Extending a land-surface model with Sphagnum moss to simulate responses of a northern temperate bog to whole-ecosystem warming and elevated CO_2

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Abstract

Mosses need to be incorporated into Earth system models to better simulate peatland functional dynamics under changing environment. *Sphagnum* mosses are strong determinants of nutrient, carbon and water cycling in peatland ecosystems. However, most land surface models do not include *Sphagnum* or other mosses as represented plant functional types (PFTs), thereby limiting predictive assessment of peatland responses to environmental change. In this study, we introduce a moss PFT into the land model component (ELM) of the Energy Exascale Earth System Model (E3SM), by developing water content dynamics and non-vascular photosynthetic processes for moss. The model was parameterized and independently evaluated against observations from an ombrotrophic forested bog as part of the Spruce and Peatland Responses Under Changing Environments (SPRUCE) project. Inclusion of a *Sphagnum* PFT with some *Sphagnum* specific processes in ELM allows it to capture the observed seasonal dynamics of *Sphagnum* gross primary production (GPP), albeit with an underestimate of peak GPP. The model simulated a reasonable annual net primary production (NPP) for moss but with less interannual variation than observed, and reproduced above ground biomass for tree PFTs and stem biomass for shrubs. Different species showed highly variable warming responses under both ambient and elevated atmospheric CO_2 concentrations, and elevated CO_2 altered the warming response direction for the peatland ecosystem. Microtopography is critical: *Sphagnum* mosses on hummocks and hollows were simulated to show opposite warming responses (NPP decreasing with warming on hummocks, but increasing in hollows), and hummock *Sphagnum* was modeled to have strong dependence on water table height. Inclusion of this new moss PFT in global ELM

simulations may provide a useful foundation for the investigation of northern peatland carbon exchange, enhancing the predictive capacity of carbon dynamics across the regional and global scales.

1. Introduction

Boreal peatlands store at least 500 Pg of soil carbon due to incomplete decomposition of plant litter inputs resulting from a combination of low temperature and water-saturated soils. Because of this capacity to store carbon, boreal peatlands have played a critical role in regulating the global climate since the onset of the Holocene (Frolking and Roulet, 2007; Yu et al., 2010). The total carbon stock is large but uncertain: a new estimation of northern peatlands carbon stock of 1055 Pg was recently reported by Nichols and Peteet (2019). The rapidly changing climate at high latitudes is likely to impact both primary production and decomposition rates in peatlands, contributing to uncertainty in whether peatlands will continue their function as net carbon

sinks in the long term (Moore et al., 1998; Turetsky et al., 2002; Wu and Roulet, 2014). Manipulative experiments and process-based models are thus needed to make defensible projections of net carbon balance of northern peatlands under anticipated global warming (Hanson et al, 2017; Shi et al., 2015).

Peatlands are characterized by a ground layer of bryophytes, and the raised or ombrotrophic bogs of the boreal zone are generally dominated by *Sphagnum* mosses that contribute significantly to total ecosystem CO_2 flux (Oechel and Van Cleve, 1986; Williams and Flanagan, 1998; Robroek et al., 2009; Vitt, 2014). *Sphagnum* mosses also strongly affect the hydrological and hydrochemical conditions at the raised bog surface (Van, 1995; Van der Schaaf, 2002). As a result, microclimate and *Sphagnum* species interactions influence the variability of both carbon accumulation rates and water and exchanges within peatland and between peatland and atmosphere (Heijmans et al., 2004a, 2004b; Rosenzweig et al., 2008; Brown et al., 2010; Petrone et al., 2011; Goetz and Price, 2015). Functioning as keystone species of boreal peatlands, *Sphagnum* mosses strongly influence the nutrient, carbon and water cycles of peatland ecosystems (Nilsson and Wardle, 2005; Cornelissen et al., 2007; Lindo and Gonzalez, 2010; Turetsky et al., 2010; Turetsky et al., 2012), and exert a substantial impact on ecosystem net carbon balance (Clymo and Hayward; 1982; Gorham, 1991; Wieder, 2006; Weston et el., 2015; Walker et al., 2017; Griffiths et al., 2018).

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Numerical models are useful tools to identify knowledge gaps, examine long-term dynamics, and predict future changes. Earth system models (ESMs) simulate global processes, including the carbon cycle, and are primarily used to make future climate projections. Poor model representation of carbon processes in peatlands is identified as a

deficiency causing biases in simulated soil organic mass and heterotrophic respiratory fluxes for current ESMs (Todd-Brown et al., 2013; Tian et al., 2015). Although most ESMs do not include moss, a number of offline dynamic vegetation models and ecosystem models do include one or more moss plant functional types (PFTs) (Pastor et al., 2002; Nungesser, 2003; Zhuang et al., 2006; Bond-Lamberty et al., 2007; Heijmans et al., 2008; Euskirchen et al., 2009; Wania et al., 2009; Frolking et al., 2010). Several peatland-specific models contain moss species and have been applied globally or at selected peatland sites. For example, the McGill Wetland Model (MWM) was evaluated using the measurements at Degerö Stormyr and the Mer Bleue bogs (St-Hilaire et al., 2010). The peatland version of the General Ecosystem Simulator - Model of Raw Humus, Moder and Mull (GUESS-ROMUL) was used to simulate the changes of daily CO_2 exchange rates with water table position at a fen (Yurova et al., 2007). The PEATBOG model was implemented to characterize peatland carbon and nitrogen cycles in the Mer Bleue bog, including moss PFTs but without accounting for microtopography (Wu et al., 2013a). The CLASS-CTEM model (the coupled Canadian Land Surface Scheme and the Canadian Terrestrial Ecosystem Model), which includes a moss layer as the first soil layer, was applied to simulate water, energy and carbon fluxes at eight different peatland sites (Wu et al., 2016). The IAP-RAS (Institute of Applied Physics – Russian Academy of Sciences) wetland methane (CH_4) model with a 10 cm thick moss layer (Mokhov et al. 2007) was run globally to simulate the distribution of CH_4 fluxes (Wania et al., 2013). The CHANGE model (a coupled hydrological and biogeochemical process simulator), which includes a moss cover layer (Launiainen et al., 2015), was used to investigate the effect of moss on soil temperature and carbon flux at a tundra site in Northeastern Siberia

(Park et al., 2018). Chadburn et al. (2015) added a surface layer of moss to JULES land surface model to consider the insulating effects and treated the thermal conductivity of moss depending on its water content to investigate the permafrost dynamics. Porada et al. (2016) integrated a stand-alone dynamic non-vascular vegetation model LiBry (Porada et al., 2013) to land surface scheme JSBACH, but JSBACH mainly represent bryophyte and lichen cover on upland forest, not for peatland ecosystem without including an organic soil layer. Druel et al. (2017) investigated the vegetation-climate feedbacks in high latitudes by introducing a non-vascular plant type representing mosses and lichens to the global land surface model ORCHIFEE. Moreover, those models did not consider microtopography and the lateral transports between hummocks and hollows. Two models, the "ecosys" model (Grant et al., 2012) and CLM_SPRUCE (Shi et al., 2015), have been parameterized to represent peatland microtopographic variability (e.g., the hummock and hollow microterrain characteristic of raised bogs) with lateral connections across the topography. Prediction of water table dynamics in the "ecosys" model is constrained by specifying a regional water table at a fixed height and a fixed distance from the site of interest, thereby missing key controlling factors of a precipitation-driven dynamic water table (Shi et al., 2015). The CLM_SPRUCE model (Shi et al., 2015) was developed to parameterize the hydrological dynamics of lateral transport for microtopography of hummocks and hollows in the raised bog environment of the SPRUCE (Spruce and Peatland Responses Under Changing Environments) experiment (Hanson et al., 2017). That model version did not include the biophysical dynamics of *Sphagnum* moss, and used a prescribed leaf area instead of allowing leaf area to evolve prognostically.

In this study, we introduce a new *Sphagnum* moss PFT into the model, and migrate the entire raised-bog capability into the new Energy Exascale Earth System Model (E3SM), specifically into version 1 of the E3SM land model (ELM v1, Ricciuto et al., 2018). The objectives of this study are to: 1) introduce a *Sphagnum* PFT to the ELM model with additional *Sphagnum*-specific processes to better capture the peatland ecosystem; and 2) apply the updated ELM to explore how an ombrotrophic, raised-dome bog peatland ecosystem will respond to different scenarios of warming and elevated atmospheric CO_2 concentration.

2. Model description

2.1 Model provenance

ELM v1 is the land component of E3SM v1, which is supported by the US Department of Energy (DOE). Developed by multiple DOE laboratories, E3SM consists of atmosphere, land, ocean, sea ice, and land ice components, linked through a coupler that facilitates across-component communication (Golaz et al., 2019). ELM was originally branched from the Community Land Model (CLM4.5, Oleson et al., 2013), with new developments that include representation of coupled carbon, nitrogen, and phosphorus controls on soil and vegetation processes, and new plant carbon and nutrient storage pools (Ricciuto et al., 2018; Yang et al., 2019; Burrows et al., 2020). Inputs of new mineral nitrogen of ELM are from atmospheric deposition and biological nitrogen fixation. The fixation of new reactive nitrogen from atmospheric N_2 by soil microorganisms is an important component of nitrogen budgets. ELM follows the approach of Cleveland et al. (1999) that uses an empirical relationship of biological

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nitrogen fixation as a function of net primary production to predict the nitrogen fixation. The model version used in this study is designated ELM SPRUCE, and includes the new implementation of Sphagnum mosses as well as the hydrological dynamics of lateral transport between hummock and hollow microtopographies. The implementation has been parameterized based on observations from the S1-Bog in northern Minnesota, USA, as described by Shi et al. (2015), with additional details provided below.

