General comments

This study addresses a critical gap in the Terrestrial Ecosystem Model by including mosses as a plant type at northern latitudes (>45 degrees). The authors do a good job of establishing the key role of moss in these ecosystems and show an improvement in model-data assimilation from the previous iteration of the model through the inclusion of mosses. In general, this is an important contribution to improving these models. However, some non-trivial caveats may have large effects on the future carbon storage potential of high latitude ecosystems, particularly the expected decreases in moss biomass with climate warming.

Specific comments:

1. Throughout the manuscript, I would suggest replacing “higher plants” with a more appropriate terminology, such as “vascular plants”. For a discussion on why (and how) to implement this change, please see McDaniel 2021 in New Phytologist (Title: Bryophytes are not early diverging land plants)

Response: Thanks for the suggestions and comments. In this revision, we replaced all “higher plants” with “vascular plants”.

2. In order to support the claim that this paper quantifies the interaction between vascular plants and mosses as mentioned in the abstract and introduction, I would like to see a more explicit explanation of how that interaction was included within the model.

Response: Thanks for the comments. In TEM_Moss, we have explicitly considered moss effects on soil thermal dynamics, soil water and soil moisture, and nutrient conditions in boreal ecosystems. Mosses compete with vascular plants for water and nutrient (nitrogen) in the modeling system. Three kinds of effects are described below:

1) Moss effects on soil thermal dynamics: In TEM 5.0, a moss plus fibric soil organic layer is considered and specified with respect to thickness through site-level parameterization. Here moss layer thickness was explicitly considered for each pixel.
2) Moss effects on water balance: In TEM 5.0, water balance is modeled as the difference between precipitation, vascular plant evapotranspiration, runoff, and percolation. In TEM_Moss, water loss through moss is considered, and soil water content is thus affected by both vascular plants and mosses. See equations 17 and 18 in the text.
3) Nutrient feedbacks, in TEM 5.0, N balance is modeled without considering moss N uptake. The change rate of soil organic N is modeled as the difference between the vascular plant N uptake and net N mineralization rate. In TEM_Moss, N uptake is modeled as:

$$\mathrm{Nuptake} = \mathrm{Nuptake_v} + \mathrm{Nuptake_m} \quad (16)$$

Thus, the change rate of soil organic N is affected and the N feedbacks to C cycling is affected by considering moss N uptake.

3. In the discussion, the authors say their simulation confirms that that mosses and vascular plants respond similarly to climate change in terms of productivity. He et al. 2016 (Title: Will bryophytes survive in a warming world?) finds an expected divergence between vascular plants

and bryophytes in response to climate change, as do many experimental manipulations (see below). It seems like the authors set up the model to have vascular plants and mosses respond similarly, rather than the model proving that they do? It may also be worth considering the higher CO2 concentration at the moss carpet—is it appropriate to use mean atmospheric CO2 concentration?

Response: Thanks for the comments. While there were a number of studies suggesting that the bryophyte act differently from vascular plants in terms of photosynthesis, nutrient uptake, and carbon allocation, and fundamental plant physiology, the algorithms of these processes of moss are not ready to be implemented in modeling activities. Here we made a number of assumptions in our Method section to model moss productivity and nutrient uptake. To further address your concerns, we added a few sentences to discuss this limitation in Discussion section. Regarding your comments on moss responses to climate change, we added "Future moss dynamics will also impact carbon dynamics in this region. For instance, a long-term warming experiments along natural climatic gradients, ranging from Swedish subarctic birch forest and subarctic/subalpine tundra to Alaskan arctic tussock tundra concluded that both diversity and abundance of mosses are likely to decrease under arctic climate warming (Long et al. 2012). Similarly, total moss cover declined in both heath and mesic meadow under experimental long-term warming (by 1.5–3 °C), driven by general declines in many species (Alatalo et al., 2020). Due to global warming, significant losses in moss diversity are expected in boreal forests and alpine biomes, leading to changes in ecosystem structure and function, nutrient cycling, and carbon balance (He et al., 2015)."

Additionally, we have to acknowledge that our modeling can not reveal moss physiology and associated carbon cycling processes, rather we strive to incorporate the knowledges into modeling to quantify carbon consequences. It is still difficult to quantify the level of CO2 concentration near /inside of mosses clusters so as to have more accurate quantification of CO2 impacts on moss productivity.

4. I think the potentially large decreases in moss biomass expected with warming are a non-trivial concern for future carbon storage expectations found in this model. I would recommend papers such as Elmendorf et al. 2012, Lang et al. 2012, and Alatalo et al. 2020 as sources on changes in moss biomass in response to simulated warming.

Response: Thanks for the comments. We cited these references to discuss the potential changes of moss diversity and abundance and their effects on ecosystem structure and functioning and carbon dynamics. "Future moss dynamics will also impact carbon dynamics in this region. For instance, a long-term warming experiments along natural climatic gradients, ranging from Swedish subarctic birch forest and subarctic/subalpine tundra to Alaskan arctic tussock tundra concluded that both diversity and abundance of mosses are likely to decrease under arctic climate warming (Long et al. 2012). Similarly, total moss cover declined in both heath and mesic meadow under experimental long-term warming (by 1.5–3 °C), driven by general declines in many species (Alatalo et al., 2020). Due to global warming, significant losses in moss diversity are expected in boreal forests and alpine biomes, leading to changes in ecosystem structure and function, nutrient cycling, and carbon balance (He et al., 2015)."

5. Soil uptake is only one pathway for mosses to access N. Studies have shown that they receive nitrogen from associations with nitrogen fixers (see Bay et al 2013 and Berg et al 2013 for examples in various types of host mosses). Mosses can translocate N from within the senescent moss body to incorporate new growth (Aldous 2002). Mosses also acquire nitrogen via deposition. The cited studies (Ayres et al. 2006 and Fritz et al. 2014) show that mosses can acquire nitrogen from soil (a previously unexpected N source due to the lack of roots and vasculature), but in Ayres et al. mosses incorporated more nitrogen via wet deposition.

Response: We recognize the limitation of current understanding of N uptake and its algorithms in our current modeling. While these N uptake pathways are potentially important to moss productivity, the data and knowledges are not sufficient to allow us represent these processes in the model. In this revision, we cited these studies to discuss future efforts to improve moss N uptake representations in modeling. We added this following to Discussion “First, due to the limited understanding of moss photosynthesis (He et al., 2015) and various moss N uptake pathways (e.g., Bay et al 2013; Berg et al 2013), a few important assumptions have been made in our modeling. For instance, we assume that mosses behave similarly to vascular plants regarding photosynthesis and soil N uptake is the only pathway for mosses without considering N uptake through N fixers and atmospheric wet N deposition (Ayres et al. 2006).”

Technical corrections

L22 ""which do not" instead of "without" moss.

Response: Changed.

L27 "nutrient" should be nutrients.

Response: Changed.

L41 “hold” instead of occupy, perhaps?

Response: Changed.

L59 Rephrase for clarity

Response: Rephrased the sentence as “However, the role of boreal forests in carbon sink or source activities has not been clear due to a number of model limitations”.

L69 "nutrient" should be nutrients.

Response: Changed.

L81 Since the degree to which mosses facilitate nitrogen fixation is not well-studied across the broad array of host mosses, rephrase to say “because of their associations with microbial nitrogen fixers” or similar.

Response: Changed.

L83 “of” not “on”

Response: Changed.

L84 “being” recognized.

Response: Changed.

L90 “exceeding” instead of “exceed”.

Response: Changed.

L98 “higher plants” <- but also, see comment above.

Response: Changed.

L103 Rephrase—perhaps exclude interaction?

Response: Excluded the word “interaction”.

L210: This sounds like a great feature of the model!

Response: Thanks.

L307-308 Very cool result. I think this is a major take-away of this study.

Response: Thanks.

L403 Please refer to a table or figure here to direct audience to that finding.

Response: We did not compare modeled NPP with observations, thus we deleted “Thus, with incorporation of moss into our models, NPP estimation in our model is improved.” in this revision.

L422-424 Past tense for past estimates?

Response: Changed.

L458 “which have their own functional traits” I would like to see a couple key traits enumerated—perhaps differing levels of insulation provided for soil, perhaps different associated microbiomes? Whichever may be most relevant to the assumptions within the model. Also remove next sentence that starts “In our model,…”.

Response: We revised the sentence to “Different kinds of mosses may provide different levels of insulation for soil, resulting in different soil thermal conditions that affect microbial activities.”.

Figure 1: Since Moss as a category was added in this model, perhaps the Moss boxes should also be green? I would find that helpful in interpreting the figure.

Response: Changed the color of Moss boxes to green.

Figure 3: Include a map as an inset or separate figure to show the location of these sites. I was surprised to see that half were on the southern end of area included in TEM_Moss, would you expect this to impact your results in any way?

Response: Added a map to show the sites for calibration. The locations for sites won't influence the calibration results.

Follow-up question: Why was 45 degrees N selected as the cut-off point? This includes temperate, boreal, and Arctic ecosystems--though the introduction and discussion seem tailored more to the Arctic and boreal ecosystems.

Response: For model comparison convenience, we generally treat 45 ºN above region as pan arctic.

Quantifying the role of moss in terrestrial ecosystem carbon dynamics in northern high-latitudes

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Key words: moss, carbon dynamics, Earth System Modeling, terrestrial ecosystems, Arctic

Abstract

In addition to woody and herbaceous plants, mosses are ubiquitous in northern terrestrial ecosystems, which play an important role in regional carbon, water and energy cycling. Current global land surface models that ~~which~~ do not ~~without~~ considering moss may bias the quantification of the regional carbon dynamics. Here we incorporate moss into a process-based biogeochemistry model, the Terrestrial Ecosystem Model (TEM 5.0), as a new plant functional type to develop a new model (TEM_Moss). The new model explicitly quantifies the interactions between ~~higher plant~~vascular plants and mosses and their competition for energy, water, and nutrients. Compared to the estimates using TEM 5.0, the new model estimates that the regional terrestrial soils store 132.7 Pg more C at present day, and will store 157.5 Pg and 179.1 Pg more C under the RCP 8.5 and RCP 2.6 scenarios, respectively, by the end of the 21st century. Ensemble regional simulations forced with different parameters for the 21st century with TEM_Moss predict that the region will accumulate 161.1±142.1 Pg C under the RCP 2.6 scenario, and 186.7±166.1 Pg C under the RCP 8.5 scenario over the century. Our study highlights the necessity of coupling moss into Earth System Models to adequately quantify terrestrial carbon-climate feedbacks in the Arctic.

1. Introduction

Northern high latitude ecosystems, which refers to the land ecosystems (>45 ºN) in northern temperate, boreal, grassland and tundra regions, hold~~occupy~~ about 30% of global terrestrial carbon (C) in soils and plants (Allison and Treseder, 2008; Jobbágy and Jackson, 2000; Kasischke, 2000; Tarnocai et al., 2009; Hugelius et al., 2014), and contain as much as 1024 Pg soil organic carbon from 0 to 3 m depth ~~-~~(Treseder et al., 2016; Schuur et al., 2008). This large amount of carbon is potentially responsive to ongoing global warming (Burke et al., 2017, Koven et al., 2015, Comyn-Platt et al., 2018)~~McGuire et al., 1995; Melillo et al., 1993; McGuire and Hobbie, 1997~~), which is especially pronounced at high latitudes (Treseder et al., 2016; IPCC, 2014). Thus, explicit investigation of carbon-climate feedback is important (Wieder et al., 2013; Bond-Lamberty and Thomson, 2010).

Ecosystem models are important tools for understanding the role of boreal ecosystems in carbon-climate feedbacks (Bond-Lamberty et al., 2005; Chadburn et al., 2017; Zhuang et al., 2002; Treseder et al., 2016). Process-based biogeochemical models such as TEM (Hayes et al., 2014; Raich et al., 1991; Melillo et al., 1993; McGuire et al., 1992; Zhuang et al., 2001, 2002, 2010, 2013), Biome-BGC (Running and Coughlan, 1988; Bond-Lamberty et al., 2007), and Biosphere Energy Transfer Hydrology scheme (BETHY) (Knorr, 2000) are increasingly employed to simulate current and future carbon dynamics. Those models estimate carbon dynamics by simulating processes such as photosynthesis, respiration, nitrogen competition, evapotranspiration and soil decomposition (Bond-Lamberty et al., 2005; Zhuang et al., 2015). The results from these models are influenced by components and processes that are built into the model (Turetsky et al., 2012; Oreskes et al., 1994). However, the role~~whether~~ of boreal forests

~~act~~ in (~~as a~~ carbon sink or source~~)~~ activities has~~ve~~ not yet reached a consensus due to a number of model limitations (Cahoon et al., 2012; Hayes et al., 2011; Todd-Brown et al., 2013).

