General comments

This study updates an existing ecosystems model (TEM 5.0) to account for mosses - including moss photosynthesis and respiration, and the influence of the moss layer on soil temperature, moisture and ecosystem N dynamics. The updated model (TEM-Moss) is then used to simulate future carbon dynamics for northern high latitudes, and by comparing the TEM-Moss simulations to those from TEM 5.0, the authors aim to understand the role of mosses in determining the future carbon balance of the region.

This is an important topic – forecasting northern high latitude C dynamics is critical for understanding global change, and mosses are an important component of northern vegetation. Attempting to understand the role of mosses on such a broad scale is novel; there has been some work incorporating the thermal properties of mosses in land-surface models, but I'm not aware of any similar analyses at this scale. It's an ambitious study and in general the manuscript is well structured and logically presented.

My main criticism is around how the TEM-Model is calibrated and validated, and whether the comparison to TEM 5.0 is valid. It may be that I haven't understood the methods fully, but it seems TEM-Moss is based on ecosystem-level calibrations of the 'moss parameters', but TEM 5.0 is not based on representative ecosystem level calibrations. If this is the case, it doesn't make sense to compare the performance of the two models. It also means that the calibrated 'moss parameters' will be compensating for un-calibrated 'non-moss parameters' i.e. the optimal moss parameters for an ecosystem will likely reflect differences in the properties of the higher plant vegetation which have not been captured by the 'default' version of TEM 5.0.

In conclusion, I think the aims of the study are worthwhile, and the general approach to update TEM 5.0 is valid, but a more robust model analysis is needed.

Specific comments

I've made line by line comments below which I hope will be helpful in revising the paper.

Line 41: Define northern high latitudes and the types of ecosystems that are included in the study.

Response: Thanks for your comments and suggestions. We changed the sentence to "Northern high latitude ecosystems, which refers to the land ecosystems (>45 ºN) in northern temperate, boreal, grassland and tundra regions".

Line 43. Add some text to highlight the uncertainty around the 1024 Pg figure.

Response: We revised the sentence as "contain as much as 1024 Pg soil organic carbon from 0 to 3 m depth".

Line 44-47. "This large amount of carbon is potentially responsive to ongoing global warming". The references supporting this statement are quite old, please cite some more recent literature (e.g. Burke et al., 2017, Koven et al., 2015, Comyn-Platt et al., 2018)

Response: Following suggestions, we updated the references.

Line 154: Please provide more detail on the function f(NA).

Response: We added "which is a scalar function that depends on monthly N available for incorporation into plant production of new tissue" to describe f(NA).

Line 238: "higher plants" rather than "higher vegetations".

Response: We revised it.

Line 238: Did you use a single set of default parameters for the standard TEM model? I'm not sure I follow the reasoning here. Zha and Zhuang 2018 is an arctic study, yet you are using data from temperate forests and grasslands to calibrate TEM-Moss. Did you use the same set of default parameters across all sites? And did you use any other site-level information – apart from the NEP data – when calibrating the model?

Response: For TEM 5.0 simulations, we used different sets of default parameters for each vegetation type. Zha and Zhuang (2018) focused on the same region, but we parameterized that TEM version with site level information. In this study, we used site level data to parameterize TEM_Moss, but use the default parameterization of TEM 5.0 to compare with TEM-Moss simulations. Site-level parameterization was conducted based NEP data in addition to site level vegetation and soil information. Some site level data of NEP were used for model validation. Additionally, soil temperature and moisture at validation sites were also evaluated.

Line 247: I don't fully understand how the posterior parameter distributions were generated. As I understand it, the SCE algorithm provides a point-estimate for each parameter, then you treat the 50 independent point estimates as samples from a posterior parameter distribution? Is this correct? Please provide some clarification on this in the text. Please also update the legend in figure 4 – what probabilities do the boxes and tails represent?

Response: Yes, the posterior parameter distribution is just the distribution for the 50 independent point estimates. We added the explanation to boxes and whiskers into the figure caption "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."

Line 250: Zhuang 2010 is a study from the Tibetan plateau, and Zhuang 2015 is northern high latitude wetlands. How do you justify using (I assume calibrated?) parameters from these studies to model C and N dynamics at temperate forest and grassland sites?

Response: The correct citation is Zhuang et al. (2003).

Zhuang, Q., A. D. McGuire, J. M. Melillo, J. S. Clein, R. J. Dargaville, D. W. Kicklighter, R. B. Myneni, J. Dong, V. E. Romanovsky, J. Harden, J. E. Hobbie (2003) Carbon cycling in extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th Century: A modeling analysis of the influences of soil thermal dynamics, Tellus, 55B, 751-776, 2003

Line 266: please explain in more detail how the six site-level calibrations for TEM-Moss are applied to the pixel by pixel simulation. Is this on the basis of vegetation class?

Response: Yes. We added a sentence "With six site-level calibrated parameters, TEM-Moss is applied to the region pixel by pixel based on vegetation distribution data.".

Line 289: If I understand correctly, TEM-Moss uses calibrated parameters for the representative ecosystems, but TEM 5.0 uses a single set of default parameters. If this is the case, it is not surprising that TEM-Moss performs better than TEM 5.0 in the validation exercise.

Response: TEM 5.0 also used the calibrated parameters for representative ecosystems and extrapolated to the region based on the same set of data of vegetation distribution.

Line 359: The number for RH for TEM 5.0 is not correct, and the figure reference should be figure 11b.

Response: We corrected the number. But the figure is figure 11a.

Line 412-414: These figures for the moss percentage contribution to NPP seem very high. 20 % of NPP may be realistic for boreal forest (note the Turetsky study is 20% of aboveground NPP, which is probably < 10 % of total NPP) but your study covers the entire northern latitudes from 45oN. Is a moss contribution of >25 % of 21st century NPP really plausible? I would want to see a much more thorough discussion of this, with references to observed data from a wider range of representative ecosystems.

Response: Thanks for the comments. Yes, Turetsky et al. (2010) suggested an average contribution of 20% of aboveground NPP from moss in boreal forests. Frolking et al. (1996) even reported a contribution of 38.4% to total NPP by moss at a boreal forest site. These estimates are for the historical periods and our estimates of 17.6% of NPP in the 20th century is at the lower end of their estimates. Our estimates of 28.8% and 27.6% in the 21st century under the RCP 2.6 410 and RCP 8.5 scenarios, respectively, are still similar to the range of existing estimates for the historical period.

Turetsky et al. (2010) conducted a long-term data analysis through literature synthesis, representing a good knowledge about moss contribution to both wetlands and upland ecosystems in Alaska. They found that mosses contributed 48% and 20% of wetland and upland productivity, respectively. In this revision, we revised the sentence to "This is comparable with the results reported by a synthesis study, indicating an average contribution of 20% of aboveground NPP from moss in upland boreal forests and the contribution is 48% in wetlands ecosystems."

Line 440: Changing vegetation is a key limitation, I recommend adding some more discussion here on the likely changes in moss abundance as climate warms, e.g. with respect to changing temperature/ hydrology/ shading by vascular plants.

Response: Thanks for the suggestion. We added a few references to explicitly discuss the potential the impacts of moss distribution and abundance on carbon budget in the region. In this revision, we also added the following to further discuss the impacts of vegetation including mosses on carbon dynamics in the region. "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). "

1 **Quantifying the role of moss in terrestrial ecosystem carbon dynamics in**

2 **northern high-latitudes**

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8 **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 °N) 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

63 ~~act~~ in (~~as a~~ carbon sink or source~~)~~ activities ha~~sve~~ not yet reached a consensus due to a number

64 of model limitations (Cahoon et al., 2012; Hayes et al., 2011; Todd-Brown et al., 2013).

65   One limitation is that ecosystems models often ignore some important components such

66 as understory processes that play crucial roles in biogeochemical cycles (Zhuang et al., 2002;

67 Treseder et al., 2011; Bond-Lamberty et al., 2005). For instance, mosses are ubiquitous in

68 northern ecosystems, and show a pattern of increasing abundance with increasing latitude

69 (Turetsky et al., 2012; Jägerbrand et al., 2006). Their functional traits, including tolerance to

70 drought and a broad response of net assimilation rates to temperature, allow them to persist in

71 high-latitude regions (Kallio and Heinonen, 1975; Harley et al., 1989). The activities of moss

72 that are related to water, nutrient~~s~~, and energy may influence several ecosystem processes such

73 as permafrost formation and thaw, peat accumulation, soil decomposition and net primary

74 productivity (NPP) (Turetsky et al., 2012; Nilsson and Wardle, 2005). Mosses can have positive

75 or negative interactions with vascular plants (Skre and Oechel, 1979; Turetsky et al., 2010). On

76 the one hand, mosses compete with vascular plants for available nutrients, negatively affecting

77 vascular plant~~s~~ productivity (Skre and Oechel, 1979; Gornall et al., 2011; Turetsky et al., 2012).

78 Besides, a thick moss cover can form an environment with water logging or low oxygen supply,

79 which is common in high-latitude regions (Skre and Oechel, 1979; Cornelissen et al., 2007). The

80 moss cover prevents absorbed solar heat from being conducted down into the soil, and tends to

81 decrease soil temperature in summer. Therefore, soil decomposition rates can be affected since

82 they are mediated by soil temperature, which will further influence growth of vascular plants

83 (Gornall et al., 2007). On the other hand, some species of mosses can serve as an important

84 source of nitrogen because of their associations with microbial nitrogen fixers ~~because of their~~

85 ~~ability of facilitating biological nitrogen fixation and their low nitrogen-use efficiency~~ (Basilier,

86   1979; DeLuca et al., 2007; Markham, 2009; Kip et al., 2011). Thus, mosses can also exert

87   positive effects on plant growth due to their regulation ofon nitrogen availability for vascular

88   plants (Hobbie et al., 2000; Gornall et al., 2007). It is gradually being recognized that mosses can

89   have comparable influences on high-latitude ecosystems to vascular plants, due to their large

90   density and essential function in plant competition, soil climate, and carbon and nutrient cycling

91   (Longton, 1988; Lindo and Gonzalez, 2010; Okland, 1995; Pharo and Zartman, 2007). They can

92   on average contribute 20% of aboveground NPP in boreal forests (Turetsky et al., 2010), and

93   their annual NPP may reach as high as 350 g C m^{-2} in some regions in the Arctic (Pakarinen and

94   Vitt 1973), even exceeding that of vascular plants (Oechel and Collins, 1976; Clarke et al.,

95   1971). Thus, ignorance of mosses, the keystone species of boreal ecosystems, can pose large

96   biases in model predictions and limit the utility of models. To date, a number of ecosystem

97   models have already included moss activities to explore the response of moss to disturbance

98   (Bond-Lamberty et al., 2007; Euskirchen et al., 2009; Frolking et al., 2010, Wania et al., 2009,

99   Chadburn et al., 2015, Porada et al., 2016, Druel et al., 2017), or improve model prediction of

100   carbon dynamics (Bond-Lamberty et al., 2005). However, the potential role of moss in the

101   regional carbon dynamics in northern high latitudes has been slowly evaluated by considering

102   the interactions between moss and higher plantvascular plants, especially with respect to their

103   competition for water, nutrient and energy.

104   This study developed a new version of Terrestrial Ecosystem Model (Raich et al., 1991;

105   McGuire et al., 1992; Zhuang et al., 2001, 2002, 2010, 2013, 2015), hereafter referred to as

106   TEM_Moss, by explicitly considering moss impacts on terrestrial ecosystem carbon dynamics.

107   The interactions and competition of water, energy and nutrient between higher plantvascular plants

108   and mosses are explicitly modeled. The verified TEM_Moss and previous TEM were compared

109   against the observed data of ecosystem carbon, soil temperature and moisture dynamics. Both

110   models were then used to analyze the regional carbon dynamics in northern high latitudes (north

111   of 45 „N) during the 20th and 21st centuries.