2.2 Non-vascular plants: *Sphagnum* mosses

To represent non-vascular plant the *Sphagnum* mosses, we modified the C3 artic grasses equations as follows. We considered *Sphagnum* biomass to be represented mainly by leaf and stem carbon (only a very shallow root). In addition, we modified the vascular C3 arctic grasses equations for photosynthesis and stomatal conductance (see the below new model development), and the associated parameters as reported by Table 1-3. We use the same framework as for C3 artic grasses, but the Ball-Berry slope term is assumed to be zero and the intercept term is the conductance term as a function of water content of *Sphagnum* mosses. For all other processes like the evapo(transpi)ration and associated parameters not described below, we used the C3 artic grasses equations (reported by Oleson et al., 2013). Drying impacts the conductance and affects evapo(transpi)ration of the internal water. The SLA and leaf C:N ratio parameters are strong controls on Vcmax, and therefore overall productivity and Sphagnum moss LAI. The high sensitivities occur because LAI is a strong control on evapo(transp)iration.

2.3 New model developments

2.3.1 Water content dynamics of *Sphagnum* mosses

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The main sources for water content of *Sphagnum* mosses are passive capillary water uptake from peat, and interception of atmospheric water on the capitulum (growing tip of the moss) (Robroek et al. 2007). Capillary water uptake, the internal *Sphagnum* moss water content, is modeled as functions of soil water content and evaporation losses. Water intercepted on the *Sphagnum* moss capitulum is modeled as a function of moss foliar biomass, current canopy water, water drip, and evaporation losses.

Since evaporation at the *Sphagnum* surface depends on atmospheric water vapor deficit, moss-atmosphere conductance and available water pool which depends on capillary wicking of water up to the surface, At SPRUCE, the peat volumetric water content is measured at several depths using automated sensors (model 10HS, Decagon Devices, Inc., Pullman, WA) calibrated for the site-specific upper peat soil using mesocosms (reference Figure S1, Hanson et al. 2017). During those calibrations, we periodically sampled the surface *Sphagnum* for gravimetric water content and water potential using a dew point potentiometer (WP4, Decagon Devices, Inc.), which also provided a surface soil water retention curve. The destructive sampling of surface *Sphagnum* was primarily hummock species but did included some hollow species. The automated measurements of peat water content at 10 cm depth were shown to be a good indicator of surface *Sphagnum* water content (Fig. 1). Based on this relationship, we model the water content of *Sphagnum* moss due to capillary rise ($W_{internal}$) (g water /g dry moss) as:

$$W_{internal} = 0.3933 + 7.6227/(1 + \exp(-(Soil_{vol} - 0.1571))/0.018 \quad (1)$$

where $Soil_{vol}$ is the averaged volumetric soil water of modeled soil layers nearest the 10cm depth horizon (layers 3 and 4 in the ELM v1 vertical layering scheme).

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The *Sphagnum* moss surface water ($W_{surface}$) was calculated using the model predicted canopy water and the dry foliar biomass as:

$$W_{surface} = can\_water/fmass \quad (2)$$

where $W_{surface}$ (g water /g dry moss) is the surface water content and $fmass$ is the foliar biomass of *Sphagnum* mosses. The can_ water is the *Sphagnum* moss canopy water and it is simulated by a function of interception, canopy drip, dew and canopy evaporation (Oleson et al., 2013).

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The total water content (W_{total}) of *Sphagnum* mosses is the sum of water taken up from peat and the surface water content (St-Hilaire et al, 2010; Wu et al., 2013).

$$W_{total} = W_{internal} + W_{surface} \quad (3)$$

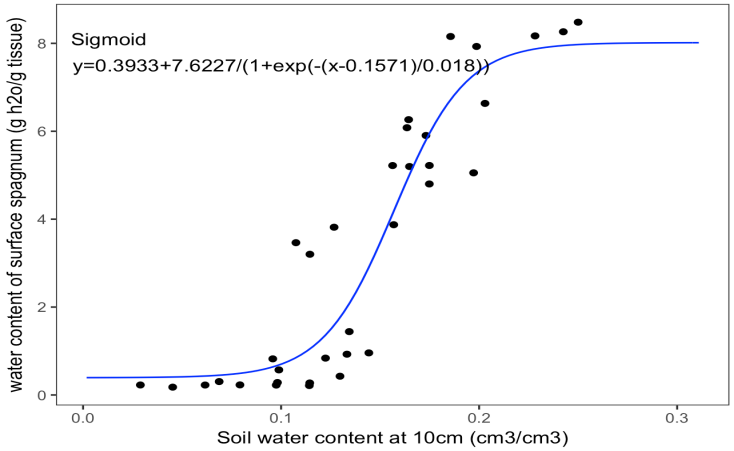

Figure 1. The measured relationship between soil water content at depth and the water content of surface Sphagnum based on destructive sampling.

2.3.2 Modeling *Sphagnum* CO_2 conductance and photosynthesis

ELM_SPRUCE computes photosynthetic carbon uptake (gross primary production, or GPP) for each vascular PFT on a half-hourly time step, based on the Farquhar biochemical approach (Farquhar et al., 1980; Collatz et al., 1991, 1992), with implementation as described by Oleson et al. (2013). While, *Sphagnum* lacks a leaf cuticle and stomata that regulate water loss and CO_2 uptake in vascular plants (Titus et al. 1983). The primary transport pathway for CO_2 is through the cells and is analogous to mesophyll conductance in higher plants. Thus, we calculate the total conductance to CO_2 for *Sphagnum* mosses by using total water content following the method reported by Williams and Flanagan (1998) described as below. Goetz and Price (2015) also indicated that capillary rise through the peat is essential to maintain a water content sufficient for photosynthesis for *Sphagnum* moss species, but that atmospheric inputs can provide small but critical amounts of water for physiological processes.

The stomatal conductance for vascular plant types in ELM_SPRUCE is derived from the Ball-Berry conductance model (Collatz et al., 1991). That model relates stomatal conductance to net leaf photosynthesis, scaled by the relative humidity and the CO_2 concentration at the leaf surface. The stomatal conductance (g_s) and boundary layer conductance (g_b) are required to obtain the internal leaf CO_2 partial pressure (C_i) of vascular PFTs:

$$C_i = C_a - \left(\frac{1.4g_s + 1.6g_b}{g_s\, g_b}\right) P_{atm} A_n \qquad (4)$$

where C_i is the internal leaf CO_2 partial pressure, C_a is the atmospheric CO_2 partial

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pressure, A_n is leaf net photosynthesis (μ mol CO_2 m^{-2} s^{-1}) P_{atm} is the atmospheric pressure, g_s is the leaf stomatal conductance, g_b is the leaf boundary layer conductance, and values 1.4 and 1.6 are the ratios of the diffusivity of CO_2 to H_2O for stomatal conductance and the leaf boundary layer conductance, respectively.

For *Sphagnum* moss photosynthesis, we followed the method from the McGill Wetland Model (St-Hilaire et al. 2010; Wu et al., 2013), which is based on the effects of *Sphagnum* moss water content on photosynthetic capacity (Tenhunen et al., 1976) and total conductance of CO_2 (Williams and Flanagan, 1998), and replaces the stomatal conductance representation used for vascular PFTs.

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$$C_i = C_a - \frac{P_{atm} A_n}{g_{tc}} \quad (5)$$

The total conductance to CO_2 (g_{tc}) was determined from a least-squares regression described by Williams and Flanagan (1998) as:

$$g_{tc} = -0.195 + 0.134 W_{total} - 0.0256 {W_{total}}^2 + 0.0028 {W_{total}}^3 - 0.0000984 {W_{total}}^4 + 0.00000168 {W_{total}}^5 \quad (6)$$

where W_{total} is as defined in equation (3). This relationship is only valid up to the maximum water holding capacity of mosses. To be noted that we assume that the boundary layer conductance is greater than moss surface layer conductance, and the moss surface layer conductance is greater than chloroplast conductance.