One limitation is that ecosystems models often ignore some important components such as understory processes that play crucial roles in biogeochemical cycles (Zhuang et al., 2002; Treseder et al., 2011; Bond-Lamberty et al., 2005). For instance, mosses are ubiquitous in northern ecosystems, and show a pattern of increasing abundance with increasing latitude (Turetsky et al., 2012; Jägerbrand et al., 2006). Their functional traits, including tolerance to drought and a broad response of net assimilation rates to temperature, allow them to persist in high-latitude regions (Kallio and Heinonen, 1975; Harley et al., 1989). The activities of moss that are related to water, nutrients, and energy may influence several ecosystem processes such as permafrost formation and thaw, peat accumulation, soil decomposition and net primary productivity (NPP) (Turetsky et al., 2012; Nilsson and Wardle, 2005). Mosses can have positive or negative interactions with vascular plants (Skre and Oechel, 1979; Turetsky et al., 2010). On the one hand, mosses compete with vascular plants for available nutrients, negatively affecting vascular plants productivity (Skre and Oechel, 1979; Gornall et al., 2011; Turetsky et al., 2012). Besides, a thick moss cover can form an environment with water logging or low oxygen supply, which is common in high-latitude regions (Skre and Oechel, 1979; Cornelissen et al., 2007). The moss cover prevents absorbed solar heat from being conducted down into the soil, and tends to decrease soil temperature in summer. Therefore, soil decomposition rates can be affected since they are mediated by soil temperature, which will further influence growth of vascular plants (Gornall et al., 2007). On the other hand, some species of mosses can serve as an important source of nitrogen because of their associations with microbial nitrogen fixers ~~because of their ability of facilitating biological nitrogen fixation and their low nitrogen-use efficiency~~ (Basilier, 1979; DeLuca et al., 2007; Markham, 2009; Kip et al., 2011). Thus, mosses can also exert positive effects on plant growth due to their regulation of~~on~~ nitrogen availability for vascular plants (Hobbie et al., 2000; Gornall et al., 2007). It is gradually being recognized that mosses can have comparable influences on high-latitude ecosystems to vascular plants, due to their large density and essential function in plant competition, soil climate, and carbon and nutrient cycling (Longton, 1988; Lindo and Gonzalez, 2010; Okland, 1995; Pharo and Zartman, 2007). They can on average contribute 20% of aboveground NPP in boreal forests (Turetsky et al., 2010), and their annual NPP may reach as high as 350 g C m^{-2} in some regions in the Arctic (Pakarinen and Vitt 1973), even exceeding that of vascular plants (Oechel and Collins, 1976; Clarke et al., 1971). Thus, ignorance of mosses, the keystone species of boreal ecosystems, can pose large biases in model predictions and limit the utility of models. To date, a number of ecosystem models have already included moss activities to explore the response of moss to disturbance (Bond-Lamberty et al., 2007; Euskirchen et al., 2009; Frolking et al., 2010, Wania et al., 2009, Chadburn et al., 2015, Porada et al., 2016, Druel et al., 2017), or improve model prediction of carbon dynamics (Bond-Lamberty et al., 2005). However, the potential role of moss in the regional carbon dynamics in northern high latitudes has been slowly evaluated by considering the interactions between moss and ~~higher plant~~vascular plants, especially with respect to their competition for water, nutrient and energy.

This study developed a new version of Terrestrial Ecosystem Model (Raich et al., 1991; McGuire et al., 1992; Zhuang et al., 2001, 2002, 2010, 2013, 2015), hereafter referred to as TEM_Moss, by explicitly considering moss impacts on terrestrial ecosystem carbon dynamics. The ~~interactions and~~ competition of water, energy and nutrient between ~~higher plant~~vascular plants and mosses are explicitly modeled. The verified TEM_Moss and previous TEM were compared against the observed data of ecosystem carbon, soil temperature and moisture dynamics. Both models were then used to analyze the regional carbon dynamics in northern high latitudes (north of 45 ¯N) during the 20th and 21st centuries.

2. Methods

2.1 Overview

First, we briefly describe how we developed the TEM_Moss by modifying the previous TEM 5.0 to consider their interactions between ~~higher plant~~vascular plants and mosses. Second, parameterization and validation of TEM_Moss using measured gap-filled carbon flux data and meteorological data at representative sites is presented. Third, we present how we have applied both models (TEM_Moss and TEM 5.0) to the northern high latitudes (above 45 °N) to quantify regional carbon dynamics during the 20th and 21st centuries.

2.2 Model description

TEM is a process-based, large-scale biogeochemical model that uses monthly climatic data and spatially explicit vegetation and soil information to simulate the dynamics of carbon and nitrogen fluxes and pool sizes of plants and soils (Raich et al., 1991; McGuire et al., 1992; Zhuang et al., 2010, 2015, 2020). However, in previous versions of TEM, the interactions between mosses and ~~higher plant~~vascular plants on carbon and nitrogen cycling have not been included. Here we developed a TEM_Moss model by modifying model structure and incorporating activities of moss into extant TEM 5.0 (Zhuang et al., 2003). Based on the structure of TEM 5.0, we added carbon and nitrogen pools and fluxes to simulate activities of moss including photosynthesis, respiration, litterfall and nutrient and water cycling (Figure 1). Thus, the structure of TEM_Moss includes the processes of both ~~higher plant~~vascular plants and mosses (Figure 1).

In TEM_Moss, moss photosynthesis (GPP_m) is described as a maximum rate, reduced by influence of photosynthetically active radiation, mean air temperature, mean atmospheric carbon dioxide concentrations, moss moisture, and indirectly, nitrogen availability (Frolking et al., 1996; Launiainen et al., 2015; Zhuang et al., 2002). For each time step, GPP_m is calculated as:

$$GPP_m = C_{max} f(PAR) f(T) f(W_m) f(CO_2) f(NA) \quad (1)$$

where C_{max} denotes the maximum rate of carbon assimilation by moss (units: gC $m^{-2}mon^{-1}$), $f(PAR)$ is a scalar function that depends on monthly photosynthetically active radiation (PAR), which is calculated as (Frolking et al., 1996; Launiainen et al., 2015; Kulmala et al., 2011):

$$f(PAR) = \frac{PAR}{b + PAR} \quad (2)$$

where b (units: μmol m^{-2} s^{-1}) is the half saturation constant for PAR use by moss as indicated by the Michaelis–Menten kinetic.

The temperature effect on moss photosynthesis is modeled as a multiplier (Frolking et al., 1996; Raich et al., 1991):

$$f(T) = \frac{(T - T_{min})(T - T_{max})}{(T - T_{min})(T - T_{max}) - (T - T_{opt})^2} \quad (3)$$

where T is the monthly mean air temperature (units: °C), and T_{min}, T_{max}, and T_{opt} are parameters (units: °C) that limit $f(T)$ to a range of zero to one.

The moisture effect is also modeled as a multiplier (Frolking et al., 1996; Raich et al., 1991):

$$f(W_m) = \frac{(W_m - W_{min})(W_m - W_{max})}{(W_m - W_{min})(W_m - W_{max}) - (W_m - W_{opt})^2} \quad (4)$$

where w_m is moss moisture (units: mm), and w_{min}, w_{max}, and w_{opt} are related parameters (units: mm) that limit $f(w_m)$ to a range of zero to one.

$f([CO_2])$ is also a scalar function that depends on monthly mean atmospheric carbon dioxide concentration (Zhuang et al., 2002; Raich et al., 1991):

$$f([CO_2]) = \frac{[CO_2]}{k_m + [CO_2]} \qquad (5)$$

where $[CO_2]$ (units: µL/L) represents monthly mean atmospheric carbon dioxide concentration, the k_m (units: µL/L) is the internal CO_2 concentration at which moss C assimilation proceeds at one-half its maximum rate.

The function $f(NA)$ models the limiting effects of plant nitrogen status on GPP (McGuire et al., 1992; Zhuang et al., 2002), which ~~is a unitless multiplier.~~ is a scalar function that depends on monthly N available for incorporation into plant production of new tissue.

Meanwhile, in TEM_Moss, we defined the moss respiration rate (R_m) as a function of moss respiration rate at 10 °C, moss respiration temperature sensitivity which was expressed as a Q_{10} function, and moss moisture (Launiainen et al., 2015; Frolking et al., 1996):

$$R_m = R_{10} \times Q_{10}^{\frac{T_m - 10}{10}} \times f'(w_m) \qquad (6)$$

where R_{10} (units: gC $m^{-2}mon^{-1}$) represents the moss respiration rate at 10 °C, the parameter Q_{10} is moss respiration temperature sensitivity, T_m is moss temperature (°C) and w_m is moss moisture (mm).

The function $f'(w_m)$ denotes the moisture effect on moss respiration. Here we used $f'(w_m)$ to distinguish with the function $f(w_m)$, which is moisture effect on moss photosynthesis as mentioned earlier. ̏Ωᶻ ×ݎ is defined as (Frolking et al., 1996; Zhuang et al, 2002):

ˬΩᶻ ×ݎ سي ρطي (يئي ٩ يئيئجئجب٩ ي بحبخ ب) / (يئي ٩ يئيئجئجب ᶻي بحبخب٨ ي بحبخب)   (7)

where ×ݖ ݖݐ (units: mm) denotes the optimal water content for moss respiration.

Besides, the carbon in litter production from mosses to soil (,ݕ) is modeled as proportional to moss carbon biomass with a constant ratio (Zhuang et al., 2002):

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where MOSSC denotes the moss carbon biomass, and cfall$_m$ is the corresponding constant proportion.

Thus, the change of moss carbon pool (MOSSC) can be modeled as:

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On the other hand, researches have shown that mosses can uptake substantial inorganic nitrogen from the bulk soil (Ayres et al., 2006, Fritz et al., 2014). In our model, nitrogen uptake by moss (Nuptake$_m$) is modelled as a function of available soil nitrogen, moss moisture, and mean air temperature, and the relative amount of energy allocated to N versus C uptake (Zhuang et al., 2002; Raich et al., 1991):

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Where N$_{max}$ is the maximum rate of nitrogen uptake by mosses (units: gC m^{-2}mon^{-1}), and N$_{av}$ (units: g m^{-2}) represents available soil nitrogen, which is treated as a state variable in our model.

Ë‸ (units: g m^{-2}) is the concentration of available soil nitrogen at which nitrogen uptake proceeds at one-half its maximum rate. T is the monthly mean air temperature (ºC), and A_m is a unitless parameter ranging from 0 to 1, which represents relative allocation of effort to carbon vs. nitrogen uptake. K_s is a parameter accounting for relative differences in the conductance of the soil to N diffusion, which can be calculated through moss moisture (Zhuang et al., 2002; Raich et al., 1991):

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where w_f (units: mm) denotes the moss field capacity.

The nitrogen in litter production from mosses to soil (,ڭت) is modeled as proportional to moss nitrogen biomass with a constant ratio (Zhuang et al., 2002):

,ڭت سي Î ÆÁ ⁊ -Ì / 3 3 . (12)

where $nfall_m$ is the constant proportion to moss nitrogen biomass (MOSSN).

Thus, the changes in moss nitrogen pool (MOSSN) can be modeled as:

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At the same time, total carbon and nitrogen in litterfall, and total nitrogen uptake from soil available nitrogen are changed due to incorporation of mosses:

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, É Ô Ô Å Ò Æ Á Ì , Ì (15)

. Õ Đ Ô Á Ë Å Õ Đ Ô Á Ë Å Õ Đ Ô Á Ë Å (16)

Where ,ڿ and ,ڿ are carbon and nitrogen in litter production from ~~higher plant~~vascular plants to soil, and . Õ Ð Ô Á Ë is nitrogen uptake by ~~higher plant~~vascular plants (Raich et al., 1991; Melillo et al., 1993; Zhuang et al., 2003).

Except above equations, other governing equations in TEM 5.0 have not been changed. More equations of TEM 5.0 have been documented in previous studies (Raich et al., 1991; McGuire et al., 1992; Zhuang et al., 2003; Zha and Zhuang, 2018).

In TEM 5.0, a soil thermal module (STM) simulates soil thermal dynamics considering the effects of moss thickness, soil moisture, and snowpack (Zhuang et al., 2001, 2002). In STM, soil profile was treated as a three soil-layer system: (1) a moss plus fibric soil organic layer, (2) a humic organic soil layer, and (3) a mineral soil layer, and temperature for each layer can be derived from STM (Zhuang et al., 2001, 2002, 2003). Temperature in moss layer is estimated with STM.

A water balance module (WBM) was also incorporated into TEM 5.0 to simulate soil hydrologic dynamics (Vörösmarty et al., 1989; Zhuang et al., 2001). The WBM receives information on precipitation, air temperature, potential evapotranspiration, vegetation, soils and elevation to predict soil moisture evapotranspiration and runoff (Vörösmarty et al., 1989). The whole soil was treated as a single profile in WBM (Vörösmarty et al., 1989; Zhuang et al., 2001). To simulate moss moisture, we added a moss layer on the soil profile by modifying the WBM (Figure 2). Similar to soil moisture, moss moisture is also treated as a state variable in the revised WBM, which is modeled as:

Ó Î Ï × Æ Ě Ă Â Ê Î Ð Å Ò Ã Ï Á Ô É Å Ï Î Á Ð Ï Ô Ò Á Î Ó Ð É Ò Á Ô É Ï Î (11) where the term “percolation” denotes the percolation from moss, which is the sum of rainfall percolation and snowmelt percolation from moss. We assume that there is no runoff from moss layer.

Accompanied by the above equation, changes in soil water (SM) is modified as:

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Calculations for these water fluxes regarding ~~higher plant~~vascular plants were not changed. More details about an earlier version of WBM were described in Vörösmarty et al. (1989) and Zhuang et al. (2001).

2.3 Model parameterization and validation

The newly introduced parameters that are associated with moss activities were documented in Table 1. We parameterized the TEM_Moss for six representative ecosystem types in northern high latitudes with gap-filled monthly net ecosystem productivity (NEP, $gCm^{-2}mon^{-1}$) data from the AmeriFlux network (Davidson et al., 2000). We assumed that the moss types are associated with the representative ecosystem types, which means we tuned the moss-related parameters for the six representative ecosystem types. Except for the moss-related parameters, other parameters related to vascular ~~high~~ plants~~vegetations~~ are default based on Zha and Zhuang, 2018. The information of six sites that we chose to calibrate the TEM_Moss was compiled in Table 2. The parameterization was conducted using a global optimization algorithm known as SCE-UA (Shuffled complex evolution) method, which aims to minimize the difference between model simulations and measurements (Duan et al., 1994). In our calibration, the cost function of the minimization is:

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Where . %چQفbچ and . %چQجbچ are the measured and simulated NEP, respectively. k is the number of data pairs for comparison. Fifty independent sets of parameters were converged to minimize the objective function, and finally the optimized parameters were derived as the mean of these 50 sets of inversed parameters. We presented the boxplot of parameter posterior distributions at sites chosen for calibration (Figure 4). At the same time, the results of model parameterization were shown in Figure 3. Besides these parameters related to moss, all other parameters use their default values in TEM 5.0 (Zhuang et al., ~~2010,~~ 2015). These optimized parameters were used for model validation and extrapolation.

We verified the TEM_Moss simulated NEP, soil moisture and soil temperature. First, we conducted site-level simulations at six sites that contain level-4 gap-filled monthly NEP data from the AmeriFlux network (Table 3). Site-level monthly gap-filled soil moisture and soil temperature data were organized from the ORNL DAAC Dataset (https://daac.ornl.gov/) to make comparison with model simulations (Table 4 and Table 5). Local climate data including monthly air temperature (°C), precipitation (mm), and cloudiness (%) were obtained to drive these model simulations.