2. Methods

2.1 Overview

114   First, we briefly describe how we developed the TEM_Moss by modifying the previous

115   TEM 5.0 to consider their interactions between ~~higher plant~~vascular plants and mosses. Second,

116   parameterization and validation of TEM_Moss using measured gap-filled carbon flux data and

117   meteorological data at representative sites is presented. Third, we present how we have applied

118   both models (TEM_Moss and TEM 5.0) to the northern high latitudes (above 45 °N) to quantify

119   regional carbon dynamics during the 20th and 21st centuries.

2.2 Model description

121   TEM is a process-based, large-scale biogeochemical model that uses monthly climatic data

122   and spatially explicit vegetation and soil information to simulate the dynamics of carbon and

123   nitrogen fluxes and pool sizes of plants and soils (Raich et al., 1991; McGuire et al., 1992; Zhuang

124   et al., 2010, 2015, 2020). However, in previous versions of TEM, the interactions between mosses

125   and ~~higher plant~~vascular plants on carbon and nitrogen cycling have not been included. Here we

126   developed a TEM_Moss model by modifying model structure and incorporating activities of moss

127   into extant TEM 5.0 (Zhuang et al., 2003). Based on the structure of TEM 5.0, we added carbon

128   and nitrogen pools and fluxes to simulate activities of moss including photosynthesis, respiration,

129   litterfall and nutrient and water cycling (Figure 1). Thus, the structure of TEM_Moss includes the

130   processes of both ~~higher plant~~vascular plants and mosses (Figure 1).

131   In TEM_Moss, moss photosynthesis (C_A) is described as a maximum rate, reduced by

132   influence of photosynthetically active radiation, mean air temperature, mean atmospheric carbon

133   dioxide concentrations, moss moisture, and indirectly, nitrogen availability (Frolking et al., 1996;

134   Launiainen et al., 2015; Zhuang et al., 2002). For each time step, C_A is calculated as:

135                     $$C_A = C_{max} \cdot f(PAR) \cdot h(T) \cdot g(M) \cdot n \qquad (1)$$

136   where C_{max} denotes the maximum rate of carbon assimilation by moss (units: gC m^{-2}mon^{-1}),

137    $f(PAR)$ is a scalar function that depends on monthly photosynthetically active radiation (PAR),

138   which is calculated as (Frolking et al., 1996; Launiainen et al., 2015; Kulmala et al., 2011):

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

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

141   the Michaelis–Menten kinetic.

142   The temperature effect on moss photosynthesis is modeled as a multiplier (Frolking et al.,

143   1996; Raich et al., 1991):

144                     $$h(T) = \frac{(T - T_{min})(T - T_{max})}{(T - T_{min})(T - T_{max}) - (T - T_{opt})^2} \qquad (3)$$

145   where T is the monthly mean air temperature (units: ºC), and T_{min}, T_{max}, and T_{opt} are parameters

146   (units: ºC) that limit h(T) to a range of zero to one.

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

148   1991):

149                     $$g(M) = \frac{M}{M + k} \qquad (4)$$

150   where $_3$ is moss moisture (units: mm), and w_{min}, w_{max}, and w_{opt} are related parameters (units:

151   mm) that limit $h(w_m)$ to a range of zero to one.

152     $h([CO_2])$ is also a scalar function that depends on monthly mean atmospheric carbon

153   dioxide concentration (Zhuang et al., 2002; Raich et al., 1991):

154                               $_{\llcorner}$ #   ————   (5)

155   where $[CO_2]$ (units: µL/L) represents monthly mean atmospheric carbon dioxide concentration,

156   the k_m (units: µL/L) is the internal CO_2 concentration at which moss C assimilation proceeds at

157   one-half its maximum rate.

158   The function $h(NA)$ models the limiting effects of plant nitrogen status on GPP (McGuire

159   et al., 1992; Zhuang et al., 2002), which ~~is a unitless multiplier.~~ is a scalar function that depends

160   on monthly N available for incorporation into plant production of new tissue.

161   Meanwhile, in TEM_Moss, we defined the moss respiration rate (R_m) as a function of

162   moss respiration rate at 10 °C, moss respiration temperature sensitivity which was expressed as a

163   Q_{10} function, and moss moisture (Launiainen et al., 2015; Frolking et al., 1996):

164   &   &   %   ———— $_3$ (6)

165   where &   (units: $gC\ m^{-2}mon^{-1}$) represents the moss respiration rate at 10 °C, the parameter

166   %   is moss respiration temperature sensitivity, T_m is moss temperature (°C) and $_3$ is moss

167   moisture (mm).

168   The function $_3$ · denotes the moisture effect on moss respiration. Here we used

169    $_3$ · to distinguish with the function $_3$, which is moisture effect on moss

170 photosynthesis as mentioned earlier. ^{3} · is defined as (Frolking et al., 1996; Zhuang et al,

171 2002):

172 ^{3} ___________ (7)

173 where ^{3} (units: mm) denotes the optimal water content for moss respiration.

174 Besides, the carbon in litter production from mosses to soil (ž) is modeled as

175 proportional to moss carbon biomass with a constant ratio (Zhuang et al., 2002):

176 ž · œ ¢ š ¨! ¨# ' ' ‗ (8)

177 where MOSSC denotes the moss carbon biomass, and $cfall_m$ is the corresponding constant

178 proportion.

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

180 ─── fi $ $ & ž (9)

181 On the other hand, researches have shown that mosses can uptake substantial inorganic

182 nitrogen from the bulk soil (Ayres et al., 2006, Fritz et al., 2014). In our model, nitrogen uptake

183 by moss ($Nuptake_m$) is modelled as a function of available soil nitrogen, moss moisture, and

184 mean air temperature, and the relative amount of energy allocated to N versus C uptake (Zhuang

185 et al., 2002; Raich et al., 1991):

186 " ± ¬ ° š §"¡ ───── ¡ ° (10)

187 Where N_{max} is the maximum rate of nitrogen uptake by mosses (units: $gC\ m^{-2}mon^{-1}$), and N_{av}

188 (units: $g\ m^{-2}$) represents available soil nitrogen, which is treated as a state variable in our model.

189   § (units: g m^{-2}) is the concentration of available soil nitrogen at which nitrogen uptake proceeds

190   at one-half its maximum rate. T is the monthly mean air temperature (^{o}C), and A_m is a unitless

191   parameter ranging from 0 to 1, which represents relative allocation of effort to carbon vs.

192   nitrogen uptake. K_s is a parameter accounting for relative differences in the conductance of the

193   soil to N diffusion, which can be calculated through moss moisture (Zhuang et al., 2002; Raich et

194   al., 1991):

195   Ž   ——   (11)

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

197   The nitrogen in litter production from mosses to soil (ž   ) is modeled as proportional to

198   moss nitrogen biomass with a constant ratio (Zhuang et al., 2002):

199   ž   ·   ª ¢ Š ¨!¨#' ' ¨   (12)

200   where nfall$_m$ is the constant proportion to moss nitrogen biomass (MOSSN).

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

202   ———   " ± ¬ ° Š §ž¡   (13)

203   At the same time, total carbon and nitrogen in litterfall, and total nitrogen uptake from

204   soil available nitrogen are changed due to incorporation of mosses:

205   ž ¥ ° ° ¡ ®ž¢ Š ¨ž¨   (14)

206   ž ¥ ° ° ¡ ®ž¢ Š ¨ž¨   (15)

207   " ± ¬ ° Š '§ ‡ ¬ ° Š § ¡± ¬ ° Š §(16)

208 Where $\check{z}$ and $\check{z}$ are carbon and nitrogen in litter production from ~~higher plant~~vascular

209 plants to soil, and $¨ ± ¬ ° \check{S} is §nitrogen$ uptake by ~~higher plant~~vascular plants (Raich et al., 1991;

210 Melillo et al., 1993; Zhuang et al., 2003).

211   Except above equations, other governing equations in TEM 5.0 have not been changed.

212 More equations of TEM 5.0 have been documented in previous studies (Raich et al., 1991;

213 McGuire et al., 1992; Zhuang et al., 2003; Zha and Zhuang, 2018).

214   In TEM 5.0, a soil thermal module (STM) simulates soil thermal dynamics considering

215 the effects of moss thickness, soil moisture, and snowpack (Zhuang et al., 2001, 2002). In STM,

216 soil profile was treated as a three soil-layer system: (1) a moss plus fibric soil organic layer, (2) a

217 humic organic soil layer, and (3) a mineral soil layer, and temperature for each layer can be

218 derived from STM (Zhuang et al., 2001, 2002, 2003). Temperature in moss layer is estimated

219 with STM.

220   A water balance module (WBM) was also incorporated into TEM 5.0 to simulate soil

221 hydrologic dynamics (Vörösmarty et al., 1989; Zhuang et al., 2001). The WBM receives

222 information on precipitation, air temperature, potential evapotranspiration, vegetation, soils and

223 elevation to predict soil moisture evapotranspiration and runoff (Vörösmarty et al., 1989). The

224 whole soil was treated as a single profile in WBM (Vörösmarty et al., 1989; Zhuang et al., 2001).

225 To simulate moss moisture, we added a moss layer on the soil profile by modifying the WBM

226 (Figure 2). Similar to soil moisture, moss moisture is also treated as a state variable in the revised

227 WBM, which is modeled as:

228 $$\overline{\quad\quad} \quad ¯ ^{a} « ^{3} ₵ ® \check{S} ¥ ^{a} ₢ \check{S} ¨®¨œ« \quad ¨ ℗ ‰ ¥_¡ «^{2a}\check{S} ¬ « ° ® \check{S} ^{a} ¯ \quad (17) ® \check{S} ° ¥ « ^{a}$$

229 where the term "percolation" denotes the percolation from moss, which is the sum of rainfall

230 percolation and snowmelt percolation from moss. We assume that there is no runoff from moss

231 layer.

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

233 $$\overline{} \quad \neg_i \quad ^{®}\text{œ}« \quad ^{¨} \quad ^{®}Š \quad ¥ \quad ^{₴}_{«} \quad \text{œ}_i \quad ^{-\;ª} \quad «_i^{\;3\;´} \quad \text{œ}_i \quad ^{-\;-} \quad Š_i \quad ^{a2\;°}Š \quad \neg \quad « \quad ^{°} \quad ^{®}Š \quad ^{a\;-} \quad \neg \; (¥8\text{Š} \quad ^{°} \quad ¥ \quad « \quad ^{a}$$

234 Calculations for these water fluxes regarding ~~higher plant~~vascular plants were not changed. More

235 details about an earlier version of WBM were described in Vörösmarty et al. (1989) and Zhuang

236 et al. (2001).

