Associate Editor Decision: Reconsider after major revisions (02 Jul 2020) by Jens-Arne Subke
Comments to the Author:
Dear Drs Zha and Zhuang,

Thank you for addressing referees concerns over the manuscript. I have reviewed your changes and have reason to request further changes before I'm able to finally accept this manuscript for publication. This addresses mostly the writing and framing of your science, not further analyses, and I hope that you will be able to perform revisions relatively swiftly.

A key concern is your framing of the study as addressing "Arctic" soils. Your study does not focus on Arctic ecosystems. Latitudes north of 45° include mostly temperate and boreal regions, with the Arctic making up a small fraction only (possibly 10 - 15%, depending on definition). Your reference sites (Table 2) include only two actual Arctic sites. It's not clear to me why you present this as a study addressing Arctic C storage; the model addresses microbial dormancy in general, why is it framed specifically around the Arctic context? Please remove or revise sections that present this study as specifically Arctic-focused (e.g. lines 48/49 and 58 in the Abstract, and lines 114-120, and 126/127). Similarly, "high latitudes" would normally be understood to be > 60°, most commonly in fact > 66° (i.e. pole-ward from Arctic Circle). Please remove reference to "high latitude" where you include areas north of 45°N.

Response: Thanks for the concern. In this revision, we use "northern temperate and boreal" instead of "Arctic" or "High Latitudes" throughout the text. Consequently, the title is changed to "*Microbial dormancy and its impacts on northern temperate and boreal terrestrial ecosystem carbon budget*".

This aside, I also think that you have to make it much clearer that this presents the potential of including microbial dormancy in models to potential outcomes, rather than providing realistic scaled numbers for northern regions. A very substantial part of land surface north of 45° is agricultural, which is entirely absent from your data sets used for parameterisation. Please make it absolutely clear that this is an exercise of using models to estimate potential regional C dynamics, but that this applies to natural ecosystems only, so it is a partial C balance for the region. I see no problem with this being a study to demonstrate the role of dormancy in principle, but want to avoid these numbers being used to claim actual source or sink functions of ecosystems in the region. Your objectives stated at the end of the introduction should make this very clear.

Response: Thanks for the suggestion. In this revision, we made clearer that the study was focusing on natural ecosystems only and revised the text accordingly.

Please note the detailed points below when you re-draft the manuscript. I hope that this will make the manuscript more focused and comprehensive.

141: Again, why the Arctic specifically? Your modeling approach is generic to any soil microbial dormancy, or not?

Response: Made correction.

166/184: Equations 1 and 3 are identical, but use different parameters. Please keep consistent (and possibly omit one of them, as they are repetitive).

Response: Deleted Eqn. 1 and re-ordered equations.

247-248: Please refer to biomes covered as "northern ecosystems ranging from temperate to Arctic", or similar. Not "high latitude".

Response: Changed.

260: This is misleading. Four of the validation sites are the same as those used for parameterisation. This has to be absolutely clear.

Response: Indeed a few sites are overlapped between Tables 2 and 3 to be able to cover all ecosystem types in this study for both parameterization and validation. However, for those overlapped sites, we used the data for different years for parameterization and validation. Specifically, the overlapped sites are Howland Forest, UCI-1964, Atqasuk, and Ivotuk. At Howland Forest site, we used the data during 01/2003-12/2003 for validation, the data during 01/2004-12/2004 for parameterization. At UCI-1964 site, the data during 01/2004-10/2005 are used for parameterization, but the data during 01/2002-12/2003 are for validation. At Atqasuk site, the data of 01/2003-12/2004 are for model validation, the data of 01/2005-12/2006 are for model parameterization. At Ivotuk site, the data during 01/2004-12/2004 are for parameterization, but the data of 01/2005-12/2005 are for validation. To make this clear, we added a sentence to clarify this in main text "*Four of these six sites were also used for parameterization (Table 2). However, we used the data of different observation periods for model validation for those overlapped sites.* "

337-339: This sentence goes beyond data presentation. Please move it to the discussion, where this interpretation is more appropriate.

Response: Deleted the sentence in these lines, but moved the citations to Discussion section to support the argument of soil decomposition, N availability and NPP differences.

352 – 360: Also here, avoid lengthy explanations in the results section. Abbreviate the entire section to: "Without considering dormancy, MIC-TEM estimates more active microbial biomass, hence overestimating both RH, and NPP (due to higher simulated N mineralization and uptake by plants), but resulting in lower NEP than that calculated by MIC-TEM-dormancy."

Response: Thanks for the suggestion. We used your more concise version in this revision.

361-373: This section is not very well phrased. Please present the key findings of the seasonal dynamics without detailed descriptions of the shape of graphs. Also no need to reference the fact that moisture and temperature are higher in summer.

Response: Following your suggestion, in this revision, we made the paragraph more concise to "*Temporally, both models projected higher NPP and RH in summer than in winter (Figures 8a and 8b) due to higher soil temperature and moisture (McGuire et al., 1992). Setting the RH projection from MIC-TEM as a baseline, MIC-TEM-dormancy projected 33% less RH in summer (May to September), and 30% more in winter (other months) (Figure 8b), indicating that without dormancy, model tends to estimate lower soil respiration due to ignorance of dormant respiration in winter, but higher soil respiration due to higher active biomass in summer. NEP seasonality estimated with two models are close to each other (Figure 8c), but the dormancy model projected slightly higher NEP in summer.*"

397-398: Delete last sentence (again, this should be picked up in the discussion).

Response: We removed this sentence.

399-400: Delete first sentence, and add "in the 2090s" after "scenarios" in the following sentence. Note that it is 2090s, not "2990s" as stated in line 399.

Response: Thanks. We corrected the error.

410, 413 and 415: Replace "predicted" by "predicts".

Response: Changed.

418 – 426: This should be deleted as it has been covered in the introduction. Focus on key findings of your study in the discussion.

Response: Following your suggestion, we deleted these sentences.

Figure 3: The figure caption states that you show parameter ranges for all six sites, but on three are shown. Text in the Results section also suggests that data are shown for all six sites.

Response: We made these consistent in this revision.

Microbial dormancy and its impacts on northern temperate and boreal ~~Arctic~~ terrestrial ecosystem carbon budget

Junrong Zha and Qianlai Zhuang

Department of Earth, Atmospheric, and Planetary Sciences and Department of Agronomy,
Purdue University, West Lafayette, IN 47907 USA

Submitted to: *Biogeoscience*

Correspondence to: qzhuang@purdue.edu

Abstract

A large amount of soil carbon in ~~the~~ northern temperate and boreal~~Arctic terrestrial ecosystem~~ regions 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 northern temperate and boreal natural terrestrial ecosystems. ~~the Arctic.~~

1. Introduction

The land ecosystems in northern temperate and boreal regions ~~high latitudes~~ (>45 ºN) 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 represent decomposition in ways that include important microbial processes that were previously ignored (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 (Wieder et al., 2015), 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, likely below 50%, metabolically active 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 use total rather than active microbial biomass as an indicator of microbial activities (Wieder et al., 2015), which could bias the estimates of soil decomposition and ecosystem carbon budget (Hagerty et al., 2014; He et al., 2015). Especially, the northern temperate and boreal ~~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). Furthermore, these ecosystems ~~Arctic~~ haves experienced a marked seasonality of active and dormant microbial cycles and the above-global-average warming, which might have increased the proportion of active microbes in soils (He et al., 2015). Thus, incorporating dormancy effects will improve model realism to provide a better projection of the northern temperate and boreal terrestrial ecosystem ~~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 northern temperate and boreal ~~Arctic~~ terrestrial ecosystems (north 45 °N above). By comparing the results of MIC-TEM-dormancy and MIC-TEM, we can show that incorporating microbial dormancy may produce a much different prediction in historical and future carbon budget.