In addition to the water content, the effects of moss submergence were taken into account in the calculation of moss photosynthesis. Walker et al. (2017) reported

significant impacts of submergence on measured *Sphagnum* GPP and modeled the effect by modifying the *Sphagnum* leaf (stem) area index. Submergence in Walker et al. (2017) was expressed as photosynthesising stem area index (SAI) as a logistic function of water table depth. A maximum SAI of 3 was used and the parameter combination that most closely described the GPP data gave a range of water table depth from -10 cm for complete submergence and SAI of ~2.5 at 10 cm. This allowed for a range of processes such as floatation of *Sphagnum* with the water table, and adhesion of water to the *Sphagnum* capitula. For simplicity, in ELM_SPRUCE, we calculated such impacts on *Sphagnum* GPP directly as a function of the height of simulated surface water, assuming that GPP from the submerged portion of photosynthetic tissue is negligible. GPP is thus reduced linearly according to the following equation:

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$$GPP_{sub} = GPP_{orig} * (h_{moss} - H_2O_{sfc}) \quad (7)$$

where GPP_{sub} is the GPP corrected for submergence effects, GPP_{orig} is the original GPP, H_2O_{sfc} is the surface water height, and h_{moss} is the height of the photosynthesizing *Sphagnum* layer above the soil surface, set to 5cm in our simulations. If H_2O_{sfc} is equal to or greater than h_{moss}, GPP is reduced to zero. Because in our simulations surface water is never predicted to occur in the hummocks, in practice this submergence effect only affects the moss GPP in the hollows.

3. Methods

3.1 Site Description

We focused on a high C, ombrotrophic peatland (the S1-Bog) that has a perched water table with limited groundwater influence (Sebestyen et al. 2011, Griffiths and Sebestyen, 2016). This southern boreal bog is located on the Marcell Experimental

Forest, approximately 40 km north of Grand Rapids, Minnesota, USA (47.50283 degrees latitude, -93.48283 degrees longitude) (Sebestyen et al. 2011), and is the site of the SPRUCE climate change experiment (http://mnspruce.ornl.gov; Hanson et al., 2017). The S1-Bog has a raised hummock and sunken hollow microtopography, and it is nearly covered by *Sphagnum* mosses. *S. angustifolium* (C.E.O. Jensen ex Russow) and *S. fallax* (Klinggr.) occupy 68% of the moss layer and exist in both hummocks and hollows. *S. magellenicum* (Brid.) occupies ~20% of the moss layer and is primarily limited to the hummocks (Norby et al., 2019). The vascular plant community at the S1-Bog is dominated by the evergreen tree *Picea mariana* (Mill.) B.S.P, the deciduous tree *Larix laricina* (Du Roi) K. Koch, and a variety of ericaceous shrubs. Trees are present due to natural regeneration following strip cut harvesting in 1969 and 1974 (Sebestyen et al., 2011). The soil of this peat bog is the Greenwood series, a Typic Haplohemist (https://websoilsurvey.sc.egov.usda.gov), and its average peat depth is 2 to 3 m (Parsekian et al., 2012)

Northern Minnesota has a subhumid continental climate with average annual precipitation of 768 mm and annual air temperature of 3.3 °C for the time period from 1965 to 2005. Mean annual air temperatures at the bog have increased about 0.4 °C per decade over the last 40 years (Verry et al., 2011).

3.2 Field measurements

Multiple observational pre-treatment data (the data were collected prior to initiation of the warming and CO_2 treatments) were used in this study. Flux-partitioned GPP of *Sphagnum* mosses was derived from measured hourly *Sphagnum*-peat net ecosystem exchange (NEE) flux (Walker et al., 2017). The GPP – NEE relationship was

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also evaluated using observed vegetation growth and productivity allometric and biomass data on tree species, stem biomass for shrub species (Hanson et al., 2018a and b), and *Sphagnum* pre-treatment net primary productivity (NPP) (Norby et al., 2019). ELM_SPRUCE was driven by climate data (temperature, precipitation, relative humidity, solar radiation, wind speed, pressure and long wave radiation) from 2011 to 2017 measured at the SPRUCE S1-Bog (Hanson et al., 2015a and b). The surface weather station is outside of the enclosures and not impacted by the experimental warming treatments that began in 2015. These data are available at https://mnspruce.ornl.gov/.

3.3 Simulation of the SPRUCE experiment

Based on measurements at the SPRUCE site, ELM_SPRUCE includes four PFTs: boreal evergreen needleleaf tree (*Picea)*, boreal deciduous needleleaf tree (*Larix)*, boreal deciduous shrub (representing several shrub species), and the newly introduced *Sphagnum* moss PFT. Currently ELM_SPRUCE does not include light competition among multiple PFTs, and thus does not represent cross-PFT shading effects. Our model also allows the canopy density of PFTs to change prognostically, and their fractional coverage is held constant. We used measurements from *Sphagnum* moss collected at a tussock tundra site in Alaska (Hobbie 1996) to set several of the model leaf litter parameters for our simulations (Table 1). The values for other parameters have been optimized based on observations at the SPRUCE site (Table 2 and 3, optimization methods described in section 3.4). We prescribe both hummock and hollow https://scratch.mit.edu/projects/411435898microtopographies to have the same fractional PFT distribution. Consistent with Shi et al. (2015), hummocks and hollows were

modeled on separate columns with lateral flow of water between them. All the ELM_SPRUCE simulations were conducted using a prognostic scheme for canopy phenology (Olesen et al., 2013).

The SPRUCE experiment at the S1-Bog consists of combined manipulations of temperature (various differentials up to +9 ºC above ambient) and atmospheric CO_2 concentration (ambient and ambient + 500 ppm) applied in 12 m diameter x 8 m tall enclosures constructed in the S1-Bog. The whole-ecosystem warming began in August 2015, elevated CO_2 started from June 2016, and various treatments are envisioned to continue until 2025. Extensive pre-treatment observations at the site began in 2009.

For the ELM_SPRUCE, we continuously cycled the 2011-2017 climate forcing (see section 3.2) to equilibrate carbon and nitrogen pools under pre-industrial atmospheric CO_2 concentrations and nitrogen deposition, and then launched a simulation starting from year 1850 through year 2017. This transient simulation includes historically varying CO_2 concentrations, nitrogen deposition, and the land-use effects of a strip cut and harvest at the site in 1974. These simulations were used to compare model performance with pre-treatment observations. A subset of these observations was also used for optimization and calibration (section 3.4).

To investigate how the bog vegetation may respond to different warming scenarios and elevated atmospheric CO_2 concentrations, we performed 11 model runs from the same starting point in year 2015. These simulations were designed to reflect the warming treatments and CO_2 concentrations being implemented in the SPRUCE experiment enclosures. The model simulations include one ambient case (both ambient temperature and CO_2 concentration), and five simulations with modified input air

temperatures to represent the whole-ecosystem warming treatments at five levels (+0 ºC, +2.25 ºC, +4.50 ºC, +6.75 ºC and +9.00 ºC above ambient) and at ambient CO_2, and another five simulations with the same increasing temperature levels and at elevated CO_2 (900 ppm). In the treatment simulations, we also considered the passive enclosure effects, which reduce incoming shortwave and increase incoming longwave radiation (Hanson et al., 2017). Following the SPRUCE experimental design, there was no water vapor added so that the simulations used constant specific humidity instead of constant relative humidity across the warming levels. All the treatment simulations were performed through the year 2025 by continuing to cycle the 2011-2017 meteorological inputs (with modified temperature and radiation to reflect the treatments) to simulate future years.

Table 1: Physiological parameters of *Sphagnum* mosses as given in Hobbie 1996

Parameters	Description	Values
lflitcn	Leaf litter C:N ratio (gC/gN)	66
lf_fcel	Leaf litter fraction of cellulose	0.737
lf_flab	Leaf litter fraction of labile	0.227
lf_flig	Leaf litter fraction of lignin	0.036

3.4. Model sensitivity analysis and calibration

The vegetation physiology parameters in ELM_SPRUCE were originally derived from CLM4.5 and its predecessor, Biome-BGC, and represent broad aggregations of plant traits over many species and varied environmental conditions (White et al., 2000).

To achieve reasonable model performance at SPRUCE, site-specific parameters and targeted parameter calibration are needed. Since the ELM_SPRUCE contains over 100 uncertain parameters, parameter optimization is not computationally feasible without first performing some dimensionality reduction. Based on previous ELM sensitivity analyses (e.g., Lu et al., 2018; Ricciuto et al., 2018; Griffiths et al., 2018), we chose 35 model parameters for further calibration (Tables 2 and 3). An ensemble of 3000 ELM_SPRUCE simulations were conducted using the procedure described in 3.3, with each ensemble member using a randomly selected set of parameter values within uniform prior ranges. This model ensemble was first used to construct a polynomial chaos surrogate model, which was then used to perform a global sensitivity analysis (Sargsyan et al., 2014; Ricciuto et al., 2018). Main sensitivity indices, reflecting the proportion of output variance that occurs for each parameter, are described in section 4.1.

To minimize potential biases in model predictions of treatment responses, we calibrated the same 35 model parameters using pre-treatment observations as data constraints. We employed a quantum particle swarm optimization (QPSO) algorithm (Lu et al., 2018). While this method does not allow for the calculation of posterior prediction uncertainties, it is much more computationally efficient than other methods such as Markov Chain Monte Carlo. The constraining data included year 2012-2013 tree growth and biomass (Hanson et al. 2018a), year 2012-2013 shrub growth and biomass (Hanson et al., 2018b), year 2012 and 2014 *Sphagnum* net primary productivity (Norby et al., 2017, 2019), enclosure-averaged leaf area index by PFT (year 2011 for tree and year 2012 for shrub and *Sphagnum*), and year 2011-2013 water table depth (WTD) observations, aggregated to seasonal averages (Hanson et al., 2015b). The goal of the

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optimization is to minimize a cost function, which we define here as a sum of squared errors over all observation types weighted by observation uncertainties. When observation uncertainties were not available, we assumed a range of ±25% from the default value. Site measurements were also used to constrain the ranges of two parameters: *leafcn* (leaf carbon to nitrogen ratio) and *slatop* (specific leaf area at canopy top). The uniform prior ranges for these parameters represent the range of plot to plot variability. Optimized parameter values are shown in Table 2 and 3. Section 4 reports the results of simulations using these optimized parameters, which were used to perform a spinup, transient (1850-2017) and set of 11 treatment simulations (2015-2025) as described above.