2.3 Model parameterization and validation

238   The newly introduced parameters that are associated with moss activities were documented

239 in Table 1. We parameterized the TEM_Moss for six representative ecosystem types in northern

240 high latitudes with gap-filled monthly net ecosystem productivity (NEP, $gCm^{-2}mon^{-1}$) data from

241 the AmeriFlux network (Davidson et al., 2000). We assumed that the moss types are associated

242 with the representative ecosystem types, which means we tuned the moss-related parameters for

243 the six representative ecosystem types. Except for the moss-related parameters, other parameters

244 related to vascular ~~high~~ plants~~vegetations~~ are default based on Zha and Zhuang, 2018. The

245 information of six sites that we chose to calibrate the TEM_Moss was compiled in Table 2. The

246 parameterization was conducted using a global optimization algorithm known as SCE-UA

247 (Shuffled complex evolution) method, which aims to minimize the difference between model

248 simulations and measurements (Duan et al., 1994). In our calibration, the cost function of the

249 minimization is:

250                                   $\# \rangle \vdots \qquad " \vdots \$ \qquad " \vdots \$$ (19)

251   Where $" \vdots \$$ and $" \vdots \$$ are the measured and simulated NEP, respectively. k is the number

252   of data pairs for comparison. Fifty independent sets of parameters were converged to minimize the

253   objective function, and finally the optimized parameters were derived as the mean of these 50 sets

254   of inversed parameters. We presented the boxplot of parameter posterior distributions at sites

255   chosen for calibration (Figure 4). At the same time, the results of model parameterization were

256   shown in Figure 3. Besides these parameters related to moss, all other parameters use their default

257   values in TEM 5.0 (Zhuang et al., ~~2010,~~ 2015). These optimized parameters were used for model

258   validation and extrapolation.

259   We verified the TEM_Moss simulated NEP, soil moisture and soil temperature. First, we

260   conducted site-level simulations at six sites that contain level-4 gap-filled monthly NEP data from

261   the AmeriFlux network (Table 3). Site-level monthly gap-filled soil moisture and soil temperature

262   data were organized from the ORNL DAAC Dataset (https://daac.ornl.gov/) to make comparison

263   with model simulations (Table 4 and Table 5). Local climate data including monthly air

264   temperature (^{o}C), precipitation (mm), and cloudiness (%) were obtained to drive these model

265   simulations.

266   2.4 Regional Extrapolation

267   With six site-level calibrated parameters, TEM-Moss is applied to the region ~~the~~ pixel by pixel

268   based on ~~simulation on the basis of~~ vegetation distribution data~~class~~. Both TEM_Moss and TEM

269   5.0 were applied to northern high latitudes (above 45 °N) for historical (the 20th century) and future

270   (the 21st century) quantifications on carbon dynamics. For historical simulations, climatic forcing

271   data including monthly air temperature, precipitation, and cloudiness and atmospheric CO_2

272   concentrations during the 20th century, were collected from the Climatic Research Unit (CRU

273   TS3.1) from the University of East Anglia (Harris et al., 2014). Other ancillary inputs including

274   gridded soil texture (Zhuang et al., 2015), elevation (Zhuang et al., 2015), and potential natural

275   vegetation (Melillo et al., 1993) were also organized. For future simulations, two contrasting

276   Intergovernmental Panel on Climate Change (IPCC) climate scenarios (RCP 2.6 and RCP 8.5)

277   were used to drive the models. The future climate forcing data and atmospheric CO_2 concentrations

278   during the 21st century under these two climate change scenarios were derived from the

279   HadGEM2-ESmodel, which is a member of CMIP5project213 (https://esgf-

280   node.llnl.gov/search/cmip5/, January 2017).

281   Simulations were conducted at a spatial resolution of 0.5° latitude × 0.5° longitude (Zhuang

282   et al., 2001, 2002). A spin-up was run to reach an equilibrium for each pixel, and the values of state

283   variables at equilibrium were treated as initial values for transient simulations (McGuire et al.,

284   1992). Specifically, we chose the first 30 years in the whole 100-year climatic forcing data to spin-

285   up the models when conducting historical and future simulations. For each of the simulations, net

286   primary production (NPP), heterotrophic respiration (R_H), and net ecosystem production (NEP)

287   were analyzed. We denoted that a positive NEP represents a CO_2 sink from the atmosphere to

288   terrestrial ecosystems, while a negative value represents a source of CO_2 from terrestrial

289   ecosystems to the atmosphere.

290   In these simulations, for each pixel, we assumed its moss distribution area is the same as

291   the ~~higher plant~~vascular plants distribution. The total carbon uptake/emission of mosses in a pixel

292   are calculated as the multiplication of pixel area with the carbon fluxes such as NEP (units: gC m^{-}

293   ^{2} month^{-1}). Moss-related parameters for representative ecosystems are calibrated (Fig. 4 and Table

294   1) or obtained from previous model parameterization and the rest of model parameters are default

295   from Zha and Zhuang (2018).

296   **3. Results**

297   **3.1 Model Validation**

298   TEM_Moss was able to reproduce the monthly NEP and performed better than TEM 5.0

299   at chosen sites, with larger R-square values and smaller RMSE (Figure 5, Table 6). R-square for

300   TEM_Moss reached 0.94 at Bartlett Experimental Forest site and 0.72 at Ivotuk site (Table 6). R-

301   square values for TEM 5.0 showed a similar pattern, reaching 0.91 and with minimum value of

302   0.43 at Bartlett Experimental Forest and Ivotuk sites, respectively (Table 6). Except for Ivotuk

303   site, R-squares for TEM_Moss are all higher than 0.8 at the chosen sites, while most R-squares

304   for TEM 5.0 are from 0.62 to 0.75 (Table 6). On the other hand, RMSE for TEM_Moss is lower

305   than that for TEM 5.0 at each site (Table 6).

306   We presented the comparisons between measured and simulated volumetric soil moisture

307   (VSM) from TEM_Moss and TEM 5.0 (Figure 6). Statistical analysis shows that TEM_Moss

308   reproduces the soil moisture well with R-squares ranging from 0.51 at US-Bkg to 0.87 at US-Atq

309   (Table 7). R-squares for TEM_Moss are substantially higher than that for TEM 5.0 at most

310   chosen sites, except for US-Atq (Table 7). RMSE for TEM_Moss is lower than that for TEM 5.0

311   at each site (Table 7). Similarly, comparisons between measured and simulated soil temperature

312   at 5 cm depth (ST_5) from TEM_Moss and TEM 5.0 indicated that TEM_Moss can reproduce

313   the soil temperature with R-squares ranging from 0.81 at US-Ho1 to 0.91 at US-Bkg, while TEM

314   5.0 reproduces the soil temperature with R-squares ranging from 0.69 at BE-Vie to 0.89 at US-

315   Bkg (Figure 7; Table 8). Although R-squares for both models are relatively high and RMSE for

316   them are relatively low, TEM_Moss still shows higher R-squares and lower RMSE than TEM

317   5.0 (Table 8).

318   **3.2 Regional carbon dynamics during the 20th century**

319   Both TEM_Moss and TEM 5.0 were used to simulate northern high-latitude regional

320   carbon balance during the 20th century (Figure 8). Higher NEP was correlated with the

321   combination of relatively higher NPP and lower heterotrophic respiration (R_H). TEM_Moss

322   indicated that the northern high latitudes acted as a carbon sink of 221.9 Pg with an inter-annual

323   standard deviation of 0.31 PgC yr^{-1} during the 20th century, which is 132.7 Pg larger than 89.2 Pg

324   simulated by TEM 5.0 (Figure 8). The simulated NEP by TEM_Moss ranges from 1.38 PgC yr^{-1}

325   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).

326   The patterns of the simulated NEP from two models were similar, both showing a general

327   increasing trend throughout the 20th century (Figure 8). By 2000, the TEM_Moss simulation

328   indicated that the northern high-latitude region stored 3.05 PgC yr^{-1}, which is more than twice as

329   the storage estimated by TEM 5.0 (1.33 PgC yr^{-1}, Figure 8). Both models indicated that carbon

330   uptake by the northern ecosystems during the second half of the 20th century was higher than the

331   first half for most part of the region, and only a small portion of the region lost carbon in last

332   century (Figure 9).

333   Simulated total NPP by TEM_Moss was 9.6 PgC yr^{-1}, ranging from 8.52 PgC yr^{-1} to

334   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~~

335   ~~plant~~vascular plants NPP (Figure 8). Moss NPP ranges from 1.23 PgC yr^{-1} to 2.14 PgC yr^{-1} and

336   the ratio of moss NPP to ~~higher plant~~vascular plants NPP is 0.21 (Figure 8). TEM 5.0 estimated

337   0.8 PgC yr^{-1} lower total NPP than TEM_Moss, but 0.87 PgC yr^{-1} higher NPP for ~~higher~~

338   ~~plant~~vascular plants (Figure 8). On the other hand, average heterotrophic respiration in the 20th

339 century was 7.38 PgC yr^{-1} and all years were within about 5% of this value (Figure 8). TEM 5.0

340 projected 0.53 PgC yr^{-1} higher R_H than TEM_Moss (7.91 PgC yr^{-1}, Figure 8). Overall,

341 TEM_Moss predicted higher total NPP but lower R_H, which jointly caused a pronounced

342 difference in NEP between two models.

343 Both models estimated that soil organic carbon and vegetation carbon were accumulating

344 continuously in the 20th century (Figure 10). TEM_Moss indicated that regional SOC and VEGC

345 accumulated 96.3 PgC and 115.2 PgC, respectively, and the carbon uptake by moss was 10.4 Pg in

346 the period (Figure 10, Table 10). As simulated by TEM_Moss, 43.4%, 51.9% and 4.7% of total

347 carbon uptake in the region was assimilated to soils, ~~higher plant~~vascular plants and mosses,

348 respectively (Table 10). TEM 5.0 simulated that SOC increased by 31.7 Pg at the end of the 20th

349 century, which is 64.6 PgC less than the value estimated by TEM_Moss (Table 10). TEM 5.0

350 estimated 57.7 PgC in plants less than the value estimated by TEM_Moss (57.5 PgC, Table 10).

351 35.5% and 64.5% of total carbon was as SOC and VEGC, respectively.

352 **3.3 Regional carbon dynamics during the 21st century**

353 Under the RCP 2.6 scenario, TEM_Moss simulated NEP of 2.07 PgC yr^{-1} with the range

354 from 0.41 PgC yr^{-1} to 3.2 PgC yr^{-1}, and the inter-annual standard deviation of 0.59 PgC yr^{-1}

355 during the 21st century (Figure 11 (a)). The regional sink shows a decreasing pattern in the 2000s

356 and then generally increases over the remaining years of the 21st century (Figure 11 (a)). For

357 comparison, TEM 5.0 predicted that the average NEP of 0.28 PgC yr^{-1} with the range from -1.48

358 PgC yr^{-1} to 1.69 PgC yr^{-1} during the 21st century (Figure 11 (a)). Thus, TEM 5.0 projected 179.1

359 PgC stored in northern ecosystems is less than the estimation from TEM_Moss in the 21st

360 century. Besides, TEM 5.0 simulated that the regional NEP showed a decreasing trend and the

361 region fluctuates between sinks and sources during the century (Figure 11 (a)). The spatial

362 patterns from two models also showed differences. TEM_Moss indicated that the region

363 accumulates carbon over this century, while TEM 5.0 simulated that some regions changed from

364 a carbon sink to a source in the second half of the century (Figure 12 (a)). Simulated regional

365 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

366 century, while average NPP predicted by TEM 5.0 is 1.46 PgC yr^{-1} lower than that value (11.52

367 PgC yr^{-1} (Figure 11(a)). TEM_Moss simulated NPP has 3.74 PgC yr^{-1} from moss and 9.24 PgC

368 yr^{-1} from ~~higher plant~~vascular plants, which account for 28.8% and 71.2% of total NPP,

369 respectively (Figure 11(a)). Meanwhile, TEM_Moss estimated that R$_H$ is 10.91 PgC yr^{-1}, while

370 TEM 5.0 predicted it as 11.24~~0.33~~ PgC yr^{-1}, which is higher (Figure 11(a)). Both models

371 projected that soil organic carbon and vegetation carbon accumulate in this century but with

372 different magnitudes (Figure 13 (a)). TEM_Moss predicted that regional SOC and VEGC

373 accumulated 84.7 PgC and 112.6 PgC, respectively, during the 21st century, while TEM 5.0

374 predicted that a smaller increase with 12.1 and 15.5 PgC in SOC and VEGC, respectively (Figure

375 13 (a), Table 12 (a)). Besides, TEM_Moss also predicted an increasing of 9.4 PgC in MOSSC,

376 accounting for 4.5% of the total carbon uptake in this region (Table 12(a)).