2.4 Regional Extrapolation

With six site-level calibrated parameters, TEM-Moss is applied to the region ~~the~~ pixel by pixel based on ~~simulation on the basis of~~ vegetation distribution data~~class~~. Both TEM_Moss and TEM 5.0 were applied to northern high latitudes (above 45 °N) for historical (the 20th century) and future (the 21st century) quantifications on carbon dynamics. For historical simulations, climatic forcing data including monthly air temperature, precipitation, and cloudiness and atmospheric CO_2

concentrations during the 20th century, were collected from the Climatic Research Unit (CRU TS3.1) from the University of East Anglia (Harris et al., 2014). Other ancillary inputs including gridded soil texture (Zhuang et al., 2015), elevation (Zhuang et al., 2015), and potential natural vegetation (Melillo et al., 1993) were also organized. For future simulations, two contrasting Intergovernmental Panel on Climate Change (IPCC) climate scenarios (RCP 2.6 and RCP 8.5) were used to drive the models. The future climate forcing data and atmospheric CO_2 concentrations during the 21st century 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/, January 2017).

Simulations were conducted at a spatial resolution of 0.5° latitude × 0.5° longitude (Zhuang et al., 2001, 2002). A spin-up was run to reach an equilibrium for each pixel, and the values of state variables at equilibrium were treated as initial values for transient simulations (McGuire et al., 1992). Specifically, we chose the first 30 years in the whole 100-year climatic forcing data to spin-up the models when conducting historical and future simulations. For each of the simulations, net primary production (NPP), heterotrophic respiration (R_H), and net ecosystem production (NEP) were analyzed. We denoted that a positive 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.

In these simulations, for each pixel, we assumed its moss distribution area is the same as the ~~higher plant~~vascular plants distribution. The total carbon uptake/emission of mosses in a pixel are calculated as the multiplication of pixel area with the carbon fluxes such as NEP (units: gC m^{-2} $month^{-1}$). Moss-related parameters for representative ecosystems are calibrated (Fig. 4 and Table

1) or obtained from previous model parameterization and the rest of model parameters are default from Zha and Zhuang (2018).

3. Results

3.1 Model Validation

TEM_Moss was able to reproduce the monthly NEP and performed better than TEM 5.0 at chosen sites, with larger R-square values and smaller RMSE (Figure 5, Table 6). R-square for TEM_Moss reached 0.94 at Bartlett Experimental Forest site and 0.72 at Ivotuk site (Table 6). R-square values for TEM 5.0 showed a similar pattern, reaching 0.91 and with minimum value of 0.43 at Bartlett Experimental Forest and Ivotuk sites, respectively (Table 6). Except for Ivotuk site, R-squares for TEM_Moss are all higher than 0.8 at the chosen sites, while most R-squares for TEM 5.0 are from 0.62 to 0.75 (Table 6). On the other hand, RMSE for TEM_Moss is lower than that for TEM 5.0 at each site (Table 6).

We presented the comparisons between measured and simulated volumetric soil moisture (VSM) from TEM_Moss and TEM 5.0 (Figure 6). Statistical analysis shows that TEM_Moss reproduces the soil moisture well with R-squares ranging from 0.51 at US-Bkg to 0.87 at US-Atq (Table 7). R-squares for TEM_Moss are substantially higher than that for TEM 5.0 at most chosen sites, except for US-Atq (Table 7). RMSE for TEM_Moss is lower than that for TEM 5.0 at each site (Table 7). Similarly, comparisons between measured and simulated soil temperature at 5 cm depth (ST_5) from TEM_Moss and TEM 5.0 indicated that TEM_Moss can reproduce the soil temperature with R-squares ranging from 0.81 at US-Ho1 to 0.91 at US-Bkg, while TEM 5.0 reproduces the soil temperature with R-squares ranging from 0.69 at BE-Vie to 0.89 at US-Bkg (Figure 7; Table 8). Although R-squares for both models are relatively high and RMSE for them are relatively low, TEM_Moss still shows higher R-squares and lower RMSE than TEM 5.0 (Table 8).

3.2 Regional carbon dynamics during the 20th century

Both TEM_Moss and TEM 5.0 were used to simulate northern high-latitude regional carbon balance during the 20th century (Figure 8). Higher NEP was correlated with the combination of relatively higher NPP and lower heterotrophic respiration (R_H). TEM_Moss indicated that the northern high latitudes acted as a carbon sink of 221.9 Pg with an inter-annual standard deviation of 0.31 PgC yr^{-1} during the 20th century, which is 132.7 Pg larger than 89.2 Pg simulated by TEM 5.0 (Figure 8). The simulated NEP by TEM_Moss ranges from 1.38 PgC yr^{-1} to 3.05 PgC yr^{-1}, while the range by TEM 5.0 was from 0.11 PgC yr^{-1} to 1.75 PgC yr^{-1} (Figure 8). The patterns of the simulated NEP from two models were similar, both showing a general increasing trend throughout the 20th century (Figure 8). By 2000, the TEM_Moss simulation indicated that the northern high-latitude region stored 3.05 PgC yr^{-1}, which is more than twice as the storage estimated by TEM 5.0 (1.33 PgC yr^{-1}, Figure 8). Both models indicated that carbon uptake by the northern ecosystems during the second half of the 20th century was higher than the first half for most part of the region, and only a small portion of the region lost carbon in last century (Figure 9).

Simulated total NPP by TEM_Moss was 9.6 PgC yr^{-1}, ranging from 8.52 PgC yr^{-1} to 10.65 PgC yr^{-1} in the 20th century, with 1.69 PgC yr^{-1} of moss NPP and 7.93 PgC yr^{-1} of ~~higher plant~~vascular plants NPP (Figure 8). Moss NPP ranges from 1.23 PgC yr^{-1} to 2.14 PgC yr^{-1} and the ratio of moss NPP to ~~higher plant~~vascular plants NPP is 0.21 (Figure 8). TEM 5.0 estimated 0.8 PgC yr^{-1} lower total NPP than TEM_Moss, but 0.87 PgC yr^{-1} higher NPP for ~~higher plant~~vascular plants (Figure 8). On the other hand, average heterotrophic respiration in the 20th century was 7.38 PgC yr^{-1} and all years were within about 5% of this value (Figure 8). TEM 5.0 projected 0.53 PgC yr^{-1} higher R_H than TEM_Moss (7.91 PgC yr^{-1}, Figure 8). Overall, TEM_Moss predicted higher total NPP but lower R_H, which jointly caused a pronounced difference in NEP between two models.

Both models estimated that soil organic carbon and vegetation carbon were accumulating continuously in the 20th century (Figure 10). TEM_Moss indicated that regional SOC and VEGC accumulated 96.3 PgC and 115.2 PgC, respectively, and the carbon uptake by moss was 10.4 Pg in the period (Figure 10, Table 10). As simulated by TEM_Moss, 43.4%, 51.9% and 4.7% of total carbon uptake in the region was assimilated to soils, ~~higher plant~~vascular plants and mosses, respectively (Table 10). TEM 5.0 simulated that SOC increased by 31.7 Pg at the end of the 20th century, which is 64.6 PgC less than the value estimated by TEM_Moss (Table 10). TEM 5.0 estimated 57.7 PgC in plants less than the value estimated by TEM_Moss (57.5 PgC, Table 10). 35.5% and 64.5% of total carbon was as SOC and VEGC, respectively.

3.3 Regional carbon dynamics during the 21st century

Under the RCP 2.6 scenario, TEM_Moss simulated NEP of 2.07 PgC yr^{-1} with the range from 0.41 PgC yr^{-1} to 3.2 PgC yr^{-1}, and the inter-annual standard deviation of 0.59 PgC yr^{-1} during the 21st century (Figure 11 (a)). The regional sink shows a decreasing pattern in the 2000s and then generally increases over the remaining years of the 21st century (Figure 11 (a)). For comparison, TEM 5.0 predicted that the average NEP of 0.28 PgC yr^{-1} with the range from -1.48 PgC yr^{-1} to 1.69 PgC yr^{-1} during the 21st century (Figure 11 (a)). Thus, TEM 5.0 projected 179.1 PgC stored in northern ecosystems is less than the estimation from TEM_Moss in the 21st century. Besides, TEM 5.0 simulated that the regional NEP showed a decreasing trend and the region fluctuates between sinks and sources during the century (Figure 11 (a)). The spatial patterns from two models also showed differences. TEM_Moss indicated that the region accumulates carbon over this century, while TEM 5.0 simulated that some regions changed from a carbon sink to a source in the second half of the century (Figure 12 (a)). Simulated regional NPP by TEM_Moss ranges from 11.2 to 13.7 PgC yr^{-1} with a mean of 12.98 PgC yr^{-1} in this century, while average NPP predicted by TEM 5.0 is 1.46 PgC yr^{-1} lower than that value (11.52 PgC yr^{-1} (Figure 11(a)). TEM_Moss simulated NPP has 3.74 PgC yr^{-1} from moss and 9.24 PgC yr^{-1} from ~~higher plant~~vascular plants, which account for 28.8% and 71.2% of total NPP, respectively (Figure 11(a)). Meanwhile, TEM_Moss estimated that R_H is 10.91 PgC yr^{-1}, while TEM 5.0 predicted it as 11.24~~10.33~~ PgC yr^{-1}, which is higher (Figure 11(a)). Both models projected that soil organic carbon and vegetation carbon accumulate in this century but with different magnitudes (Figure 13 (a)). TEM_Moss predicted that regional SOC and VEGC accumulated 84.7 PgC and 112.6 PgC, respectively, during the 21st century, while TEM 5.0 predicted that a smaller increase with 12.1 and 15.5 PgC in SOC and VEGC, respectively (Figure 13 (a), Table 12 (a)). Besides, TEM_Moss also predicted an increasing of 9.4 PgC in MOSSC, accounting for 4.5% of the total carbon uptake in this region (Table 12(a)).

Under the RCP 8.5 scenario, TEM_Moss simulated annual NPP of 13.84 PgC yr^{-1} with a range from 11.09 to 16.94 PgC yr^{-1}, which is 1.31 PgC yr^{-1} higher than the projection from TEM 5.0 (Figure 11 (b)). Total NPP estimated by TEM_Moss has 3.84 PgC yr^{-1} from moss and 10 PgC yr^{-1} from ~~higher plant~~vascular plants (Figure 11(b)). Annual R_H was 11.28 PgC yr^{-1} estimated by TEM_Moss and 11.54 PgC yr^{-1} by TEM 5.0, respectively (Figure 11(b)). Consequently, TEM_Moss projected NEP was 2.56 PgC yr^{-1} with the inter-annual standard deviation of 0.93 PgC yr^{-1} in this century (Figure 11 (b)). NEP ranges from 0.67 PgC yr^{-1} to 4.78 PgC yr^{-1} estimated with TEM_Moss, while from -1.69 PgC yr^{-1} to 2.65 PgC yr^{-1} with a mean of

0.99 PgC yr-1 was estimated by TEM 5.0 (Figure 11 (b)). TEM_Moss predicted more carbon uptake of 157.5 Pg than TEM 5.0 during the 21st century. Both models predicted that NEP showed an increasing trend during the 21st century (Figure 11 (b)). Moreover, similar spatial patterns of carbon sinks and sources appeared in the projections from two models (Figure 12 (b)). Soil organic carbon and vegetation carbon shows an increasing trend from both models (Figure 13 (b)). Regional SOC and VEGC increased by 92.5 PgC and 153.6 PgC, respectively by the end of the 21st century predicted by TEM_Moss. In contrast, the increase of 44.2 PgC and 54.5 PgC of SOC and VEGC, respectively, was predicted by TEM 5.0 (Figure 13 (b), Table 12 (b)). TEM_Moss predicted an increase of 10.1 PgC in MOSSC (Table 12(b)).

4. Discussion

4.1 The role of moss in the regional carbon dynamics

Global warming has been pronounced in recent decades, particularly at high latitudes (IPCC, 2014; Tape et al., 2006; Stow et al., 2004). An enormous amount of soil organic carbon stored in northern high-latitude regions (Tarnocai et al., 2009; Schuur et al., 2008) is expected to affect a broad spectrum of ecological and human systems, and cause rapid changes in the Earth system when undergoing substantial climate change (Serreze and Francis 2006; Davidson and Janssens, 2006; McGuire et al., 2009). Improving projections for carbon budget of high latitude terrestrial ecosystems is essential for understanding global carbon–climate feedbacks (Melillo et al., 2011; Todd-Brown et al., 2013).

Our simulations suggest that mosses play an important role in the regional carbon dynamics, which is consistent with previous studies (McGuire et al., 2009; Turetsky et al., 2012). First of all, mosses are productive with carbon assimilation even during low temperature, water content and irradiance (Kallio and Heinonen, 1975; Harley et al., 1989). For example, mosses can tolerate drought through physiological responses, such as by suspending metabolism and by withstanding cell dessication (Turetsky et al., 2012; Oechel and Van Cleve, 1986). The key functional traits related to water, nutrient, and thermal tolerances of mosses enable them to fit in harsh northern conditions (Shetler et al., 2008; Turetsky et al., 2012). Thus, with incorporation of moss into our models, the total NPP estimation in our model is affected. ~~improved (The referee requires me to direct a figure to prove this sentence, but I am not sure which figure should I direct).~~ Mosses also act as a powerful competitor with vascular plants for nutrient uptake. Their rapid nutrient acquisition and slow nutrient loss through slow decomposition may constrain concentrations of plant-available nitrogen (Hobbie et al., 2000; Turetsky et al., 2010; Oechel and Van Cleve, 1986; Gornall et al., 2007), which will further decrease NPP of ~~higher plant~~vascular plants. Our model results suggested that the NPP of ~~higher plant~~vascular plants considering moss is indeed lower than previous NPP estimates without considering moss, but the total NPP is larger than before. We estimated that mosses contribute 17.6% of NPP in the 20th century, and 28.8% and 27.6% in the 21st century under the RCP 2.6 and RCP 8.5 scenarios, respectively. This is comparable with the results reported by a synthesis study, ~~Turetsky et al. (2010),~~ ~~which~~indicating ~~suggested~~ an average contribution ~~of~~ 20% of aboveground NPP from moss in upland boreal forests and the contribution is 48% in wetlands ecosystems. Frolking et al. (1996) even reported a contribution of 38.4% to total NPP by moss at a boreal forest site. Moreover, mosses can also influence heterotrophic respiration (R_H) through their effects on soil thermal and hydrologic dynamics (Zhuang et al., 2001). With the layer of moss, soil temperature tends to decrease but soil moisture tends to increase (Oechel and Van Cleve, 1986), which will further decrease soil respiration in summer. This supports our results that TEM_Moss simulated R_H is lower than that by TEM 5.0. With a combination of higher NPP and lower R_H, NEP predicted by

TEM_Moss is larger than that by TEM 5.0. The two contrasting regional simulations by TEM_Moss and TEM 5.0 indicated the region is currently a carbon sink, which is consistent with previous studies (White et al., 2000; McGuire et al., 2009; Schimel et al., 2001). Our study estimates~~d~~ that regional NEP during the 20th century is 2.2 Pg C yr^{-1} by TEM_Moss and 0.89 Pg C yr^{-1} by TEM 5.0, respectively. In the 1990s, the regional sink is projected to be 2.7 and 1.1 Pg C yr^{-1} by TEM_Moss and TEM 5.0 respectively. Compared with other existing studies, our regional estimates of NEP are within the reasonable range from other existing studies. McGuire et al. (2009) estimated a land sink of 0.3–0.6 Pg C yr^{-1} for the pan-arctic region for the 1990s, which is closer to our estimation by TEM 5.0 but less than the projection by TEM_Moss. The top-down atmospheric analyses indicate that the sink of pan-arctic region is between 0 and 0.8 Pg C yr^{-1} in the 1990s (Menon et al. 2007). Besides, Schimel et al. (2001) reported an estimation of the northern extratropical NEP is from 0.6 to 2.3 PgC yr^{-1} in the late 20th century, which is comparable to our estimates. Our simulations also confirmed that mosses and ~~higher plant~~vascular plants respond to climate change similarly in terms of their productivity (Turetsky et al. 2010).

