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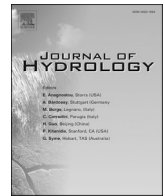
Hydrological feedbacks on peatland CH$_4$ emission under warming and elevated CO$_2$: A modeling study

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ABSTRACT

Peatland carbon cycling is critical for the land–atmosphere exchange of greenhouse gases, particularly under changing environments. Warming and elevated atmospheric carbon dioxide (eCO$_2$) concentrations directly enhance peatland methane (CH$_4$) emission, and indirectly affect CH$_4$ processes by altering hydrological conditions. An ecosystem model ELM-SPRUCE, the land model of the E3SM model, was used to understand the hydrological feedback mechanisms on CH$_4$ emission in a temperate peatland under a warming gradient and eCO$_2$ treatments. We found that the water table level was a critical regulator of hydrological feedbacks that affect peatland CH$_4$ dynamics; the simulated water table levels dropped as warming intensified but slightly increased under eCO$_2$. Evaporation and vegetation transpiration determined the water table level in peatland ecosystems. Although warming significantly stimulated CH$_4$ emission, the hydrological feedbacks leading to a reduced water table mitigated the stimulating effects of warming on CH$_4$ emission. The hydrological feedback for eCO$_2$ effects was weak. The comparison between modeled results with data from a field experiment and a global synthesis of observations supports the model simulation of hydrological feedbacks in projecting CH$_4$ flux under warming and eCO$_2$. The ELM-SPRUCE model showed relatively small parameter-induced uncertainties on hydrological variables and their impacts on CH$_4$ fluxes. A sensitivity analysis confirmed a strong hydrological feedback in the first three years and the feedback diminished after four years of warming. Hydrology-moderated warming impacts on CH$_4$ cycling suggest that the indirect effect of warming on hydrological feedbacks is fundamental for accurately projecting peatland CH$_4$ flux under climate warming.

1. Introduction

Peatlands store 16–33% of the global terrestrial soil carbon (Bridgham et al., 2006; Gorham, 1991), and play an important role in regulating climate change. Peatlands act as net sinks of carbon dioxide (CO$_2$) and net sources of atmospheric methane (CH$_4$) due to the prevalence of waterlogged conditions (Dinsmore et al., 2009; Harriss et al., 1985; Huttunen et al., 2003; McNamara et al., 2008). Therefore, water table level (WT) is a vital parameter controlling peatland CH$_4$ emission (Dise et al., 1993, 2011; Laine et al., 1996; Moore and Roulet, 1993; White

et al., 2008). Any level of climate warming might alter hydrological processes and soil microbial physiology (Nykänen et al., 1998), thereby modifying CO$_2$ and CH$_4$ emission and changing C storage in peatlands (Bridgham et al., 1995; Keller et al., 2004). A rise in the WT might strengthen CH$_4$ emission by stimulating the activities of methanogens ((Nykänen et al., 1998; Turetsky et al., 2008) or reduce CH$_4$ emission by reducing the transport rate of CH$_4$ to the atmosphere (Blodau and Moore, 2003; Brown et al., 2014; Knorr et al., 2008). A WT drop might promote the oxidation of CH$_4$ and thus reduce CH$_4$ emission (Zhang et al., 2007).

Warming and elevated CO_2 (eCO_2) represent two critical global change factors affecting CH_4 flux in peatlands (Xu et al., 2010; Xu and Tian, 2012; Turetsky et al., 2008; Updegraff et al., 2001). For example, warming stimulates peatland CH_4 emission by directly enhancing CH_4 transport from soil to the atmosphere (Turetsky et al., 2008). In addition, warmer temperatures stimulate methanogenesis more than methanotrophy (Dunfield et al., 1993), and thus reinforces CH_4 emission. Elevated eCO_2 has the potential to enhance CH_4 emission by increasing plant biomass, thereby providing a C substrate for CH_4 production (Dijkstra et al., 2012; Hutchin et al., 1995; Inubushi et al., 2003; Saarnio et al., 1998). However, peatlands are complex ecohydrological systems and the hydrological feedbacks linked to the WT can reinforce the climatic impacts on CH_4 emission (Waddington et al., 2015). Water table dynamics are a function of precipitation, evaporation, transpiration, and drainage (near-surface runoff or deeper vertical drainage to aquifers). A WT drop is expected to increase aerobic C mineralization (Song et al., 2018), which in turn provides more available C substrates for methanogenesis. On the contrary, a low WT may also suppress peatland CH_4 emission due to an expansion of the CH_4 oxidation zone associated with aerobic soil and a contraction of the methanogenesis zone associated with anoxic saturated soil (Whalen and Reeburgh, 1996; 2000; White et al., 2008). Thus, warming affects the WT level via strengthened evapotranspiration, reduced soil moisture, and altered precipitation regimes (Allison and Treseder, 2008; Verburg et al., 1999). Meanwhile, the stimulating effects of eCO_2 on vegetation biomass might lead to increases in water loss via canopy evaporation and transportation, and decreases in water input via canopy interception (Waddington et al., 2015). Such hydrological changes might interact with warming and eCO_2 to complicate CH_4 cycling represented in peatland ecosystem models.

Large uncertainties exist in projecting the responses of CH_4 emission to warming and eCO_2 in peatland ecosystems (Bridgham et al., 2013; Ma et al., 2017), due to the unknown mechanisms of CH_4 production and emission associated with complicated hydrological feedbacks. A shift in microbial community composition associated with vegetation dynamics might occur under long-term warming and eCO_2, which may offset the effects of short-term changes in WT level (Blodau, 2002; Szumigalski and Bayley, 1997; Tveit et al., 2015). In particular, changes in plant species composition can affect ecosystem functions (Weltzin et al., 2000), including evapotranspiration and CO_2 and CH_4 fluxes. A few biogeochemical models have accounted for WT fluctuation and impacts on CH_4 fluxes (Kettunen, 2003; Ma et al., 2017; Segers et al., 2001a,b,c; Xu et al., 2016). However, the mechanisms by which soil hydrological processes respond to warming and eCO_2 and affect peatland CH_4 fluxes remain elusive (Ricciuto et al., 2021).

This study focuses on the hydrological feedbacks on CH_4 emissions under a warming gradient and an ambient and an elevated CO_2 (800 ppm) atmosphere in a Minnesota peatland using the ELM-SPRUCE model (Ricciuto et al., 2021; Yuan et al., 2021), which is a new version of the Energy Exascale Earth System (E3SM) land model (ELM). Uncertainty and sensitivity analyses were carried out to evaluate the hydrological processes controlling peatland CH_4 emission. With this study we aimed to address: 1) how do hydrological processes respond to warming and eCO_2? 2) what are the mechanisms by which hydrological processes feedback to warming and eCO_2 in terms of affecting CH_4 flux?

2. Methodology

2.1. Data source and model experiment

Our study was based on the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment (Hanson et al. 2017), located at the S1 bog (47° 30.476′ N; 93° 27.162′ W) of the USDA Forest Service Marcell Experimental Forest (MEF) in northern Minnesota, USA (Kolka et al., 2011). One control treatment (+0°C) and four warming levels (i.e., +2.25 °C, +4.50 °C, +6.75 °C, and + 9.00 °C above ambient)

of whole-ecosystem warming under ambient CO_2 (~400 ppm) and the same five temperature treatments at elevated atmospheric CO_2 concentration (+400 ppm or ~ 800 ppm) were implemented in the SPRUCE field experiment within 10 open-top enclosures (Hanson et al., 2017). Six of these 10 treatments were selected for model simulations using ELM-SPRUCE (+0°C and four warming levels at ambient CO_2 and + 0 °C at eCO_2). Within the enclosures, hydrology is isolated using a subsurface corral system (Sebestyen and Griffiths, 2016), so that the treatments may cause shifts in water table levels without inducing lateral flows from the bog surrounding the enclosures. This model was originally developed upon CLM4.5 with improved representations of hydrology (Shi et al., 2015), moss (Shi et al., 2021), and CH_4 cycling (Xu et al., 2015; Wang et al., 2019; Ricciuto et al., 2021; Yuan et al., 2021). The initial atmospheric forcing data (from 2001 to 2014) used in the model were developed by the SPRUCE team (Ricciuto et al., 2021). The model was implemented for three stages, including the accelerated spin-up (Thornton and Rosenbloom, 2005), final spin-up, and transient runs. Then, six independent experimental simulations from 2015 to 2019 were conducted to examine how CH_4 emission responds to warming and eCO_2 over a 5-year period, for a comparison with the field experiment. The cumulative changes in modeled variables in response to warming and eCO_2 were calculated relative to the control treatment (unwarmed, ambient + eCO_2) responses. More information and evaluations of model experiments are available in our previous publications (Ricciuto et al., 2021; Yuan et al., 2021). All positive CH_4 fluxes indicate emission while negative CH_4 fluxes indicate uptake.