2. Methods

2.1 Overview

Due to the importance of microbial dormancy, some recent work has been done to consider the metabolic activation and deactivation of microbes in soil and its effects on soil carbon (C) dynamics and climate feedbacks. For example, Wang et al. (2015) has incorporated transformation processes between active and dormant states to develop two versions of MEND, that is, MEND with and without dormancy. The two versions of the model have been applied to quantify the carbon decomposition in laboratory incubations of four soils. Salazar et al. (2018) have also taken microbial dormancy into account to compare their predictions of microbial biomass and soil heterotrophic respiration (R_H) under simulated cycles of stressful (dryness) and favorable (wet pulses) conditions. Our study extends those modeling studies to the northern temperate and boreal terrestrial ecosystems ~~whole Arctic region~~ by developing a more detailed biogeochemistry model considering the dormancy impacts. Below, we first 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, we discuss how parameterization and validation of MIC-TEM-dormancy model were conducted using observed net ecosystem exchange data, and heterotrophic respiration data at representative sites. Third, we presented how the model was applied to natural ecosystems in the region ~~northern high latitudes~~ (above 45 °N) for the 20th and 21st centuries and discussed the dormancy effects on their regional carbon budget.

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., 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 northern temperate and boreal terrestrial ecosystems~~whole northern high-latitudes 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 (Figure 1), which was ignored in MIC-TEM.

In previous MIC-TEM, heterotrophic respiration (R_H) is simply calculated as the product of ~~:~~

~~R_H=ASSIM × (1-CUE) (1)~~

~~Where~~ ASSIM and CUE, which are ~~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 MIC-TEM-dormancy, the soil heterotrophic respiration R_H is revised to include ~~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):

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

(1~~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 β is the ratio of dormant maintenance rate to active maintenance rate. Thus, βm_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).

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

$$CO_2 = ASSIM \times (1-Y_g)$$

(2~~3~~)

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

$$\mathrm{ASSIM} = \frac{1}{Y_g}\,\frac{\Phi}{\alpha}\,m_R\,Q_{10enz}^{\frac{temp-15}{10}}\;\mathrm{Ba}\,\left(\frac{CN_{soil}}{CN_{mic}}\right)^{0.6}$$ (3~~4~~)

Here parameter α is maintenance weight (h^{-1}), CN_{soil} and CN_{mic} denotes the C:N ratios of soil and that of microbial biomass. Besides, Φ is the substrate saturation level and defined as in He et al. (2015) and Wang et al. (2014):

$$\Phi = \frac{S}{K_S+S}$$ (4~~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):

$$S = \mathrm{Soluble\ C} \times D_{liq} \times \theta^3$$ (5~~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:

$$D_{liq} = 1/(1-BD/PD)^3$$ (~~7~~6)

Where BD is the bulk density and PD is the soil particle density. θ is the volumetric soil moisture. Different from MIC-TEM, the transitions between active and dormant microbial biomass are included in MIC-TEM-dormancy.

$$B_{a\to d} = (1-\Phi)m_R Q_{10mic}^{\frac{temp-15}{10}}\,B_a$$ (7~~8~~)

$$B_{d\to a} = \Phi m_R Q_{10mic}^{\frac{temp-15}{10}}\,B_d$$ (8~~9~~)

Where $B_{a\rightarrow d}$ and $B_{d\rightarrow a}$ denote the transition from the active to dormant microbe and from the dormant to active microbe, respectively (He et al., 2015; Wang et al., 2014). Thus, dormancy rate is affected by active and dormant biomass, soil temperature (temp) and soil moisture (θ in Φ).

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

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

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):

$$DEATH = r_{death} \times Ba$$ (10~~1~~)

$$EPROD = r_{EnzProd} \times Ba$$ (11~~2~~)

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):

$$\frac{dB_d}{dt} = -\beta m_R Q_{10mic}^{\frac{temp-15}{10}} B_d + B_{a\rightarrow d} - B_{d\rightarrow a}$$ (12~~3~~)

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

$$\frac{d\ Soluble\ C}{dt} = DECAY - ASSIM + ELOSS + DEATH$$ (13~~4~~)

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):

$$DECAY = V_{max} \times Q_{10enz}^{\frac{temp-15}{10}} \times ENZ \times \frac{SOC}{Km_{uptake} + SOC} \times (120 - CN_{soil})$$ (14~~5~~)

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:

$$\mathrm{ELOSS} = r_{enzloss} \times \mathrm{ENZ} \qquad (15\cancel{6})$$

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

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

$$\frac{dSOC}{dt} = \mathrm{Litterfall} - \mathrm{DECAY} \qquad (16\cancel{7})$$

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

Last, enzyme pool (ENZ) is modeled as:

$$\frac{dENZ}{dt} = \mathrm{EPROD} - \mathrm{ELOSS} \qquad (17\cancel{8})$$

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 much less. 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 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 temperate and boreal regions ~~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:

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

Where $\mathrm{NEP}_{\mathrm{obs},i}$ and $\mathrm{NEP}_{\mathrm{sim},i}$ 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). Four of these six sites were also used for parameterization (Table 2). However, we used the data of different observation periods for model validation for those overlapped sites. 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 available RH data, we could not conduct a regional validation for all pixels in northern temperate and boreal regions~~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 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 20th 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). We also used gridded data of soil texture (Zhuang et al., 2003), elevation (Zhuang et al., 2015), and potential natural vegetation (Melillo et al., 1993) from literatures. 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.

2.5 Parameter equifinality effects

Our previous studies using TEM has demonstrated that equifinality derived from site-level parameterization will affect the uncertainty in the estimation of regional carbon dynamics (Tang and Zhuang, 2008, 2009). Here equifinality refers to that a number of sets of parameters result in model simulations that all match the data similarly well. To quantify this effect on our simulation uncertainty, we conducted ensemble regional simulations with 50 sets of parameters for both historical and future studies. The 50 sets of parameters were obtained according to the method in Tang and Zhuang (2008).