4.2 Model Uncertainty and limitations

There are a number of uncertainty sources in our model simulations. First, due to the limited understanding of moss photosynthesis (He et al., 2015) and various moss N uptake pathways (e.g., Bay et al 2013; Berg et al 2013), a few important assumptions have been made in our modeling. For instance, we assume that mosses behave similarly to vascular plants regarding photosynthesis and soil N uptake is the only pathway for mosses without considering N uptake through N fixers and atmospheric wet N deposition (Ayres et al. 2006). Second, ~~First,~~ the errors in the observed data will influence our parameterization results, which will bias our regional estimates of carbon dynamics. Second, climatic driving data are also a source of uncertainty for historical and future simulations. Third, model assumptions will also induce additional uncertainties. For instance, we assumed that vegetation distribution will remain unchanged during the transient simulation. However, vegetation will change in response to warming climate and disturbances such as fire and insect outbreaks in the region (Hansen et al., 2006), which will affect carbon budget. Missing potential responses to disturbances in our model shall introduce additional uncertainties (Soja et al. 2007; Kasischke and Turetsky, 2006). Future moss dynamics will also impact carbon dynamics in this region. For instance, a long-term warming experiments along natural climatic gradients, ranging from Swedish subarctic birch forest and subarctic/subalpine tundra to Alaskan arctic tussock tundra concluded that both diversity and abundance of mosses are likely to decrease under arctic climate warming (Long et al. 2012). Similarly, total moss cover declined in both heath and mesic meadow under experimental long-term warming (by 1.5–3 °C), driven by general declines in many species (Alatalo et al., 2020). Due to global warming, significant losses in moss diversity are expected in boreal forests and alpine biomes, leading to changes in ecosystem structure and function, nutrient cycling, and carbon balance (He et al., 2015).

We conducted ensemble regional simulations with 50 sets of parameters to quantify model uncertainty due to uncertain parameters. The 50 sets of parameters were obtained using the method in Tang and Zhuang (2008). The ensemble means and the inter-simulation standard deviations are used to measure the model uncertainty (Figure 14). TEM_Moss predicted that the regional cumulative carbon ranges from a carbon loss of 266 Pg C to a carbon sink of 567.3 Pg C by different ensemble members, with a mean of 161.1±142.1 Pg during the 21st century under the

RCP 2.6 scenario. Under the RCP 8.5 scenario, TEM_Moss predicted that the region acts from a carbon source of 79.1 Pg C to a carbon sink of 625.9 Pg C, with a mean of 186.7±166.1 Pg during the 21st century (Figure 14).

This study took an important step to incorporate moss into an extant ecosystem model that has not explicitly consider the role of moss and its interactions with ~~higher plant~~vascular plants. Our model simulations showed that mosses have strong influences on regional ecosystem carbon cycling, by affecting the soil thermal, nitrogen availability, and water conditions of terrestrial ecosystems. However, there are still limitations in our model. First, we did not differentiate various kinds of mosses because they have their own functional traits.~~,~~ Different kinds of mosses may ~~differ in levels~~ provide different levels of insulation ~~provided~~ for soil, resulting in different soil thermal conditions that ~~and their associated~~ affect microbial activities~~iomes~~. ~~In our model, the moss types are just differentiated by the vegetation types.~~ The structural and physiological traits of mosses will differ largely in different moss groups, such as feather moss versus Sphagnum (Turetsky et al., 2010). In addition, we lack spatially explicit information of moss distribution in the region, which will lead to a large regional uncertainty of carbon quantification. We assumed that moss area distribution is the same as its associated vegetation distribution. Another limitation is that some important physiological traits of moss have not been modeled. For example, moss abundance may change following shifts in vascular species composition due to shading or burial by vascular litter (Turetsky et al., 2010; Cornelissen et al., 2007). Furthermore, disturbance such as wildfires can also influence moss activities.

5. Conclusions

This study explicitly incorporated moss into an extant process-based terrestrial ecosystem model to investigate the carbon dynamics in the Arctic for present day and future. Historical regional simulations with TEM_Moss indicated that the region is a carbon sink of 221.9 PgC over the 20th century, and this sink may decrease to 206.7 PgC under the RCP 2.6 scenario or increase to 256.2 PgC under the RCP 8.5 scenario during the 21st century. Compared with an earlier version of TEM that has not explicitly modeled moss, TEM_Moss projected that the region stored 132.7 Pg more C over the last century, 179.1 Pg and 157.5 Pg more C under the RCP 2.6 and RCP 8.5 scenarios, respectively. This study demonstrated that moss activities have large effects on ecosystem soil thermal, water, and carbon dynamics through their interactions with ~~higher plant~~vascular plants~~s~~. This study highlights the importance of considering the moss dynamics in Earth System Models to adequately quantify the carbon–climate feedbacks in the Arctic.

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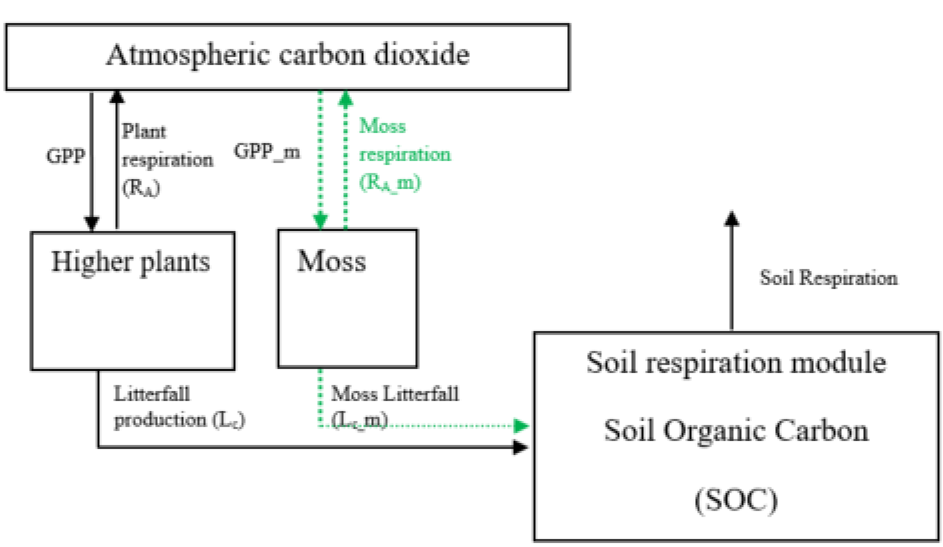
Atmospheric carbon dioxide
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Moss respiration (R_A_m)
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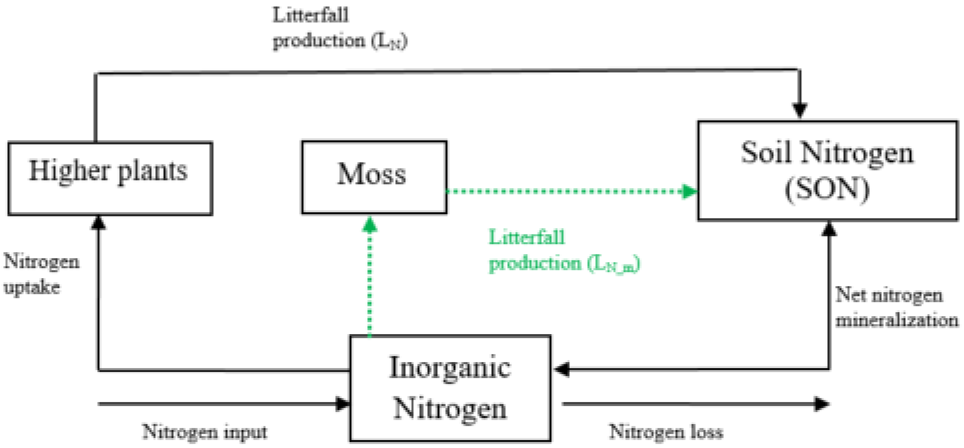
Soil Organic Carbon (SOC)
Litterfall production (L_c)
Moss Litterfall (L_c_m)


Litterfall production (L_N)
Higher plants
Moss
Soil Nitrogen (SON)
Litterfall production (L_N_m)
Nitrogen uptake
Net nitrogen mineralization
Inorganic Nitrogen
Nitrogen input
Nitrogen loss

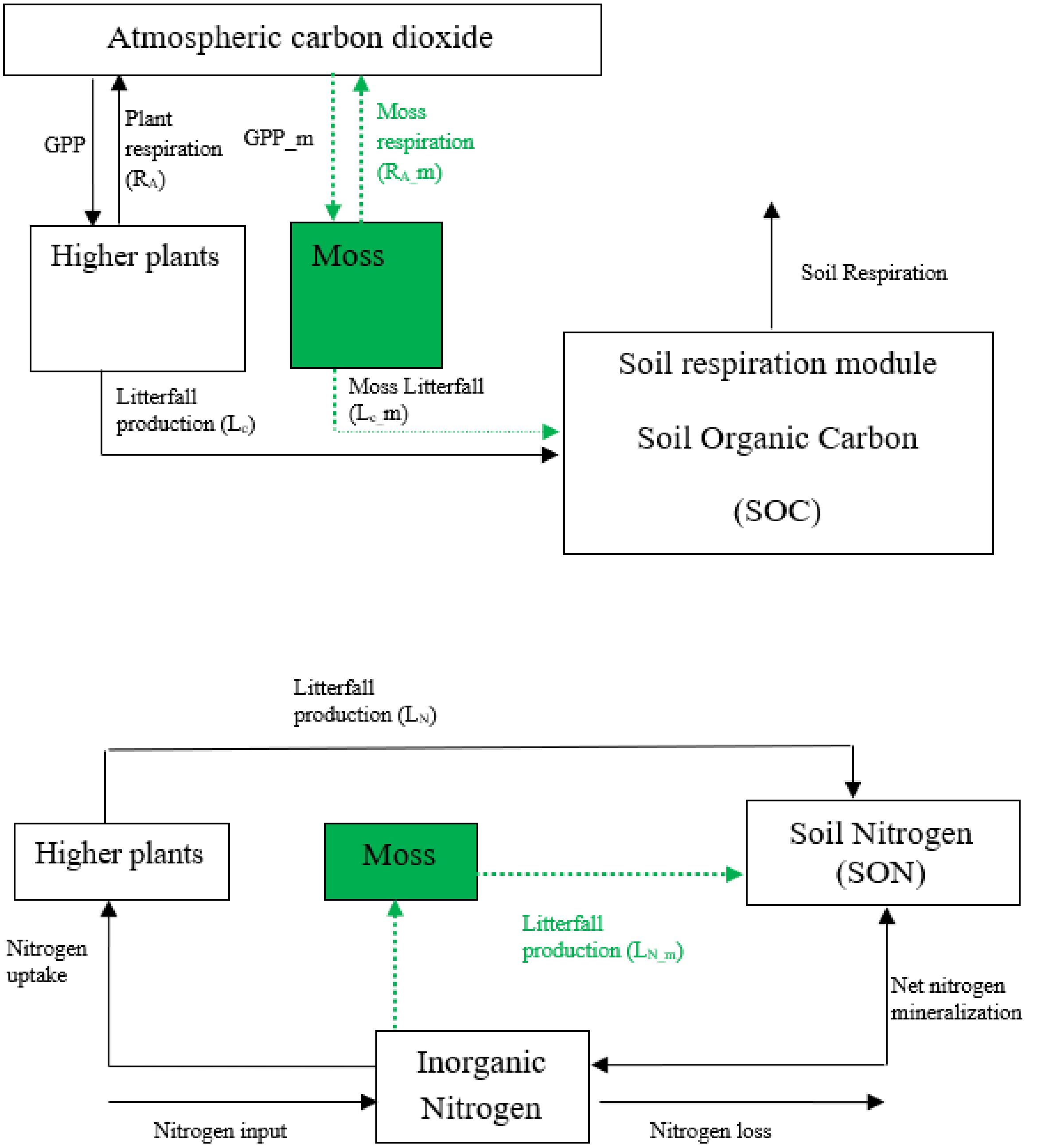


Figure 1. Schematic diagram of TEM_Moss: Green dashed arrows are new carbon and nitrogen fluxes, representing moss production, moss respiration and litterfall of moss. Black arrows were in TEM 5.0 (Zhuang et al., 2013).