Uncertainty of model outputs was quantified by focusing on ten key parameters related to hydrological processes. These parameters are primarily relevant to soil water potential, soil organic matter content, saturation suction for soil organic matter, porosity of organic soil, soil hydraulic conductivity and heat capacity, surface runoff, and inundated fraction, as *qflx_h2osfc_ surfrate, smpso, smpsc, om_hksat, om_sucsat,om_b, organic_max, om_csol, om_watsat, finundated, fff (surface)* and *fff (subsurface)*, respectively (Table 1). A total of 100 model simulations for 2015–2019 for each of the manipulative experiments were set up for this uncertainty analysis.

Table 1

Key parameters and their optimized values and uncertainty (as standard deviation).

Parameters	Description	Unit	Value	Standard deviation
qflx_h2osfc_ surfrate*	Surface water drainage rate per mm	s^{-1}	1.02e-07	1.56e-08
smpso*	Soil water potential at full stomatal opening	mm	−72250	11058.67
smpsc*	Soil water potential at full stomatal closure	mm	−303250	46415.82
om_hksat*	Saturated hydraulic conductivity of organic soil	mm s^{-1}	0.1	0.0153
om_sucsat*	Saturated suction for organic matter		10.3	1.58
om_b*	Clapp Hornberger parameter for organic soil		2.7	0.41
organic_max	organic matter content where soil is assumed to act like peat	kg m^{-3}	130	19.90
om_csol	Heat capacity of peat soil *10^6	JK m^{-3}	2.5	0.38
om_watsat*	Porosity of organic soil		0.9	0.14
finundated	Fractional inundated area in soil column (excluding dedicated wetland columns)		0.97	0.01
fff (surface) *	The decay factor for surface runoff	m^{-1}	0.5	0.1
fff (subsurface) *	The decay factor for subsurface runoff	m^{-1}	2.5	0.5

* represent the parameters used in the sensitivity analysis.

Additionally, to further identify the most important hydrological processes in regulating the WT level and affecting CH_4 emissions from peatlands, a global sensitivity analysis was conducted. Based on a previous study on the default CLM (Hou et al., 2012), nine parameters were selected and set up with $+ 20\%$ and -20% changes for model runs for 2015–2019 in this study (Table 1). An index S is used to quantify the sensitivity of the model output to parameter change, and is calculated as the ratio of the standardized change in the model response to the standardized change in the parameter values (equation (1)).

$$S = \frac{(R_a - R_n)/R_n}{(P_a - P_n)/P_n} \tag{1}$$

R_a and R_n are model responses for altered and nominal parameters, respectively, and P_a and P_n are the altered and nominal parameters, respectively. S is negative if the direction of modelled response opposes the direction of the parameter changes (Xu et al., 2015; Wang et al., 2019; Yuan et al., 2021).

3. Research synthesis and field observational data

Both the field observational data and a compiled dataset from the literature were used to validate model performance. Experimental data from the SPRUCE project were used to evaluate the site-level simulation (Hanson et al., 2020; McPartland et al., 2019; Norby et al., 2019). The evapotranspiration (ET) (Warren et al., 2021), transpiration, leaf area index (LAI), WT, runoff (Sebestyen and Griffiths, 2016), and soil water content are at the S1 bog measured by the SPRUCE team (Hanson et al., 2020). Measurements of runoff or lateral flow are known to have errors

during high water periods and, therefore, were not a clear quantitative measure of warming and eCO_2 responses. Nevertheless, the observational data of runoff support the warming-induced WT drop as simulated by the model.

Additionally, published literature was surveyed to generate a global synthesis of warming and eCO_2 experimental results in peatlands to evaluate the broader applicability of the ELM-SPRUCE model. We executed a keyword search algorithm: searching ("warming" or "rising temperature") or ("elevated CO_2" or "rising CO_2") or ("fumigation CO_2" or "enrichment CO_2") and ("CH_4" or "methane") and ("wetland" or "peatland" or "bog" or "marsh" or "swamp" or "fen") in the Web of Science and Google Scholar databases. The latest search was completed in March 2020. Published literature was screened and the data were included if they (a) had exact values or graphs for variables related to CH_4 emissions and hydrological processes, and (b) provided detailed information on the wetland type(s) and treatment setting(s). Eight eCO_2 studies and five warming studies met these criteria (Table S1). Five variables were chosen and extracted from these relevant publications, including ET, Trans, LAI, WT, and SW. For these selected studies, the air temperature increased by 0.85 – 4.10 °C in warming experiments, and the atmospheric CO_2 concentrations were elevated by 120–350 ppm in the eCO_2 experiments. The duration of experiments ranged from 0.13 to 12 years. All data from warming experiments were standardized to per °C of warming (% °C^{-1}), while the data from eCO_2 experiments were standardized to per 100 ppm (v) elevated CO_2 (% 100 ppm^{-1}).
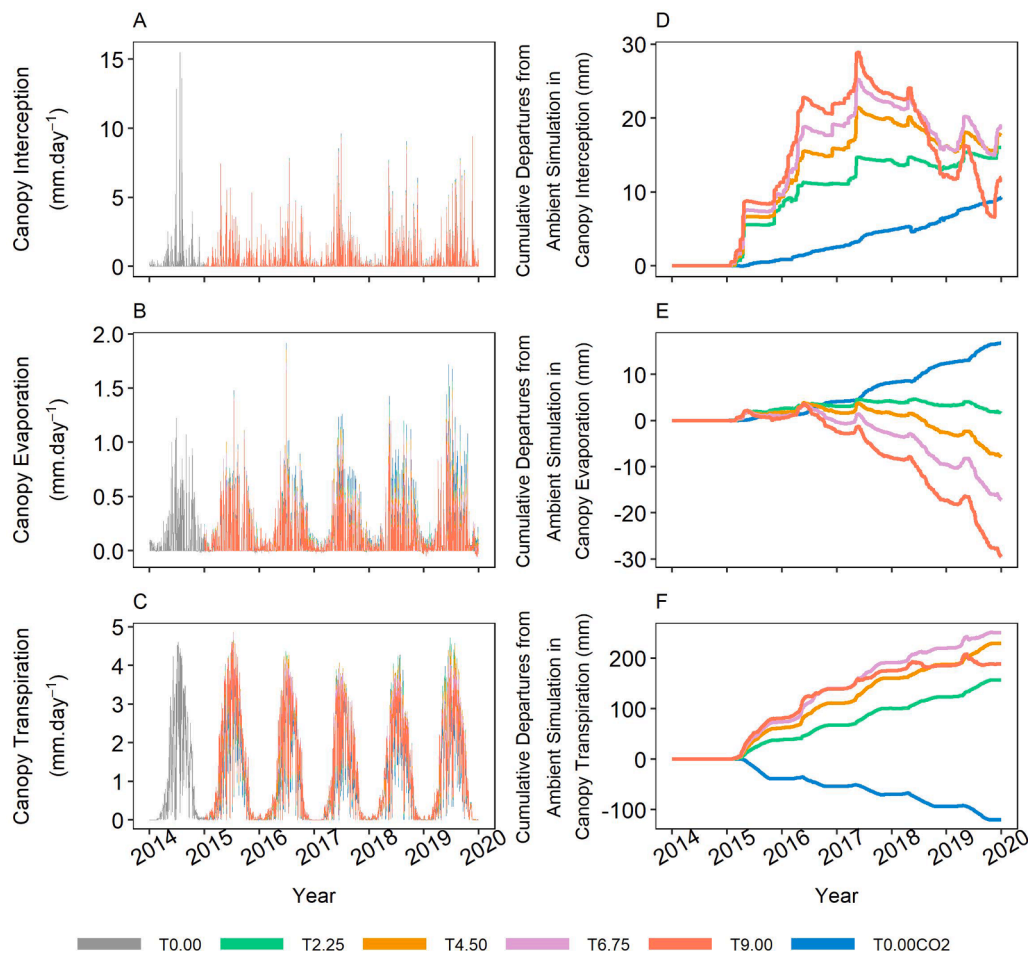