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, growth yield was 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 higher in tundra types than in forests. From the plot for parameter beta, the ratio of dormant maintenance rate to specific maintenance rate for active biomass in tundra types is lower than that in forest types. 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 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, dormancy model performs better for alpine tundra, temperate coniferous forest, and grassland. For other sites, both models show similar performance (Table 5). Besides, a set of monthly soil respiration data were selected to evaluate the estimated R_H. The comparisons between monthly observed R_H and simulated R_H from two contrasting models were conducted (Figure 5). MIC-TEM-dormancy has higher R^2 and lower root mean square error (RMSE) (Table 6). Sixty-one sites with average annual R_H in northern temperate and boreal regions~~high-latitude regions~~ 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 R_H by considering microbial dormancy. ~~This difference in R_H further affects soil available nitrogen dynamics, influencing nitrogen uptake by plants, the rate of photosynthesis and NPP (Zhuang et al., 2015; Zha et al., 2018; Thullner et al., 2005).~~

3.2 Regional carbon dynamics during the 20th century

Regional extrapolation with both models estimated a regional terrestrial ecosystem carbon sink but with different magnitudes (Figure 7c). 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 20th 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 (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 (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 since NEP is calculated as the difference between NPP and R_H. Without considering dormancy, MIC-TEM estimates more active microbial biomass, hence overestimating both R_H and NPP (due to higher simulated N mineralization and uptake by plants), but resulting in lower NEP than that calculated by MIC-TEM-dormancy.~~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 affect organic matter 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 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). Setting the R_H projection from MIC-TEM as a baseline, MIC-TEM-dormancy ~~averagely~~ projected 33% less R_H in summer (May to September), and 30% more in winter (other months) (Figure 8b), ~~which~~ indicating ~~es~~ 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). Though R_H and NPP show the similar seasonal patterns, NEP can still show different pattern.~~ NEP s~~Here s~~easonality estimated ~~cycles of NEP~~ with two models are close to each other (Figure 8c), but the dormancy model projected slightly higher NEP in summer.

3.3 Regional carbon dynamics during the 21st century

Under the RCP 8.5 scenario, both models estimated the regional natural terrestrial ecosystems act~~s~~ as a carbon sink (Figure 9). The MIC-TEM-dormancy predicted a C accumulation of 129.9 Pg by the end of this century. with the interannual standard deviation of 0.13 Pg C yr^{-1}, whereas MIC-TEM estimates a C accumulation of 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, with less interannual variation (Figure 9). Under this scenario, 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 21st century. In contrast, MIC-TEM-dormancy projected the region acts as a carbon sink of 123.6 Pg C with an 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). Moreover, simulations under the 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).~~

~~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 in the 2090s (Figure 10). NPP is the same in winter with or without dormancy, and in the late summer is higher than that without dormancy, especially in the RCP 8.5 scenario. 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 lower NEP from January to April compared 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).

3.4 Regional uncertainty considering equifinality effects during 20th and 21st centuries

The ensemble simulations for the 20th century is shown in Figure 11. Given the uncertainty in parameters, MIC-TEM-dormancy predicts~~ed~~ that the regional cumulative carbon ranges from a carbon loss of 28.2 Pg to a carbon sink of 362.1 Pg by different ensemble members, with a mean of 71.2±54.8 Pg (Figure 11). For the 21st century, MIC-TEM-dormancy predicts~~ed~~ that the region acts from a carbon source of 49.3 Pg C to a carbon sink of 296.5 Pg C, with a mean of 112.7±116.5 Pg under the RCP 2.6 scenario (Figure 12). Under the RCP 8.5 scenario, MIC-TEM-dormancy predicts~~ed~~ that the region acts from a carbon source of 27.1 Pg C to a carbon sink of 401.1 Pg C, with a mean of 143.1±162.5 Pg (Figure 12).

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 stored in northern high latitudes (Tarnocai et al., 2009). Besides, the magnitude of the warming in these regions is larger, almost twice, that of the global average (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 regional natural terrestrial ecosystems acted ~~was~~ as 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 21st 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. Estimations based on models without dormancy could fit observations of R_H as well as estimations with dormancy, but at the cost of underestimating microbial biomass (Wang et al., 2014). Differences in predicted R_H with and without dormancy increase with temperature and with the length of the dry periods between wetting events (Salazar et al., 2018). 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, many 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). 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 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; ~~).~~ ~~This difference in R_H further affects soil available nitrogen dynamics, influencing nitrogen uptake by plants, the rate of photosynthesis and NPP (~~Zhuang et al., 2015; Zha & Zhuang~~et al.~~, 2018; Thullner et al., 2005).

Therefore, NPP will be higher due to the N enrichment from higher R_H. However, how NEP will change is still unclear. Our estimates of the northern extratropical NEP in the 1980s (1.61 Pg C yr^{-1} with MIC-TEM-dormancy and 0.84 Pg C yr^{-1} with MIC-TEM) are within ranges (0.6 to 2.3 PgC yr^{-1}) reported in the literature for northern regions (Schimel et al.,2001). Moreover, our predicted time trajectory of NEP in the 21st century under the RCP 2.6 scenario 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. Although our dormancy model can project reasonable carbon fluxes and indicate the importance of incorporating microbial dormancy when compared with 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). 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). Moreover, microbial acclimation, a mechanism of adaption to a new temperature regime, is another important trait to affect soil decomposition. Recent studies have found that the warming-induced elevated respiration of the microbial community could decrease over time because of acclimation (Melillo et al. 1993; Todd-Brown et al., 2011). This mechanism shall be factored into future soil decomposition analysis.

Except for model limitations mentioned above, 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 temperate and boreal regions~~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.

While our analysis suggests it is important to incorporate microbial dormancy dynamics into a process-based biogeochemistry model to more adequately simulate carbon dynamics in northern temperate and boreal regions~~high latitudes~~, we do confront modeling dilemmas. First, our process-based models have a relatively large number of parameters, which unavoidably creates the "equifinality" problem as recognized in our previous studies for the model (e.g., Tang and Zhuang, 2008, 2009). To alleviate this problem in this analysis, we have conducted parameter ensemble simulations at both site and regional levels and presented our results with uncertainties, which could be a standard approach for process-based complex biogeochemistry modeling analyses. Second, incorporating more ecosystem processes increases the number of parameters in our model, inducing even larger uncertainties for both site level and regional simulations. On the one hand, the more complex model to a certain degree helps capture observations, on the other hand, the model uncertainty has not been constrained or even enlarged. We highlight the need to further investigate this trade-off within the modeling research community.

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 storage in northern temperate and boreal natural terrestrial ecosystems under changing climate conditions. Regional simulations using MIC-TEM-dormancy indicated that, over the 20th century, the region is a carbon sink of 166.8 ± 97.7 Pg. This sink could decrease to 175.9 ± 105.4 Pg under the RCP 8.5 scenario or 125.4 ± 85.5 Pg under the RCP 2.6 scenario during the 21st 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 of ~~in~~ natural terrestrial ecosystems in northern temperate and boreal regions.~~high latitudes.~~

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Materials & Correspondence. Correspondence and material requests should be addressed to qzhuang@purdue.edu.

