



RESEARCH ARTICLE

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Key Points:

- We used in situ whole-ecosystem manipulations to evaluate peatland carbon cycle changes to a range of warming conditions and elevated CO₂
- Warming caused variable responses for vegetation and losses of CO₂ and CH₄ for a linear response of 31.3 g C·m⁻²·year⁻¹·°C⁻¹
- Models are capable of capturing C cycle responses to temperature under ambient CO₂ conditions but overpredict sensitivity to elevated CO₂

Supporting Information:

- Supporting Information S1
- Original Version of Manuscript
- Peer Review History
- Authors' First Response to Peer Review Comments
- First Revision of Manuscript
- Authors' Second Response to Peer Review Comments
- Second Revision of Manuscript [Accepted]

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Rapid Net Carbon Loss From a Whole-Ecosystem Warmed Peatland

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Abstract To evaluate boreal peatland C losses from warming, novel technologies were used to expose intact bog plots in northern Minnesota to a range of future temperatures (+0°C to +9°C) with and without elevated CO₂ (eCO₂). After 3 years, warming linearly increased net C loss at a rate of 31.3 g C·m⁻²·year⁻¹·°C⁻¹. Increasing losses were associated with increased decomposition and corroborated by measures of declining peat elevation. Effects of eCO₂ were minor. Results indicate a range of C losses from boreal peatlands 4.5 to 18 times faster than historical rates of accumulation, with substantial emissions of CO₂ and CH₄ to the atmosphere. A model of peatland C cycle captured the temperature response dominated by peat decomposition under ambient CO₂, but improvements will be needed to predict the lack of observable responses to elevated CO₂ concentrations thus far.

Plain Language Summary Northern bogs and fens have accumulated carbon in deep deposits of peat—dead and decaying plant material high in carbon content—for millennia under wet, cold, and acidic conditions. We experimentally warmed and added CO₂ to a series of bog plots in northern Minnesota to investigate whether warming and drying would lead to the increased decomposition and loss of carbon from bogs to the atmosphere, where it would contribute further to warming. We found that warming changed the nature of these bogs from carbon accumulators to carbon emitters—where carbon was increasingly lost to the atmosphere in the form of greenhouse gases CO₂ and CH₄ as the level of warming increased. This carbon loss was faster than historical rates of carbon accumulation, demonstrating the significant impact of global warming on naturally stored carbon. Improved peatland ecosystem models are capable of capturing the temperature responses but overpredict responses to the elevated CO₂ treatments.

1. Introduction

The disproportionate contribution of extant peatlands to the long-term storage of terrestrial carbon (C) is well documented (Yu, 2012), and recent analyses suggest that the size of the global storage pool may be double previous estimates, now projected to be over 1,000 Gt of C (Nichols & Peteet, 2019). Likewise, concerns about the stability of this pool of C in the face of a warming climate have also been repeatedly published (Bridgman et al., 2006; Charman et al., 2013; Dise, 2009; Gorham, 1991; Roulet & Moore, 2006). These concerns are important given that losses of C from warming may be proportionate to the size of extant C stocks that are especially large in high-latitude systems (Crowther et al., 2016). Thus, peatlands represent a key ecosystem for evaluation of warming responses and the underlying mechanisms controlling such responses. Concomitant with future warming are increases in atmospheric CO₂ concentration, which has the potential to bring C from the atmosphere into ecosystems via enhanced photosynthesis (Ainsworth & Long, 2005). This study used in situ enclosures designed to be large enough to encompass the diversity of vegetation (from deep deposits of peat to short-statured mosses to tall trees) found in temperate raised-dome bogs. An overarching goal was to improve our understanding of ecosystem-level responses to continuous warming (air warming and deep-soil warming) not previously possible in a manipulative setting. Key questions were as follows: How will C loss and C gain balance under various future climates? Will peatlands remain a C sink or become a source of enhanced global greenhouse gas emissions?

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The Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment (Hanson, Riggs, et al., 2017) is a large-scale climate change manipulation that focuses on the combined response of multiple levels of warming at both ambient and elevated CO₂ concentration (eCO₂). The experiment was designed to provide a one-of-a-kind platform for testing and discovering the mechanisms that control the vulnerability of organisms and ecosystems to important climate change variables (e.g., thresholds for species decline or mortality, limitations to regeneration, biogeochemical regulations of productivity, and the cycling and release of CO₂ and CH₄ to the atmosphere). Because this ecosystem is located at the southern extent of the spatially expansive boreal peatland forests, it is considered especially vulnerable to climate change and may have important C cycle feedbacks to the atmosphere with global climate implications.