Fig. 1. Time series of simulated canopy interception, canopy evaporation, and canopy transpiration in a peatland under warming and elevated CO_2 concentration (800 ppm) for 5-year simulations. (A-C) Raw model output, and (D-F) cumulative impacts of warming or eCO_2 relative to the ambient (control) condition.

4. Results

4.1. Canopy hydrological processes

As modeled using ELM-SPRUCE, warming and eCO2 largely influenced canopy hydrological processes: the cumulative effects of eCO2 over the 5-year simulation were positive on whole-ecosystem canopy interception and transpiration, whereas warming effects were negative for canopy evaporation and transpiration (Fig. 1D-F). Simulated canopy interception, evaporation, and transpiration showed the same seasonal patterns: increasing in spring, reaching a maximum in summer, and decreasing in fall (Fig. 1A-C). The warming effects on canopy interception followed the gradient of warming treatments. Canopy interception increased with warming in the first 3-years of warming, primarily driven by earlier leaf-out, but then decreased (Fig. 1A) as

driven by the projected decrease in peak LAI (Figure S1). The cumulative responses of canopy interception (departure from ambient simulation) also intensified rapidly in the first 3 years, then weakened after reaching peaks of 16.0 mm, 17.7 mm, 18.9 mm, and 12.0 mm in 2017 under + 2.25 °C, +4.50 °C, +6.75 °C and + 9.00 °C, respectively (Fig. 1D); even the cumulative effects under + 4.50 °C, +6.75 °C and + 9.00 °C tended to diminish after the third warming year. On the other hand, the cumulative eCO2 effects on canopy interception continued increasing over the entire period, and eventually reached 9.2 mm (Fig. 1D) after 5-years.

The cumulative effects of simulated warming on canopy evaporation were negative (Fig. 1E) due to the declining LAI (Figure S1) and drying soil (Fig. 3D, H). In contrast, warming effects were consistently positive on canopy transpiration (Fig. 1F). The magnitude of the cumulative effects increased with warming strength. The cumulative warming effects reinforced canopy evaporation in the first two years, then started to
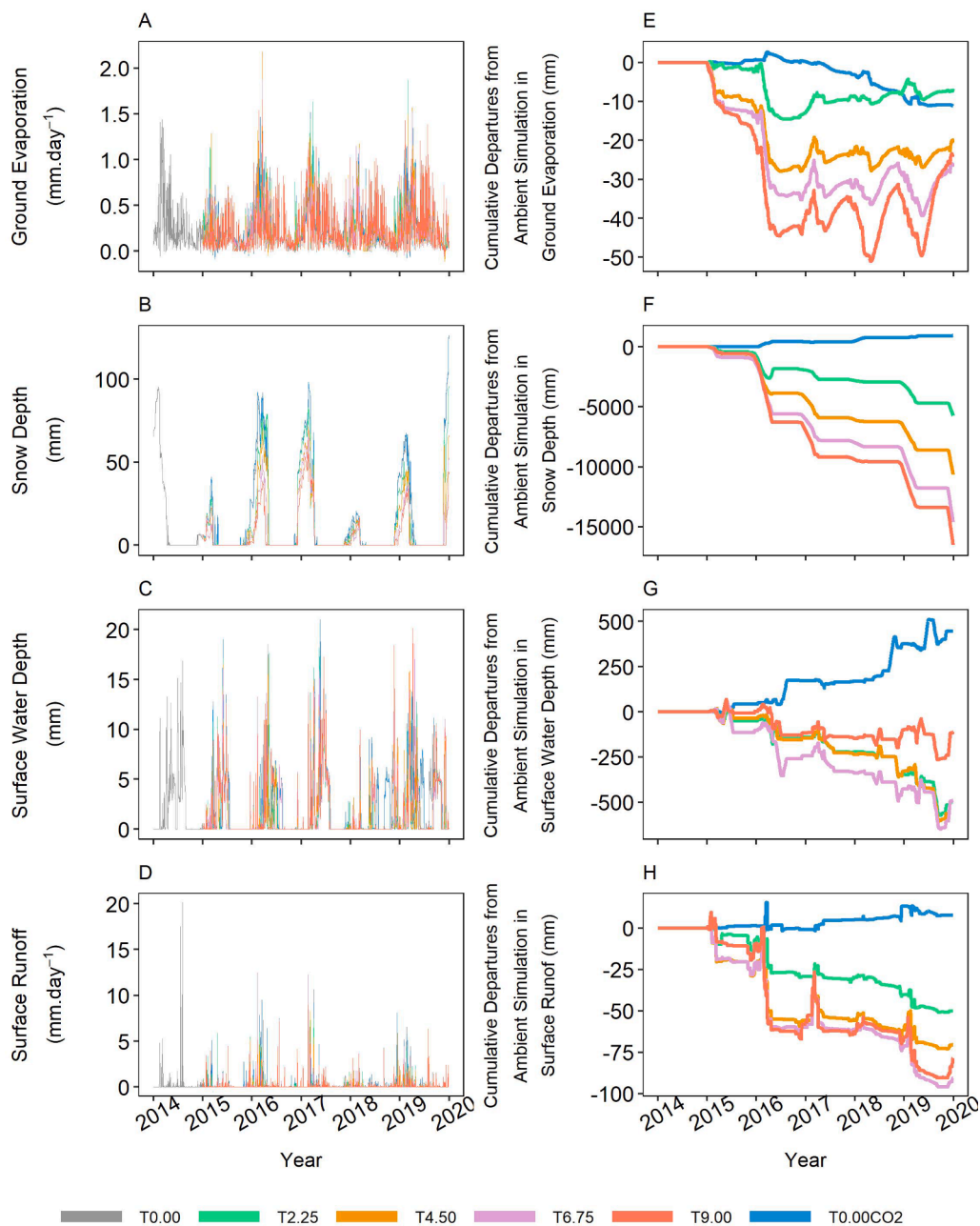

Fig. 2. Time series of simulated ground evaporation, snow depth, surface water depth, and surface runoff in a peatland under warming and elevated CO2 concentration (800 ppm) for 5-year simulations. (A-D) Raw model output, and (E-H) cumulative impacts of warming or eCO2 relative to the ambient (control; +0°C and ambient CO2) condition.

decrease in the following years. The cumulative canopy evaporation changed by $+1.6$ mm, -7.9 mm, -17.2 mm, and -29.5 mm under the four warming treatments, respectively. The cumulative canopy transpiration was enhanced by 156.8 mm, 228.9 mm, 250.7 mm, and 188.1 after the 5-year warming period. The cumulative (5-year) effect of warming on canopy transpiration under $+9.00\ ^\circ C$ reduced from the fourth warming year, despite increasing under $+2.25\ ^\circ C$, $+4.50\ ^\circ C$, and $+6.75\ ^\circ C$ and the cumulative magnitude increased with the warming strength. In contrast, the eCO_2 treatment cumulatively strengthened the canopy evaporation response and slowly weakened the canopy transpiration response relative to the ambient CO_2 treatment (Fig. 1E-F). The cumulative canopy evaporation increased by 16.8 mm, whereas cumulative canopy transpiration decreased by 119.9 mm by the end of the fifth year.