377 Under the RCP 8.5 scenario, TEM_Moss simulated annual NPP of 13.84 PgC yr^{-1} with a

378 range from 11.09 to 16.94 PgC yr^{-1}, which is 1.31 PgC yr^{-1} higher than the projection from TEM

379 5.0 (Figure 11 (b)). Total NPP estimated by TEM_Moss has 3.84 PgC yr^{-1} from moss and 10

380 PgC yr^{-1} from ~~higher plant~~vascular plants (Figure 11(b)). Annual R$_H$ was 11.28 PgC yr^{-1}

381 estimated by TEM_Moss and 11.54 PgC yr^{-1} by TEM 5.0, respectively (Figure 11(b)).

382 Consequently, TEM_Moss projected NEP was 2.56 PgC yr^{-1} with the inter-annual standard

383 deviation of 0.93 PgC yr^{-1} in this century (Figure 11 (b)). NEP ranges from 0.67 PgC yr^{-1} to 4.78

384 PgC yr^{-1} estimated with TEM_Moss, while from -1.69 PgC yr^{-1} to 2.65 PgC yr^{-1} with a mean of

385 0.99 PgC yr⁻1 was estimated by TEM 5.0 (Figure 11 (b)). TEM_Moss predicted more carbon

386 uptake of 157.5 Pg than TEM 5.0 during the 21st century. Both models predicted that NEP

387 showed an increasing trend during the 21st century (Figure 11 (b)). Moreover, similar spatial

388 patterns of carbon sinks and sources appeared in the projections from two models (Figure 12

389 (b)). Soil organic carbon and vegetation carbon shows an increasing trend from both models

390 (Figure 13 (b)). Regional SOC and VEGC increased by 92.5 PgC and 153.6 PgC, respectively by

391 the end of the 21st century predicted by TEM_Moss. In contrast, the increase of 44.2 PgC and 54.5

392 PgC of SOC and VEGC, respectively, was predicted by TEM 5.0 (Figure 13 (b), Table 12 (b)).

393 TEM_Moss predicted an increase of 10.1 PgC in MOSSC (Table 12(b)).

394 **4. Discussion**

395 **4.1 The role of moss in the regional carbon dynamics**
396
397   Global warming has been pronounced in recent decades, particularly at high latitudes

398 (IPCC, 2014; Tape et al., 2006; Stow et al., 2004). An enormous amount of soil organic carbon

399 stored in northern high-latitude regions (Tarnocai et al., 2009; Schuur et al., 2008) is expected to

400 affect a broad spectrum of ecological and human systems, and cause rapid changes in the Earth

401 system when undergoing substantial climate change (Serreze and Francis 2006; Davidson and

402 Janssens, 2006; McGuire et al., 2009). Improving projections for carbon budget of high latitude

403 terrestrial ecosystems is essential for understanding global carbon–climate feedbacks (Melillo et

404 al., 2011; Todd-Brown et al., 2013).

405   Our simulations suggest that mosses play an important role in the regional carbon

406 dynamics, which is consistent with previous studies (McGuire et al., 2009; Turetsky et al., 2012).

407 First of all, mosses are productive with carbon assimilation even during low temperature, water

408 content and irradiance (Kallio and Heinonen, 1975; Harley et al., 1989). For example, mosses

409 can tolerate drought through physiological responses, such as by suspending metabolism and by

410 withstanding cell dessication (Turetsky et al., 2012; Oechel and Van Cleve, 1986). The key

411 functional traits related to water, nutrient, and thermal tolerances of mosses enable them to fit in

412 harsh northern conditions (Shetler et al., 2008; Turetsky et al., 2012). Thus, with incorporation of

413 moss into our models, the total NPP estimation in our model is affected. ~~improved (The referee~~

414 ~~requires me to direct a figure to prove this sentence, but I am not sure which figure should I~~

415 ~~direct).~~ Mosses also act as a powerful competitor with vascular plants for nutrient uptake. Their

416 rapid nutrient acquisition and slow nutrient loss through slow decomposition may constrain

417 concentrations of plant-available nitrogen (Hobbie et al., 2000; Turetsky et al., 2010; Oechel and

418 Van Cleve, 1986; Gornall et al., 2007), which will further decrease NPP of ~~higher plant~~vascular

419 plants. Our model results suggested that the NPP of ~~higher plant~~vascular plants considering moss

420 is indeed lower than previous NPP estimates without considering moss, but the total NPP is

421 larger than before. We estimated that mosses contribute 17.6% of NPP in the 20th century, and

422 28.8% and 27.6% in the 21st century under the RCP 2.6 and RCP 8.5 scenarios, respectively.

423 This is comparable with the results reported by a synthesis study, ~~Turetsky et al. (2010),~~

424 ~~which~~indicating ~~suggested~~ an average contribution ~~of~~ 20% of aboveground NPP from moss in

425 upland boreal forests and the contribution is 48% in wetlands ecosystems. Frolking et al. (1996)

426 even reported a contribution of 38.4% to total NPP by moss at a boreal forest site. Moreover,

427 mosses can also influence heterotrophic respiration (R_H) through their effects on soil thermal and

428 hydrologic dynamics (Zhuang et al., 2001). With the layer of moss, soil temperature tends to

429 decrease but soil moisture tends to increase (Oechel and Van Cleve, 1986), which will further

430 decrease soil respiration in summer. This supports our results that TEM_Moss simulated R_H is

431 lower than that by TEM 5.0. With a combination of higher NPP and lower R_H, NEP predicted by

432 TEM_Moss is larger than that by TEM 5.0. The two contrasting regional simulations by

433 TEM_Moss and TEM 5.0 indicated the region is currently a carbon sink, which is consistent

434 with previous studies (White et al., 2000; McGuire et al., 2009; Schimel et al., 2001). Our study

435 estimates that regional NEP during the 20th century is 2.2 Pg C yr^{-1} by TEM_Moss and 0.89 Pg

436 C yr^{-1} by TEM 5.0, respectively. In the 1990s, the regional sink is projected to be 2.7 and 1.1 Pg

437 C yr^{-1} by TEM_Moss and TEM 5.0 respectively. Compared with other existing studies, our

438 regional estimates of NEP are within the reasonable range from other existing studies. McGuire

439 et al. (2009) estimated a land sink of 0.3–0.6 Pg C yr^{-1} for the pan-arctic region for the 1990s,

440 which is closer to our estimation by TEM 5.0 but less than the projection by TEM_Moss. The

441 top-down atmospheric analyses indicate that the sink of pan-arctic region is between 0 and 0.8

442 Pg C yr^{-1} in the 1990s (Menon et al. 2007). Besides, Schimel et al. (2001) reported an estimation

443 of the northern extratropical NEP is from 0.6 to 2.3 PgC yr^{-1} in the late 20th century, which is

444 comparable to our estimates. Our simulations also confirmed that mosses and ~~higher~~

445 ~~plant~~vascular plants respond to climate change similarly in terms of their productivity (Turetsky

446 et al. 2010).

4.2 Model Uncertainty and limitations

448 There are a number of uncertainty sources in our model simulations. First, due to the

449 limited understanding of moss photosynthesis (He et al., 2015) and various moss N uptake

450 pathways (e.g., Bay et al 2013; Berg et al 2013), a few important assumptions have been made in

451 our modeling. For instance, we assume that mosses behave similarly to vascular plants regarding

452 photosynthesis and soil N uptake is the only pathway for mosses without considering N uptake

453 through N fixers and atmospheric wet N deposition (Ayres et al. 2006). Second, ~~First,~~ the errors

454 in the observed data will influence our parameterization results, which will bias our regional

455 estimates of carbon dynamics. Second, climatic driving data are also a source of uncertainty for

456 historical and future simulations. Third, model assumptions will also induce additional

457 uncertainties. For instance, we assumed that vegetation distribution will remain unchanged

458 during the transient simulation. However, vegetation will change in response to warming climate

459 and disturbances such as fire and insect outbreaks in the region (Hansen et al., 2006), which will

460 affect carbon budget. Missing potential responses to disturbances in our model shall introduce

461 additional uncertainties (Soja et al. 2007; Kasischke and Turetsky, 2006). Future moss dynamics

462 will also impact carbon dynamics in this region. For instance, a long-term warming experiments

463 along natural climatic gradients, ranging from Swedish subarctic birch forest and

464 subarctic/subalpine tundra to Alaskan arctic tussock tundra concluded that both diversity and

465 abundance of mosses are likely to decrease under arctic climate warming (Long et al. 2012).

466 Similarly, total moss cover declined in both heath and mesic meadow under experimental long-

467 term warming (by 1.5–3 °C), driven by general declines in many species (Alatalo et al., 2020).

468 Due to global warming, significant losses in moss diversity are expected in boreal forests and

469 alpine biomes, leading to changes in ecosystem structure and function, nutrient cycling, and

470 carbon balance (He et al., 2015).

471

472   We conducted ensemble regional simulations with 50 sets of parameters to quantify

473 model uncertainty due to uncertain parameters. The 50 sets of parameters were obtained using

474 the method in Tang and Zhuang (2008). The ensemble means and the inter-simulation standard

475 deviations are used to measure the model uncertainty (Figure 14). TEM_Moss predicted that the

476 regional cumulative carbon ranges from a carbon loss of 266 Pg C to a carbon sink of 567.3 Pg C

477 by different ensemble members, with a mean of 161.1 ± 142.1 Pg during the 21st century under the

478   RCP 2.6 scenario. Under the RCP 8.5 scenario, TEM_Moss predicted that the region acts from a

479   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

480   during the 21st century (Figure 14).

481   This study took an important step to incorporate moss into an extant ecosystem model

482   that has not explicitly consider the role of moss and its interactions with ~~higher plant~~vascular

483   plants. Our model simulations showed that mosses have strong influences on regional ecosystem

484   carbon cycling, by affecting the soil thermal, nitrogen availability, and water conditions of

485   terrestrial ecosystems. However, there are still limitations in our model. First, we did not

486   differentiate various kinds of mosses because they have their own functional traits.~~.~~ Different

487   kinds of mosses may ~~differ in levels~~provide different levels of insulation ~~provided~~ for soil,

488   resulting in different soil thermal conditions that ~~and their associated~~affect microbial

489   activities~~iomes~~. ~~In our model, the moss types are just differentiated by the vegetation types.~~ The

490   structural and physiological traits of mosses will differ largely in different moss groups, such as

491   feather moss versus Sphagnum (Turetsky et al., 2010). In addition, we lack spatially explicit

492   information of moss distribution in the region, which will lead to a large regional uncertainty of

493   carbon quantification. We assumed that moss area distribution is the same as its associated

494   vegetation distribution. Another limitation is that some important physiological traits of moss

495   have not been modeled. For example, moss abundance may change following shifts in vascular

496   species composition due to shading or burial by vascular litter (Turetsky et al., 2010; Cornelissen

497   et al., 2007). Furthermore, disturbance such as wildfires can also influence moss activities.