Experimental manipulations are critical to projections of ecosystem structural and functional responses to climatic and atmospheric change (Hanson & Walker, 2020; Mooney et al., 2013; Osmond et al., 2004). Mechanistic response curves and multidimensional surfaces are needed for models to project beyond conclusions that can be extracted from current and historical observations. Hypotheses for this ecosystem response to warming with or without an elevated CO₂ atmosphere include the following:

- enhanced production and subsequent loss of both CO₂ and CH₄ from warming-stimulated microbial activity across the range of warming conditions (Bridgman et al., 2006, 2008),
- negative growth responses of *Sphagnum* and other moss species that depend on surface water availability (Bragazza, 2008),
- positive growth responses of vascular plants associated with enhanced nutrient availability (López-Bucio et al., 2003), and
- enhanced net primary production (NPP) from warming and elevated CO₂ accelerations of physiological processes (Parton et al., 2007).

A key component of our research approach is also to construct and evaluate a peatland ecosystem model that includes rigorous mechanisms for application within regional and global models and to fill a recognized gap in the representation of peatlands in these models (Limpens et al., 2008). A regression-based experimental design was chosen for the SPRUCE experiment to allow better evaluation and improvement of model mechanistic responses across a wide range of warming treatments.

2. Methods

2.1. SPRUCE Project and Site Description

The experiment was conducted in the S1 Bog which is an 8.1-ha *Picea mariana* (black spruce)-*Sphagnum* spp. raised-dome, ombrotrophic bog in northern Minnesota in the United States Department of Agriculture Forest Service Marcell Experimental Forest (Lat. 47.503, Long. -93.483). The whole-ecosystem warming manipulations were provided via 12.8-m diameter × 7-m tall, open-top enclosures (Hanson, Riggs, et al., 2017; Figure S1 in the supporting information) enabling both air and soil warming for a range of warming levels: +0°C, +2.25°C, +4.5°C, +6.75°C, and +9°C (Figures S2 and S5). Air warming was accomplished through the use of four propane-fired furnaces per enclosure that generated warm air from recirculated air drawn from within the enclosure. The warmed air was blown back into each enclosure via eight diffusers distributed around the enclosure and located above the shrub height (approximately 1 m above the bog surface). Belowground warming was conducted using an array of 67 low wattage 3-m long resistance heaters positioned throughout the plot and enclosed in coated pipes (Hanson, Riggs, et al., 2017). The 19 belowground heaters within the plot measurement space only heated peat depths from -2 to -3 m to avoid direct heating of the measured peat profiles. The temperature control points were at +2 m for air temperature and -2 m for soil temperature. All warming treatments were conducted at both ambient and elevated CO₂, the latter in the range of 800 to 900 ppm.

Whole-ecosystem warming began in August 2015 following a year of belowground-only warming which commenced in 2014 (Wilson et al., 2016), and eCO₂ treatments were initiated in June 2016. Warming treatments were run continuously (24/7/365), while eCO₂ treatments were restricted to the growing season and daylight hours. Two plots without enclosures (Plots 7 and 21) were also fully instrumented and evaluated as “ambient” reference plots to allow assessment of the influence of the enclosures themselves. Ambient plot data are not part of the main regression analyses, but ambient plot data are included in Table 1, Figures 1

and 2, and within the supporting information environmental figures (Figures S1 to S6) as a reference for the reader of the responses to be expected for nonmanipulated plots. The experiment is intended and expected to run for a full decade.

Overstory vegetation within the S1 Bog is dominated by two tree species: *Picea mariana* (Mill.) Britton, Sterns, and Poggenburg and *Larix laricina* (Du Roi) K. Koch underlain by a bryophyte layer dominated by *Sphagnum* spp mosses (*S. magellanicum*, *S. angustifolium*, and *S. fallax*). The understory includes a layer of ericaceous shrubs including *Rhododendron groenlandicum* (Oeder) Kron and Judd (Labrador tea) and *Chamaedaphne calyculata* (L.) Moench. (leatherleaf) with a minor component of other woody shrubs. The bog also supports a limited number of herbaceous species including the summer-prevalent *Maianthemum trifolium* (L.) Sloboda (three-leaf false Solomon's seal) and a variety of graminoid species including *Eriophorum vaginatum* (cotton-grass). The peatland soil is the Greenwood series, a Typic Haplohemist (<http://websoilsurvey.nrcs.usda.gov>) with average peat depths to the Wisconsin glacial-age lake bed of -2 to -3 m (Parsekian et al., 2012). Peat at the experimental site within the S1 Bog has been accumulating at the -3 -m reference depth since around 11,000 years before present (McFarlane et al., 2018).