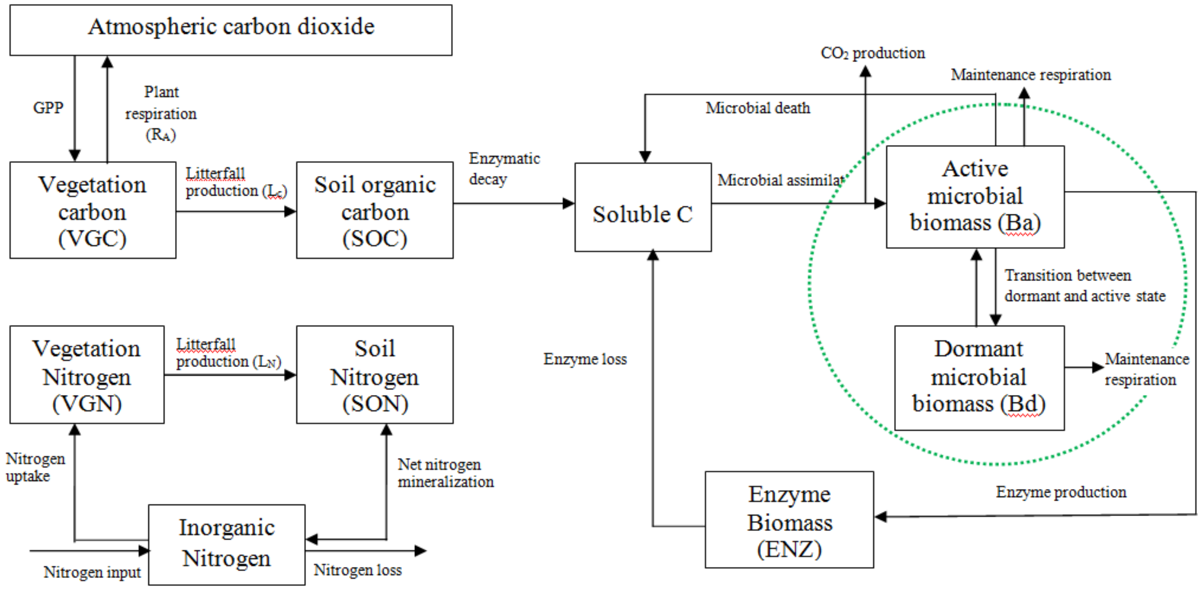


Figure 1. Framework of the dormancy model: microbial biomass is split into two parts, active microbial biomass and dormant microbial biomass (shown in the green dashed circle). Maintenance respiration from these two parts, and the CO_2 production through microbial assimilation contributes to heterotrophic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

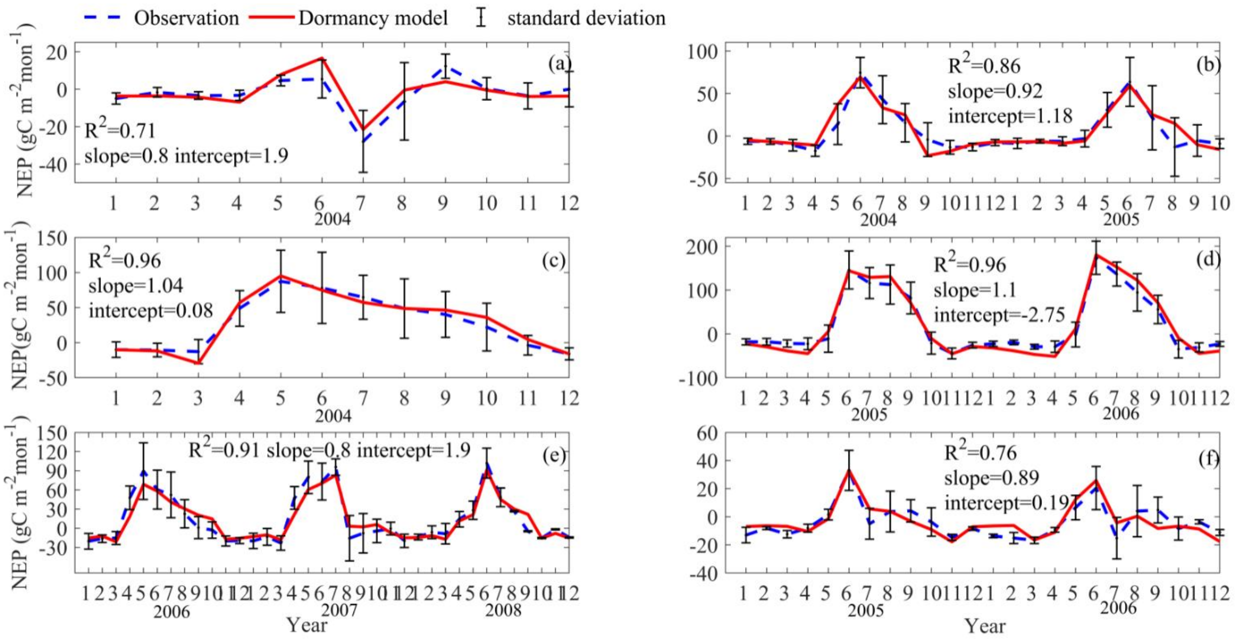


Figure 2. Comparison between observed and simulated NEP (gC $m^{-2}mon^{-1}$) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Univ. of Mich. Biological Station (Temperate deciduous forest), (e) KUOM Turfgrass Field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

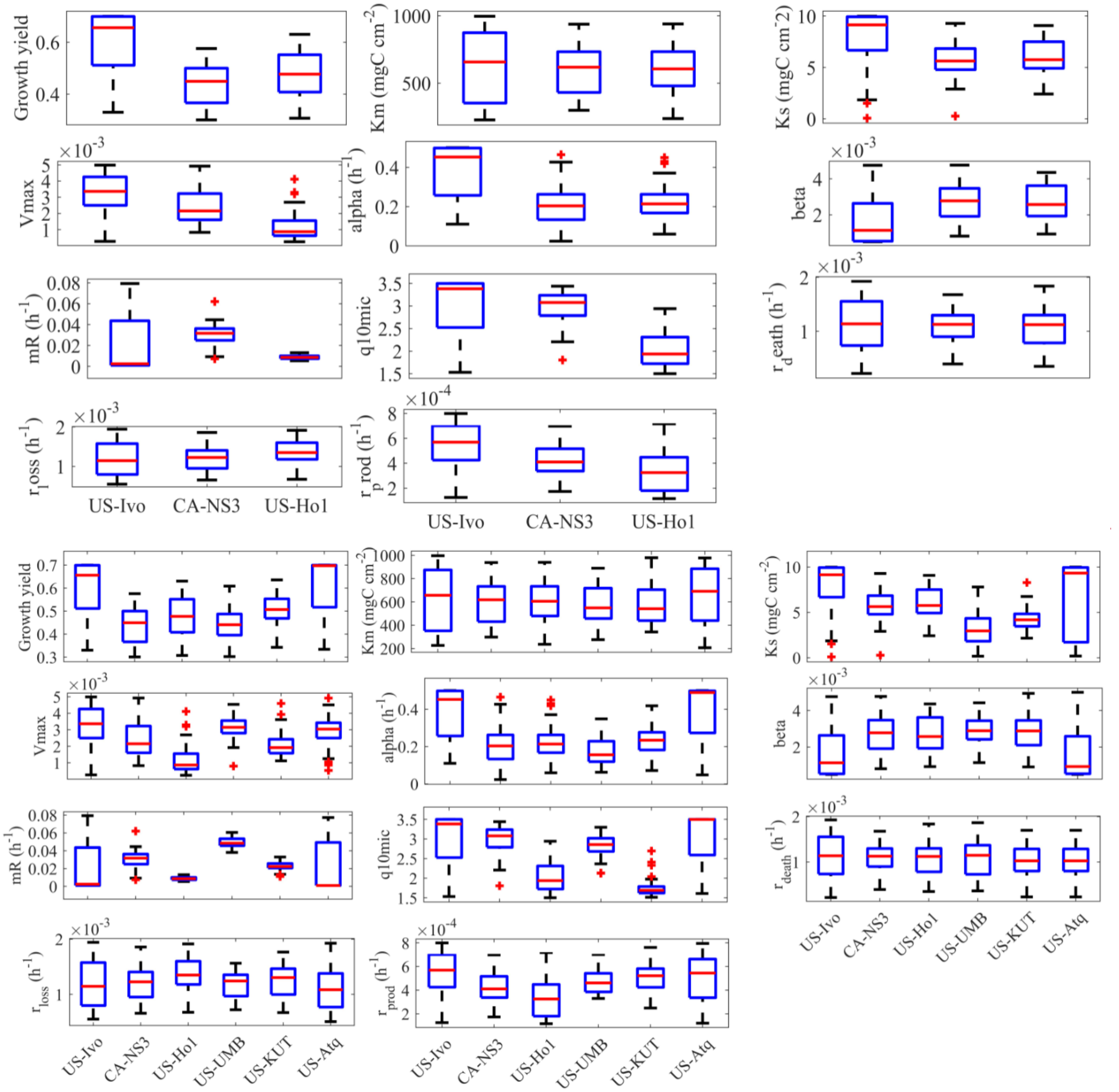


Figure 3. Boxplot of parameter posterior distribution that are obtained after ensemble inverse modeling for MIC-TEM-dormancy all six sites: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-1964 burn site (boreal forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB: Univ. of Mich. Biological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