498   **5. Conclusions**

499   This study explicitly incorporated moss into an extant process-based terrestrial ecosystem model

500   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 plant~~s~~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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Author contributions. Q.Z. designed the study. J.Z. conducted model development, simulation

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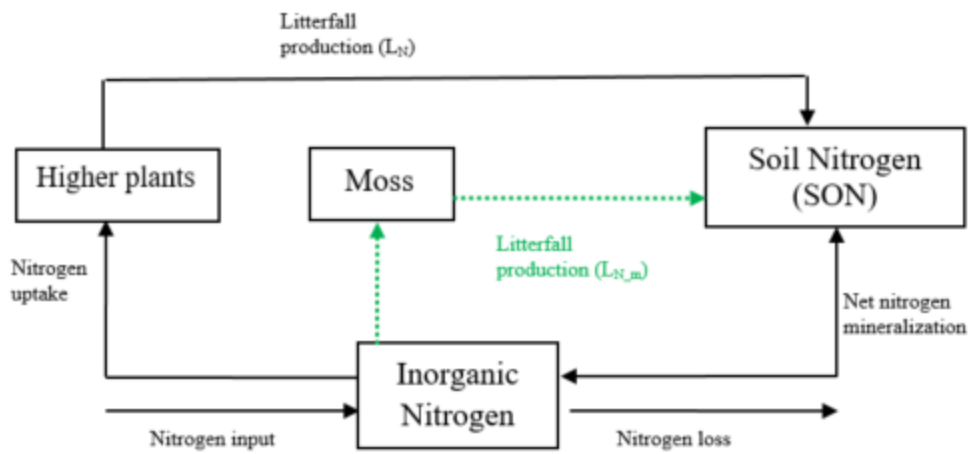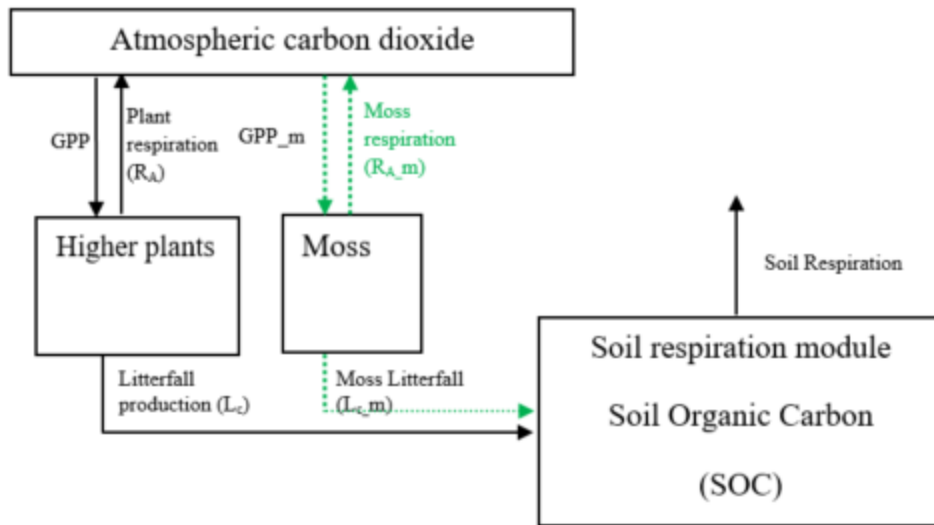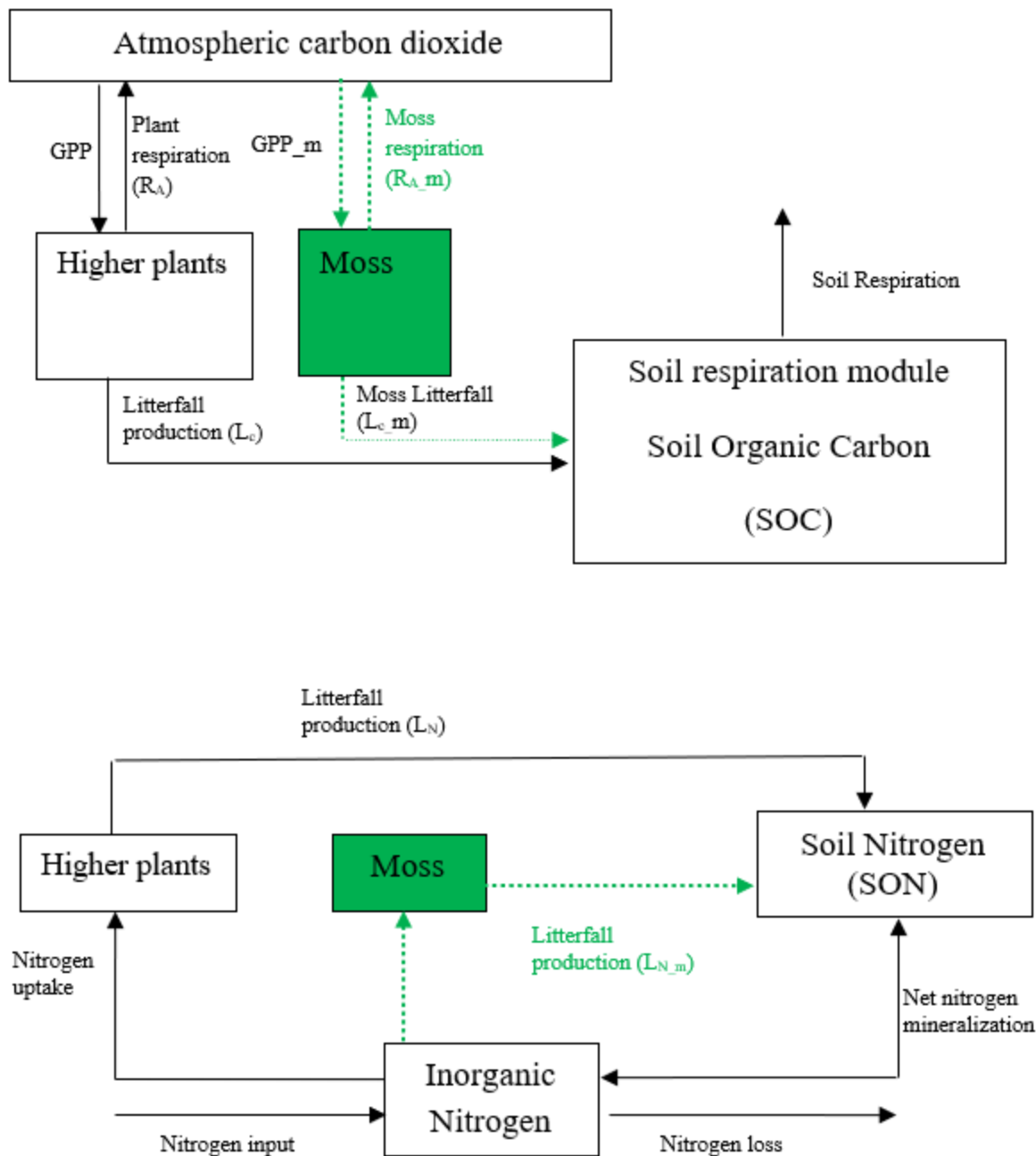
Figure 1. Schematic diagram of TEM_Moss: Green dashed arrows are new carbon and nitrogen fluxes, representing moss production, moss respiration and litterfall of moss. Black arrows were in TEM 5.0 (Zhuang et al., 2013).

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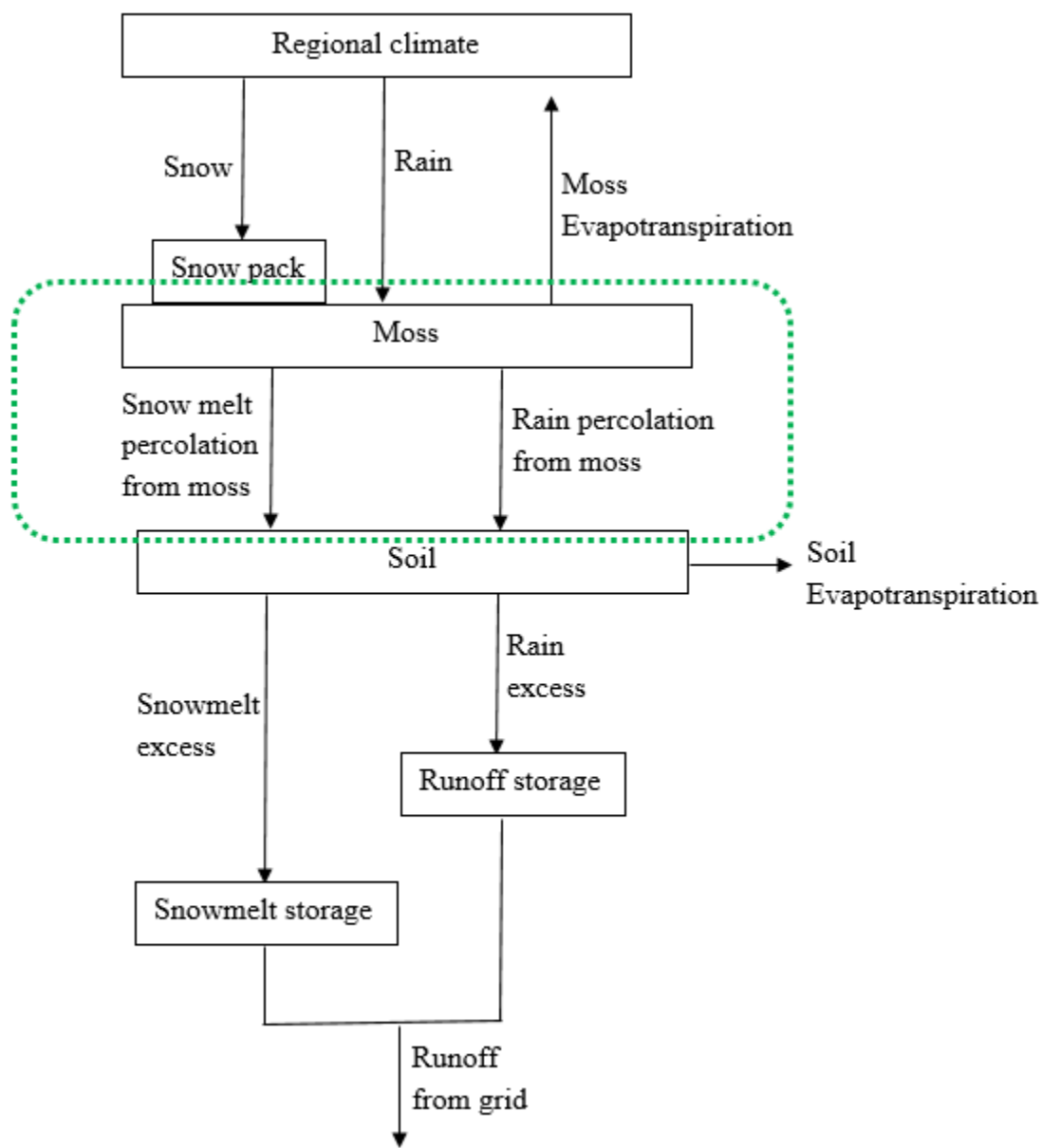
Figure 2. The revised Water Balance Model: Green dashed circle represents the hydrology
dynamics for moss (Vörösmarty et al., 1989).