4.2. Surface hydrological processes

Ground evaporation, snow depth, surface water depth (depth of water table on soil surface), and surface lateral runoff varied seasonally over the 5-year simulation period (Fig. 2A-D). Overall, warming cumulatively led to lower while eCO_2 cumulatively led to higher snow depth, surface water depth, and surface runoff (Fig. 2F, G, H). Both warming and eCO_2 diminished ground evaporation (Fig. 2E). The cumulative effects of warming and eCO_2 on surface hydrological processes were stronger when the hydrological metrics reached their maximums during spring snowmelt periods. All measures of ground-level hydrology reached maximums in March due to snow melt, and then were drawn down to lower levels throughout the rest of the year; lower levels persisted until the next melting season, with slight fluctuations depending on the timing of precipitation events (Hanson et al., 2020).

The magnitudes of the cumulative effects of warming on three ground hydrological variables (evaporation, snow depth, and surface water table) increased with the warming gradient, and tended to be comparable under the $+6.75\ ^\circ C$ and $+9.00\ ^\circ C$ treatments especially in the last year of the simulations (Fig. 2E-G). Surface lateral runoff under $+9.00\ ^\circ C$ showed the same magnitude of response as the $+6.75\ ^\circ C$ treatment in the second warming year, and then had a smaller cumulative effect than under $+6.75\ ^\circ C$ in the fourth warming year (Fig. 2H). The rates of ground evaporation cumulatively decreased by 7.2 mm, 20.0 mm, 26.3 mm, and 23.8 mm along the warming gradient after 5 years, while eCO_2 decreased the ground evaporation rate by 11.1 mm which was similar to the response of ground evaporation under $+2.25\ ^\circ C$ (Fig. 2E). Warming cumulatively reduced snow depth, and displayed a larger suppression effect in the fifth year compared with the first four years, especially in the warmest treatment (Fig. 2F). At the end of the simulations, the cumulative reductions in snow depth, when compared to the ambient treatment, showed the decreases of 5.7 m, 10.6 m, 14.6 m, and 16.5 m along the warming gradient. In contrast, the eCO_2 treatment had a slight positive effect on snow depth, and snow depth cumulatively increased only by 0.9 m over five simulation years (Fig. 2F).

The surface water depth and surface runoff declined under the warming treatments, and the cumulative reductions gradually strengthened over time. In contrast, both surface water depth and runoff cumulatively increased under eCO_2. Furthermore, surface water depth was more responsive than the surface runoff to warming and eCO_2. At the end of the 5-year simulations, cumulative surface water depth decreased by 499.0 mm, 493.6 mm, 491.3 mm, and 112.4 mm along the warming gradient, and increased by 446.3 mm under eCO_2. Warming cumulatively diminished surface runoff by 49.9 mm, 70.4 mm, 90.7 mm, and 78.5 mm from the $+2.25\ ^\circ C$ to $+9.00\ ^\circ C$ warming treatments, respectively, whereas eCO_2 cumulatively enhanced runoff by 7.7 mm at the end of the simulations.

4.3. Belowground hydrologic and thermal processes

Water infiltration to deep soils and soil temperature along the soil profile exhibited similar seasonality, increasing in warm seasons and decreasing in cold seasons. However, the total WT level and soil water content showed opposite seasonal dynamics, declining with high soil temperature and rising with low soil temperature, respectively (Fig. 3A-D). Overall, warming and eCO_2 had opposite cumulative effects on soil temperature, water table level, and soil water content, but both cumulatively raised soil infiltration after four years and the final effect of eCO_2 was minimal compared to the effect of $+2.25\ ^\circ C$ warming treatment (Fig. 3E-H). Warming reinforced the soil water infiltration (especially under $>+2.25\ ^\circ C$ treatments), but decreased the water table level and soil water content (Fig. 3A-D). The cumulative effects on the belowground hydrothermal metrics were intensified along with warming, and tended to be comparable over time for the soil water infiltration and water table level under $+6.75\ ^\circ C$ and $+9.00\ ^\circ C$. However, eCO_2 reduced infiltration during the first 4-years while water table level and soil water content increased (Fig. 3E-H).

The cumulative changes in infiltration showed highly seasonal patterns, displaying a greater response to warming in warm seasons. The rates of the infiltration cumulatively increased, by 103.5 mm, 147.1 mm, 283.0 mm, and 305.8 mm along the warming gradient, and the rate cumulatively increased by 92.7 mm under eCO_2, at the end of simulations. Soil temperature increased more under more intense warming (Fig. 3E). After the 5-year simulations, warming cumulatively increased the soil temperature by 1263.2 $^\circ C$, 2759.8 $^\circ C$, 4390.7 $^\circ C$, and 5687.2 $^\circ C$ under $+2.25\ ^\circ C$, $+4.50\ ^\circ C$, $+6.75\ ^\circ C$ and $+9.00\ ^\circ C$, respectively. eCO_2 cumulatively decreased the soil temperature by 107.1 $^\circ C$, and the effects of eCO_2 were considerably very small comparing with the cumulative effects of warming.

Water table level and soil water content generally declined with warming over the simulation period, but they showed larger responses to $+6.75\ ^\circ C$ than other warming treatments (Fig. 3G and 3H). The cumulative reductions of the water table level diminished in the fifth warming year. At the end of 5 years of warming, the water table level cumulatively decreased by 20.0 mm, 32.3 mm, 28.8 mm, and 28.3 mm, and the soil water content cumulatively decreased by 1.3%, 3.6%, 2.6%, and 1.4% along the warming gradient. Meanwhile, at the end of the eCO_2 simulations, the soil water content increased by 1.5% and water table level cumulatively rose by 17.4 mm (Fig. 3G and 3H).

4.4. A mechanistic framework for hydrological feedbacks on CH_4 cycling under warming and eCO_2

The mechanisms of warming and eCO_2 impacts on CH_4 cycling were distinct due to their differing effects on hydrological processes (Fig. 4). Warming suppressed net primary productivity (NPP) and LAI (Figure S1), and therefore diminished canopy evaporative loss mainly via reducing evaporative area. Conversely, warming enhanced canopy interception by increasing interception duration despite decreasing LAI. The reason is that warming led to an earlier and extended growing season for deciduous tree species (Table S2), such as tamarack (*Larix laricina*) and various understory shrubs in the S1 bog, thereby suppressing throughfall inputs as a source for surface moisture and ground evaporation. Canopy transpiration was also intensified by warming due to higher vapor pressure deficiencies in the enclosures. In addition, rising canopy transpiration dominated the rapid water loss under warming, and the enhanced water loss was 6.4–98 times larger than the decreases in ground and canopy evaporation at the end of 5-year simulations.