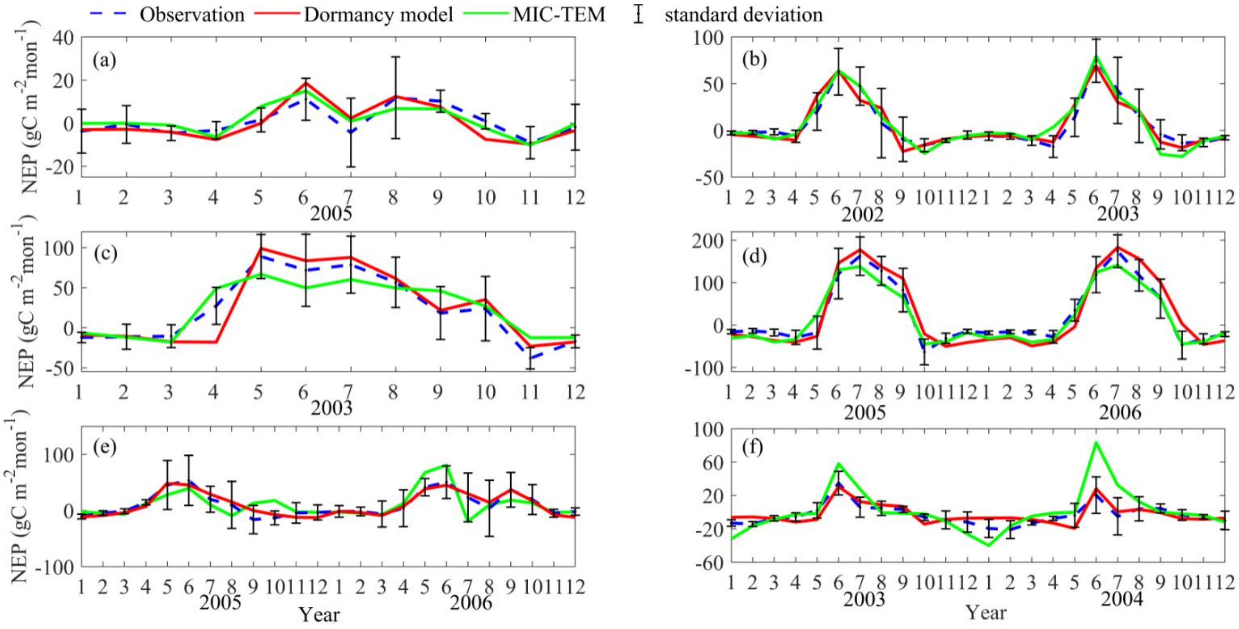


Figure 4. Comparison between observed and simulated NEP (gC m^{-2}mon^{-1}) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Bartlett Experimental Forest (Temperate deciduous forest), (e) Brookings (Grassland),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

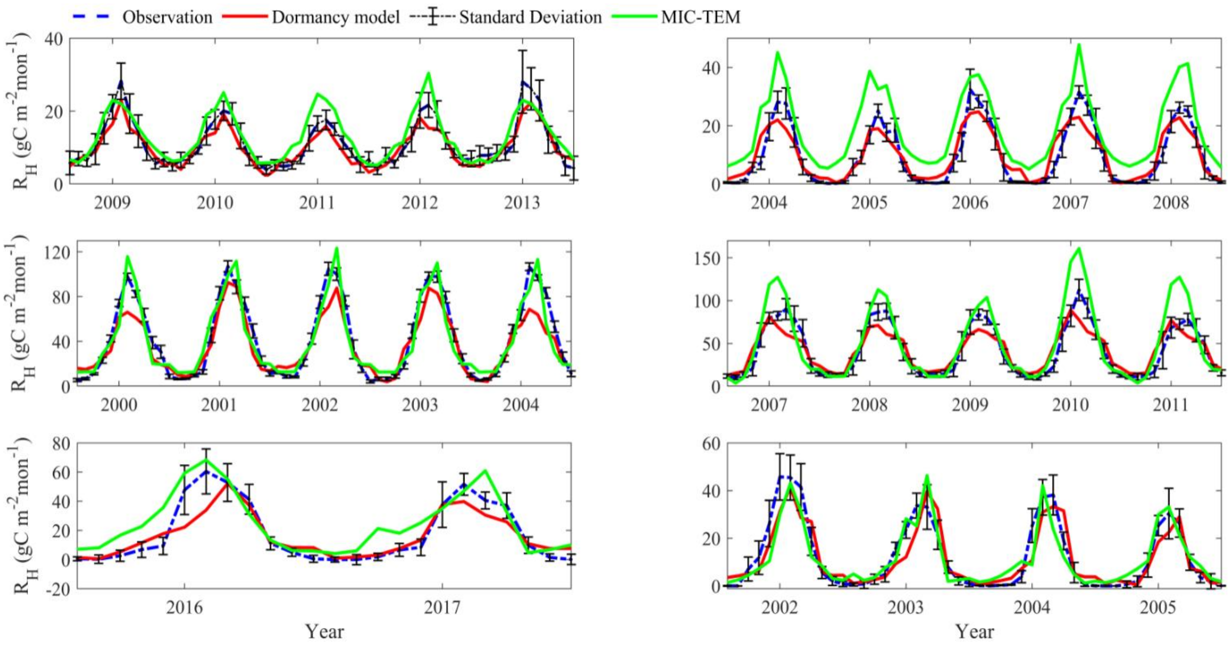


Figure 5. Comparison between observed and simulated R_H (gC $m^{-2}mon^{-1}$) at: (a) US-EML (alpine tundra), (b) CA-SJ2 (boreal forest), (c) US-Ho2 (temperate coniferous forest), (d) US-UMB (Temperate deciduous forest), (e) US-Ro4 (Grassland), and (f) RU-Che (Wet tundra). Note: scales are different.