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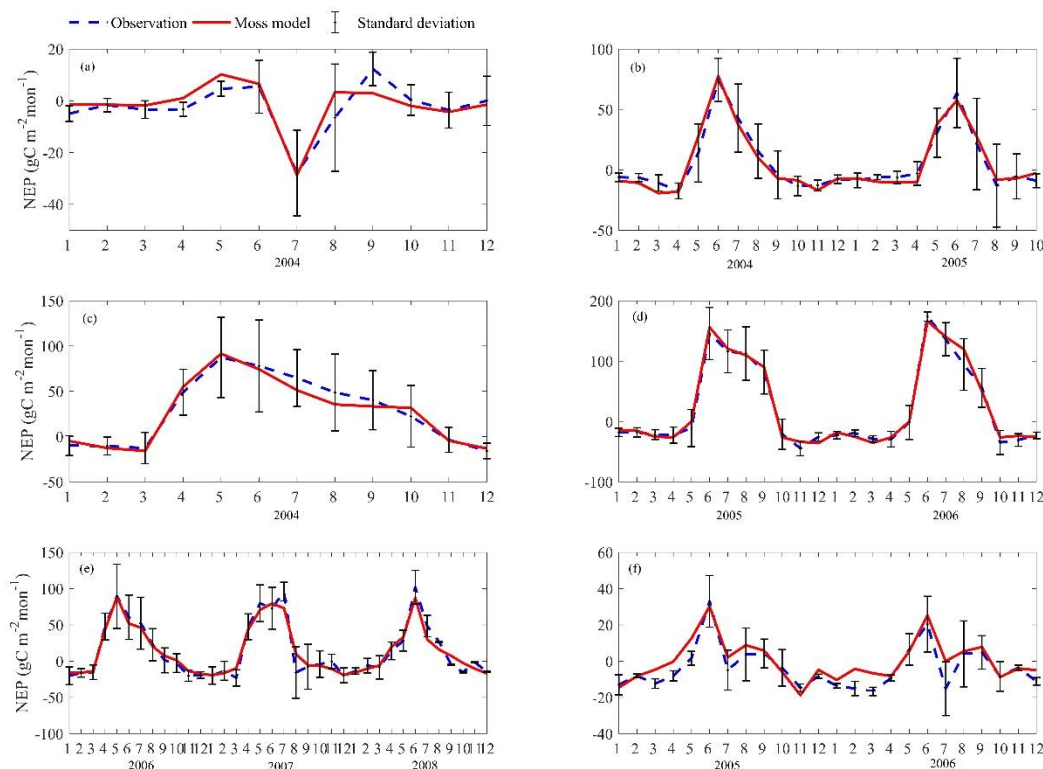
Figure 3. Comparison between observed and simulated NEP (gC m^{-2}mon^{-1}) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Univ. of Mich. Biological Station (Temperate deciduous forest), (e) KUOM Turfgrass Field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

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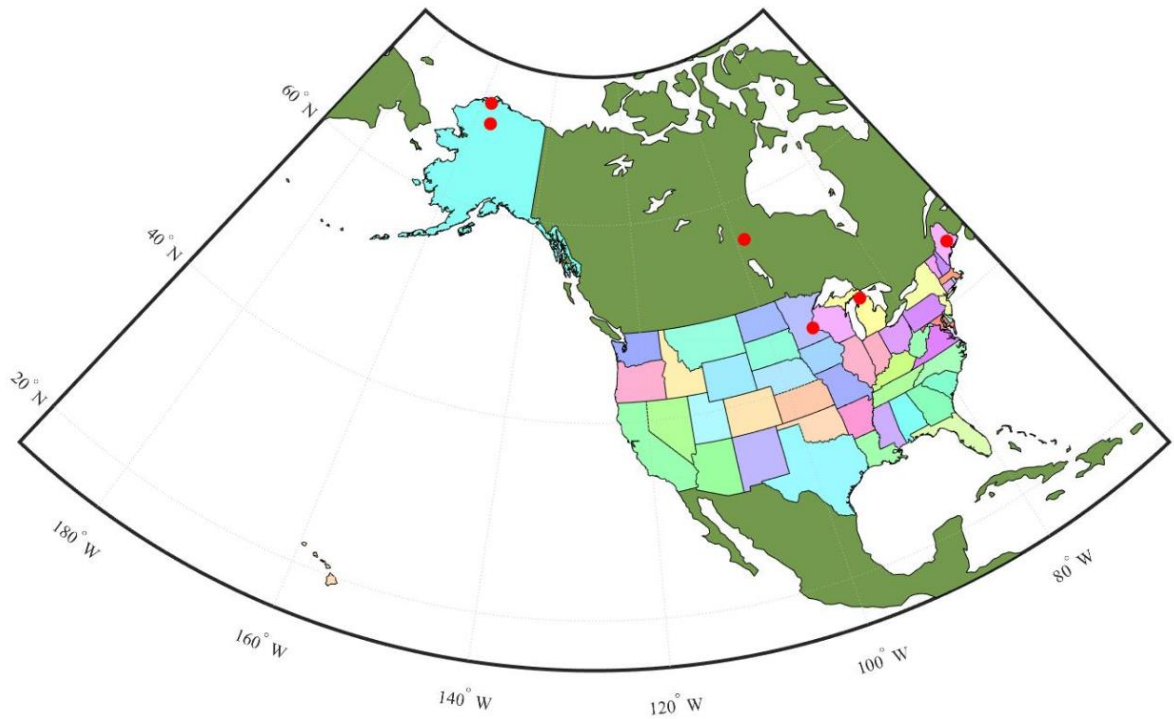
859 Figure 4. Map showing six sites used for TEM_Moss calibration. The red points represent the six
860 sites, which are all in US: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-1964 burn site (boreal
861 forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB: Univ. of Mich.
862 Biological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

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

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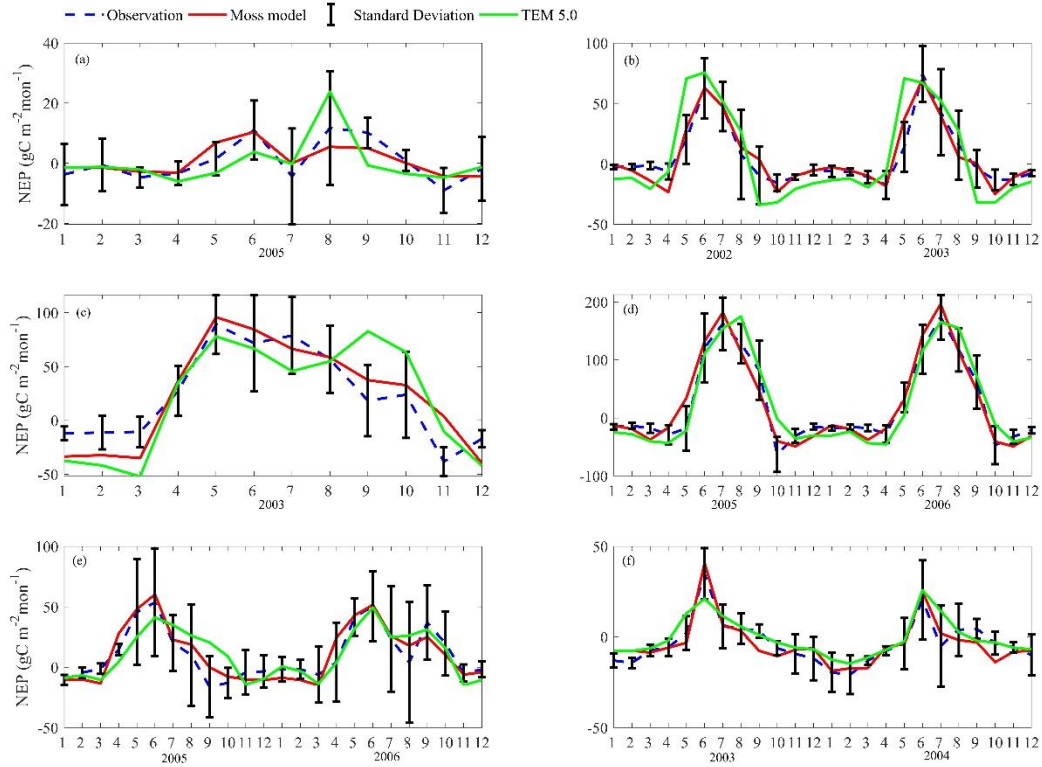
Figure 5. Comparison between observed and simulated NEP (gC m⁻²mon⁻¹) at: (a) Ivotuk (alpine tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Bartlett Experimental Forest (Temperate deciduous forest), (e) Brookings (Grassland), and (f)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

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

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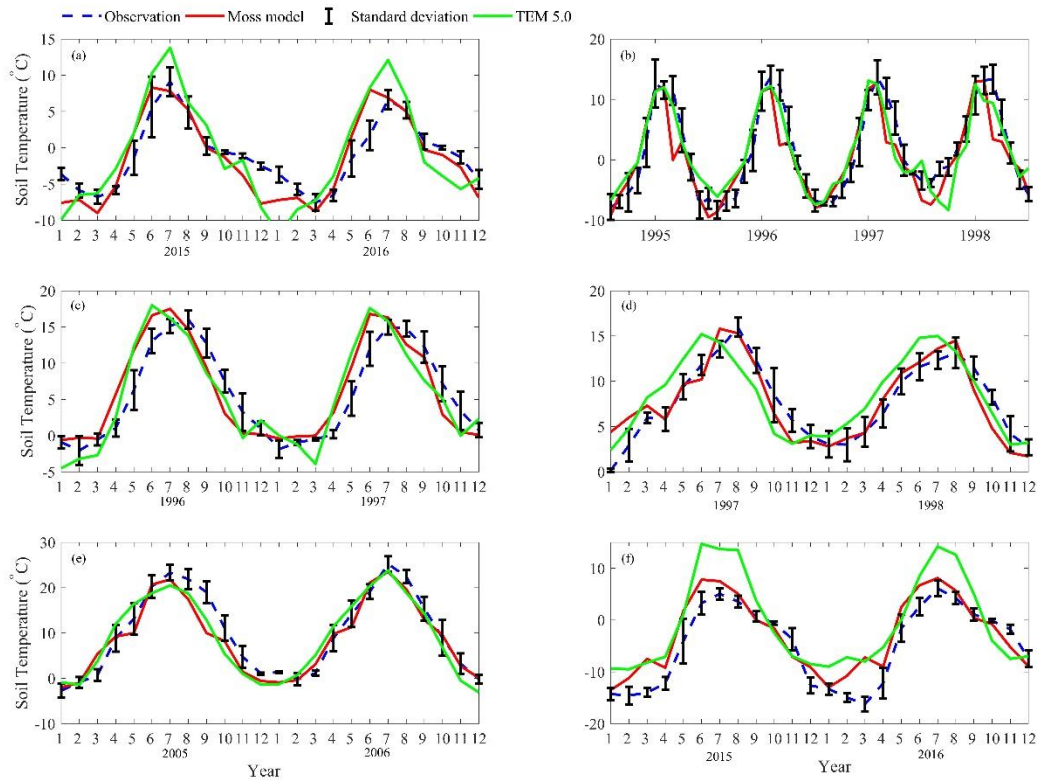
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928 Figure 7. Comparison between observed and simulated soil temperature at 5cm depth (°C) at: (a)
929 US-Ivo (alpine tundra), (b) BOREAS NSA-OBS (boreal forest), (c) US-Ho1 (temperate
930 coniferous forest), (d) BE-Vie (Temperate deciduous forest),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

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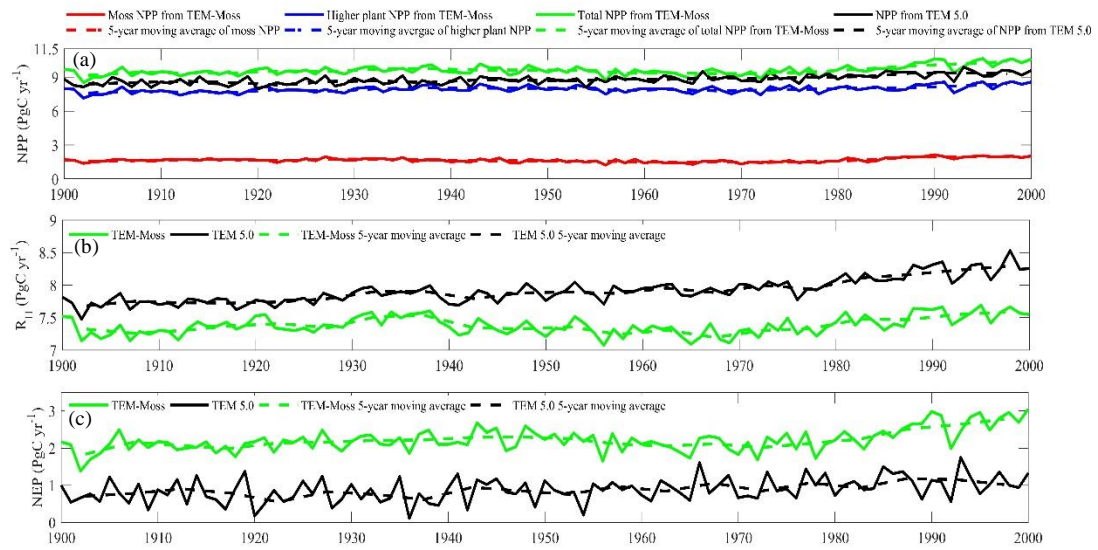
945   Figure 8. Simulated annual net primary production (NPP, a), heterotrophic respiration (R_H, b),
946   and net ecosystem production (NEP, c) during the 20th century by TEM_Moss and TEM 5.0.