Ombrotrophic bogs like the S1 Bog studied in the SPRUCE experiment represent a very common northern latitude peatland with belowground characteristics similar to other peatlands occurring on the nutrient-poor end of the ombrotrophic-minerotrophic gradient ranging from precipitation-fed bogs to more nutrient-rich fens with connections to the groundwater table (Päivänen & Hännel, 2012; Wright et al., 1992). Further definitions of peatland types needed to place the SPRUCE ombrotrophic spruce bog in a broader regional context (Zalman et al., 2018), and global peatlands can be found in the supporting information.

2.2. Environmental Measurements

Environmental measurements collected in support of the SPRUCE experiment are detailed in Hanson, Riggs et al. (2017) and are available from the data archive Hanson, Riggs et al. (2016). An aboveground vertical profile of air temperature was measured at $+0.5$, $+1$, $+2$, and $+4$ m at half-hour intervals. Relative humidity was also assessed at all vertical measurement locations. Half-hour belowground temperatures within all plots were recorded at a central, middle, and edge location at the following depths: 0, -0.05 , -0.1 , -0.2 , -0.3 , -0.4 , -0.5 , -1 and -2 m, where 0 m is the peatland hollow height. Half-hour water table depth measurements were collected at the center of each plot (see supporting information Figure S6). While hummock and hollow surface drying was evident in the warmest treatment plots during midsummer periods, local precipitation inputs were sufficient to keep all plots above critical moisture deficit levels for rooted vegetation though there were periods where specific plant species indicated enhanced hydraulic stress. Nevertheless, all warming treatments include a component of atmospheric drying (greater vapor pressure deficit) and enhanced evapotranspiration leading to reductions in near-surface moisture availability (Hanson, Riggs et al., 2017). Other data on surface moisture, radiation levels, and enclosure CO_2 concentrations were also recorded at half-hour intervals and are available from archived data sets (Hanson, Riggs, et al., 2016).

2.3. Components of NPP

The aboveground NPP for tree species in the experimental plots (*Picea mariana* and *Larix laricina*) was derived from annual measures of tree diameter at breast height (1.3 m; Hanson et al., 2018) and periodic assessments of tree height combined with allometric relationships for total aboveground tree dry mass converted to C units assuming 48% C by mass (Griffiths et al., 2017). Aboveground NPP for shrubs (Hanson et al., 2018a) was obtained from annual destructive clipped plots (0.5 to 1-m² total area per plot depending on the year). Clipped materials were separated into current year versus older aboveground plant materials and then oven dried to uniform mass (several days at 70°C). Current year stem and leaf growth is defined here as the shrub-layer aboveground NPP. Actual C content for all tissues (leaves or stems) and species ranged from 46% to 53%, but this ecosystem-scale assessment of net carbon exchange (NCE) assumes all tissues to be 48% C. *Sphagnum* annual NPP assessments were as described by Norby et al. (2019). Briefly, annual *Sphagnum* community growth was assessed in defined columns and combined with measurements of the *Sphagnum* community cover. Mean C content of *Sphagnum* tissue was 42.9%.

Belowground fine-root contribution to net primary production (BNPP) was estimated from root ingrowth cores (Iversen et al., 2018; Malhotra et al., 2020). The ingrowth cores were constructed of 7.28-cm diameter extruded plastic mesh cylinders with 50% open area (Industrial Netting, Inc., RN7480) and filled with

Table 1
Components of NCE in $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ and the Combined Treatment Totals for Each Year of Warming and the Mean Annual and Active Season (Day of Year 122 to 244) Temperatures for All SPRUCE Plots