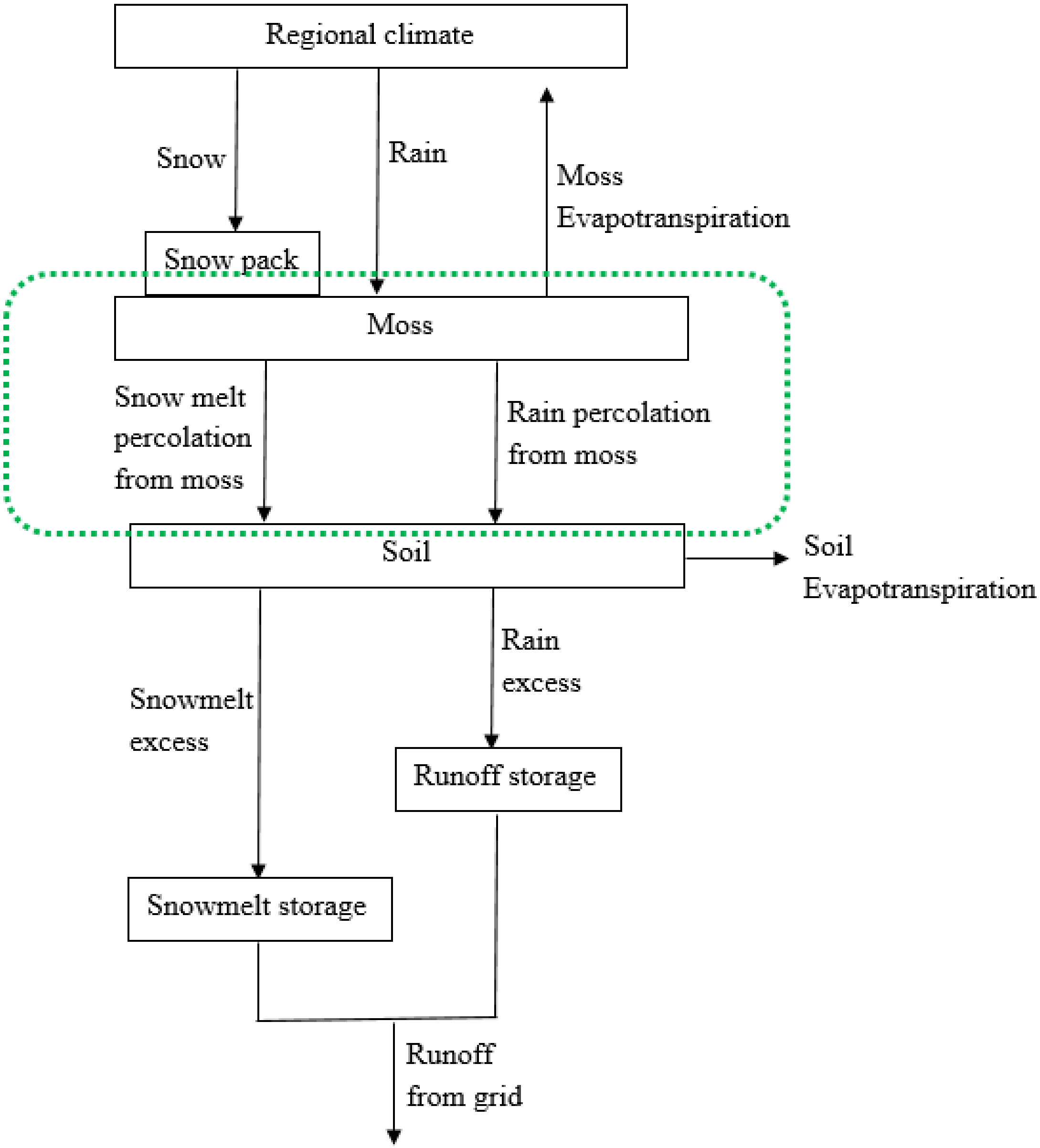


Figure 2. The revised Water Balance Model: Green dashed circle represents the hydrology dynamics for moss (Vörösmarty et al., 1989).

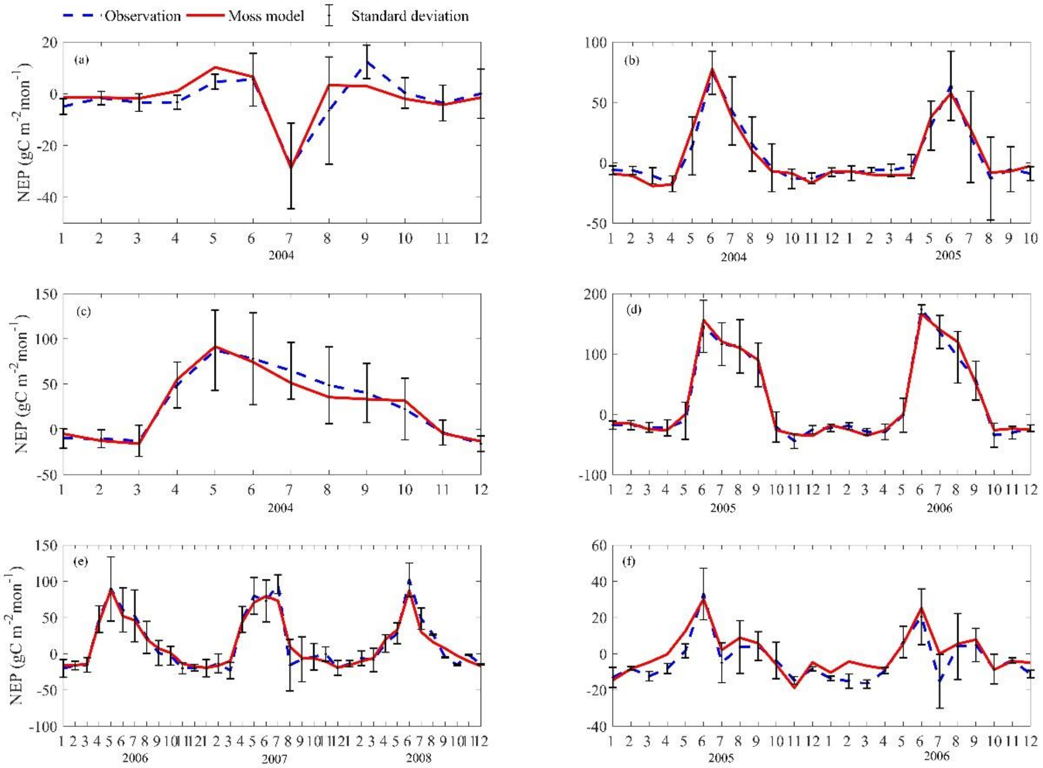


Figure 3. Comparison between observed and simulated NEP (gC $m^{-2}mon^{-1}$) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Univ. of Mich. Biological Station (Temperate deciduous forest), (e) KUOM Turfgrass Field (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different. Error bars represent standard errors among daily measure data in one month.

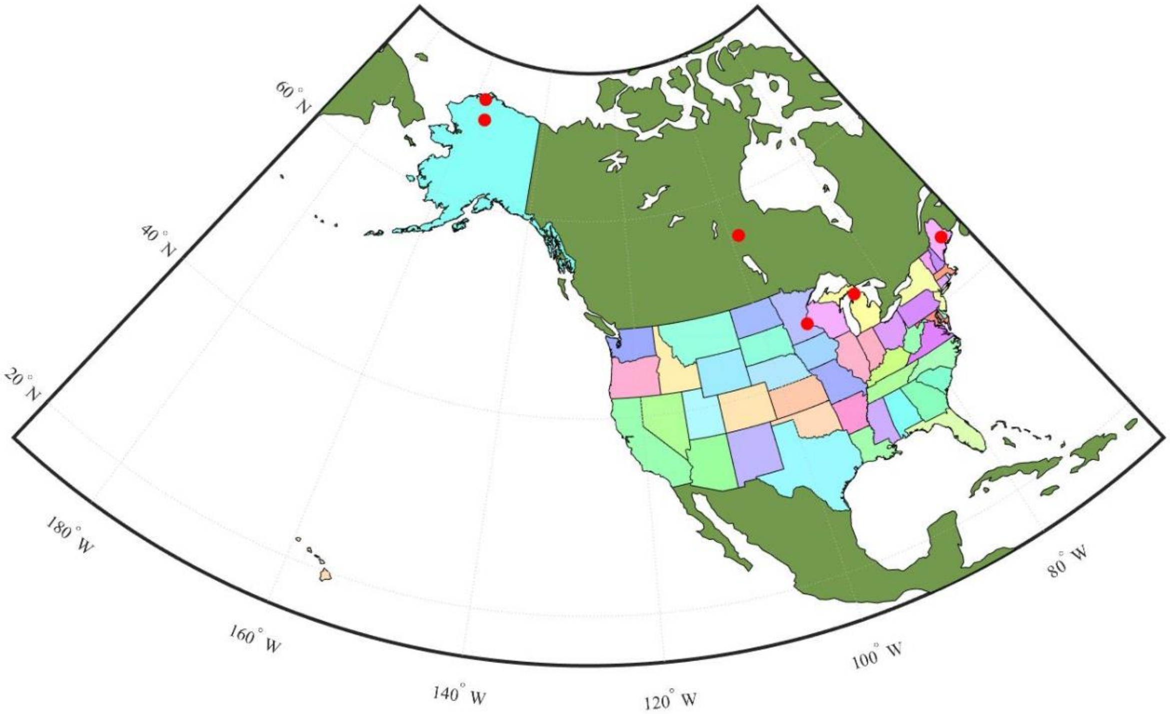


Figure 4. Map showing six sites used for TEM_Moss calibration. The red points represent the six sites, which are all in US: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-1964 burn site (boreal forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB: Univ. of Mich. Biological Station (temperate deciduous forest), US-KUT: KUOM Turfgrass Field (grassland), US-Atq: Atqasuk (wet tundra).

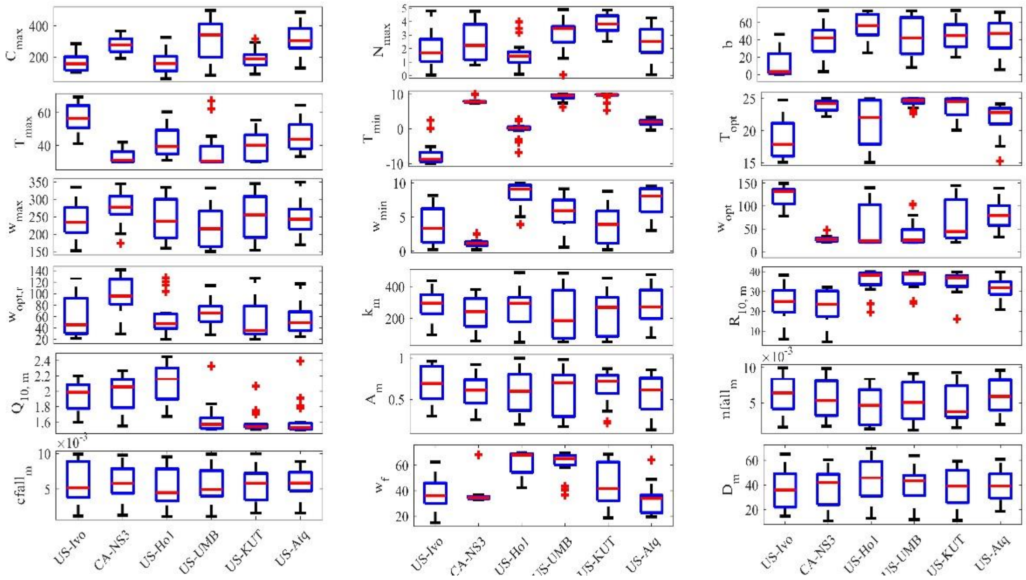


Figure 4. Boxplot of parameter posterior distribution that are obtained after ensemble inverse modeling for TEM_Moss at all six sites: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-1964 burn site (boreal forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB: Univ. of Mich. Biological Station (temperate deciduous forest), US-KUT: KUOM Turfgrass Field (grassland), US-Atq: Atqasuk (wet tundra). Boxes represent the range between the first quartile and the third quartile of the parameter values, the red line within box represents the second quartile or the mean of the values. The bottom and top whiskers represent minimum and maximum parameter values, respectively.

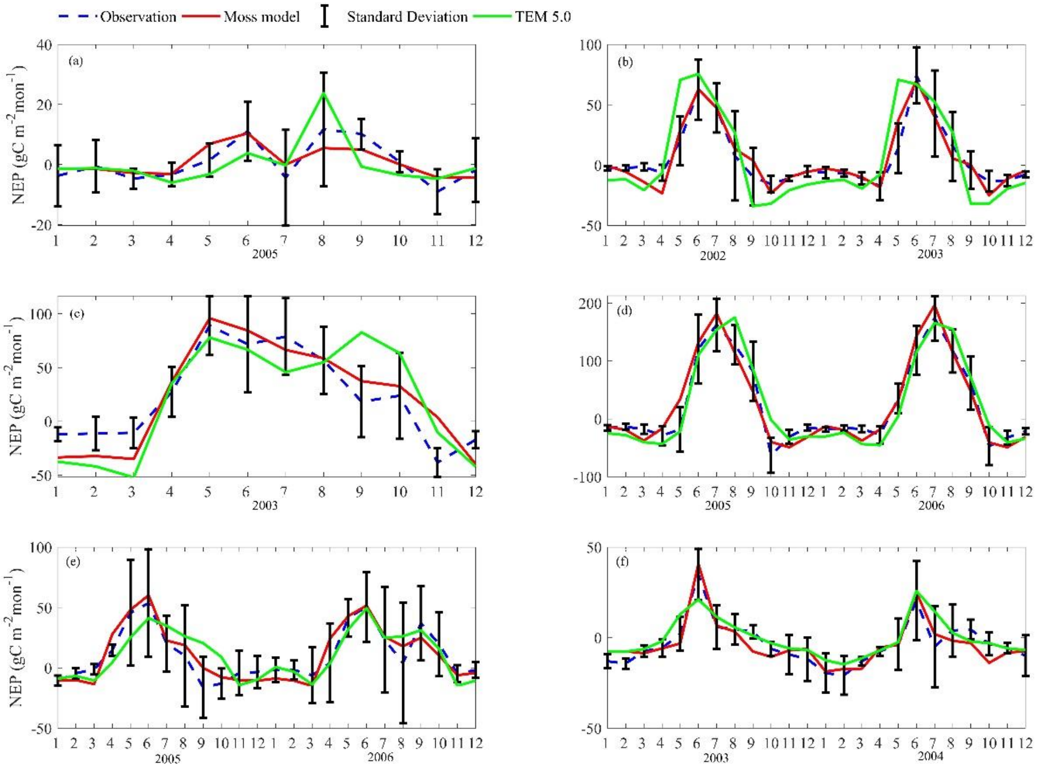


Figure 5. Comparison between observed and simulated NEP (gC m^{-2}mon^{-1}) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Bartlett Experimental Forest (Temperate deciduous forest), (e) Brookings (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different.

