson et al. (2006) |
| US-UMB | 84.71W/ 45.56N | 234 | Temperate deciduous forest | 01/2005-12/2006 | Gough et al. (2013) |
| US-Ro4 | 93.07W/ 44.68N | 274 | Grasslands | 01/2016-12/2017 | Griffis et al. (2011) |
| RU-Che | 161.34E/ 68.61N | 6 | Wet tundra | 01/2002-12/2005 | Merbold et al. (2009) |

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**Table 5. Model validation statistics for Dormancy model and MIC-TEM at six sites with NEP data**

| Site Name | Vegetation type | Models | Intercept | Slope | R-square | Adjusted R-square | p-value |
|---|---|---|---|---|---|---|---|
| Ivotuk | Alpine tundra | MIC-TEM | 0.85 | 0.83 | 0.70 | 0.67 | <0.001 |
| | | Dormancy | -0.51 | 1.09 | 0.75 | 0.73 | <0.001 |
| UCI-1964 burn site | Boreal forest | MIC-TEM | 0.18 | 1.03 | 0.912 | 0.9080 | <0.001 |
| | | Dormancy | -0.21 | 0.96 | 0.90 | 0.894 | <0.001 |
| Howland Forest (main tower) | Temperate coniferous forest | MIC-TEM | 7.29 | 0.72 | 0.85 | 0.83 | <0.001 |
| | | Dormancy | 0.27 | 1.05 | 0.89 | 0.88 | <0.001 |
| Bartlett Experimental Forest | Temperate deciduous forest | MIC-TEM | -6.05 | 0.91 | 0.944 | 0.941 | <0.001 |
| | | Dormancy | -2.34 | 1.13 | 0.93 | 0.924 | <0.001 |
| Brookings | Grassland | MIC-TEM | 3.05 | 0.71 | 0.84 | 0.83 | <0.001 |
| | | Dormancy | 0.17 | 0.95 | 0.90 | 0.898 | <0.001 |
| Atqasuk | Wet tundra | MIC-TEM | 7.22 | 1.85 | 0.71 | 0.70 | <0.001 |
| | | Dormancy | 0.19 | 0.82 | 0.67 | 0.66 | <0.001 |

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939 **Table 6. Model validation statistics for Dormancy model and MIC-TEM at six sites with $R_H$ data**
940

| Site ID | Vegetation type | Models | Intercept | Slope | R-square | Adjusted R-square | RMSE | p-value |
|---|---|---|---|---|---|---|---|---|
| US-EML | Alpine tundra | MIC-TEM | 2.90 | 0.91 | 0.79 | 0.78 | 3.55 | <0.001 |
| | | Dormancy | 1.81 | 0.74 | 0.87 | 0.85 | 2.69 | <0.001 |
| CA-SJ2 | Boreal forest | MIC-TEM | 7.59 | 1.12 | 0.84 | 0.83 | 9.8 | <0.001 |
| | | Dormancy | 2.6 | 0.74 | 0.86 | 0.85 | 3.97 | <0.001 |
| US-Ho2 | Temperate coniferous forest | MIC-TEM | 4.07 | 0.89 | 0.86 | 0.84 | 12.39 | <0.001 |
| | | Dormancy | 6.59 | 0.71 | 0.91 | 0.89 | 11.83 | <0.001 |
| US-UMB | Temperate deciduous forest | MIC-TEM | -4.73 | 1.32 | 0.81 | 0.8 | 20.05 | <0.001 |
| | | Dormancy | 13.6 | 0.67 | 0.85 | 0.84 | 12.94 | <0.001 |
| US-Ro4 | Grassland | MIC-TEM | 9.34 | 0.87 | 0.81 | 0.79 | 11.25 | <0.001 |
| | | Dormancy | 4.81 | 0.65 | 0.86 | 0.84 | 9.21 | <0.001 |
| RU-Che | Wet tundra | MIC-TEM | 2.5 | 0.67 | 0.72 | 0.71 | 6.24 | <0.001 |
| | | Dormancy | 1.96 | 0.77 | 0.81 | 0.79 | 5.95 | <0.001 |