Table 2: PFT-specific optimized model parameters

Parameter	Description	*Sphagnum*	*Picea*	*Larix*	Shrub	Range
flnr	Rubisco-N fraction of leaf N	0.2906	0.0678	0.2349	0.2123	[0.05,0.30]
croot_stem	Coarse root to stem allocation ratio	N/A	0.2540	0.1529	0.7540	[0.05,0.8]
stem_leaf[1]	Stem to leaf allocation ratio	N/A	1.047	1.016	0.754	[0.3,2.2]
leaf_long	Leaf longevity (yr)	0.9744	5[3]	N/A	N/A	[0.75, 2.0]
slatop	Specific leaf area at canopy top (m^2 gC^{-1})	0.00781	0.00462	0.0128	0.0126	[0.004,0.04]
leafcn	Leaf C to N ratio	35.56	70.17	64.84	33.14	[20,75]
froot_leaf[2]	Fine root to leaf allocation ratio	0.3944	0.8567	0.3211	0.6862	[0.15, 2.0]
mp	Ball-Berry stomatal conductance slope	N/A	7.50	9.32	10.8	[4.5, 12]

Optimized values of PFT-specific parameters. The range column values in brackets indicate the range of acceptable parameter values used in the sensitivity analysis and the optimization across all four PFTs in the format [minimum, maximum]. N/A indicates that parameter is not relevant for that PFT.

[1] for tree PFTs, this parameter depends on NPP. The value shown is the allocation at an NPP of 800 gC m^{-2} yr^{-1}.

[2] the fine root pool is used as a surrogate for non-photosynthetic tissue in *Sphagnum*

[3] This parameter was not optimized; we used the default value.

Table 3: Non PFT-specific optimized model parameters

	Description	Optimized value	Default	Range
r_mort	Vegetation mortality	0.0497	0.02	[0.005, 0.1]
decomp_depth_efolding	Depth-dependence e-folding depth for decomposition (m)	0.3899	0.5	[0.2, 0.7]
$q_{drai,0}$	Maximum subsurface drainage rate (kg m^{-2} s^{-1})	3.896e-6	9.2e-6*	[0, 1e-3]
Q_{10}_mr	Temperature sensitivity of maintenance respiration	2.212	1.5	[1.2, 3.0]
br_mr	Base rate for maintenance respiration (gC gN m^2 s^{-1})	4.110e-6	2.52e-6	[1e-6, 5e-6]
crit_onset_gdd	Critical growing degree days for leaf onset	99.43	200	[20, 500]
lw_top_ann	Live wood turnover proportion (yr^{-1})	0.3517	0.7	[0.2, 0.85]
gr_perc	Growth respiration fraction	0.1652	0.3	[0.12, 0.4]
$r_{drai,0}$	Coefficient for surface water runoff (kg m^{-4} s^{-1})	6.978e-7	8.4e-8*	[1e-9, 1e-6]

Optimized and default values for non PFT-specific parameters. The range column values in brackets indicate the range of acceptable parameter values used in the sensitivity analysis and the optimization in the format [minimum, maximum].

* Previously calibrated value from Shi et al (2015)

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4. Results

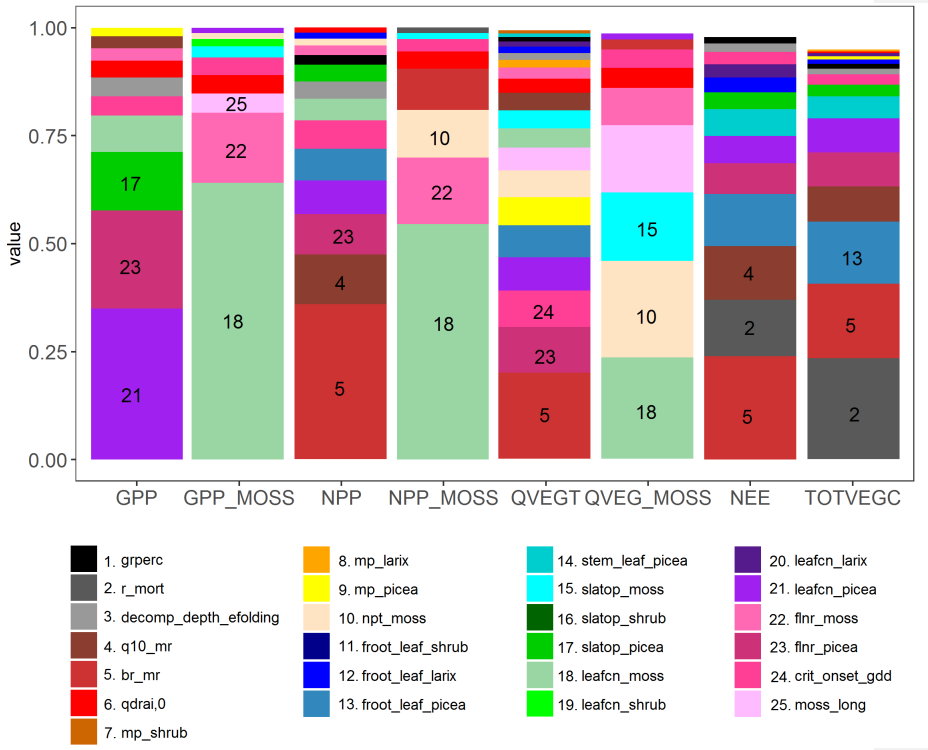
4.1 Model sensitivity analysis

Main effect (first-order) sensitivities are shown for eight model output quantities of interest: Total site gross primary productivity (GPP), GPP for the moss PFT only (GPP_moss), total site net primary productivity (NPP), NPP for the moss PFT only (NPP_moss), total site vegetation transpiration (QVEGT), evaporation from the moss surface (QVEG_moss), net ecosystem exchange (NEE) and site total vegetation carbon

(TOTVEGC) (Fig. 2). Out of 35 parameters investigated, 25 show a sensitivity index of at least 0.01 for one of the quantities of interest, and these are plotted on figure 2. In that figure, sensitivities are stacked in order from highest to lowest for each variable, with the height of the bar equal to the sensitivity index. The first order sensitivities sum to at least 0.95 for all variables, indicating that higher order sensitivities (i.e., contributions to the sensitivity from combinations of two or more parameters) contribute relatively little to the variance for these quantities of interest.

According to this analysis, the variance in total site GPP is dominated by three *Picea* parameters: the fraction of leaf nitrogen in RuBiCO (*flnr_picea)*, leaf carbon to nitrogen ratio (*leafcn_picea)* and the specific leaf area at canopy top (*slatop_picea*). GPP sensitivity for the moss PFT is dominated by the same three parameters, but for the moss PFT instead of *Picea* (*flnr_moss*, *leafcn_moss*, and *slatop_moss*). For NPP, QVEGT and NEE, the highest sensitivity the maintenance respiration base rate *br_mr*, similar to earlier results in Griffiths et al. (2017). The maintenance respiration temperature sensitivity Q_{10}*_mr* is also a key parameter for NPP and NEE. The critical onset growing degree day threshold (*crit_onset_gdd*), which drives deciduous phenology in the spring for the *Larix* and shrub PFTs, is an important parameter for NPP and NEE. *flnr_picea* is important for both NPP and QVEGT. For NPP_moss and QVEG_moss, *leafcn_moss* is and the ratio of non-photosynthesizing tissue to photosynthesizing tissue (*npt_moss)* are sensitive. For TOTVEGC and NEE, vegetation mortality (*r_mort)* is also a sensitive parameter. For the site-level quantities of interest, at least 10 parameters contribute significantly to the uncertainty, illustrating the complexity of the model and large number of processes contributing to uncertainty in SPRUCE predictions. For the moss variables,

499 there are some cases where significant sensitivities exist for non-moss PFT parameters.
500 For example, *leafcn_shrub* is the seventh most sensitive parameter for GPP_moss,
501 indicating that competition between the PFTs for resources may be important. In this
502 case, uncertainty about parameters on one PFT may drive uncertainties in the simulated
503 productivity of other PFTs.