Year and treatment temp. differential	Plot #	CO ₂ ppm	Mean annual temp. at 2 m °C	Mean active season temp. at 2 m °C	ANPP tree	ANPP shrub	NPP <i>Sphagnum</i> .	BNPP trees, shrubs, and graminoids	R _{H-CO2}	CH ₄	TOC + DIC Loss ^a	NCE
2014–2015 ^b					51 ± 37	104 ± 34	208 ± 67	32 ± 39	−283 ± 45	−16.0 ± 1.8	−14.2 ± 0.3	82 ± 101
2016												
Ambient	7	Amb	6.0	16.6–17.0	44.6	56.4	93.1	9.4	−374.3	−56.9	−40 ^a	−267.7
Ambient	21	Amb	6.0	15.0	59.8	105.3	265.8	41.3	−390.0	−56.2	−40 ^a	−14.1
+0°C	6	+0	8.2	17.0	22.2	55.3	110.1	63.5	−361.4	−34.9	−50.2	−195.4
+0°C	19	+500	7.9	16.7	82.3	99.3	157.2	33.9	−381.2	−39.0	−31.0	−78.4
+2.25°C	20	+0	10.5	19.5	94.0	131.4	91.4	107.6	−461.2	−30.0	−95.9	−162.7
+2.25°C	11	+500	10.4	19.4	44.5	118.3	95.6	28.4	−487.9	−31.1	−45.8	−278.0
+4.5°C	13	+0	12.8	21.6	21.3	84.8	117.8	88.4	−461.2	−49.4	−55.3	−253.6
+4.5°C	4	+500	12.7	21.5	26.8	171.0	105.6	104.9	−541.5	−56.3	−65.3	−254.8
+6.75°C	8	+0	14.5	23.5	43.1	116.9	107.6	105.5	−509.9	−201.5	−47.4	−385.7
+6.75°C	16	+500	14.6	23.5	40.2	111.7	117.5	39.3	−545.3	−243.9	−34.6	−515.1
+9°C	17	+0	16.8	25.7	−1.4	153.7	111.8	34.4	−503.4	−121.5	−24.0	−350.4
+9°C	10	+500	16.5	25.6	29.9	126.8	81.5	98.2	−513.8	−122.9	−26.9	−327.2
2017												
Ambient	7	Amb	5.0	16.4	29.2	77.0	124.4	10.7	−361.9	−53.4	−33 ^a	−207.0
Ambient	21	Amb	5.8	16.5	43.6	112.8	265.8	52.2	−386.9	−57.3	−33 ^a	−2.8
+0°C	6	+0	6.8	18.5	9.0	142.5	101.8	71.9	−331.2	−31.0	−35.3	−72.2
+0°C	19	+500	6.5	18.2	48.7	154.4	118.5	17.6	−362.5	−36.6	−30.0	−90.0
+2.25°C	20	+0	9.2	21.0	76.8	90.2	119.6	73.6	−435.0	−28.4	−41.3	−144.5
+2.25°C	11	+500	9.2	21.1	27.9	83.0	59.6	48.7	−403.1	−29.1	−23.3	−236.2
+4.5°C	13	+0	11.2	23.0	30.7	112.8	94	85.7	−408.8	−45.1	−29.1	−160.2
+4.5°C	4	+500	11.3	23.1	22.7	169.9	23.9	108.8	−461.1	−49.9	−45.2	−230.9
+6.75°C	8	+0	13.3	25.1	37.9	107.3	53.6	75.1	−484.4	−180.3	−42.5	−433.3
+6.75°C	16	+500	13.4	25.3	35.9	142.9	70.9	150.8	−525.4	−222.3	−25.3	−372.5
+9°C	17	+0	15.5	27.2	12.4	101.8	25.5	163.6	−474.6	−110.3	−15.1	−296.7
+9°C	10	+500	15.4	27.1	28.4	253.4	14.6	134.3	−490.6	−113.9	−22.2	−196.0
2018												
Ambient	7	Amb	4.0	18.0	44.5	91.4	140 ^c	10.0	−362.2	−56.4	−33 ^a	−165.6
Ambient	21	Amb	4.4	18.4	29.7	79.3	140 ^c	46.7	−372.2	−55.8	−33 ^a	−165.3
+0°C	6	+0	6.4	20.8	15.2	97.6	204.5	67.7 ^c	−332.4	−28.4	−38.8	−14.7
+0°C	19	+500	6.0	20.3	66.4	111.3	81.8	25.7 ^c	−336.3	−33.1	−28.1	−112.2
+2.25°C	20	+0	8.5	22.8	70.8	59.2	190.9	90.6 ^c	−408.0	−26.3	−65.3	−88.1
+2.25°C	11	+500	8.7	23.2	44.0	100.9	114	38.55 ^c	−405.4	−26.6	−33.7	−168.2
+4.5°C	13	+0	10.9	25.3	39.5	105.4	84.6	87.05 ^c	−399.8	−42.4	−37.0	−162.7
+4.5°C	4	+500	10.8	25.3	52.7	114.7	29.1	106.85 ^c	−461.7	−48.7	−59.3	−266.4
+6.75°C	8	+0	13.0	27.5	32.8	171.2	42.5	90.3 ^c	−476.3	−189.5	−59.9	−388.9
+6.75°C	16	+500	12.9	27.5	41.4	100.3	29.2	95.05 ^c	−514.9	−232.1	−41.6	−522.7
+9°C	17	+0	15.0	29.5	9.4	103.4	13.2	99 ^c	−467.5	−108.6	−47.3	−398.3
+9°C	10	+500	15.1	29.6	47.3	140.6	46.9	116.25 ^c	−481.3	−109.5	−35.5	−275.3