Additionally, warming promoted the melting of snow and ice, thereby decreasing snow accumulation. With snow melt, surface water depth and surface runoff increased. Following the further enhancement of soil water infiltration with soil freezing, surface water depth dropped, and then ground evaporation diminished. However, during the dry
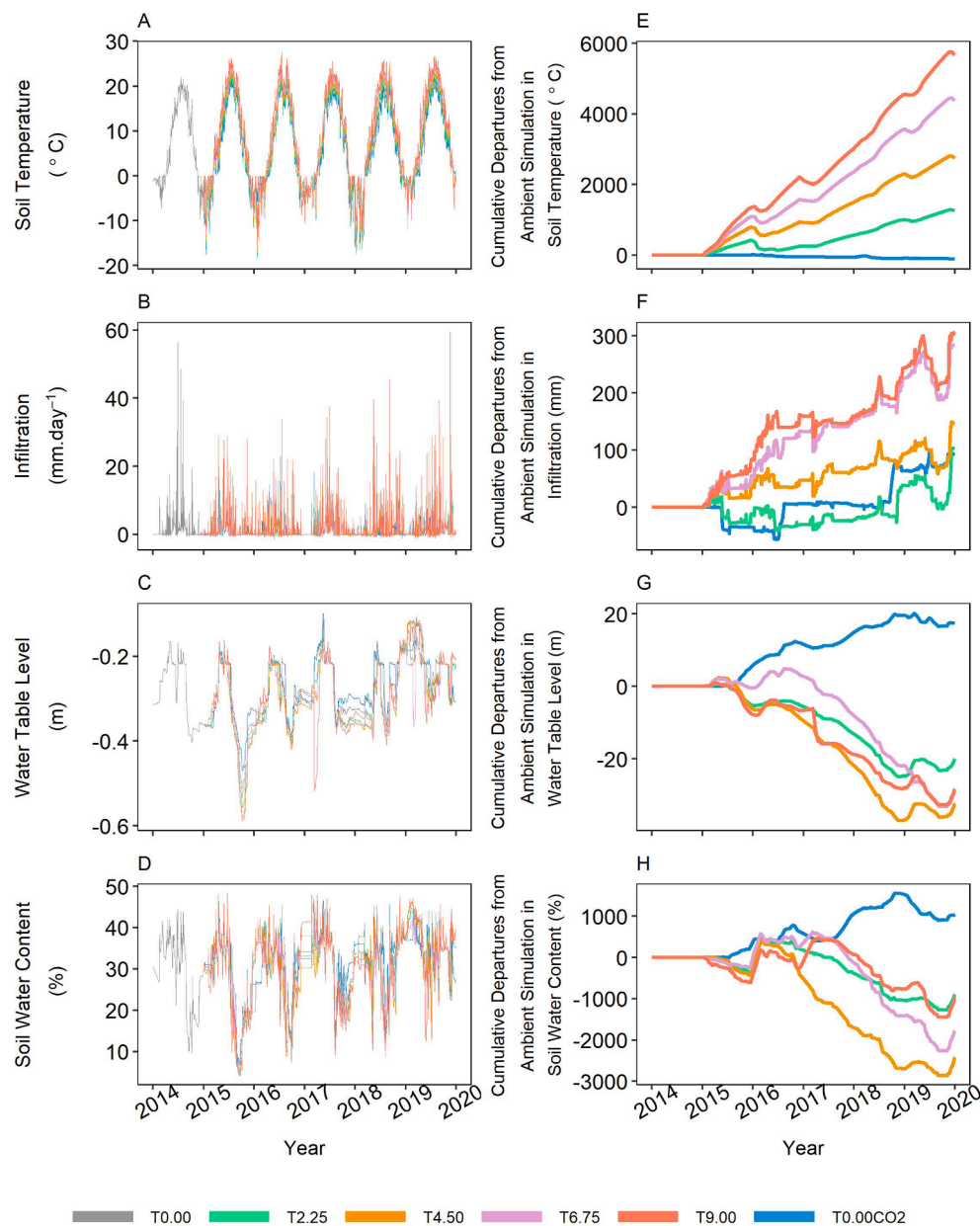
Fig. 3. Time series of simulated soil temperature, infiltration, water table level, and soil water content (at 9 cm depth) in a peatland under warming and elevated CO_2 concentration (800 ppm) for 5-year simulations. (A-D) Raw model output, and (E-H) cumulative impacts of warming or eCO_2 relative to the ambient (control) condition.

summer seasons under warming, water table levels, surface runoff, and soil water content decreased as a result of the rising water uptake by vegetation. This drainage of surface peat also created more storage above the water table and allowed for high infiltration when precipitation inputs were adequate to offset transpiration losses.

Lower water table levels inhibited CH_4 production by shrinking the anoxic zone for methanogenesis. However, soil temperature increased due to warming and enhanced CH_4 production in the regions that remained anoxic (Ricciuto et al., 2021; Yuan et al., 2021). The decreased water table level, which allowed more oxygen to penetrate into soils and promoted mineralization of soil organic matter (SOM), led to an increased production of substrates for methanogenesis. CH_4 production was stimulated by warmer temperature, leading to the consumption of available substrates that resulted in an actual loss of substrate availability. Warming had little impact on simulated CH_4 oxidation (Yuan et al., 2021), but enhanced the transport of CH_4 from peat to the atmosphere. The soil CH_4 concentrations temporarily increased because of

stimulated CH_4 production, but eventually declined due to enhanced transport of CH_4 through a combination of plant-mediated transport, diffusion, and ebullition (Ricciuto et al., 2021; Yuan et al., 2021). Overall, despite the inhibition of CH_4 production via a lower water table, the net effect of warming was an increase in CH_4 emission because of the enhancement of methanogenesis and CH_4 transport.

CH_4 emission was reinforced in the eCO_2 treatment, but the hydrological feedback to eCO_2 showed different effects on CH_4 dynamics (Fig. 4). The NPP increase under eCO_2 resulted in a rise in canopy interception and a decline in ground evaporation. Canopy evaporation increased with greater canopy interception, whereas canopy transpiration was suppressed under eCO_2. Overall, water loss from soils decreased due to the decrease in the canopy transpiration under eCO_2. Additionally, due to the increasing canopy shade under higher leaf area stimulated by eCO_2, soil temperature and ground evaporation decreased, which led to higher snow depth and increased surface runoff when snow melted. The higher water table level and soil water content facilitated
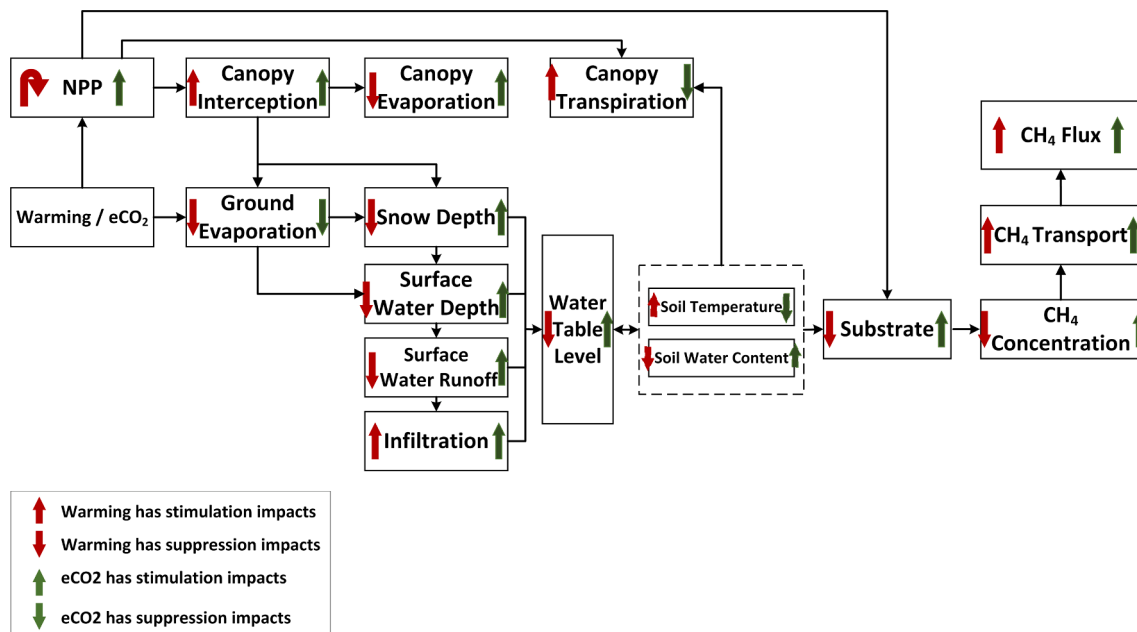
Fig. 4. Diagram showing the mechanisms of warming and elevated CO_2 impacts on CH_4 cycling indirectly through the influence on the hydrologic processes (i.e., canopy, surface, and belowground hydrological processes). Black arrows represent the crucial processes in CH_4 cycling, while red and green arrows are used to distinguish the impacts of warming and elevated CO_2, respectively Regular upward or downward arrows represent the positive or negative effects under treatments, respectively. Curved downward arrows indicate that the impacts of treatments are first positive and then negative. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

methanogenesis; meanwhile, increased NPP stimulated substrate supply and higher SOM mineralization strengthened CH_4 production. More CH_4 was produced by methanogens, which led to higher CH_4 concentrations in soils, intensified by the trivial changes in CH_4 oxidation (Yuan et al., 2021). Overall, the hydrological feedback to eCO_2 resulted in positive feedback on CH_4 emission.