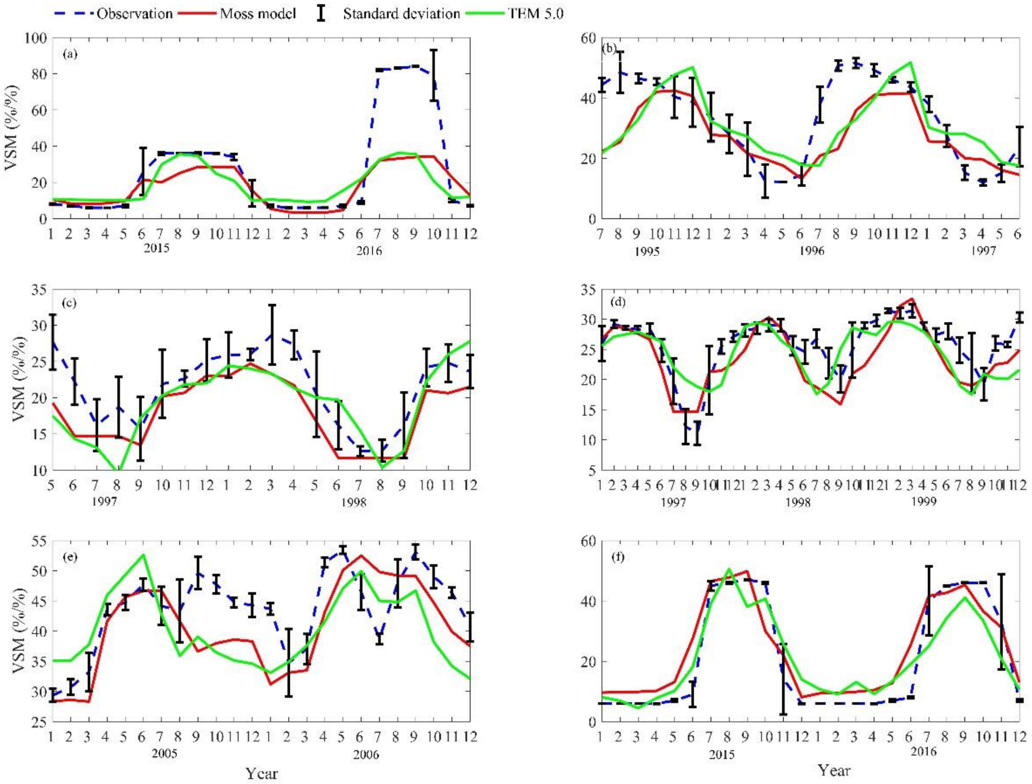


Figure 6. Comparison between observed and simulated volumetric soil moisture (VSM, %/%) at: (a) US-Ivo (alpine tundra), (b) BOREAS NSA-OBS (boreal forest), (c) NL-Loo (temperate coniferous forest), (d) DK-Sor (Temperate deciduous forest), (e) US-Bkg (Grassland), and (f) US-Atq (Wet tundra). Note: scales are different.

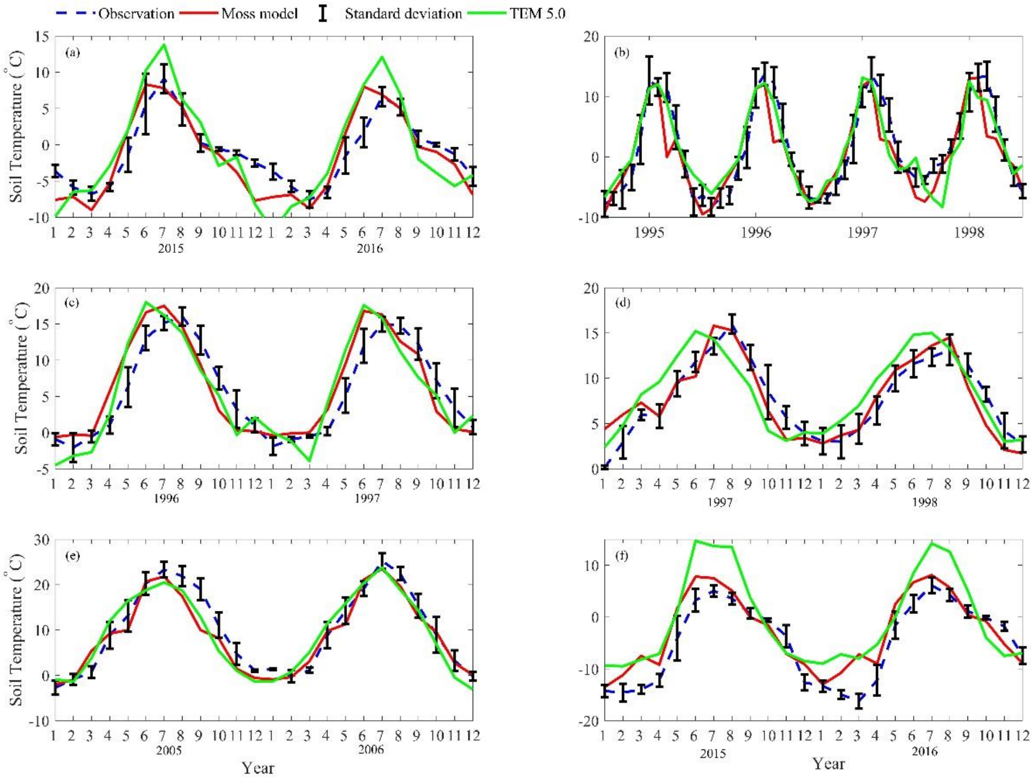


Figure 7. Comparison between observed and simulated soil temperature at 5cm depth (℃) at: (a) US-Ivo (alpine tundra), (b) BOREAS NSA-OBS (boreal forest), (c) US-Ho1 (temperate coniferous forest), (d) BE-Vie (Temperate deciduous forest), (e) US-Bkg (Grassland), and (f) US-Atq (Wet tundra). Note: scales are different.

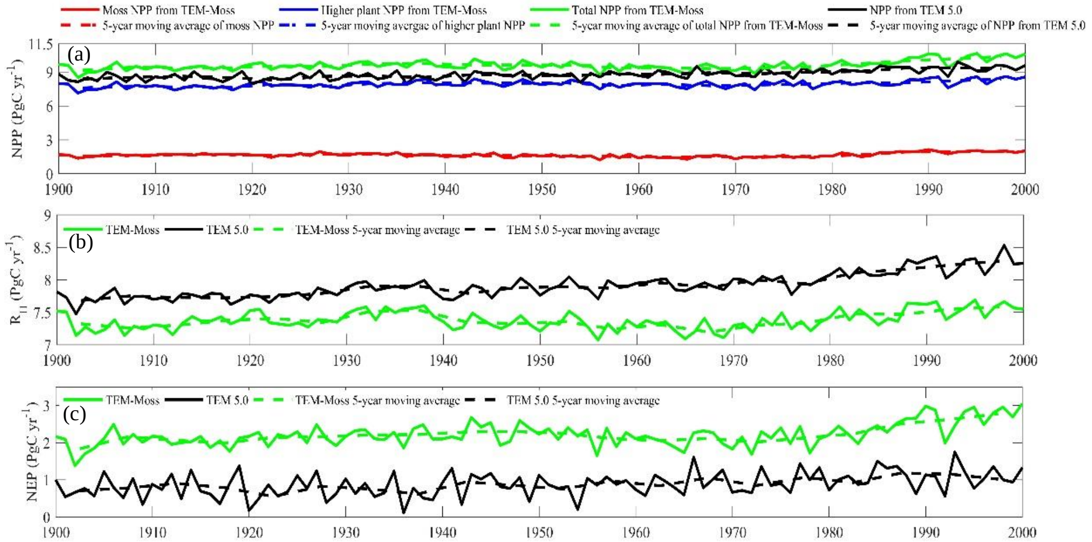


Figure 8. Simulated annual net primary production (NPP, a), heterotrophic respiration (R_H, b), and net ecosystem production (NEP, c) during the 20th century by TEM_Moss and TEM 5.0.

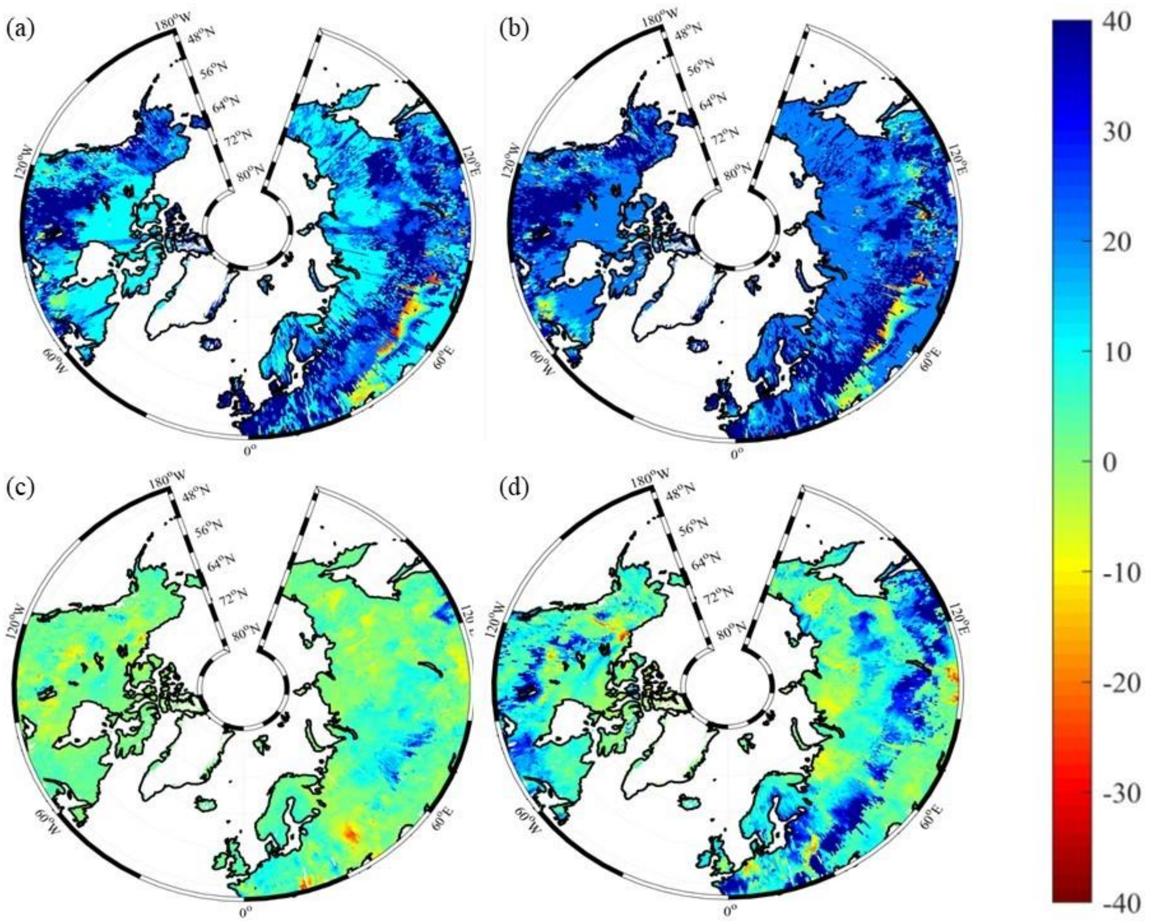


Figure 9. Spatial distribution of NEP simulated by TEM_Moss for the periods (a) 1900–1950, (b) 1951–2000, and by TEM 5.0 for the periods (c) 1900–1950, (d) 1951–2000. Positive values of NEP represent sinks of CO_2 into terrestrial ecosystems, while negative values represent sources of CO_2 to the atmosphere.

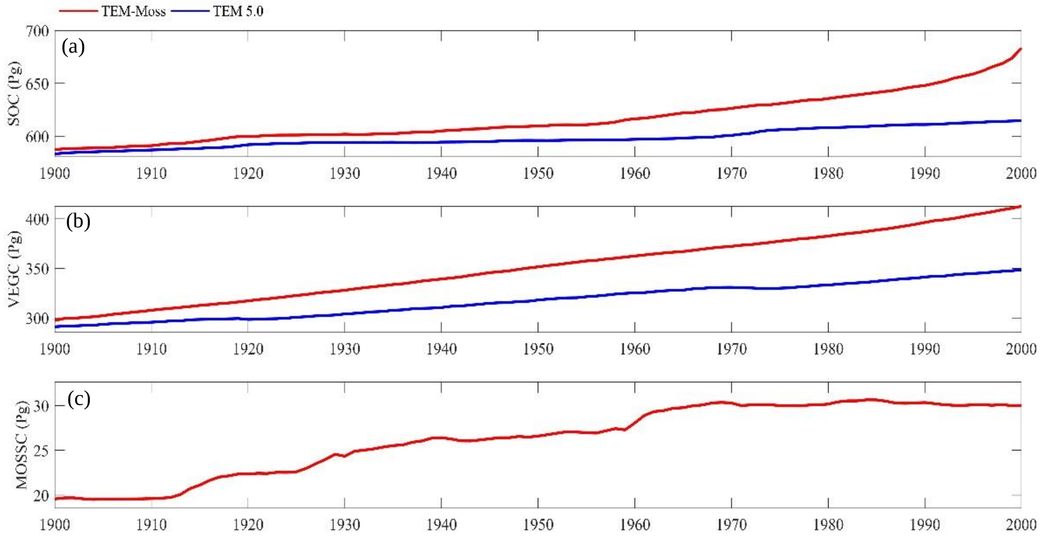


Figure 10. Simulated annual soil organic carbon (SOC, a), vegetation carbon (VEGC, b), and moss carbon (MOSSC, c) during the 20th century by TEM_Moss and TEM 5.0.