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505 Figure 2 Sensitivity analysis of ELM-SPRUCE for selected parameters (Table 2 and 3). The
506 Colored bars indicate the fraction of variance in site gross primary productivity (GPP), moss-only
507 NPP (GPP_MOSS), site net primary productivity (NPP), moss-only NPP (NPP_MOSS), total
508 vegetation transpiration (QVEGT), moss evaporation (QVEG_MOSS), site net ecosystem
509 exchange (NEE) and total vegetation carbon (TOTVEGC) controlled by each parameter. The
510 legend shows the top 25 most influential parameters; the remaining parameters not shown have
511 sensitivities of no more than 0.01 for any of the outputs. All variables represent 2011-2017

average values over the ambient conditions. For parameters that are treated as PFT-dependent, the PFT is indicated with a suffix (picea, larix, shrub or moss)

4.2 Model evaluation

Our model simulates GPP for vascular plants and *Sphagnum* moss in both hummock and hollow settings, with separate calculations for each PFT. Here we use the model estimate of GPP prior to downregulation by nutrient limitation from the ambient case, based on recent studies indicating that nutrient limitation effects are occurring downstream of GPP (Raczka et al. 2016; Metcalfe et al., 2017; Duarte et al. 2017). This treatment of nutrient limitation on GPP has been modified in a more recent version of ELM, and our moss modifications will be merged to that version as a next step. For now, by referring to the pre-downregulation GPP we are capturing the most significant impact of those changes for the purpose of comparison to observations.

Our model simulated two seasonal maxima of *Sphagnum* moss GPP, one at the end of May, and the other in August (Figure 3). Both peaks are lower than the maximum of observed (flux-partitioned) GPP, which occurs in August. Based on results of the sensitivity analysis, it could be that the base rate for maintenance respiration for moss is too high, causing an underestimate of NPP and biomass, which leads to a low bias in peak GPP.

During June and October, observations suggest that ELM_SPRUCE over-predicts GPP. The model does limit GPP as a function of the depth of standing water on the bog surface (Eq. 7). The water table height (WTH) above the bog surface is being predicted by the model (dashed red line in Fig. 3), and while the seasonal pattern of higher water

table in the spring and lower water table in the fall agrees well with observations (dashed black line in Fig. 3), the predicted WTH is generally too low by 5-10 cm. The modeled WTH here is for hollow. We turned off the lateral transport when there is ice on the soil layers above the water table to avoid an unreasonable amount of ice accumulation on the frozen layers, which results in there is no flow from hummock to hollow. Forcing the modeled GPP to respond to observed WTH (during the period with observations) gives a pattern of increasing GPP through June and July which is more consistent with observations (blue line in Fig. 3). We do not have observations for GPP earlier than June, due to limitations of the instrumentation when the bog surface is flooded.

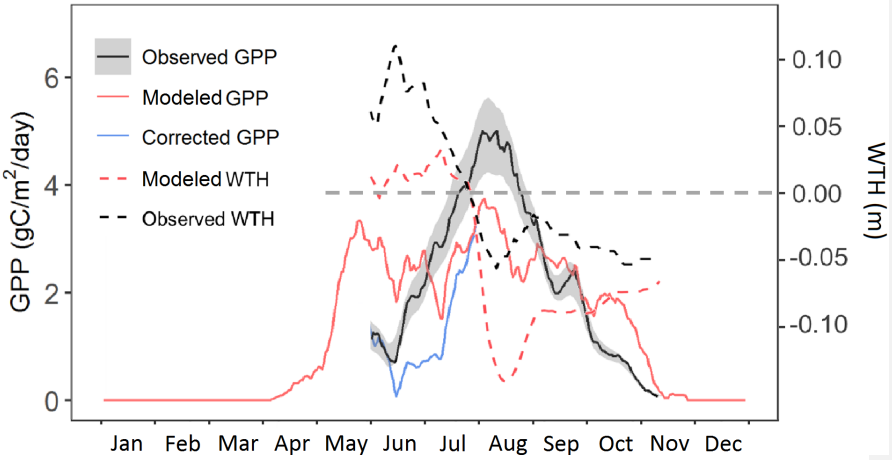

Figure 3. Predicted GPP (red solid line) compared with flux-partitioned GPP (black solid line, GPP data was not used in the parameters optimization) of *Sphagnum* mosses for the year 2014. The blue line is the predicted GPP corrected with the observed water table height. The dashed black and red lines are observed and modeled water table height (the dashed gray line is the hollow surface).

The model simulated reasonable annual values for *Sphagnum* NPP for the period 2014-2017 but showed much lower NPP compared with observation (139 vs. 288 g

555 C/m^2/yr) for the year 2012 (Fig. 4a). Measurement uncertainties are larger in 2016-2017
556 than in earlier years, perhaps related to a new measurement protocol for those years, and
557 the model estimates are within measurement uncertainty bounds for years 2014-2017
558 (Griffiths et al., 2018; Norby et al., 2019). The observed *Sphagnum* NPP was measured at
559 different plots and each plot included different species abundances. As a result, the scaled
560 NPP includes spatial variations and uncertainty in species distribution (Norby and Childs,
561 2017).

562 Simulated tree above ground biomass is within the observed inter-plot variability
563 (Fig. 4b). Observations suggest an increasing trend in tree biomass, which was not
564 predicted by the model. The optimized parameters show increased mortality and
565 autotrophic respiration rate parameters compared to the default model (Table 3), which
566 causes the simulations to approach steady state relatively quickly after the 1974
567 disturbance. However, the sensitivity analysis also identifies theses mortality and
568 maintenance respiration parameters as highly sensitive, therefore this simulated response
569 is uncertain. For the shrub stem carbon, the simulated mean from year 2012 to 2015 was
570 140.4 g C/m^2, slightly higher than the observation (133.9 g C/m^2) but well within the
571 observed range of inter-plot variability (Fig. 4c).

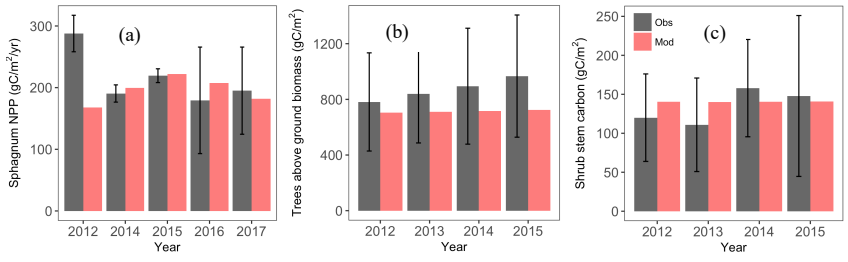

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Figure 4. Predicted (red bars) *Sphagnum* NPP (left), aboveground tree biomass (middle) and shrub stem carbon (right) compared with the observations (black bars). Observed NPP data are based on growth of 12-17 bundles of 10 Sphagnum stems in 2012-2015 (unpublished data) and in two ambient plots by the method described by Norby et al. (2019) in 2016-1017 (data in Norby et al. 2017). The Sphagnum NPP data of year 2015-2017, and aboveground tree biomass and shrub stem carbon of year 2014-2015 are independent of the related parameters opitimizaton.

4.3 Simulated carbon cycle response to warming and elevated atmospheric CO_2 concentration

Different PFTs demonstrated different warming responses for both ambient CO_2 and elevated CO_2 concentration conditions (Fig. 5). Both *Larix* and shrub NPP increased with warming under both CO_2 concentration conditions (Fig. 5 b, c, h and i). In addition, CO_2 fertilization stimulates the growth of these two PFTs and the fertilization effect further increases with warming (Fig. S1, GPP increases more under elevated CO_2 condition than the ambient case). In contrast, *Picea* NPP decreased with warming levels (Fig. 5 a and g) for both CO_2 conditions. For *Sphagnum,* NPP decreased in hummocks but increased in hollows with increasing temperature (Fig. 5 d, e, j and k). The CO_2 fertilization also stimulate the grow of the Picea and *Sphagnum* PFTs (Fig. 5 a, d, e g, j and k). The enclosure-total NPP for all PFTs responded differently to the warming only and warming with elevated CO_2 (Fig. 5 f and l). The enclosure-total NPP for each warming level changed less under the ambient CO_2 condition than those with elevated CO_2 condition, and NPP decreased with warming in most of years under ambient CO_2 condition but increased under elevated CO_2 condition (Fig.5 f and l). This result demonstrated that the elevated CO_2 scenario changes the sign of the NPP warming response for the bog peatland ecosystem.