Note. R_{H-CO2} values are based on measured assessments showing that 39.7% of total integrated community efflux of CO₂ is attributed to the heterotrophic community. Pretreatment estimates for the S1 Bog (2014, 2015) and ambient plot data for each year are provided for reference.
^aTotal organic carbon (TOC; 2016, 2017 and 2018) plus dissolved inorganic carbon (2017 and 2018). These data are estimated for the ambient plots.
^bPre-treatment data collected over multiple years prior to 2016 as summarized by Griffiths et al., (2017), but with a recalculation of the R_{H-CO2} contribution based on our most recent assessment of heterotrophic CO₂ release by the community.
^cEstimated for 2018.

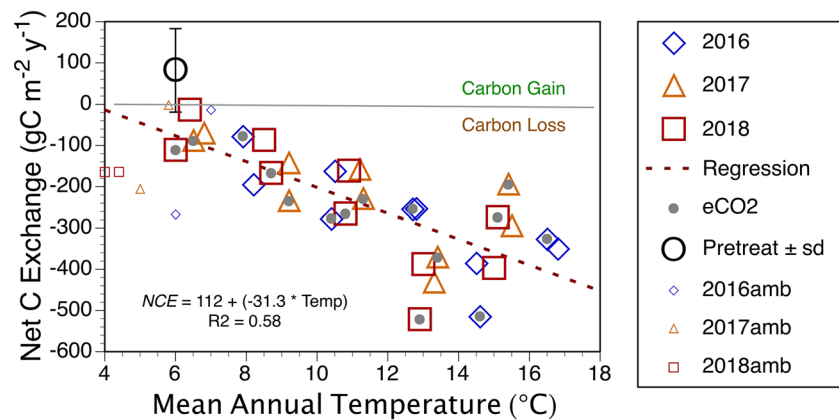


Figure 1. Measured ecosystem net C exchange (NCE; $\text{g C m}^{-2} \cdot \text{year}^{-1}$) for all treatment plots ($+0^\circ\text{C}$, $+2.25^\circ\text{C}$, $+4.5^\circ\text{C}$, $+6.75^\circ\text{C}$, and $+9^\circ\text{C}$ treatments) plotted against the mean annual air temperature at $+2\text{ m}$ for each plot in 2016, 2017, and 2018. NCE was calculated as the difference in measures of aboveground and belowground net primary production and C losses via heterotrophic CO_2 efflux, net CH_4 efflux, and combined total organic C and dissolved inorganic C efflux. Treatment plots receiving elevated atmospheric CO_2 exposures (eCO_2) are indicated by a solid gray circle within the plot symbol. Also shown is the NCE for pretreatment conditions in 2014–2015 (open circle \pm SD from Griffiths et al. (2017) modified based on new estimates of heterotrophic contributions). Nonenclosed ambient plot data for 2016, 2017, and 2018 are shown as small open symbols and are provided for reader reference.

prewetted, root-free, commercially available milled peat (Greensmix *Sphagnum* peat moss) harvested from a nearby bog. Two ingrowth cores were deployed in each plot into premade holes; one was deployed in a hollow to 30-cm depth below the peat surface, and the other was deployed in an adjacent raised hummock over the entire depth of the hummock to a depth of 10 cm below the surface of the adjacent hollow. The cores were deployed in June 2016 and collected in October 2016 when they were replaced with a new set of cores; this process was repeated seasonally (October 2016 to June 2017, June–October 2017, and October 2017 to June 2018). After collection, the cores were frozen at -20°C until processing at Oak Ridge National Laboratory where jewelers' glasses and tweezers were used to remove newly grown fine roots from thawed peat; roots were then oven dried at 70°C for $>48\text{ hr}$ before weighing to determine biomass. The living fine roots ($<2\text{ mm}$ in diameter) removed from each core included trees *P. mariana* or *L. laricina*, as well as ericaceous roots and graminoid roots which could not be differentiated by species. No dead roots were observed. Fine-root biomass production was summed over the depth of each ingrowth core, multiplied by 48% to determine root C content and standardized per core volume to a 30-cm depth. We averaged hummock and hollow BNPP assuming 62% hummock ground area (Graham et al., 2019). Here we present summed summer and winter fine-root growth ("winter" growth was observed only in warmed plots with an extended growing season) for 2016 and 2017; these data were averaged to represent 2018 fine-root growth for comparison with other measures of the C budget.