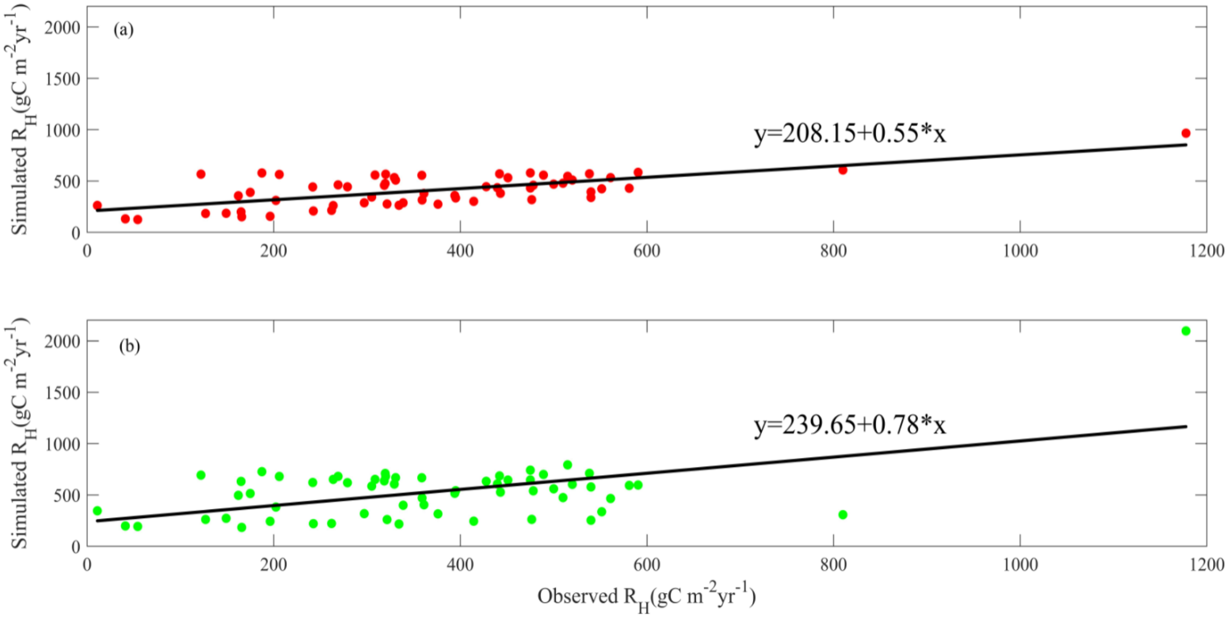


Figure 6. Linear regression between simulated and observed annual R_H (gC m^{-2}yr^{-1}) for: (a) MIC-TEM-dormancy, and (b) MIC-TEM.

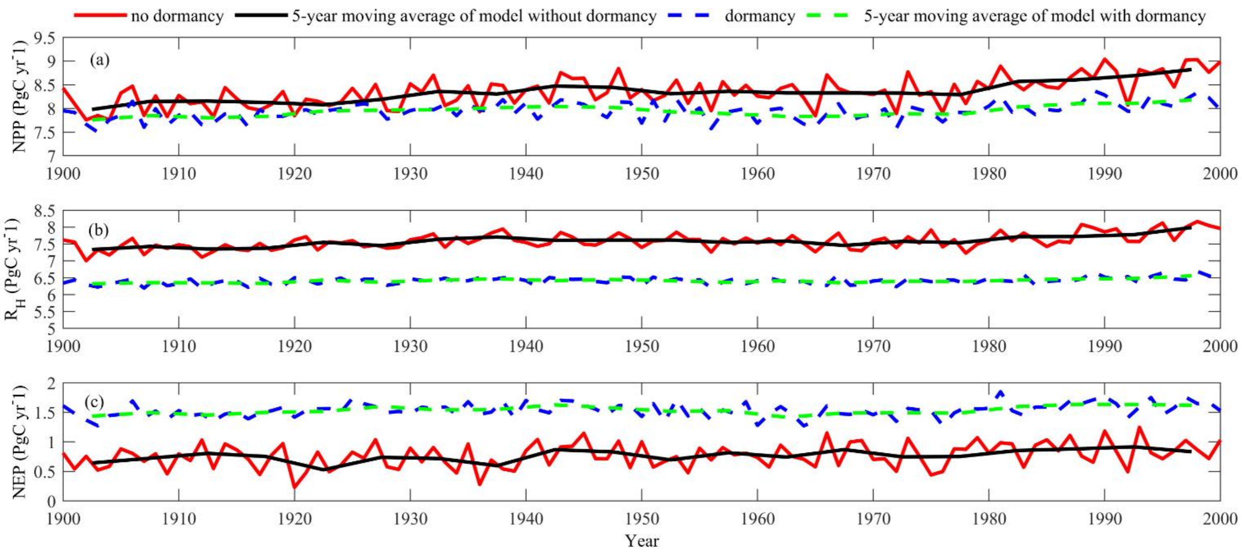


Figure 7. Simulated annual net primary production (NPP, top panel), heterotrophic respiration (R_H, center panel) and net ecosystem production (NEP, bottom panel) during the 20th century by dormancy model and MIC-TEM, respectively.

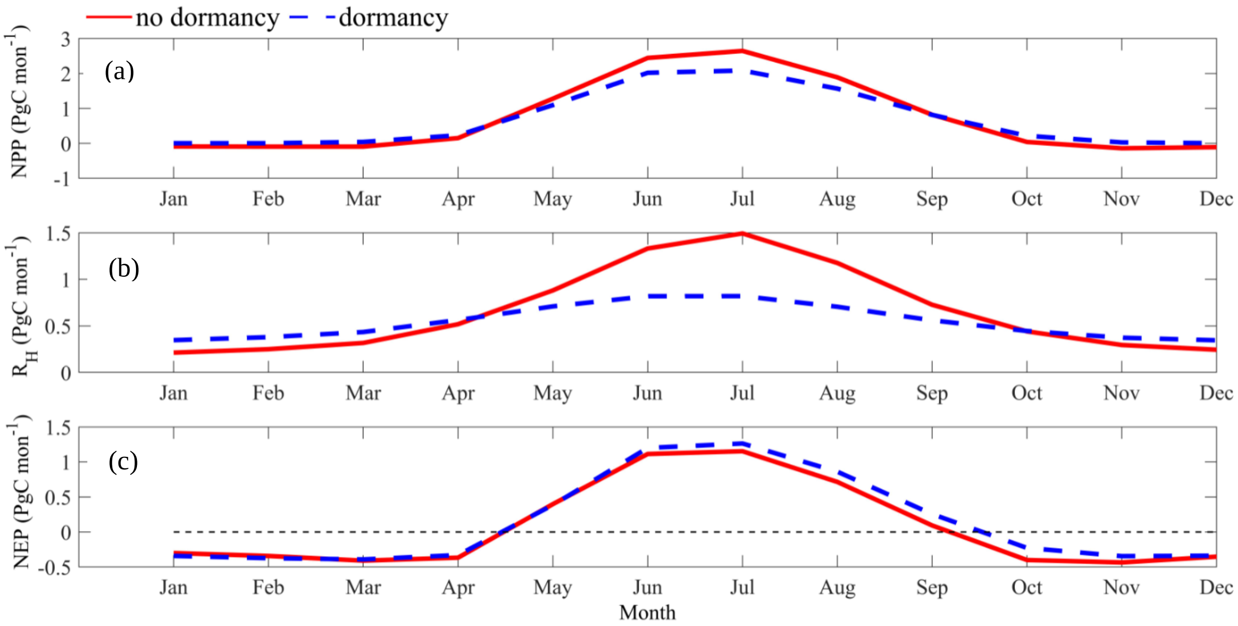


Figure 8. Regional annual seasonal pattern of simulated (a) net primary production (NPP, top panel), (b) heterotrophic respiration (R_H, center panel) and (c) net ecosystem production (NEP, bottom panel) during the 1990s from dormancy model and MIC-TEM. The region is all land areas north of 45 °N.