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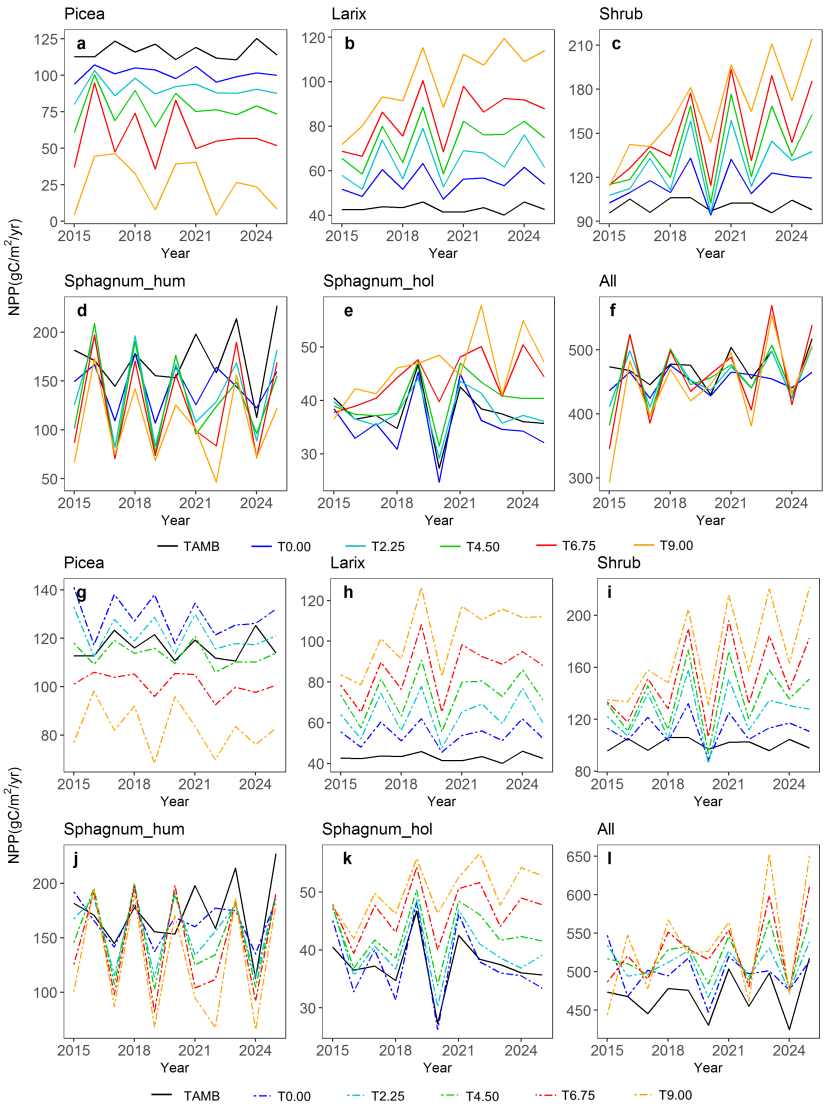

Figure 5 predicted NPP response to warming with ambient atmospheric CO_2 (a-f, solid lines) and warming with elevated atmospheric CO_2 concentration (g-l, dash lines), the black solid line TAMB is the ambient temperature and CO_2 case, T0.00 to T9.00 means increasing temperature from 0ºC to 9ºC

Compared with the ambient biomass, the biomass of black spruce (*Picea*) significantly decreased but the biomass of *Larix* significantly increased under the greatest warming treatment (+9.00°C, Fig.6). Biomass of shrub and hollow *Sphagnum* also increased, but less than did *Larix*. The hummock *Sphagnum* biomass also showed strong correlation with water table height at roughly a 3-month lag (the maximum correlation occurs with an 82-day lag, R^2=0.56). NPP is allocated instantaneously into biomass. A positive NPP anomaly caused by water table shifts leads to higher LAI, which also increases future productivity for some amount of time even if the water table returns to normal. *Sphagnum* biomass has a 1-year turnover time in the simulation. This combination of effects leads to a roughly 3-month timelag. Due to the relative lower height of the water table in the hummock than the hollow, the simulated hummock *Sphagnum* were more significantly water-stressed than the hollow *Sphagnum* as the water table height declines. This is consistent with multiple studies finding an increase in temperatures associated with drought (low water table height) reducing *Sphagnum* growth (Bragazza et al., 2016; Granath et al., 2016; Mazziotta et al., 2018). We plotted the predicted canopy evaporation for hummock and hollow *Sphagnum* responses to warming and found that both hummock and hollow *Sphagnum* canopy evaporation increase with warming for both ambient and elevated atmospheric CO_2 conditions despite the Larix and shrubs are growing with warming. Moreover, the hollow *Sphagnum* canopy evaporation warming response is stronger than that of the hummock *Sphagnum* (Fig. S2). In summary, the growth of bog vegetation is predicted to have species-specific warming responses that differ in sign and magnitude.

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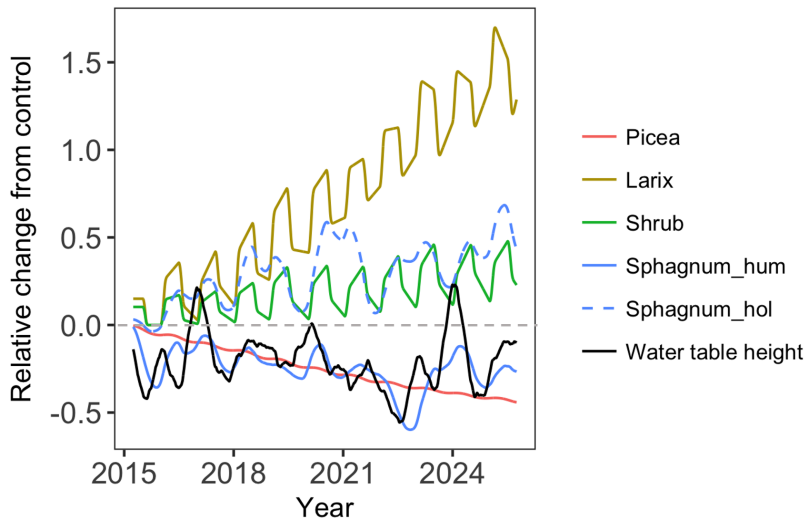

Figure 6 The relative changes of biomass for different PFTs and water table height (the weighted average between hummock and hollow) between +9.00 ºC treatment case and the ambient case (+9.00 ºC / ambient – 1)

5. Discussion

Sphagnum moss is the principal plant involved in the peat accumulation in peatland ecosystems, and effective characterization of its biophysical and physiological responses has implications for predicting peatland and global carbon, water and climate feedbacks. This study moves us closer to our long-term goal of improving the prediction of peatland water, carbon and nutrient cycles in ELM_SPRUCE, by introducing a new *Sphagnum* moss PFT, implementing water content dynamics and photosynthetic processes for this nonvascular plant. The *Sphagnum* model development combined with our previous hummock-hollow microtopography representation and laterally-coupled two-column hydrology scheme enhance the capability of ELM_SPRUCE in simulating high-carbon wetland hydrology and carbon interactions and their responses to plausible environmental changes.

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5.1 Uncertainties in simulating *Sphagnum* productivity

Our predicted peak GPP is similar to the results found by Walker et al. (2017) when they calculated the internal resistance to CO_2 diffusion as a function of *Sphagnum* water content using a stand-alone photosynthesis model. In both cases, the predicted peak GPP is lower than observations. Walker et al. (2017) were, however, able to capture the observed peak magnitude with a combination of light extinction coefficient, canopy clumping coefficient, maximum shoot area index (SAI), and a logistic function describing the effective *Sphagnum* SAI in relation to water table. Here we used model default values for the light extinction and canopy clumping coefficients. While the water table impacts *Sphagnum* productivity in our simulation, modeled leaf (or shoot) area index (LAI) is mainly controlled by NPP and turnover. In addition, we use the default formulation for acclimation of Vcmax in ELM which is based on a 10-day mean growing temperature. At this point we don't have sufficient measurements to test this assumption, but we can prioritize these measurements in the future. *Sphagnum* temperature is computed from surface energy balance but because the current model doesn't have the capacity to estimate the shading effects from trees and shrubs, this may be overestimated. Moreover, biases in predicted water table height contribute to errors in the calculated submergence effect. Improving these biases and assuming an exponential rather than a linear CO_2 uptake profile may improve representation of the submergence effect. All these aspects may be attribute to the biases of the simulated *Sphagnum* GPP. We can consider this in the future when we have more detailed measurements. Further investigation is thus needed to understand how representative the chamber-based

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observations from Walker et al. (2017) are of the larger-scale SPRUCE enclosures, and to reconcile these GPP estimates with plot-level NPP observations (Norby et al., 2019).

The hydrology cycle, especially water table depth (WTD) is also a key factor that influences the seasonality of GPP in *Sphagnum* mosses (Lafleur et al., 2005; Riutta 2007, Sonnentag et al, 2010; Grant et al., 2012; Kuiper et al., 2014; Walker et al, 2017). One key feedback is if the water table declines, there can be enhanced decomposition and subsidence of the peat layer, which brings the surface down closer to the water table again. But we currently did not consider the peat layer elevation changes in our model and this will be one of the future development directions. The capillary rise plays into the *Sphagnum* hydrological balance, which varies depending on water table depth and evaporative demand. At short timescales or under rapidly changing conditions, there may not be equilibration between the Sphagnum water content and the peat moisture. Generally, the *sphagnum* water content will equilibrate with the peat on a daily basis outside the plot since the dew point is often reached at night. But inside the warmer plots since the vapor pressure deficit does not go to zero some disequilibration could remain. High-frequency latent heat flux data from the site are currently lacking, but could help to constrain these effects in the future. The current phenology observations also include if *Sphagnum* hummock and hollow are wet or dry, and we could look at the relationship with soil water content sensors in the future. Moreover, the equilibration time between peat moisture and moss water content is reasonable fast, but the timescales for rewetting should change as the peat dries since the cross section for capillary rise will decline and thus the maximum flux to the surface will decline. So, at some point, between gravity potential and reduced hydraulic conductivity the capillarity will not satisfy evaporative