2.4. Efflux of Heterotrophic CO_2 and CH_4

Efflux of CO_2 and CH_4 (Hanson, Gill et al., 2016; Hanson, Phillips et al., 2017) was measured from in situ circular collars within each enclosure (1.2-m diameter) and evaluated approximately monthly during the active season (day of year 122 through 244; Richardson et al., 2018) and also during some dormant periods for all 3 years. To estimate annual heterotrophic fluxes of CO_2 , only darkened chamber measurements were used. All data were used to estimate CH_4 efflux. The measurement data sets were fitted to exponential curves (Tables S3 and S4) as a function of reference peat depth temperatures (-0.05 m for CO_2 flux, Figure S3 and -0.2 m for CH_4 flux, Figure S4) producing a significant apparent seasonal temperature response surface. Within an annual cycle, these fitted curves were used to integrate annual efflux of CO_2 and net CH_4 flux lost from the ecosystem using mean daily temperatures for the target peat depth appropriate to each gas (Figures S3 and S4). To obtain an estimate of annual CO_2 flux from heterotrophic respiration ($R_{\text{H-CO}_2}$) in the absence of autotrophic respiration, six paired dark collars (one intact vs. one with all autotrophic vegetation removed) located in ambient plots were evaluated for differences used to estimate the amount of heterotrophic respiration associated with the heterotrophic community (FractionH). These estimates were