4.5. Uncertainty analysis

The hydrological-parameter-induced uncertainties in hydrological processes are relatively small when compared to the uncertainties in ecosystem carbon processes from biogeochemical parameters in the current ELM-SPRUCE model (Yuan et al., 2021). Among the main hydrological and CH_4 processes under different warming and eCO_2 levels, the prediction intervals of canopy transpiration, canopy evaporation, ground evaporation, and CH_4 fluxes showed narrower and less seasonal variation than WT (Fig. 5A-E). This suggested that a relatively high uncertainty existed in WT simulations due to the choices of hydrological parameters, and there may be seasonal differences in the determination of hydrological parameters for simulating WT. Under different warming levels and eCO_2, we did not find large differences in uncertainty intervals of hydrological and CH_4 processes caused by hydrological parameters. However, the uncertainties from hydrological parameters increased with the simulation duration, particularly for the WT level and CH_4 fluxes (Fig. 5F-J and Figure S2).

4.6. Sensitivity analysis

The hydrological feedbacks regulating water table level and CH_4 fluxes showed substantially different patterns among the six treatments during the 5-year simulations (Fig. 6). No consistency was observed in the sensitivities of WT and net CH_4 fluxes to each hydrological parameter. For example, the *fff* (*subsurface*) (i.e., the decay factor for surface runoff) seemed to be a stronger factor controlling the water table level in the control, +2.25 °C, and + 4.50 °C treatments (Fig. 6A), while the CH_4 fluxes tended to be more sensitive to the surface water drainage rate

(*qflx_h2osfc_surfrate*), soil water potential at full stomatal opening (*smpso*) and *fff* (*subsurface*) in 2018 and 2019 under the + 4.50 °C warming treatment (Fig. 6B).

To further analyze responses of WT and CH_4 fluxes to warming and eCO_2 with simulation duration, the experimental and control simulations were set up with the same climate forcing of 2015 data. Increases in CH_4 fluxes were associated with the decreases in WT under warming, whereas under eCO_2, CH_4 fluxes were also enhanced with the increase of WT (Fig. 7). The WT dropped under warming, with a larger decline corresponding with more intense warming. Additionally, the warming effects on water table level weakened over time, and the water table levels under most of warming levels even started increasing beginning in the third warming year (Fig. 7A). Accordingly, the increased CH_4 emission among the warming treatments became smaller and smaller over time, and reached their smallest values at the end of the simulations (Fig. 7B). In contrast to the strong warming effects, there was a weaker eCO_2 impact - an increase of ~ 7.2% in water table level (Fig. 7A). The CH_4 emission under eCO_2 also showed a continuous increase and it intensified over time (Fig. 7B).