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demand (Personal discussion with field expert Jeffrey Warren). Previous studies have reported that drier and warmer future climates can lower the water table, affecting the resilience of long-term boreal peatland carbon stocks (Limpens et al., 2008, Dise, 2009, Frolking et al., 2011). WTD drawdown affects the net ecosystem productivity of boreal peatlands through its effects on ecosystem respiration and GPP. The interactions between WTD and GPP, however, vary across peatlands and influence both vascular and nonvascular plant GPP in different ways (Lafleur et al., 2005). For instance, nonvascular plants mostly access water in the near surface shallow peat layers. These layers, however, can drain quickly with receding WTD and high nonvascular evaporative demand, and thus depend on water supply through capillary rise or precipitation (Dimitrov et al., 2011, Peichl et al., 2014, Druel et al., 2017). If recharge is not adequate, near-surface peat desiccation occurs thereby cutting off the supply of water to Sphagnum, which subsequently dries, leading to rapid decline in GPP (Lafleur et al., 2005, Riutta 2008, Sonnentag et al ., 2010, Sulman et al., 2010, Dmitrov et al., 2011, Kuiper et al., 2014, Peichl et al., 2014). Thus, for the Sphagnum mosses desiccation occurs and the time needed before recovery to optimum photosynthetic capacity should be taken into account in our future work. Alternately, under saturated conditions when the water table is close to the *Sphagnum* surface, *Sphagnum* photosynthesizing tissue can become submerged or surrounded by a film of water that is likely to reduce the effective LAI of the *Sphagnum* and thus reduce photosynthesis (Walker et al., 2017). Submerged Sphagnum can take up carbon derived from CH4 via symbiotic methanatrophs (Raghoebarsing et al., 2005), but in any cases CO_2 diffusion for photosynthesis will dramatically decrease under water. Larmola et al. (2014) also reported that the activity of oxidizing bacteria provides not

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only carbon but also nitrogen to peat mosses and, thus, contributes to carbon and nitrogen accumulation in peatlands, which store approximately one-third of the global soil carbon pool. We currently didn't consider this kind of CH_4 associated carbon and nitrogen uptake by *Sphagnum*.

The live green *Sphagnum* moss layer buffers the exchange of energy and water at soil surface and regulates the soil temperature and moisture because of its high-water holding capacity and the insulating effect (McFadden et al., 2003; Block et al., 2011; Turesky et al, 2012; Park et al., 2018). Currently, we apply the same method for the hummock and hollow *Sphagnum* water content prediction and can test the model against the measured data when more data are available. Our model still can predict *Sphagnum* water content differences between these microtopographies as expected, with the water content of hollows greater than that of hummocks though. In addition, our model is able to represent the self-cooling effect, although we do not yet have measurements available to validate the model. The relationship of the differences between vegetation temperature (TV) and 2m air temperature (TBOT) (TV-TBOT) and canopy evaporation for both hummock and hollow *Sphagnum* demonstrated that the differences of TV-TBOT was negative and the canopy evaporation had a negative relationship with TV-TBOT (Fig. S3). Moreover, Walker et al., (2017) reported that the function of *Sphagnum* water content to soil water content or to water table depth they used for the SPRUCE site was empirical and may not be representative for peatland ecosystem. To better represent the peatland ecosystem in our model, we will eventually treat the *Sphagnum* mosses as the "top" soil layer with a lower thermal conductivity and higher hydraulic capacity (Beringer et al., 2001; Wu et al., 2016; Porada et al., 2016).

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5.2 Predicted warming and elevated CO_2 concentration response uncertainties

Our model warming simulations suggested that increasing temperature reduced the *Picea* growth but increased the growth of *Larix* under both ambient and elevated atmospheric CO_2 conditions. The main reason for this model difference in response for the two tree species is that despite their similar productivity under ambient conditions, *Picea* has more respiring leaf and fine root biomass because of lower specific leaf area, longer leaf longevity, and higher fine root allocation. Therefore, warming results in a much larger increase in maintenance respiration relative to changes in NPP for *Picea* compared to *Larix* (Fig. 5 and Fig. S4). Increased tree growth and productivity in response to the recent climate warming for high-latitude forests has been reported (Myneni et al., 1997, Chen et al. 1999, Wilming et al. 2004, Chavardes, 2013). On the other hand, reductions in tree growth and negative correlations between growth and temperature also have been shown (Barber et al., 2000; Wilmking et al., 2004; Silva et al., 2010; Juday and Alix 2012; Girardin et al., 2016; Wolken et at., 2016).

Our model also predicted increasing growth of shrubs with increased temperature, similar to simulated increase in shrub cover caused mainly by warmer temperatures and longer growing seasons reported by Miller and Smith (2012) using their model LPJ-GUESS. In addition, several other modelling studies have also found increased biomass production and LAI related to shrub invasion and replacement of low shrubs by taller shrubs and trees in response to increased temperatures in tundra regions (Zhang et al., 2013; Miller and Smith, 2012; Wolf et al., 2008; Porada et al., 2016; Rydssa et al., 2017).

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The responses of *Sphagnum* mosses to warming simulated by ELM_SPRUCE showed that *Sphagnum* growth in hollows was consistently higher with increased temperatures, where water availability was not limiting. *Sphagnum* growing on hummocks, on the other hand, showed negative warming responses that are related to the strong dependency on water table height. A Recent study of the same SPRUCE site (Norby et al. 2019) had suggested that the hummock-hollow microtopography had a larger influence on *Sphagnum* responses to warming than species-specific traits. In addition, the previous studies had demonstrated that the most dominant mechanism of *Sphagnum* warming response was probably through the effect of warming on depth to the water table and water content of the acrotelm, both of them responded to increasing temperature (Grosvernier et al., 1997; Rydin, 1985; Weltzin et al., 2001; Norby et al., 2019). Moreover, desiccation of capitula due to increased evaporation associated with higher temperatures and vapor pressure deficits can reduce *Sphagnum* growth independent of the water table depth (Gunnarsson et al., 2004). We currently used the same parameters for both hummock and hollow, but could consider species differences in the future. Norby et al. (2019) investigated different *Sphagnum* species at the same site and reported there was no support for the hypothesis that species more adapted to dry conditions (e.g., *S. magellanicum* and *Polytrichum* mainly on hummocks) would be more resistant to the stress and would increase in dominance, and both hummock and hollow *sphagnum* are declining with warming despite the differences between them. This declining trend may be in part due to increased shading from the shrub layer, which is expanding with warming.

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Ecosystem warming can have direct and indirect effects on *Sphagnum* moss growth. The growth of Sphagnum may be reduced directly by higher air temperature, due to the relatively low temperature optima of moss photosynthesis (Hobbie et al.,1999; Van Gaalen, 2007; Walker et al., 2017). On the other hand, increased shading by the shrub canopy and associated leaf litter could indirectly decrease moss growth (Chapin et al., 1995; Hobbie and Chapin 1998; Van der Wal et al., 2005; Walker et al., 2006; Breeuwer et al., 2008). In contrast, other studies suggest that *Sphagnum* growth can be promoted via a cooling effect of shading on the peat surface, by alleviating photo-inhibition of photosynthesis and also by reducing evaporation stress (Busby et al., 1978; Murray et al., 1993; Man et al., 2008; Walker et al., 2015, Bragazza et al., 2016, Mazziotta et al., 2018). Our model sensitivity analysis also indicated that the parameters of Shrub showing significant sensitivities to *Sphagnum* mosses GPP, indicating that competition between the PFTs for resources might be important. Moreover, ELM_SPRUCE did predict enhancement of shrub and *Larix* tree with increased temperatures with both ambient and elevated CO_2 conditions (the leaf area increasing with warming, Fig. S3). Currently ELM_SPRUCE does not include light competition among multiple PFTs, and thus does not represent cross-PFT shading effects, which may contribute to the warming and elevated CO_2 response differences between our model prediction and observed result of Norby et al. (2019). Meanwhile, we have fixed cover fraction for PFTs in our model may also contribute to the disagreement of predicted and observed warming responses. While Norby et al. (2019) showed that the fractional cover of different *Sphagnum* species declined with warming.

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Sphagnum mosses are sitting on top of high CO_2 sources. CH_4 can be a significant carbon sources of submerged *Sphagnum* (Raghoebarsing et al., 2005; Larmola et al, 2014); refixation of CO_2 derived from decomposition processes also is an important source of carbon for *Sphagnum* (Rydin and Clymo, 1989; Turetsky and Wieder, 1999). The effects of the elevation of atmospheric CO_2 on *Sphagnum* moss are currently disputed, with studies indicating an increase in growth rate (Jauhiainen and Silvde 1999; Heijmans et al. 2001a; Saarnio et al. 2003), decreases in growth rate (Grosvernier et al. 2001; Fenner et al. 2007) and no response (Van der Hejiden et al. 2000; Hoosbeek et al. 2002; Toet et al. 2006). Norby et al. (2019) indicated that no growth stimulation of both hummock and hollow *Sphagnum* under elevated CO_2 condition, but significant negative effects of elevated CO_2 on *Sphagnum* NPP in year 2018 at the same study site. Contrasting responses between *Sphagnum* species are thought to be coupled with the water availability. In contrast, our model results showed that both hummock and hollow *Sphagnum* growths were stimulated by the elevated CO_2 concentration, which may be attributed to the fact thatvwe did not consider the light competition between the PFTS (shrub and tree shading effects) and use a fixed cover fraction of *Sphagnum*.