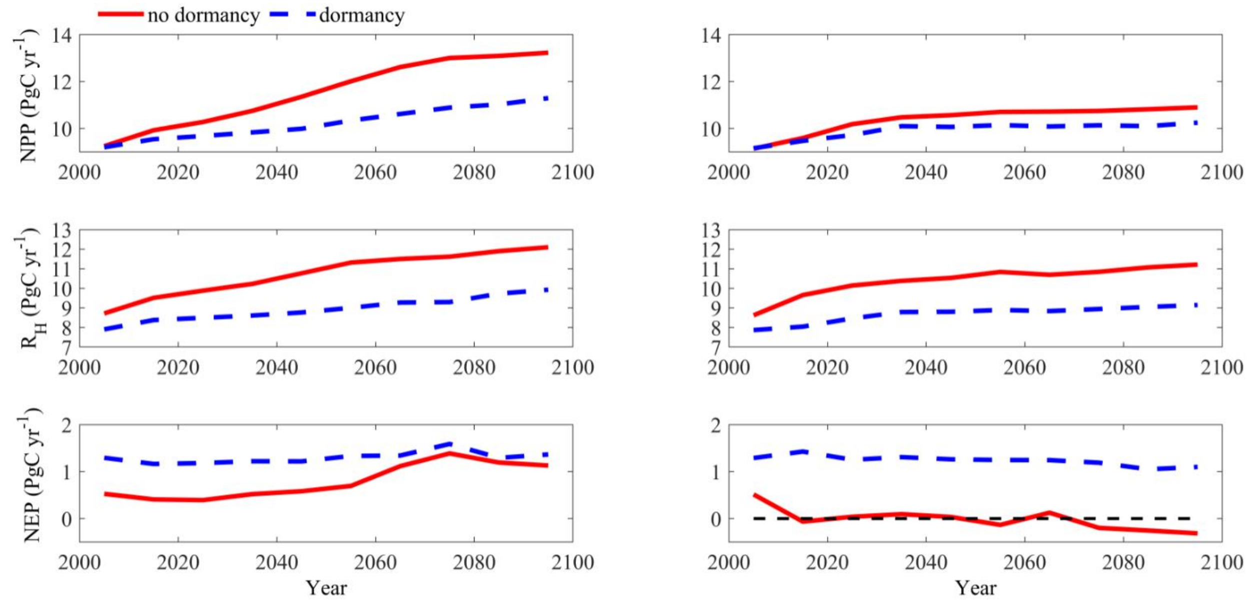
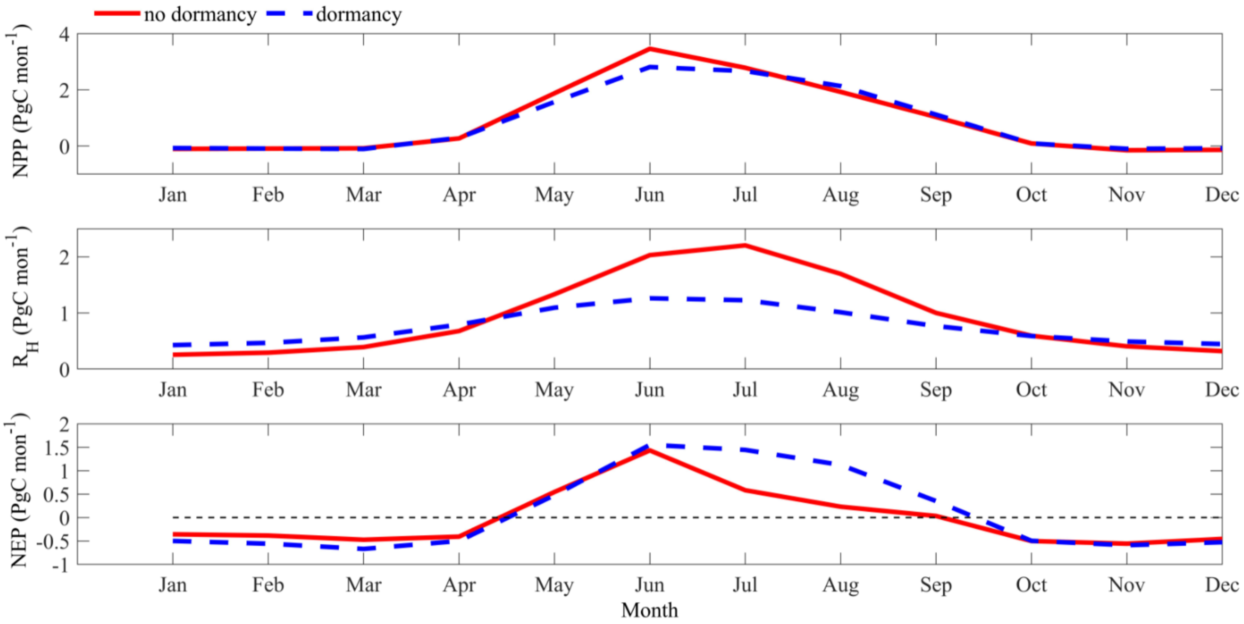


Figure 9. Predicted changes in carbon fluxes: (i) NPP, (ii) R_H, and (iii) NEP for all land areas north of 45 ºN in response to transient climate change under the RCP 8.5 scenario (left panel) and RCP 2.6 scenario (right panel) with dormancy model and MIC-TEM, respectively. The decadal running mean is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

(a)



(b)