5. Discussion

5.1. Model comparison with synthesis and observational results

Our model simulations are in good agreement with the observational results from the SPRUCE study and a global synthesis (Fig. 8). Both SPRUCE observations and model simulations showed that the WT declines were caused by enhanced ET under the warming treatments (Hanson et al., 2020; McPartland et al., 2019; Norby et al., 2019), but such changes did not lead to a substantial reduction in soil moisture due to the high-frequency precipitation over the simulation period. Both field observational data and our simulations showed minor eCO_2 impacts on ET and therefore canopy transpiration and soil moisture. Simulated runoff declined under both warming and eCO_2, consistent with the SPRUCE experimental results. However, there are still inconsistencies between SPRUCE observations and the ELM-SPRUCE
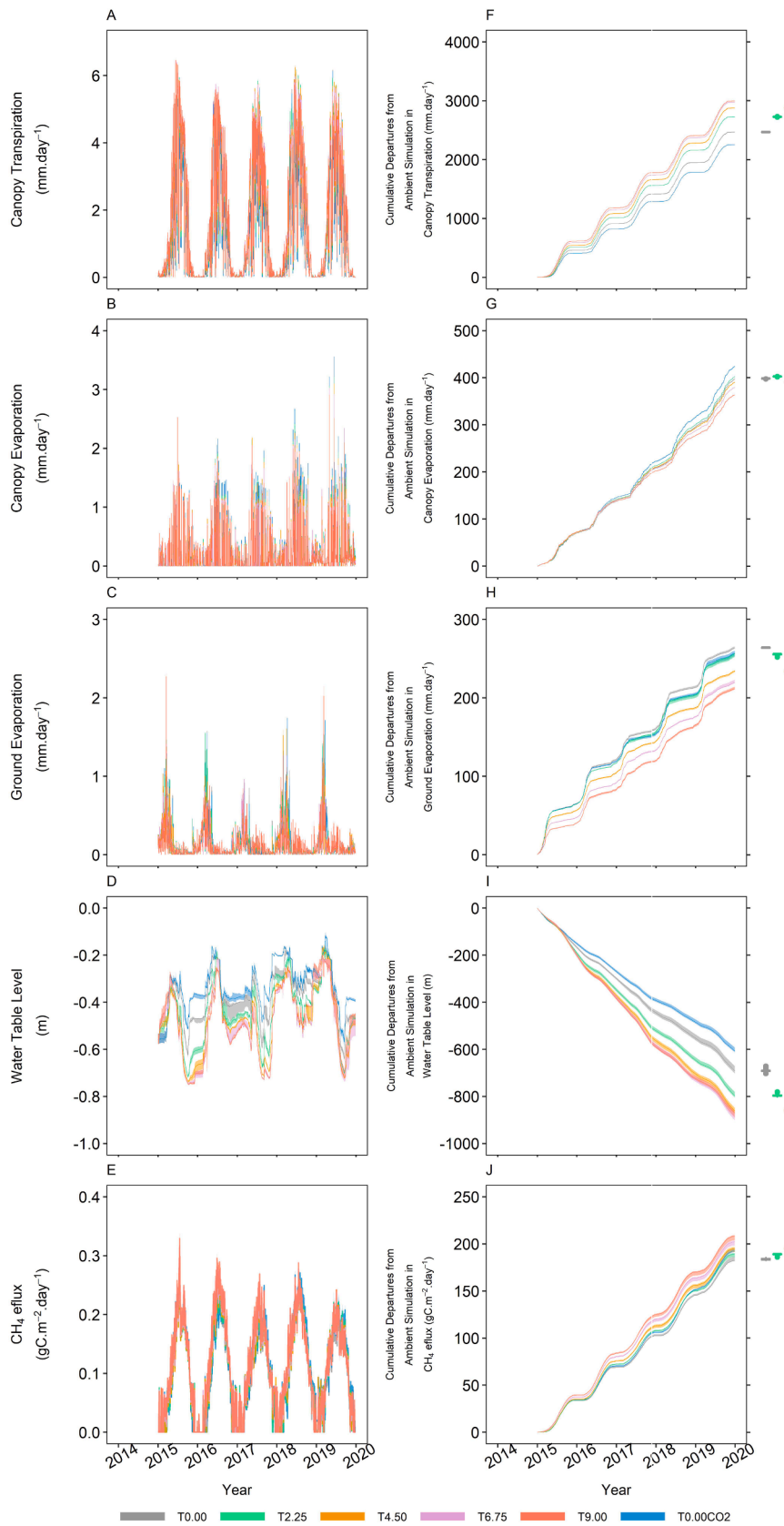
Fig. 5. Uncertainty analysis of canopy transpiration, canopy evaporation, ground evaporation, water table level, and CH_4 efflux in a peatland under + 2.25 °C, +4.50 °C, +6.75 °C, and + 9.00 °C warming and elevated CO_2 concentration (800 ppm). All assembled simulations from 100 different change parameters are shown with the multi simulation mean (solid lines) and the 5–95% range (±1.64 standard deviation) across the distribution of individual simulations (shading). Box and whiskers (mean, one standard deviation, and minimum to maximum range) at the right side of the figure show the differences on the end day of manipulation among all assembled simulations with the same manipulation.
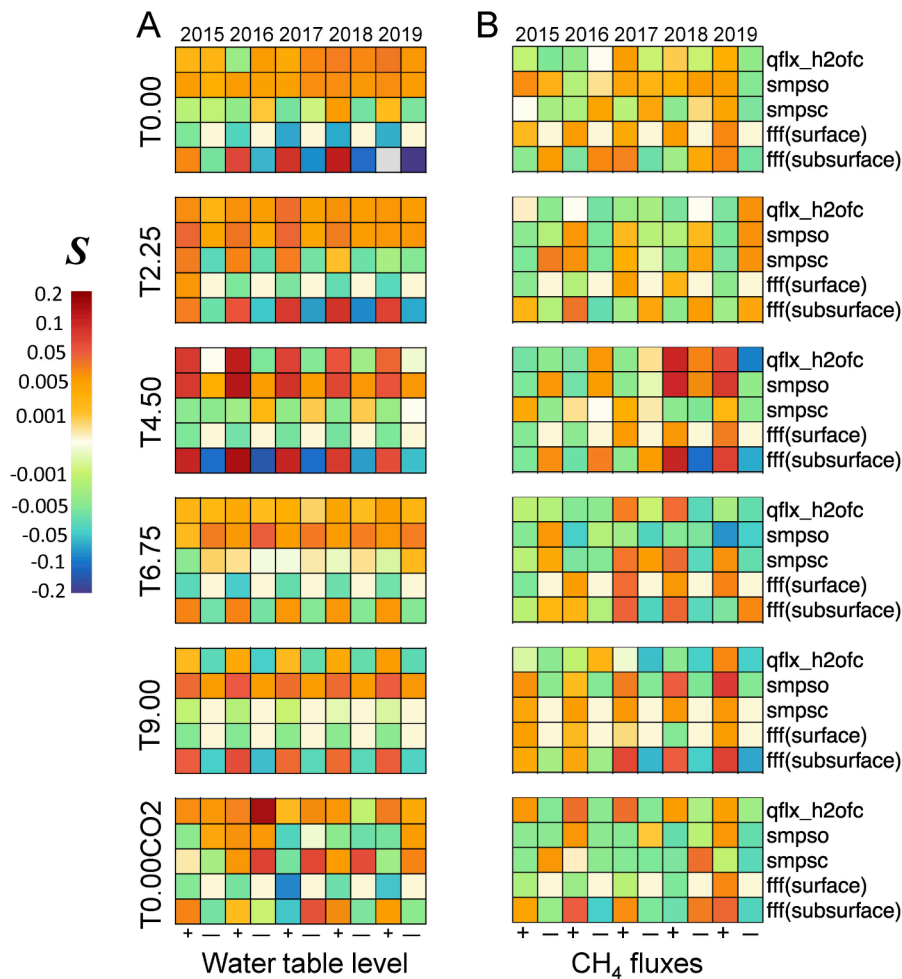
Fig. 6. Sensitivity analysis for model responses of (A) water table level, and (B) net CH_4 fluxes to five parameters (*qflx_h2osfc_surface, smpso, smpsc, fff (surface)* and *fff (subsurface)*) during 2015–2019 under warming and eCO_2. The symbols "+" and "−" indicate a 20% increase or 20% decrease of parameter values. Darker green and blue indicate a stronger negative model response to parameter change and darker orange and red indicate a stronger positive model response to parameter change. S is negative if the direction of model response opposes the direction of parameter change. Note: The sensitivities of water table level and CH_4 fluxes to other four parameters (i.e., *om_hksat, om_sucsat, om_b and om_watsat*) were not displayed due to their extremely small scales. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
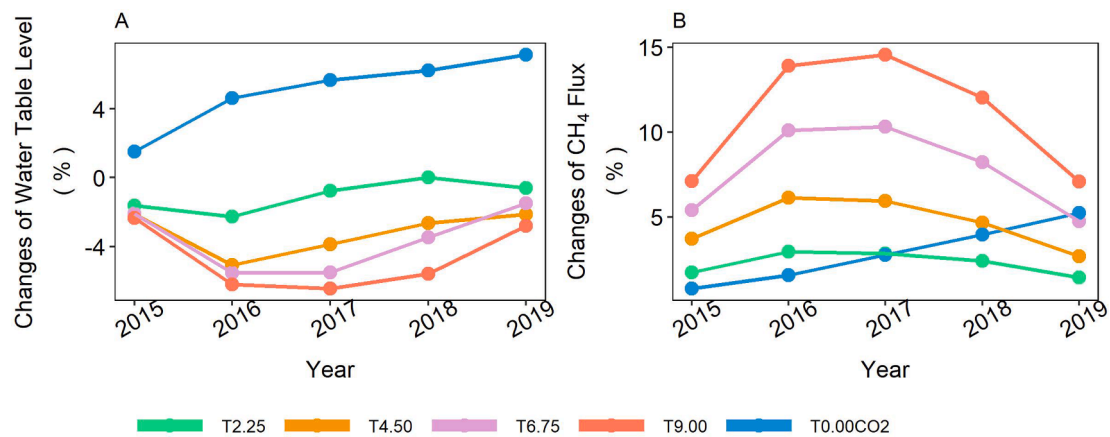

Fig. 7. Changes in simulated (A) water table level and (B) CH_4 fluxes under warming and eCO_2 compared to the control treatment (T0.00) in 2015–2019 using the same climate forcing variables in each year. Different colors and shapes indicate different treatments.

model outputs. Measured LAI had positive responses to both warming and eCO_2 treatments, while our model outputs showed smaller LAI changes under warming treatments (Fig. 8). This difference is likely due to the complicated plant community responses to nutrient availability and environmental factors. In the first three years, community-level vegetation carbon gains are attributable to eCO_2 (Hanson et al., 2020). It should be noted that although sealing of subsurface leaks into the SPRUCE experimental plots was completed in November 2020, there

were still few available data to evaluate the effectiveness of sealing efforts on surface runoff. Despite the occurrence of many observable hydrological responses to date, further observation is needed to validate the performance of the ELM-SPRUCE model for understanding the warming and eCO_2 impacts on peatland CH_4 emission.
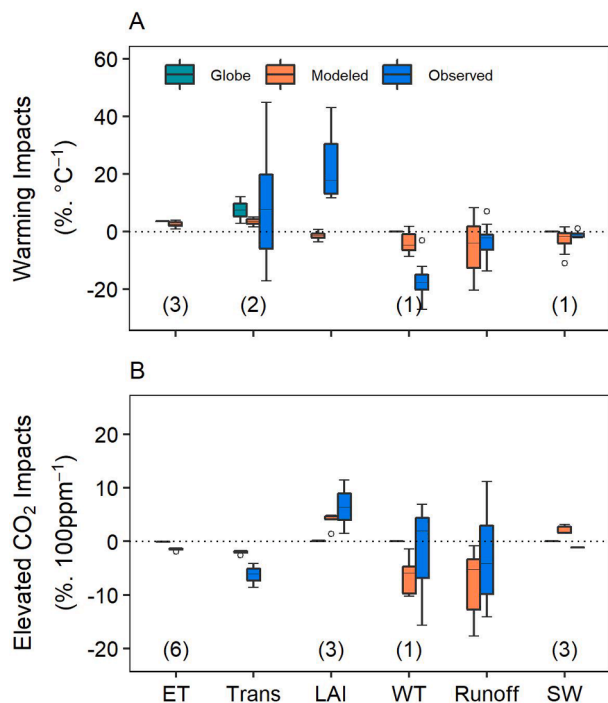
Fig. 8. Response of selected variables (ET: evapotranspiration; Trans: transpiration; LAI: leaf area index; WT: water table level; Runoff: surface runoff; SW: soil water content) to warming and elevated CO_2 treatments reported in global field observational studies (green), measured in the SPRUCE field experiment (blue), and simulated in the present modeling study (red). For boxplots, the upper and lower hinges correspond to the first and third quartiles; the upper/ lower whiskers extend to the highest/lowest value within 1.5 times the interquartile range; horizontal lines within boxes correspond to the median; outlier dots represent data beyond the end of the whiskers. The number of observations for each variable is given above the × axis in graphs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5.2. Controls of thermal and hydrological processes on CH₄ flux under warming and eCO₂

Soil biogeochemical processes are jointly controlled by hydrological and thermal regimes (Waddington et al., 2015; Bubier et al., 1995). We predicted that the WT would drop as a result of warming in peatlands, which is consistent with previous studies (Nykänen et al., 1998; Turetsky et al., 2008). The lower WT affects CH₄ production not only by changing anoxic conditions, but also by controlling energy transfer to deeper soil profiles (Turetsky et al., 2008). Meanwhile, less surface runoff reduced lateral flows of heat and nutrients, which may result in sporadic areas of higher soil temperature above the water table and thus spatial heterogeneity in CH₄ flux. Nonetheless, CH₄ flux showed a decreasing tendency under these treatments, indicating a diminishing impact of WT on CH₄ flux. Therefore, without hydrological feedbacks, the response of CH₄ flux to climate warming could be overestimated.