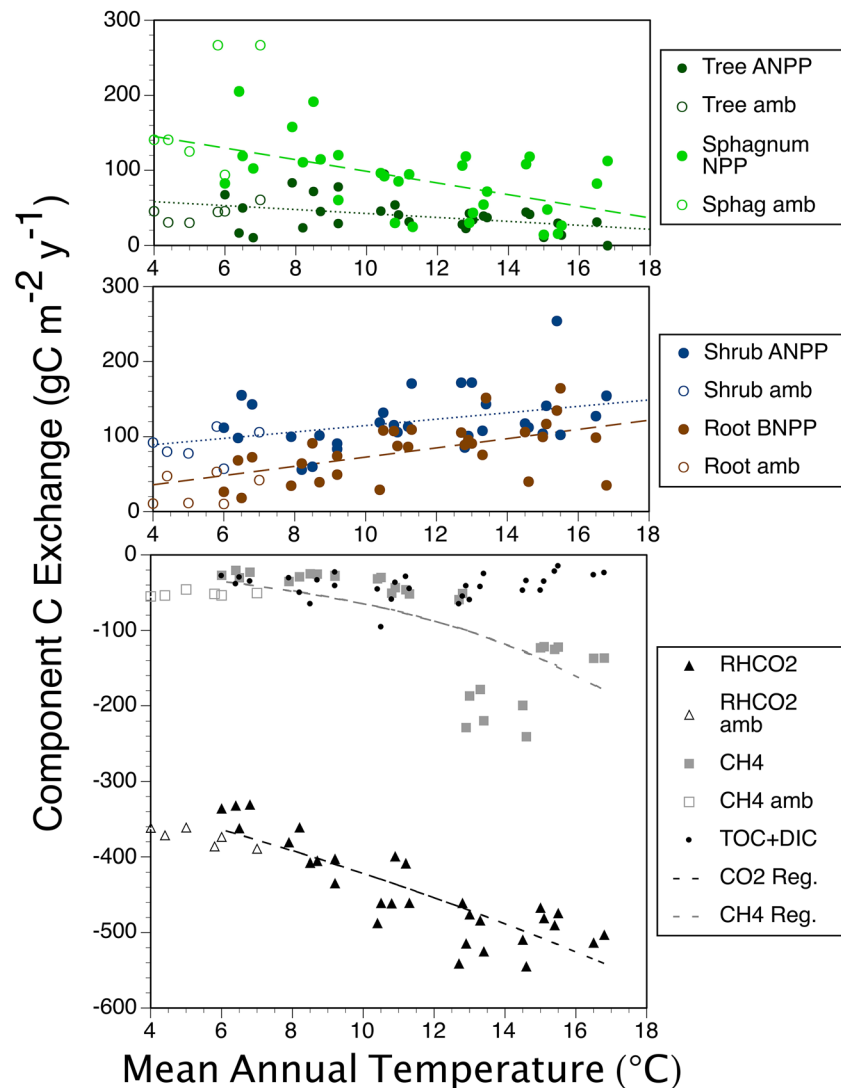


Figure 2. Response of the components of net C exchange (NCE; g C·m⁻²·year⁻¹) to mean annual air temperature for each plot in 2016, 2017, and 2018. Positive numbers are net gain, and negative numbers are losses from the bog. Components of NCE include the aboveground net primary production (ANPP) of trees, shrubs, and *Sphagnum*, belowground fine-root net primary production (BNPP), C losses from heterotrophs in the form of CO₂ (R_H-CO₂) and CH₄, and the lateral losses of total organic and dissolved inorganic C (TOC + DIC). Individual data points are for 1 year for each experimental plot. Regression coefficients and associated *p* values are available in the supplemental files (Table S1). Nonenclosed ambient plot data for 2016, 2017, and 2018 are shown for each variable as small open symbols and are provided for reader reference but are not included in the regressions.

averaged over 2-year postvegetation removal (Figure S7). This period excluded initial values subject to rapid C exudates and detached root decomposition. The final comparative CO₂ emission data yielded an estimate of the fraction of heterotrophic emissions as 0.40 ± 0.18 SD of total CO₂ efflux. Ecosystem-level flux data for these gases are available from Hanson, Phillips, et al. (2017).

2.5. Lateral Flux of TOC and DIC

Losses of total organic C (TOC) and dissolved inorganic C (DIC) in lateral flow (i.e., “stream flow”) were measured via a subsurface corral and outflow system as described in Sebestyen and Griffiths (2016). Briefly, an octagonal subsurface corral made of interlocking vinyl sheet piles was installed around each enclosure approximately to the mineral deposits below the peat. Two horizontal and slightly sloping slotted pipes, one just below the peat surface and one −37.5 cm deep, allowed water to flow passively out of the

enclosure/corral system into an external sump basin. Water level was measured in the sump basin over time and was used to calculate outflow (L min^{-1}). Flow-weighted, composite water samples were collected from the sump via an autosampler, and the sample was stored in a clean 20-L carboy inside a refrigerator until retrieval. The composite sample was retrieved weekly and analyzed for TOC concentration. Grab samples for analyses of DIC concentration were collected once a week from a standpipe inside the external sump basin to avoid the potential for degassing in the composite sample. TOC concentration was measured on a Shimadzu® TOC-VCP using the high-temperature combustion method. DIC was collected in preevacuated serum vials, followed by acidification with 0.5-mL 20% H_3PO_4 and subsequent head space analysis on a Hewlett Packard® gas chromatograph coupled to a Thermo® Finnigan isotope ratio mass spectrometer. TOC and DIC flux were calculated as the weekly TOC or DIC concentration multiplied by the daily lateral outflow of water, and these data were summed for years 2016, 2017, and 2018. Because ambient plots do not have a subsurface corral, TOC and DIC outflow for those plots was estimated as the TOC concentration in near-surface porewater multiplied by lateral flow from a prototype subsurface corral installed in the southern end of the S1 Bog (Sebestyen & Griffiths, 2016).

2.6. Measures of the Components of NCE

The annual NCE for each experimental plot was derived following the methods of Griffiths et al. (2017) where positive values are net C uptake into the ecosystem:

$$\text{NCE} = \text{NPP}_E - R_{\text{H-CO}_2} - F_{\text{CH}_4} - (\text{TOC} + \text{DIC}) \quad (1)$$

$$R_{\text{H-CO}_2} = R_{\text{CO}_2\text{total}} \times \text{FractionH} \quad (2)$$

$$\text{NPP}_E = \text{ANPP}_{\text{tree}} + \text{ANPP}_{\text{shrub}} + \text{NPP}_{\text{Sphag}} + \text{BNPP} \quad (3)$$