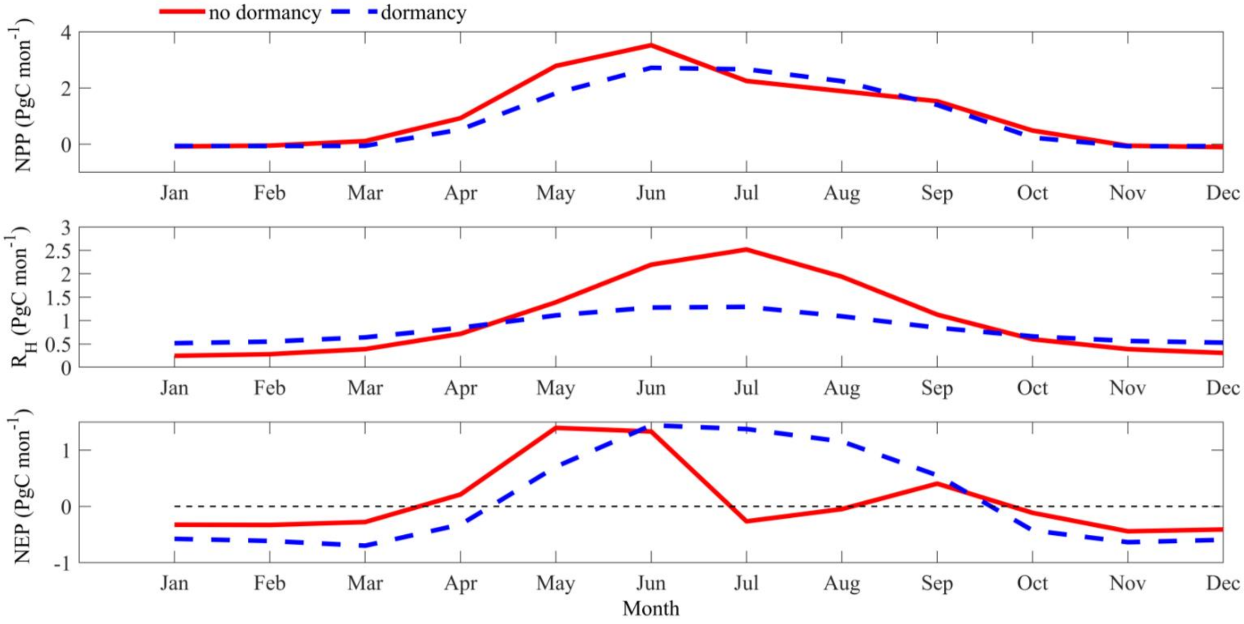


Figure 10. Regional annual seasonal pattern of simulated net primary production (NPP, top panel), heterotrophic respiration (R_H, center panel) and net ecosystem production (NEP, bottom panel) during the 2090s from dormancy model and MIC-TEM under: (a) RCP 2.6 scenario (top panel) and (b) RCP 8.5 scenario (bottom panel). The region is all land areas north of 45 ºN.

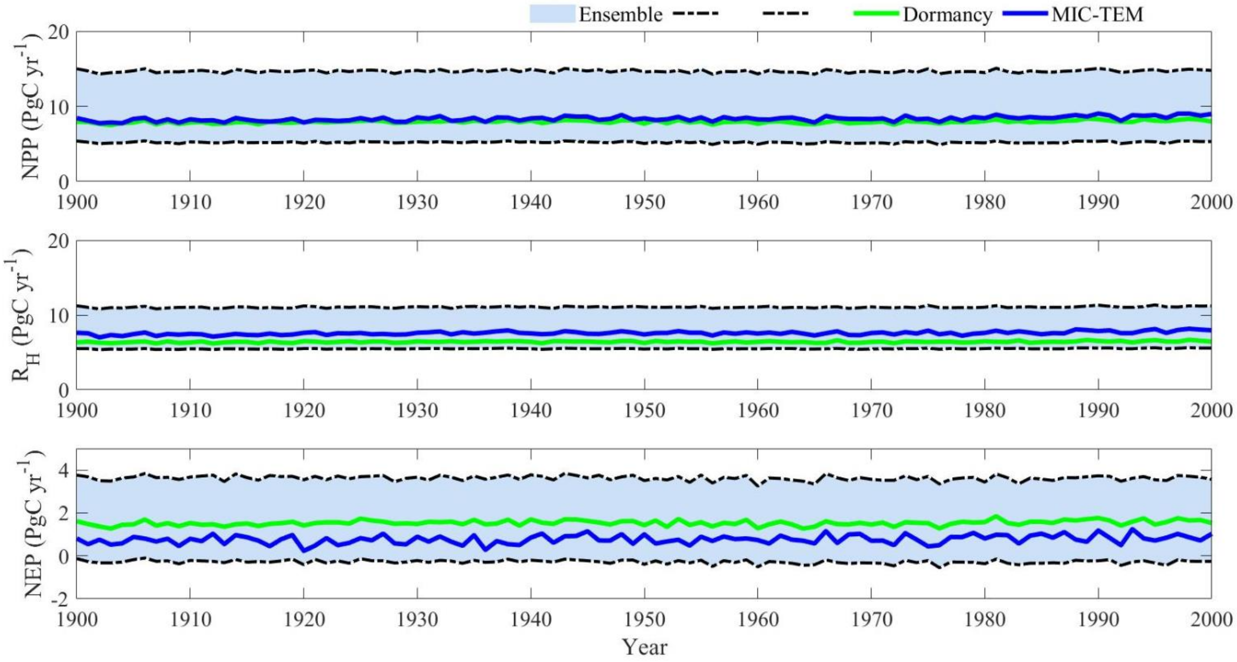


Figure 11. Simulated annual net primary production (NPP, top panel), heterotrophic respiration (R_H, center panel) and net ecosystem production (NEP, bottom panel) by MIC-TEM-dormancy with ensemble of parameters.

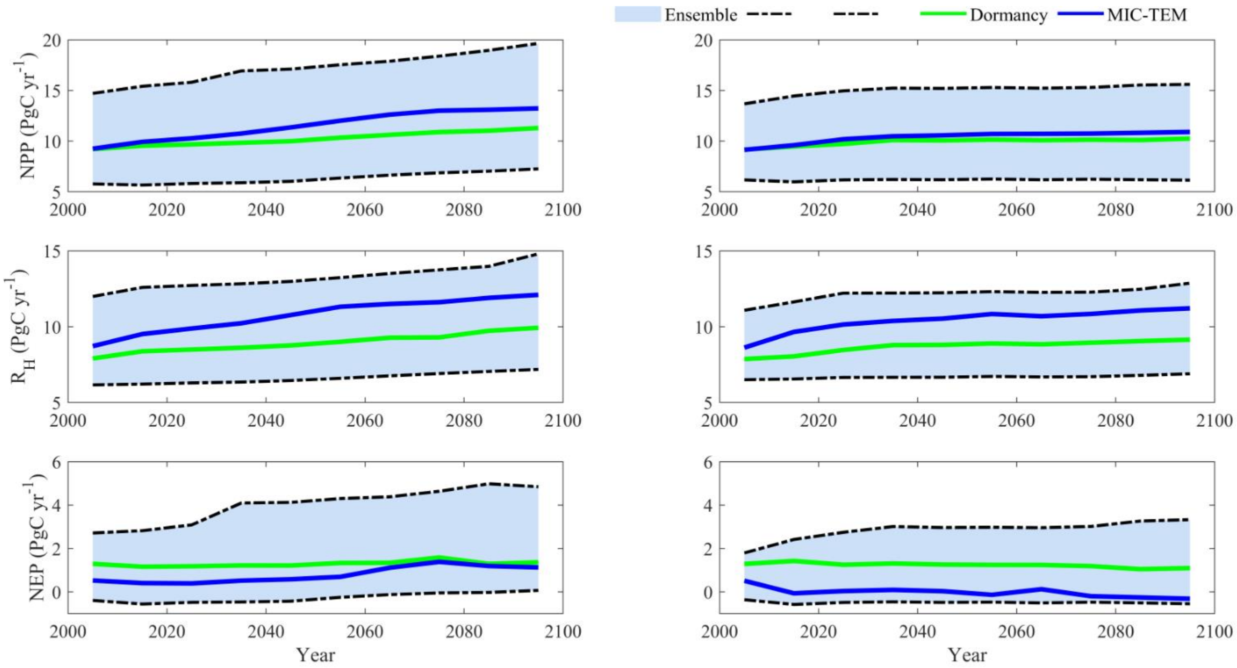


Figure 12. Simulated annual net primary production (NPP, top panel), heterotrophic respiration (R_H, center panel) and net ecosystem production (NEP, bottom panel) under RCP 8.5 scenario (left panel) and RCP 2.6 scenario (right panel) by MIC-TEM-dormancy with ensemble of parameters. The decadal running mean is applied. The grey area represents the upper and lower bounds of simulations.

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)
α	-	the ratio of m_R to the sum of maximum specific growth rate	[0.01, 0.5]	Wang et al. (2014)
β	-	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)

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)

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

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)

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)

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

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

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