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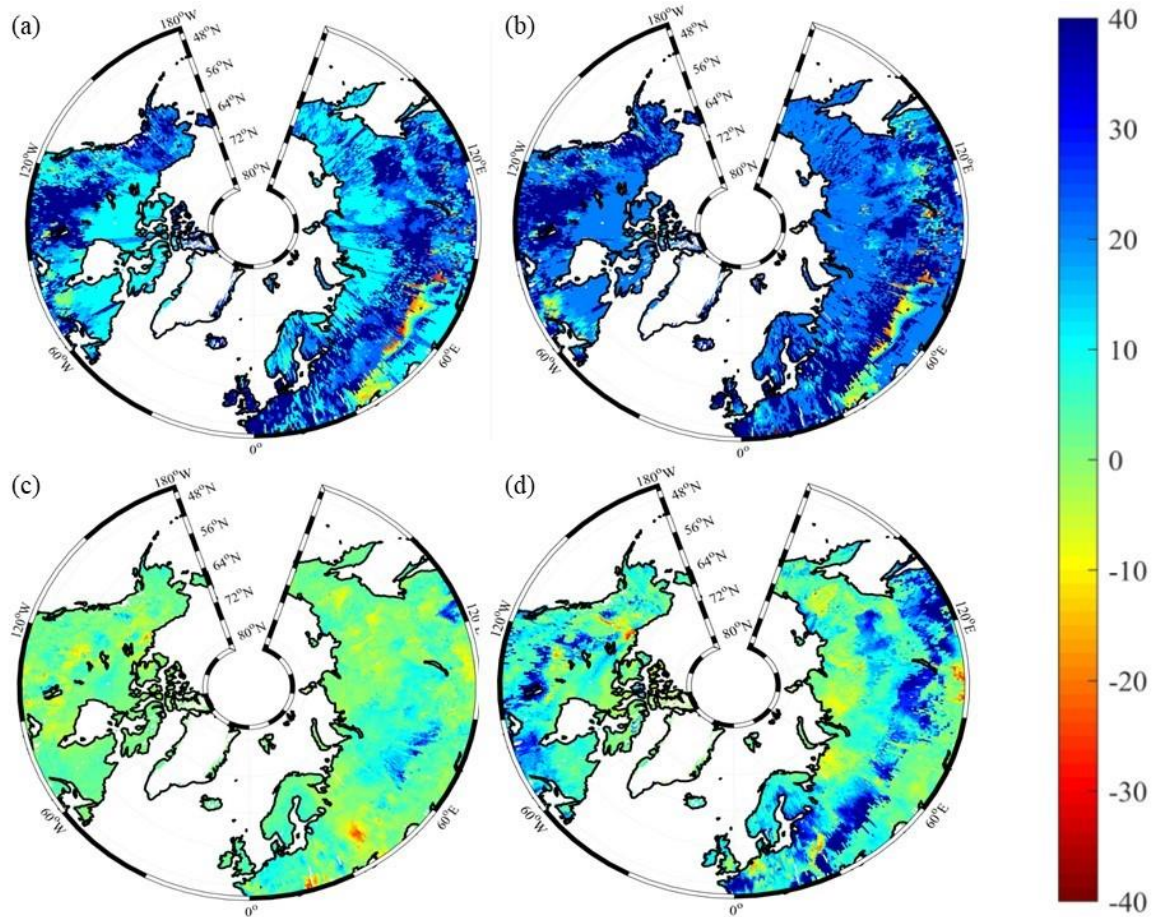
964 Figure 9. Spatial distribution of NEP simulated by TEM_Moss for the periods (a) 1900–1950, (b)
965 1951–2000, and by TEM 5.0 for the periods (c) 1900–1950, (d) 1951–2000. Positive values of
966 NEP represent sinks of CO_2 into terrestrial ecosystems, while negative values represent sources
967 of CO_2 to the atmosphere.

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

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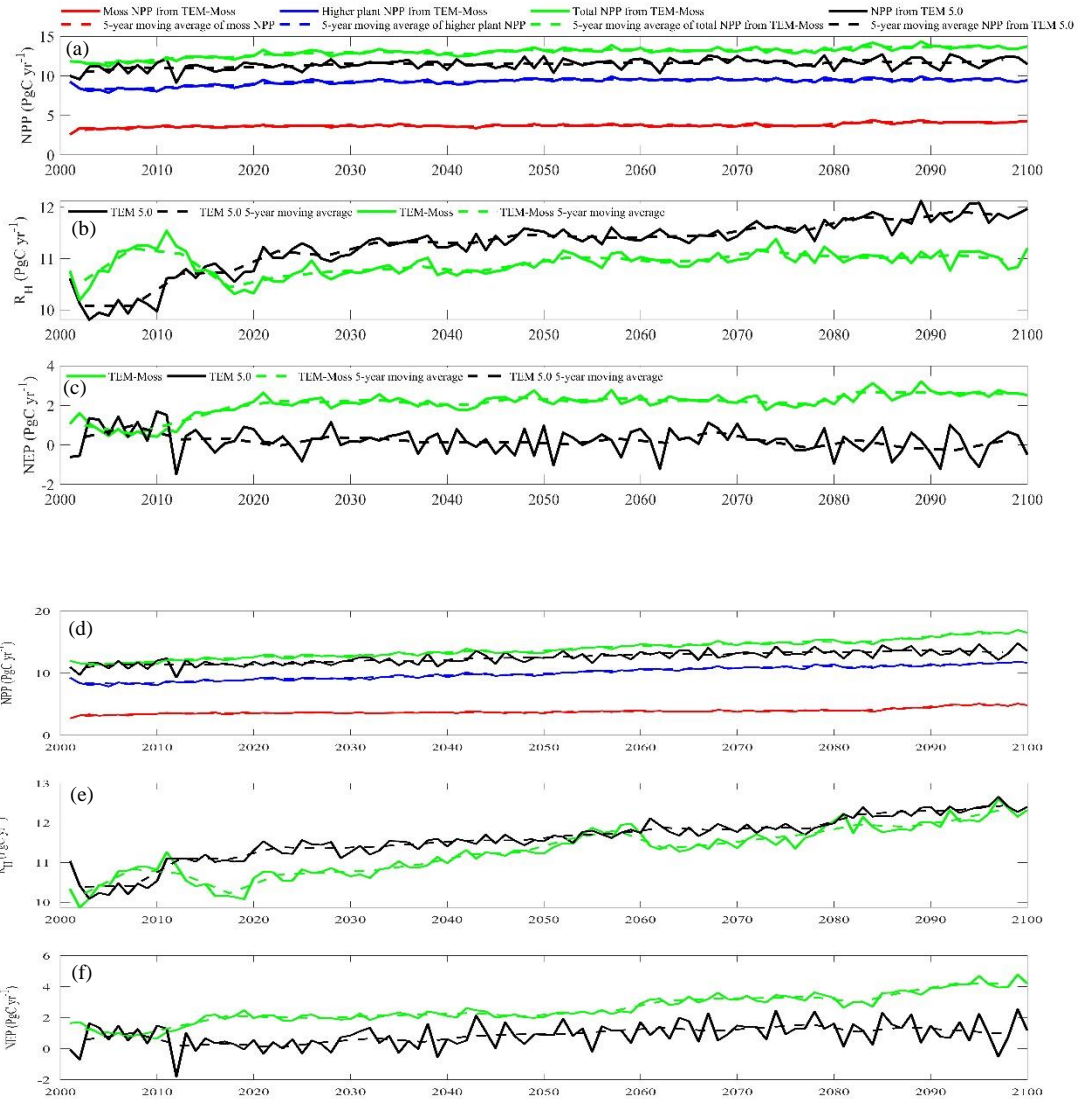
Figure 11. Predicted changes in carbon fluxes: annual net primary production (NPP, (a, d)), heterotrophic respiration (R_H, (b, e)), and net ecosystem production (NEP, (c, f)) during the 21st century under RCP 2.6 scenario (a, b, c, upper panel) and RCP 8.5 scenario (d, e, f, bottom panel) by TEM_Moss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