The CO_2 vertical concentration profile is assumed to be uniform in the simulations. In the experiment, the enclosure's regulated additions of pure CO_2 are distributed to a manifold that splits the gas into four equal streams feeding each of the four air handling units (Hanson et al., 2017 Fig. 2a), and is injected into the ductwork of each furnace just ahead of each blower and heat exchanger. Horizontal and vertical mixing within each enclosure homogenizes the air volume distributing the CO_2 along with the heated air. The horizontal blowers in the enclosures together with external wind

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eddies ensure vertical mixing. We do not have routine automated CO_2 concentration data below 0.5m. The moss layer may well be experiencing higher concentrations than assumed by the model, but such an impact will be minimized during daylight hours. Preliminary isotopic measurements imply a significant fraction of carbon assimilated by the moss may come from subsurface respired CO_2 (i.e., CO_2 with older ^{14}C signatures predating bomb carbon that can only be sourced from deeper peat, Hanson et al., 2017). However, the observed elevated CO_2 response is smaller than simulated (Hanson et al., 2020). Understanding the drivers of elevated CO_2 response or lack thereof is a key topic for future work and we will consider this effect in future assessments of the isotopic carbon budgets for the SPRUCE study.

To better investigate the *Sphagnum* warming and elevated CO_2 responses, we should also focus on revealing the interactions with Shrub and nitrogen availability (Norby et al., 2019). Nitrogen (N_2) fixation is a major source of available N in ecosystems that receive low amounts of atmospheric N deposition, like boreal forests and subarctic tundra (Lindo et al., 2013, Weston et al, 2015, Rousk et al., 2016, Kostka et al., 2016). For example, diazotrophs are estimated to supply 40-60% of N input to peatlands (Vile et at., 2014) with high accumulation of fixed N into plant biomass (Berg et al., 2013). Nevertheless, N_2 fixation is an energy costly process and is inhibited when N availability and reactive nitrogen deposition is high (Gundale et al., 2011; Ackermann et al., 2012; Rousk et al., 2013). This could limit ecosystem N input via the N_2 fixation pathway. We are measuring Sphagnum associated N2 fixation at the SPRUCE site and found that rates decline with increasing temperature (Carrell et al. 2019 Global Change Biology). We are continuing these measurements to see if they correlate with the GPP empirical relationship from

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Clevand (1999), or if temperature disrupts that association. Once finished, results will be used to represent N fixation by the Sphagnum layer and testing with measurements.

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It is also encouraging that while we did not use leaf-level gas exchange observations in our optimization, the increased maintenance respiration base rate and temperature sensitivity compared to default (table 2) is largely consistent with pre-treatment leaf level observations (Jensen et al., 2019). In the future, a multi-scale optimization framework that can assimilate leaf and plot-level observations simultaneously should lead to improved model predictions and reduced uncertainties for the treatment simulations. If similar patterns observed in ambient conditions continue during the treatments, incorporating seasonal variations in leaf photosynthetic parameters may also further improve the simulated response to warming (Jensen et al., 2019).

Overall, while the sensitivity analysis is useful to indicate the key parameters and mechanisms responsible for uncertainty, our ability to quantify prediction uncertainty is limited because we consider only a single simulation with optimized parameters. Ideally, we should perform a model ensemble that represents the full range of posterior uncertainty over simulations that are consistent with the pre-treatment observations, and also a range of possible future meteorological conditions. This is currently being done for SPRUCE with the TECO carbon cycle model (Jiang et al., 2018), but the computational expense of ELM_SPRUCE currently prohibits this approach. By combining new surrogate modeling approaches (e.g. Lu et al., 2019) with MCMC techniques, it may be possible to achieve this in the near future. This will help to reduce prediction uncertainties, which currently prevail in the future carbon budget of peatlands and its feedback to climate change (McGuire et al., 2009).

The algorithms used to represent moss (e.g. Williams and Flanagan) are transferable to and have been applied by other modeling groups in other peatlands. However, we expect that certain parameters will vary, for example, the microtopographic parameters, the relationship between peat moisture and internal water content, and moss properties such as C:N ratio. The parameter sensitivity analysis informs us as to the most important parameters responsible for prediction uncertainty, and can inform how to prioritize these measurements. Collecting these measurements from a variety of sites will be a necessary preliminary exercise. In addition to the simulations aimed at improved understanding of bog response to experimental manipulations at the plot-scale, we are pursuing model implementations at larger spatial scales. The model framework described in this study is capable of performing regional simulations, although the current simulations were designed for mechanistic understanding of *Sphagnum* mosses hydrological and physiological dynamics at the plot-level.

6. Summary

In this study, we reported the development of a *Sphagnum* moss PFT and associated processes within the ELM_SPRUCE model. Before being used to examine the ecosystem response to warming and elevated CO_2 at a temperate bog ecosystem, the updated model was evaluated against the observed *Sphagnum* GPP and annual NPP, aboveground tree biomass and shrub stem biomass. The new model can capture the seasonal dynamics of moss *Sphagnum* GPP, but with lower peak GPP compared to site-level observations, and can predict reasonable annual values for *Sphagnum* NPP but with

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5.3 Outstanding issues and future directions¶

→The present modeling framework works well for hydrological dynamics (Shi et al., 2015), vegetation responses (this study), and reconstructing CH_4 dynamics (Ricciuto et al., in review) within the S1-Bog in Minnesota. It will thus be migrated into the E3SM. However, more developments of ELM_SPRUCE are still needed before widespread applications.¶

The live green moss layer buffers the exchange of energy and water at soil surface and regulates the soil temperature and moisture because of its high-water holding capacity and the insulating effect (McFadden et al., 2003; Block et al., 2011; Turesky et al, 2012; Park et al., 2018). Nevertheless, we currently include only one *Sphagnum* moss PFT, and will eventually treat the *Sphagnum* mosses as the "top" soil layer with a lower thermal conductivity and higher hydraulic capacity than a mineral soil layer (Wu et al., 2016). We also intend to model light competition, the shading effect of shrub expansion, and the changes of Sphagnum community composition. Moreover, the new implementation would allow for the simulation of the moss layer acting as a barrier for the water and energy exchange from the underlying organic soil layer with the atmosphere. In addition, we also plan to investigate the ecosystem consequences of loss of Sphagnum from this ecosystem.¶

→The current model version is not able to simulate the biogeophysical changes that occur due to the long-term accumulation of peat in the bog; however, previous literature reported that there is a need to develop relatively realistic peatland growth models where the rates of ecosystem processes are a function of climate and the inherent autogenic properties of peatlands (Frolking et al., 2010, Belyea and Baird, 2006; Dies, 2009). Thus, future work requires modeling the peat accumulation and associated feedbacks among hydrology, vegetation communities, and peat properties. This would also facilitate the simulation of basic patterns of peat accumulation over millennia in northern peatlands, including accumulation rates, vegetation and fen-bog transitions, and future impacts from the potential loss of peat under warming scenarios.¶

→Nitrogen (N_2) fixation is a major source of available N in ecosystems that receive low amounts of atmospheric N deposition, like boreal forests and subarctic tundra (Lindo et al., 2013, Weston et al, 2015, Rousk et al., 2016, Kostka et al., 2016). For example, diazotrophs are estimated to supply 40-60% of N input to peatlands (Vile et at., 2014) with high accumulation of fixed N into plant biomass (Berg et al., 2013). Nevertheless, N_2 fixation is an energy costly process and is inhibited when N availability and reactive nitrogen deposition is high (Gundale et al., 2011; Ackermann et al., 2012; Rousk et al., 2013). This could limit ecosystem N input via the N_2 fixation pathway. A recent study showed that N_2 fixation activity in the S1-bog was negatively correlated with temperature (Carrell at al., 2019). However, for the current ELM_SPRUCE, N_2 fixation process is only tied to the whole-ecosystem NPP for all PFTs and is not mechanistic. We will focus on this process in future model development.¶

In addition to the simulations aimed at improved understanding of bog response to experimental ... [1]

lower interannual variation. Our model largely agrees with observed tree and shrub biomass. The model predicts that different PFTs responded differently to warming levels under both ambient and elevated CO_2 concentration conditions. The NPP of the two dominant tree PFTs (black spruce and *Larix*) showed contrasting responses to warming scenarios (increasing with warming for *Larix* but decreasing for black spruce), while shrub NPP had similar warming response to *Larix*. Hummock and hollow *Sphagnum* showed opposite warming responses: hollow *Sphagnum* shows generally higher growth with warming, but the hummock *Sphagnum* demonstrates more variability and strong dependence with water table height. The ELM predictions further suggest that the effects of CO_2 fertilization can change the direction of the warming response for the bog peatland ecosystem, though observations of *Sphagnum* species at the site does not yet appear to support this (Norby et al. 2019).

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Data availability. The model code we used is available here: https://github.com/dmricciuto/CLM_SPRUCE. The datasets and scripts were used for the figures is here: https://github.com/dmricciuto/CLM_SPRUCE/tree/master/analysis/Shietal2020

Acknowledgements

Research was supported by the U. S. Department of Energy, Office of Science, Biological and Environmental Research Program. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the US Department of Energy under contract DE-AC05–00OR22725.

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