Under warming condition, more precipitation fell in the form of rain rather than snow (Figure S3), and more water evaporated. Furthermore, the WT dropped and suppressed the activity of methanogens by expanding the oxic zone, reducing CH₄ emission (Gedney et al., 2004; Nykänen et al., 1998; Yrjälä et al., 2011). On the other hand, the expansion of the oxic zone promoted microbial decomposition of organic matter, which produced more acetate, CO₂, and other organic substrates for methanogenesis. Methanogens cannot immediately utilize substrates in oxic conditions, and there could be a time lag between the substrate supply and utilization by methanogens. Overall, CH₄ production was strengthened primarily by the stimulating effects of warming

on methanogens, instead of suppression effects of WT drawdown. Among the hydrological variables, canopy transpiration was identified as the key factor that directly caused the drawdown of the WT.

The emission of CH₄ can be underestimated under eCO₂ if one ignores the hydrological feedbacks because the increased WT was associated with enhanced CH₄ emission. We found that eCO₂ enhanced NPP and LAI (Figure S1), directly leading to an increase in canopy interception and evaporation. Meanwhile, due to the increased shading from greater plant cover and less throughfall, ground evaporation declined. Furthermore, the cooling effect of vegetation cover suppressed canopy transpiration. Higher surface runoff and infiltration reduced the surface water depth, with less snow accumulation. Given that water loss from plant transpiration greatly decreased under eCO₂, soil water storage increased and then the WT rose. The increased WT intensified the opportunities for soil saturation and anaerobic conditions, thereby favoring methanogenesis and suppressing methanotrophy. The eCO₂ impacts on increasing WT, in turn, strengthened positive feedbacks of eCO₂ on CH₄ production and emission. Although the magnitude of the hydrological feedbacks under eCO₂ remains unclear, these simulations emphasize the importance of hydrological processes in strengthening understanding of peatland CH₄ emissions. Overall, there are strong interactions between hydrology and thermal dynamics (Bohn et al., 2007), and these interactions further feed back to CH₄ flux.

5.3. Implications

We established a mechanistic framework for evaluating the indirect effects of warming and eCO₂ on peatland CH₄ production, concentration, and transport, and ultimately provided a mechanistic explanation of hydrological feedbacks that affect CH₄ emissions. Furthermore, the finding derived from the ELM-SPRUCE model of how warming and eCO₂ impact hydrological processes highlights the importance of including hydrological feedbacks in modeling CH₄ cycling. The ELM-SPRUCE model and its application on the peatland CH₄ flux under warming and elevated CO₂ scenarios represent a critical step towards an explicit representation of microbial processes and hydrological processes with lateral transfers between hummock and hollow columns (Shi et al., 2015). The mechanistic understanding of how hydrology affects CH₄ cycling under warming and elevated CO₂ provides insightful information for considering how to manage peatlands under changing climate and rising atmospheric CO₂.

5.4. The way forward

We explored how hydrological feedbacks influence CH₄ production, concentration, and transport pathways by using the ELM-SPRUCE model. In addition to key insights, we identified a few limitations that will be addressed in our future work. First, in the field experiment, air and soil temperatures were simultaneously warmed by 2.25 °C, 4.50 °C, 6.75 °C, and 9.00 °C. However, in the model simulations where horizontal boundaries are infinite, only the air temperature was increased by 2.25 °C, 4.50 °C, 6.75 °C, and 9.00 °C, while soil temperature was simulated by the model and was less than the change of air temperature for each warming treatment. Second, more field observations are needed to validate model simulations of lateral and vertical hydrological processes at multiple temporal and spatial scales, as well as other in peatlands types (fens vs. bog).

Third, the effects of warming and eCO₂ on peatland CH₄ cycling vary at different temporal scales. Given the predicted shift in vegetation communities that will likely occur under long-term climate change, it is necessary to incorporate the dynamics of plant species and community composition in the model for a more accurate estimation. For example, the coverage of *Sphagnum* mosses is sharply declining with warming in the SPRUCE experiment (Norby et al., 2019), which is currently poorly simulated in ELM-SPRUCE but may have strong implications for site hydrology and carbon cycling.

Fourth, an early start to the growing season in spring with warming was simulated with the ELM-SPRUCE model which influenced the water balance between water loss via canopy evapotranspiration and input via canopy interception. For example, changes in phenology have been considered as a critical factor for CO_2 uptake in wetlands (Richardson et al. 2018). In association with their effects on soil hydrology and CH_4 cycling, phenology shifts need to be taken into account to improve modeling of hydrology and biogeochemistry. Warming-induced phenology changes may reinforce the impacts of long-term warming and eCO_2 on peatland CH_4 cycling. Several models have accounted for these processes, but they might underestimate or overestimate the climatic effects on CH_4 fluxes without an explicit representation of microbial functions in CH_4 processes (Koven et al., 2015; Koven et al., 2011).

Fifth, vegetation C allocation is affected by warming and eCO_2. Previous studies indicated that plants allocate more C for root growth to enhance water uptake in dry sites (Chapin et al., 2011). The shoot to root ratio is an important indicator for soil water conditions, and it has been well considered in model simulations. Thus, to fully understand the role of hydrological feedbacks in controlling CH_4 cycling, the process-based biogeochemical models need to be improved to explicitly represent vegetation dynamics, phenology, and plant C allocation. Lastly, peat surface elevation declines potentially as a result of decomposition and drying have been observed (Hanson et al., 2020) and may cause further hydrological feedbacks that are not currently considered in our modeling framework, which assumes a fixed surface.

6. Conclusions

This study provides insight on various effects of warming and eCO_2 on hydrology that feedback to CH_4 production, transport, concentration, and emission. Hydrological feedbacks to warming mitigate the stimulating effects of warming on CH_4 emission. In contrast, hydrological feedbacks to eCO_2 strengthened the eCO_2 effects that reinforce CH_4 emission from peatlands. Water table level is the primary control on peatland CH_4 dynamics, and WT levels dropped along the warming gradient but rose with eCO_2. Model simulations showed that warming induced higher plant transpiration which contributed to water table drawdown. Our synthesis of previous studies corroborated our interpretation that hydrological feedbacks under warming have numerous mechanistic effects on CH_4 fluxes. This study showed relatively small uncertainties in the hydrological framework of the ELM-SPRUCE model. The magnitude of warming effects on water table level and CH_4 fluxes increased along the warming gradient and decreased over time, whereas no such tendency was modelled under eCO_2.

7. Data availability

The data used in this paper have been archived on the SPRUCE project website (https://mnspruce.ornl.gov/). Model code used in these simulations is available on the GitHub repository at https://github.com/dmricciuto. Model simulation output used in this analysis will be made publicly available at https://mnspruce.ornl.gov and archived at the ESS-DIVE repository (https://data.ess-dive.lbl.gov/).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2021.127137.

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