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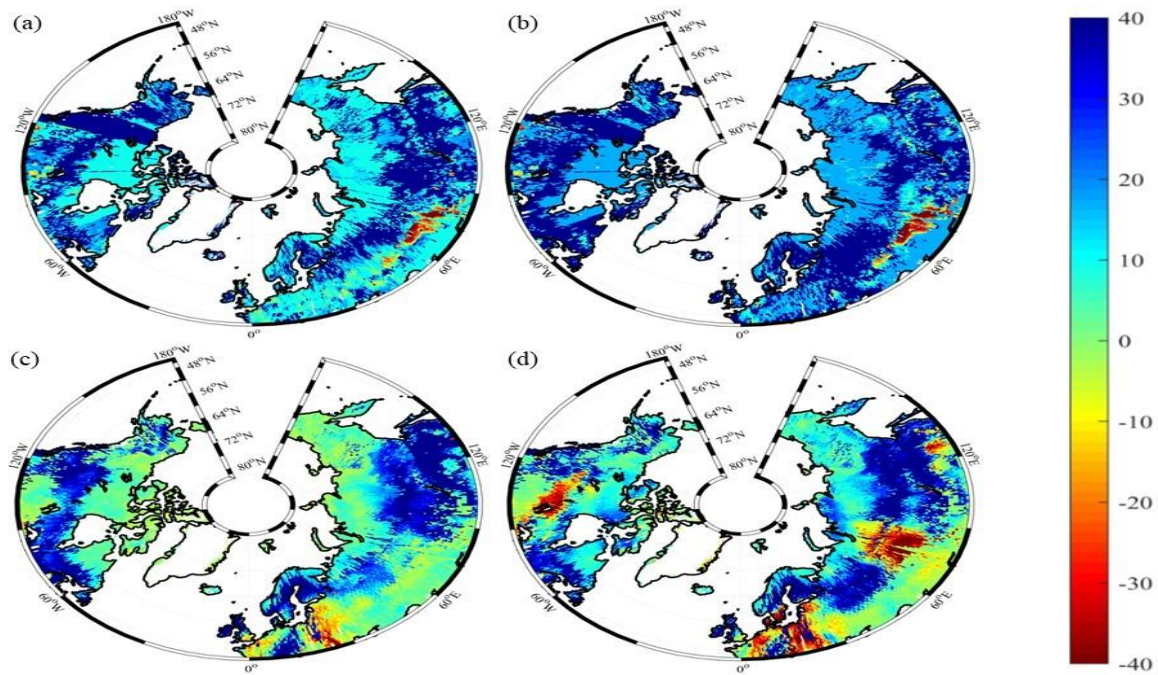
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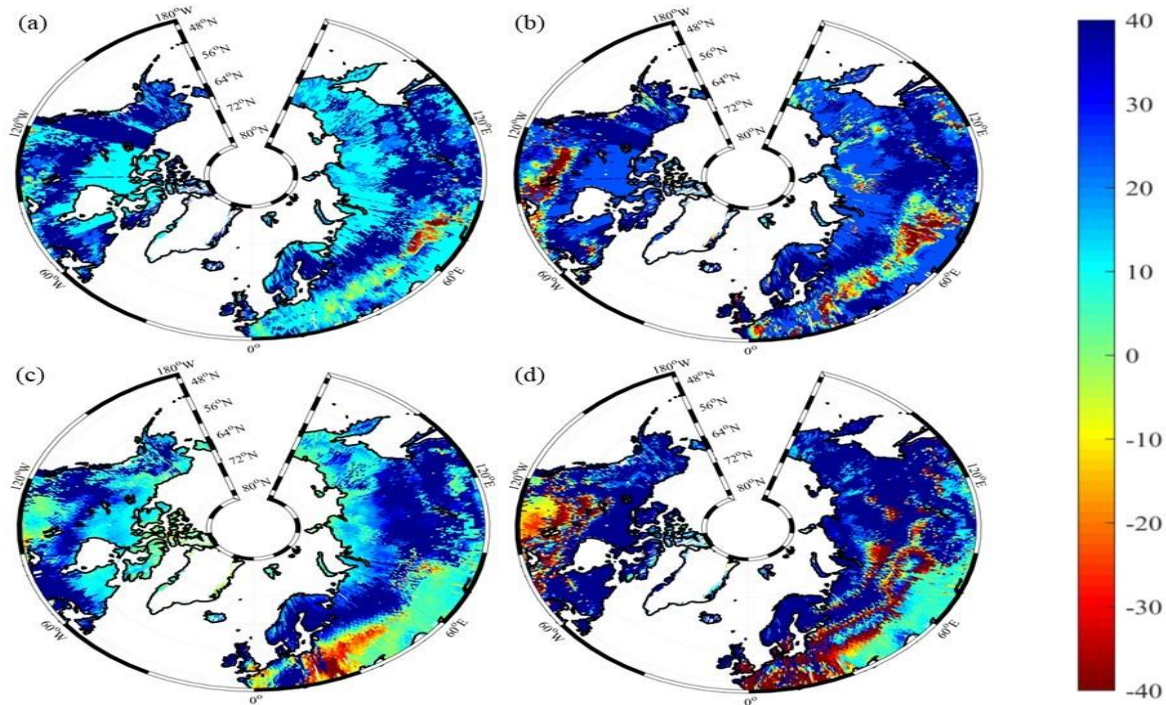
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1013 Figure 12. Spatial distribution of NEP simulated for the periods (a) 2000–2050, (b) 2051–2099
1014 by TEM_Moss, and by TEM 5.0 (c, d) during the 21st century under RCP 2.6 scenario (upper
1015 panel) and RCP 8.5 scenario (bottom panel). Positive values of NEP represent sinks of CO_2 into
1016 terrestrial ecosystems, while negative values represent sources of CO_2 to the atmosphere.

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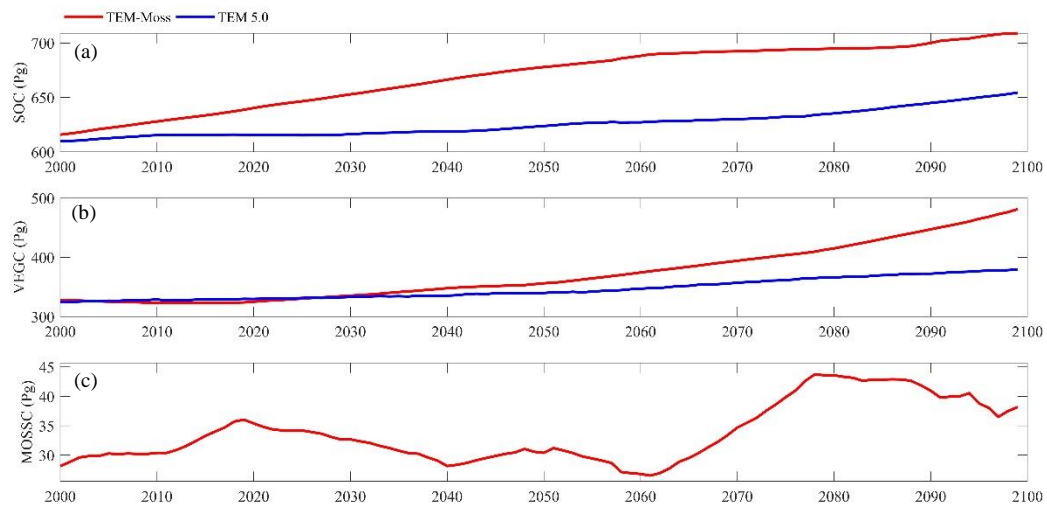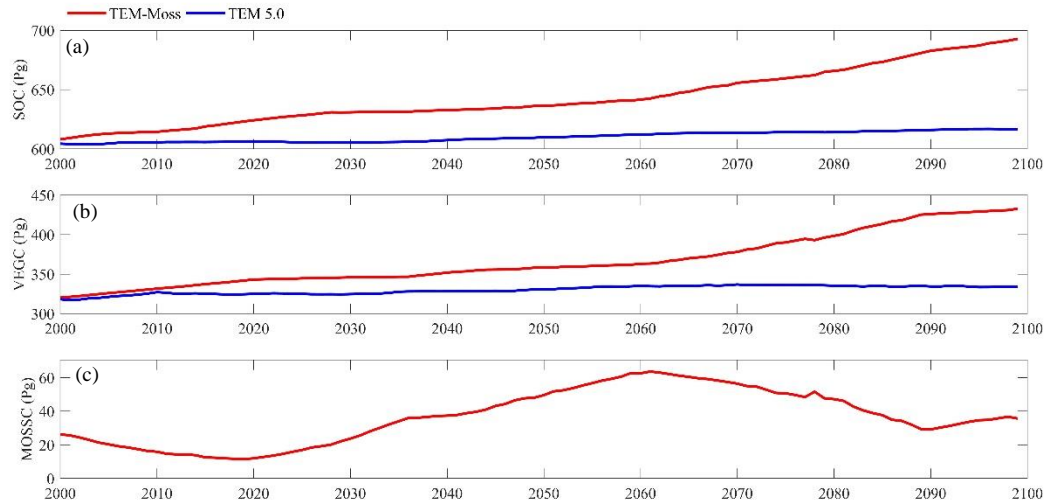
1020 Figure 13. Simulated annual soil organic carbon (SOC, a), vegetation carbon (VEGC, b), and
1021 moss carbon (MOSSC, c) during the 21st century by TEM_Moss and TEM 5.0 under RCP 2.6
1022 scenario (upper panel) and RCP 8.5 scenario (bottom panel).

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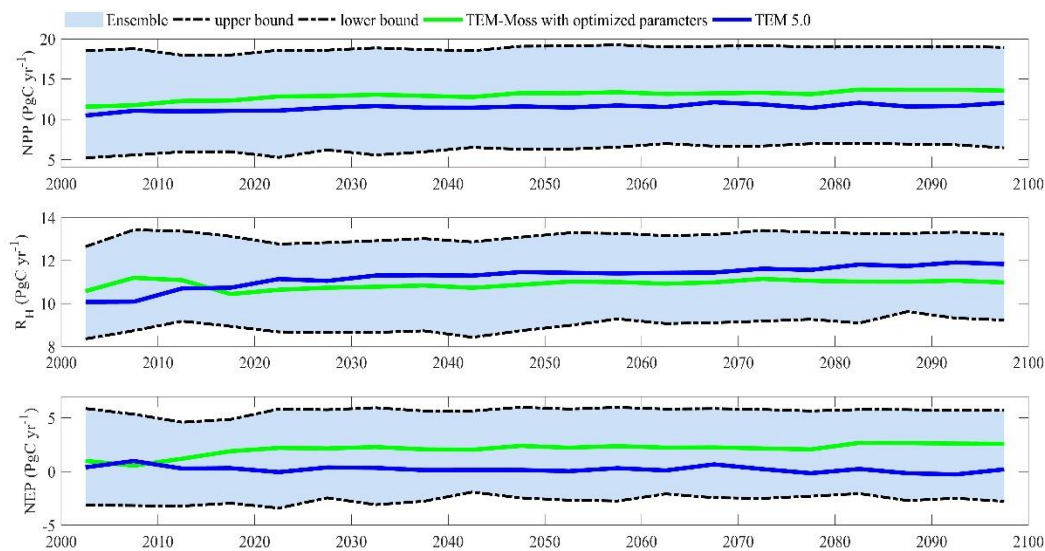
1030   (a)

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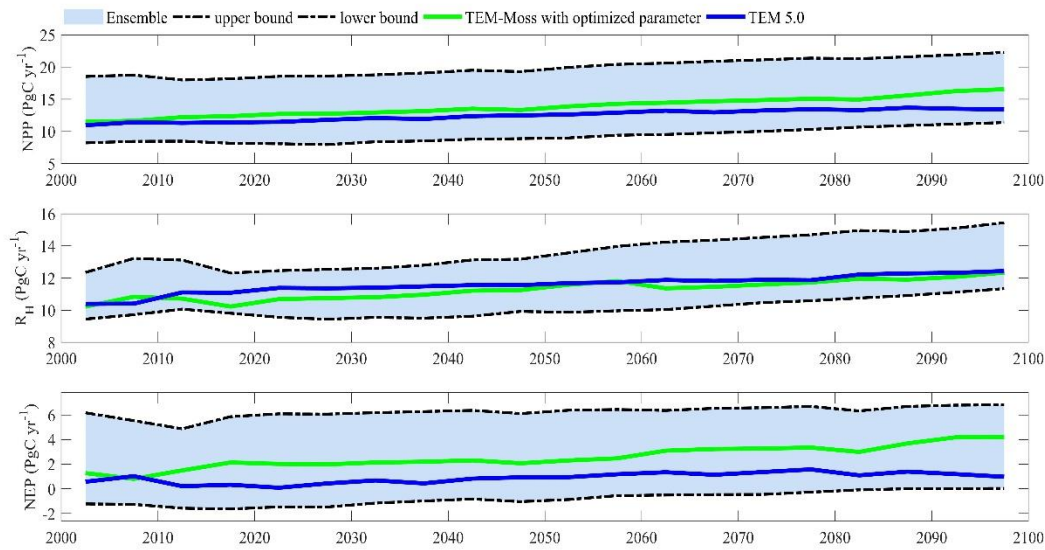
1032   (b)

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1034   Figure 14. 5-year moving average plots for carbon fluxes under the (a) RCP 2.6 scenario and (b)
1035   RCP 8.5 scenario. The blue area represents the upper and lower bounds of simulations.

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1039 **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	$\mu mol\ m^{-2}\ s^{-1}$	Light half-saturation level	[5, 150]	Launiainen et al. (2015); Raich et al. (1991)
T_{min}	°C	minimum temperature	[-10, 10]	Frolking et al. (1996); Raich et al. (1991)
T_{max}	°C	maximum temperature	[30, 80]	Frolking et al. (1996); Raich et al. (1991)
T_{opt}	°C	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	$\mu L/L$	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 °C	[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 5.83°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. (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
	Moss NPP	3.84	-	-	38.4%
NPP	~~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
	Moss NPP	3.74	-	-	40.5%
NPP	~~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