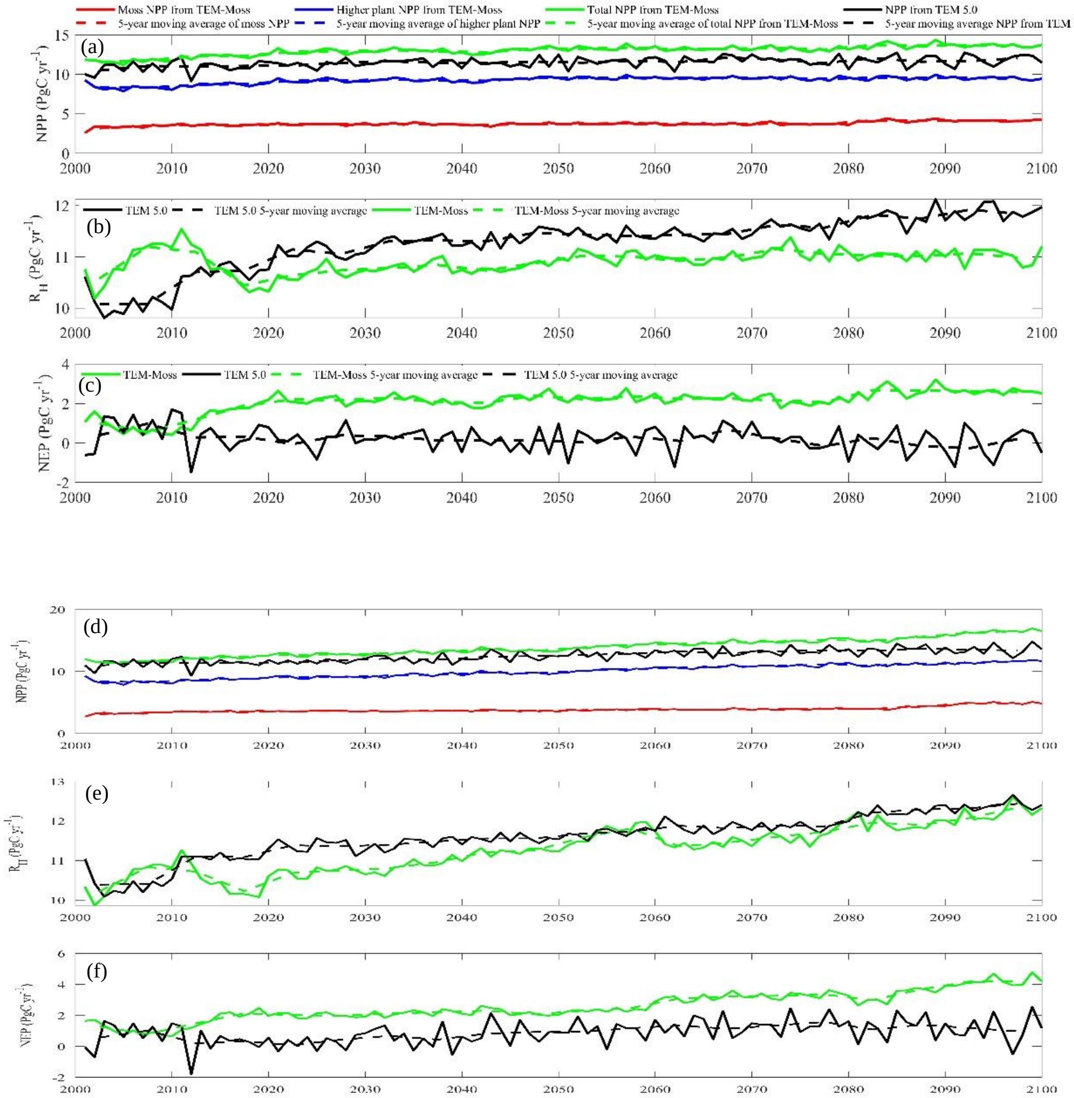


Figure 11. Predicted changes in carbon fluxes: annual net primary production (NPP, (a, d)), heterotrophic respiration (R_H, (b, e)), and net ecosystem production (NEP, (c, f)) during the 21st century under RCP 2.6 scenario (a, b, c, upper panel) and RCP 8.5 scenario (d, e, f, bottom panel) by TEM_Moss and TEM 5.0.

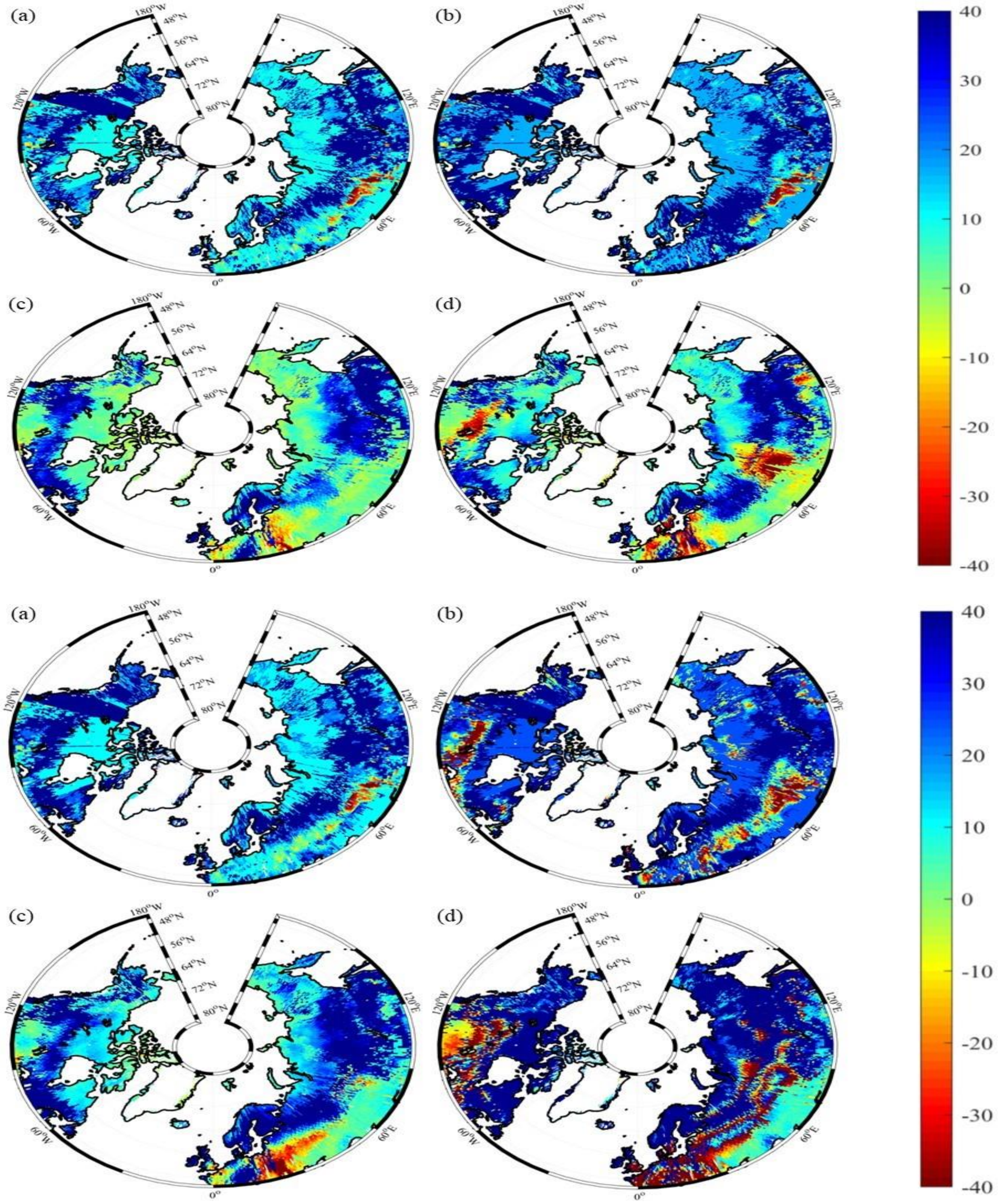


Figure 12. Spatial distribution of NEP simulated for the periods (a) 2000–2050, (b) 2051–2099 by TEM_Moss, and by TEM 5.0 (c, d) during the 21st century under RCP 2.6 scenario (upper panel) and RCP 8.5 scenario (bottom panel). Positive values of NEP represent sinks of CO_2 into terrestrial ecosystems, while negative values represent sources of CO_2 to the atmosphere.

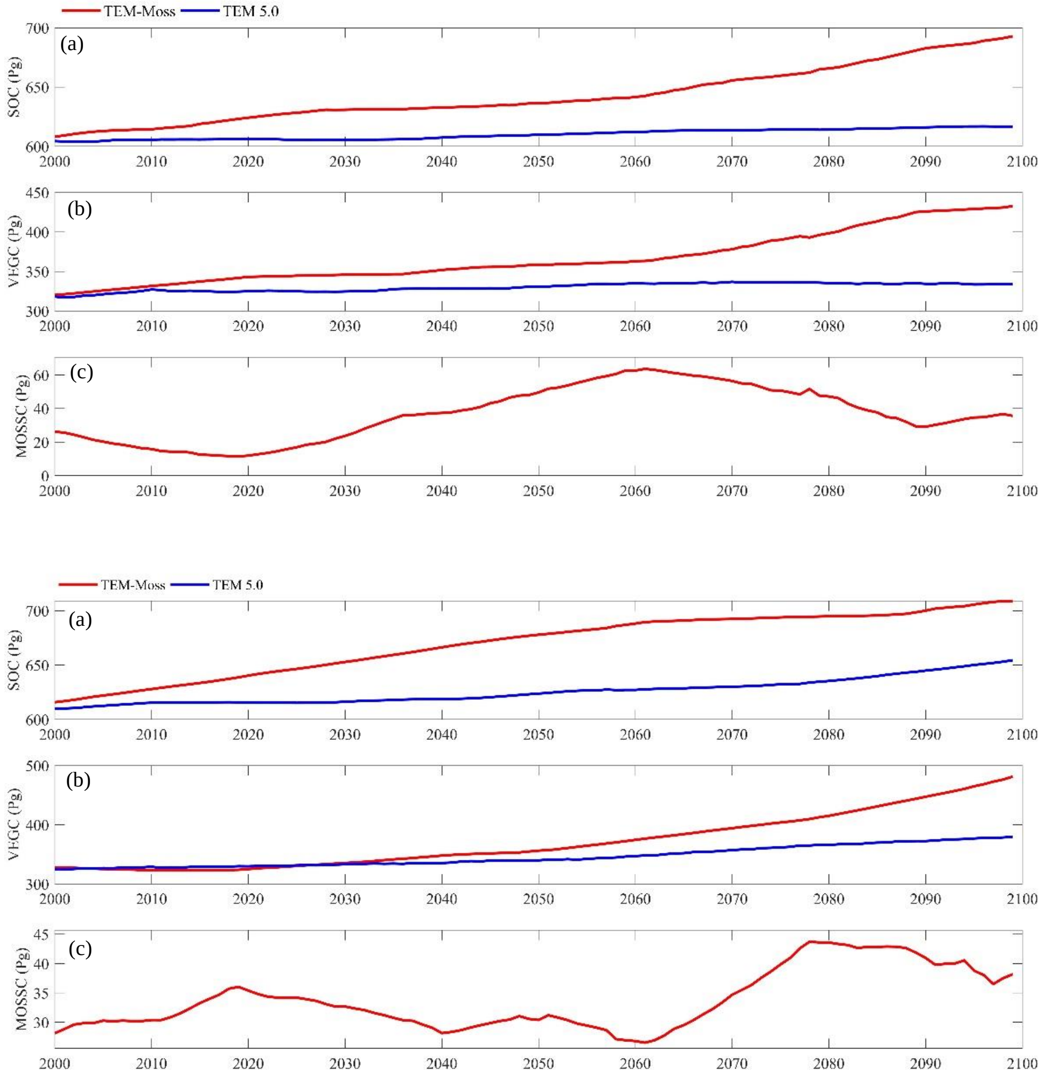
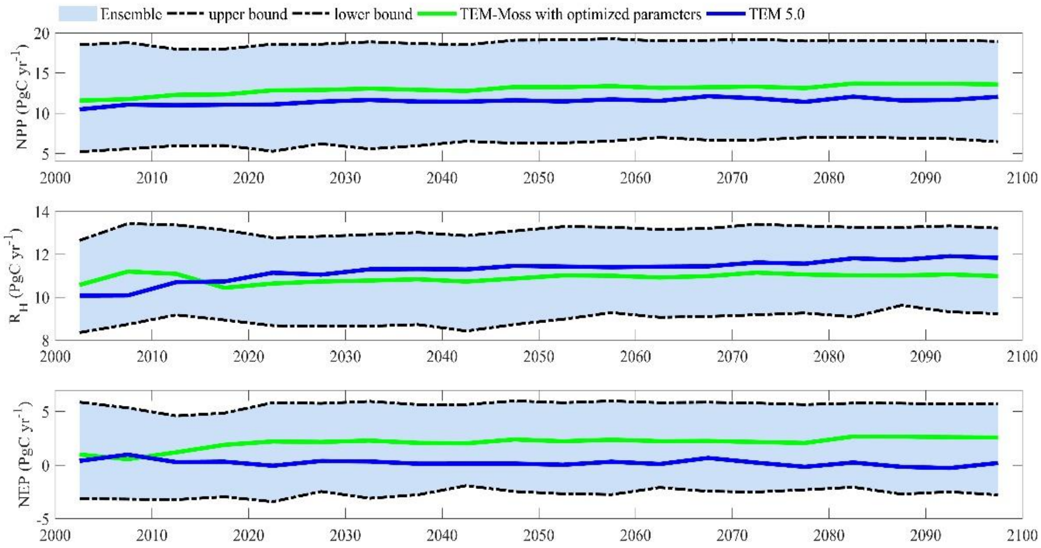


Figure 13. Simulated annual soil organic carbon (SOC, a), vegetation carbon (VEGC, b), and moss carbon (MOSSC, c) during the 21st century by TEM_Moss and TEM 5.0 under RCP 2.6 scenario (upper panel) and RCP 8.5 scenario (bottom panel).

(a)



(b)

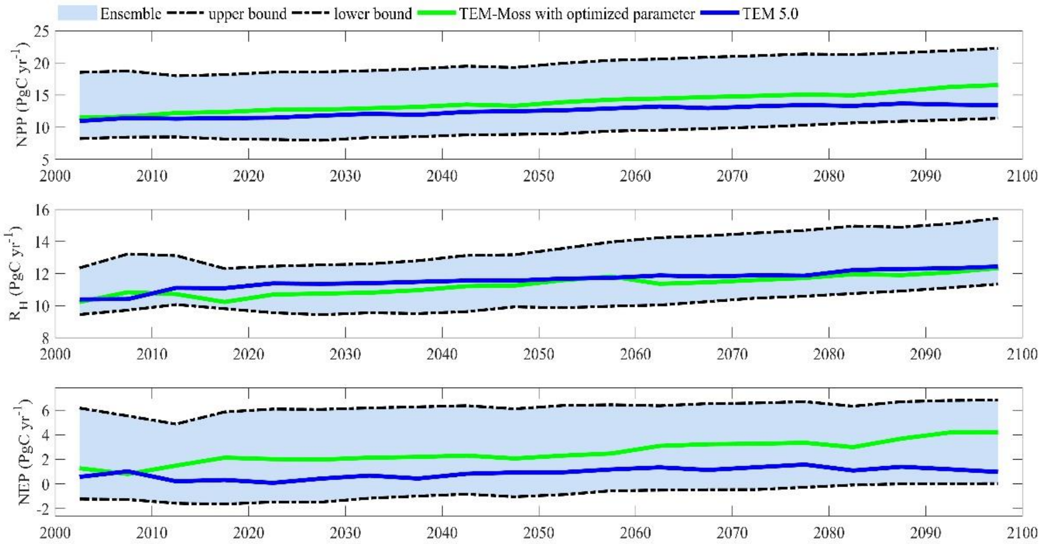


Figure 14. 5-year moving average plots for carbon fluxes under the (a) RCP 2.6 scenario and (b) RCP 8.5 scenario. The blue area represents the upper and lower bounds of simulations.

Table 1. Parameters associated with moss activities in TEM_Moss

Parameters	Units	descriptions	Parameter range (value)	references
C_{max}	gC m^{-2} mon^{-1}	maximum rate of C assimilation	[50,500]	Launiainen et al. (2015); Williams & Flanagan (1998)
b	μmol m^{-2} s^{-1}	Light half-saturation level	[5, 150]	Launiainen et al. (2015); Raich et al. (1991)
T_{min}	℃	minimum temperature	[-10, 10]	Frolking et al. (1996); Raich et al. (1991)
T_{max}	℃	maximum temperature	[30, 80]	Frolking et al. (1996); Raich et al. (1991)
T_{opt}	℃	optimal temperature	[15, 30]	Frolking et al. (1996); Raich et al. (1991)
w_{min}	mm	minimum water content for moss photosynthesis	[0.5, 15]	Frolking et al. (1996); Launiainen et al. (2015)
w_{max}	mm	maximum water content for moss photosynthesis	[150, 380]	Frolking et al. (1996); Launiainen et al. (2015)
w_{opt}	mm	optimal water content for moss photosynthesis	[10, 150]	Frolking et al. (1996); Zhuang et al. (2002)
k_m	μL/L	CO_2 concentration half-saturation level	[50, 500]	Zhuang et al. (2002); Raich et al. (1991)
$R_{10, m}$	gC m^{-2} mon^{-1}	moss respiration rate at 10 ℃	[0,40]	Frolking et al. (1996); Launiainen et al. (2015)
$Q_{10, m}$	–	moss respiration temperature sensitivity	[1.5, 2.5]	Frolking et al. (1996); Launiainen et al. (2015)
$w_{opt, r}$	mm	optimal water content for moss respiration	[10, 150]	Frolking et al., 1996; Zhuang et al. (2002)
$cfall_m$	g^{-1}g^{-1} mon^{-1}	constant proportion for carbon litterfall from moss	[0.001, 0.01]	Zhuang et al. (2002); Raich et al. (1991)
N_{max}	gN m^{-2} mon^{-1}	maximum rate of N uptake by mosses	[0.1,5]	Zhuang et al. (2002); Raich et al. (1991)
k_n	g m^{-2}	Half-saturation constant for N uptake by moss	1.0	Zhuang et al. (2002); Raich et al. (1991)
A_m	-	relative allocation of effort to C vs. N uptake	[0,1]	Raich et al. (1991)
w_f	mm	moss field capacity	[10, 80]	Frolking et al. (1996); Raich et al. (1991)
$nfall_m$	g^{-1}g^{-1} mon^{-1}	constant proportion for nitrogen litterfall from moss	[0.001, 0.01]	Zhuang et al. (2002); Raich et al. (1991)
D_m	mm	Moss thickness	[0, 100]	Zhuang et al. (2002)

Table 2. Site description and measured NEP data used to calibrate TEM_Moss

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 5.83̊ 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. (2010)
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 TEM_Moss

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 volumetric soil moisture data used to validate TEM_Moss

Site	Location (Longitude (degrees) /Latitude (degrees))	Elevation (m)	Vegetation type	Data range	Citations
US-Ivo	155.75W/ 68.49N	579	Alpine tundra	01/2015-12/2016	Oechel & Kalhori (2018)
BOREAS NSA-OBS	98.48W/ 55.88N	259	Boreal forest	07/1995-06/1997	Stangel & Kelly (1999)
NL-Loo	5.74E/ 52.17N	25	Temperate coniferous forest	05/1997-12/1998	Falge et al. (2005)
DK-Sor	11.64E/ 55.49N	40	Temperate deciduous forest	01/1997-12/1999	Falge et al. (2005)
US-Bkg	96.84W/ 44.35N	510	Grasslands	01/2005-12/2006	Gilmanov et al. (2005)
US-Atq	157.41W/ 70.47N	25	Wet tundra	01/2015-12/2016	Oechel & Kalhori (2018)

Table 5. Site description and measured soil temperature at 5cm depth data used to validate TEM_Moss

Site	Location (Longitude (degrees) /Latitude (degrees))	Elevation (m)	Vegetation type	Data range	Citations
US-Ivo	155.75W/ 68.49N	579	Alpine tundra	01/2015-12/2016	Oechel & Kalhori (2018)
BOREAS NSA-OBS	98.48W/ 55.88N	259	Boreal forest	01/1995-12/1998	Stangel & Kelly (1999)
US-Ho1	68.74W/ 45.2N	60	Temperate coniferous forest	01/1996-12/1997	Falge et al. (2005)
BE-Vie	6.0E/ 50.3N	493	Temperate deciduous forest	01/1997-12/1998	Falge et al. (2005)
US-Bkg	96.84W/ 44.35N	510	Grasslands	01/2005-12/2006	Gilmanov et al. (2005)
US-Atq	157.41W/ 70.47N	25	Wet tundra	01/2015-12/2016	Oechel & Kalhori (2018)

Table 6. Model validation statistics for TEM_Moss and TEM 5.0 at six sites with NEP data

Site Name	Vegetation type	Models	Intercept	Slope	R-square	Adjusted R-square	RMSE	p-value
Ivotuk	Alpine tundra	TEM_Moss	0.46	0.61	0.72	0.70	3.57	<0.001
		TEM 5.0	-0.22	0.75	0.43	0.41	5.88	0.02
UCI-1964 burn site	Boreal forest	TEM_Moss	-0.13	1.01	0.91	0.90	8.33	<0.001
		TEM 5.0	-2.45	1.29	0.75	0.74	20.1	<0.001
Howland Forest (main tower)	Temperate coniferous forest	TEM_Moss	-1.28	1.05	0.83	0.81	19.69	<0.001
		TEM 5.0	-2.22	0.97	0.62	0.61	31.23	0.002
Bartlett Experimental Forest	Temperate deciduous forest	TEM_Moss	-0.49	1.03	0.94	0.94	19.06	<0.001
		TEM 5.0	-2.49	1.04	0.91	0.89	23	<0.001
Brookings	Grassland	TEM_Moss	0.36	1.02	0.85	0.84	8.95	<0.001
		TEM 5.0	2.58	0.75	0.62	0.6	13.07	<0.001
Atqasuk	Wet tundra	TEM_Moss	-0.36	0.97	0.84	0.83	5.13	<0.001
		TEM 5.0	1.99	0.75	0.75	0.74	6.56	<0.001

Table 7. Model validation statistics for TEM_Moss and TEM 5.0 at six sites with volumetric soil moisture data

Site ID	Vegetation type	Models	Intercept	Slope	R-square	Adjusted R-square	RMSE	p-value
US-Ivo	Alpine tundra	TEM_Moss	8.56	0.34	0.74	0.72	20.8	<0.001
		TEM 5.0	10.67	0.29	0.64	0.62	21.76	<0.001
BOREAS NSA-OBS	Boreal forest	TEM_Moss	10.71	0.51	0.52	0.51	11.1	<0.001
		TEM 5.0	16.47	0.43	0.32	0.31	11.96	<0.001
NL-Loo	Temperate coniferous forest	TEM_Moss	0.47	0.82	0.83	0.81	4.0	<0.001
		TEM 5.0	3.75	0.72	0.49	0.48	4.5	<0.001
DK-Sor	Temperate deciduous forest	TEM_Moss	1.39	0.86	0.67	0.65	3.65	<0.001
		TEM 5.0	10.41	0.54	0.4	0.39	4.06	<0.001
US-Bkg	Grassland	TEM_Moss	5.64	0.8	0.51	0.49	6.05	<0.001
		TEM 5.0	22.24	0.41	0.21	0.2	7.34	0.027
US-Atq	Wet tundra	TEM_Moss	7.76	0.77	0.87	0.85	7.38	<0.001
		TEM 5.0	6.74	0.68	0.85	0.84	7.63	<0.001

Table 8. Model validation statistics for TEM_Moss and TEM 5.0 at six sites with soil temperature at 5cm depth data

Site ID	Vegetation type	Models	Intercept	Slope	R-square	Adjusted R-square	RMSE	p-value
US-Ivo	Alpine tundra	TEM_Moss	-0.34	1.16	0.83	0.82	2.54	<0.001
		TEM 5.0	0.54	1.36	0.75	0.73	3.94	<0.001
BOREAS NSA-OBS	Boreal forest	TEM_Moss	-0.05	0.91	0.9	0.88	2.24	<0.001
		TEM 5.0	0.27	0.81	0.84	0.82	2.9	<0.001
US-Ho1	Temperate coniferous forest	TEM_Moss	0.7	0.95	0.81	0.79	2.93	<0.001
		TEM 5.0	-0.06	0.99	0.77	0.76	3.41	<0.001
BE-Vie	Temperate deciduous forest	TEM_Moss	0.57	0.92	0.83	0.81	1.82	<0.001
		TEM 5.0	1.88	0.85	0.69	0.68	2.56	<0.001
US-Bkg	Grassland	TEM_Moss	0.17	0.87	0.91	0.89	2.87	<0.001
		TEM 5.0	-0.01	0.91	0.89	0.87	3.04	<0.001
US-Atq	Wet tundra	TEM_Moss	1.36	0.86	0.84	0.82	3.63	<0.001
		TEM 5.0	4.33	0.99	0.75	0.74	6.17	<0.001

Table 9. Average annual NPP, R_H and NEP (as Pg C per year) during the 20th century estimated by two models.

Average annual carbon fluxes (PgC yr^{-1})		TEM_Moss	TEM 5.0	Difference	Moss NPP/ ~~Higher plant~~Vascular plants NPP
NPP	Moss NPP	1.69	-	-	21.3%
	~~Higher plant~~Vascular plants NPP	7.93	8.8	-	
	Total NPP	9.6	8.8	0.8	
R_H		7.38	7.91	-0.53	
NEP		2.22	0.89	1.33	

Table 10. Increasing of SOC, vegetation carbon (VGC), and moss carbon (MOSSC) from 1900 to 2000, and total carbon storage during the 20th century predicted by two models.

Models	Carbon pools	Carbon pool amounts in 1900/2000 (units: Pg)	Changes in carbon pools during the 20th century (units: Pg)
TEM_Moss	SOC	587.1/683.4	96.3
	VEGC	297.5/412.7	115.2
	MOSSC	19.6/30	10.4
	Total	904.2/1126.1	221.9
TEM 5.0	SOC	583.2/614.9	31.7
	VEGC	291.1/348.6	57.5
	Total	874.3/963.5	89.2

Table 11. Average annual NPP, R_H and NEP (as Pg C per year) during the 21st century estimated by two models under (a) RCP 8.5 scenario and (b) RCP 2.6 scenario.

(a)

Average annual carbon fluxes (PgC yr^{-1})		TEM_Moss	TEM 5.0	Difference	Moss NPP/ ~~Higher plant~~Vascular plants NPP
NPP	Moss NPP	3.84	-	-	38.4%
	~~Higher plant~~Vascular plants NPP	10	12.53	-	
	Total NPP	13.84	12.53	1.31	
R_H		11.28	11.54	-0.21	
NEP		2.56	0.99	1.57	

(b)

Average annual carbon fluxes (PgC yr^{-1})		TEM_Moss	TEM 5.0	Difference	Moss NPP/ ~~Higher plant~~Vascular plants NPP
NPP	Moss NPP	3.74	-	-	40.5%
	~~Higher plant~~Vascular plants NPP	9.24	11.52	-	
	Total NPP	12.98	11.52	1.46	
R_H		10.91	11.24	-0.33	
NEP		2.07	0.28	1.79	

Table 12. Increasing of SOC, vegetation carbon (VGC), and moss carbon (MOSSC) from 1900 to 2000, and total carbon storage during the 21st century predicted by two models under (a) RCP 2.6 scenario and (b) RCP 8.5 scenario.

(a)

Models	Carbon pools	Carbon pool amounts in 2000/2099 (units: Pg)	Changes in carbon pools during the 21st century (units: Pg)
TEM_Moss	SOC	608.1/692.8	84.7
	VEGC	320.2/432.8	112.6
	MOSSC	26.2/35.6	9.4
	Total	954.5/1161.2	206.7
TEM 5.0	SOC	604.4/616.5	12.1
	VEGC	318.2/333.7	15.5
	Total	922.6/950.2	27.6

(b)

Models	Carbon pools	Carbon pool amounts in 2000/2099 (units: Pg)	Changes in carbon pools during the 21st century (units: Pg)
TEM_Moss	SOC	615.9/708.4	92.5
	VEGC	327.8/481.4	153.6
	MOSSC	28.1/38.2	10.1
	Total	971.8/1228.0	256.2
TEM 5.0	SOC	610.2/654.4	44.2
	VEGC	324.9/379.4	54.5
	Total	935.1/1033.8	98.7