where NCE is the net C exchange from the ecosystem ($\pm \text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), NPP_E is the cumulative NPP from all contributing autotrophs ($\pm \text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), $R_{\text{H-CO}_2}$ is the fraction of CO_2 lost from the ecosystem attributable to heterotrophs ($-\text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), F_{CH_4} is the C equivalent loss from net methane efflux ($-\text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), and $\text{TOC} + \text{DIC}$ is DIC and TOC lost via the lateral transport of water away from the plots ($-\text{g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$). NPP_E is the cumulative annual NPP from aboveground assessments of trees including foliar production associated with annual litterfall ($\text{ANPP}_{\text{tree}}$), shrubs ($\text{ANPP}_{\text{shrub}}$), the *Sphagnum* community ($\text{NPP}_{\text{Sphag}}$), and annual belowground contributions from all fine roots (BNPP). Shrub stem and coarse-root increment for ANPP (e.g., annual xylem ring tissue growth) was not assessed annually but was assumed to be a small component of NPP_E . Losses from herbivory were negligible in 2016, 2017, and 2018 and were not quantitatively evaluated. Losses of volatile organic substances, wind-extracted pollen, and other plant tissue particles were not accounted for but were assumed to be partly balanced by inputs from other ecosystems (Curtis et al., 2002).

Assessments were conducted for the first 3 years of year-round continuous warming (2016, 2017, and 2018) and were plotted versus the mean annual air temperatures at +2 m in each plot. Mean annual temperatures or temperatures for some other day sequence or position within the experimental ecosystems could have been used instead, but +2-m air temperatures were similar to all other air temperatures (Hanson, Riggs et al., 2016) and seemed appropriate for correlation to the annual cycle for the ANPP components. Annual losses of heterotrophic CO_2 and net CH_4 efflux were derived for each annual cycle from fitted equations (Tables S3 and S4) of the apparent temperature response curves for each gas fitted to the mean annual temperature for a defined peat depth with best correlation to the annual data. TOC and DIC losses were the cumulative total of subsurface corral flux of water times the C concentration in exported water.

2.7. Modeling Peatland NCE

We used an updated version of the ELM-SPRUCED model to simulate ecosystem responses to warming and elevated CO_2 and compare to observations. ELM-SPRUCED is based on the Community Land Model version 4.5 (Oleson et al., 2013) with modifications to enable representation of bog hydrology and microtopography (Shi et al., 2015). Previous versions of ELM-SPRUCED were used to conduct uncertainty analyses of net C exchange (Griffiths et al., 2017), and those simulations indicated relatively modest responses to warming. Here we modified ELM-SPRUCED to include land biogeochemistry improvements for version 1 of the Energy Exascale Earth System Model (E3SM and thus ELM for the land model component; Golaz

et al., 2019; Yang et al., 2019). Key model improvements include the addition of phosphorus cycling, C and nutrient storage pools, and improved phenology. In addition, we modified parameters associated with the vertical transport of soil C and the impact of O₂ limitation on decomposition, allowing the model to equilibrate to realistic vertical profiles of soil organic C. Previous studies using ELM-SPRUCED (Griffiths et al., 2017) applied an initialization adjustment to force the model to match the observed profiles. We also adopted the observation-based leaf and fine-root C:N and C:P ratios for model parameterization. Methane fluxes were simulated using the CLM4Me model (Riley et al., 2011). This version of ELM-SPRUCED does not consider lateral outflow of TOC and DIC, but they are a small component of NCE (Figure 2).

Four dominant plant functional types were simulated: deciduous conifer (*L. laricina*), evergreen conifer (*P. mariana*), a generic deciduous shrub type (representing *Rhododendron groenlandicum*, *Chamaedaphne calyculata*, and other species), and a generic *Sphagnum* type (representing *S. angustifolium*, *S. fallax*, and *S. magellanicum*). Through continuously cycling of the ambient meteorology observed at the S1 Bog between 2011 and 2017, we first performed spin-up simulations in both accelerated and regular modes (Thornton & Rosenbloom, 2005) to equilibrate the C stocks using preindustrial CO₂ concentrations, N deposition, and land use and land cover change. A transient simulation, in which we continue to cycle the 2011–2017 forcing but with historically varying CO₂ concentrations and N deposition, was then conducted from 1850–2014. This simulation also included the 1974 strip cuts at the site (represented as a 99% removal of aboveground tree biomass). The endpoint of that simulation served as the initial condition for 11 simulations from 2015–2018, including an ambient plot and the five warming treatment levels (+0°C, +2.25°C, +4.5°C, +6.75°C, and +9°C) at both ambient and elevated CO₂ concentrations (+500 ppm). Warming treatments were simulated beginning in August 2015 by adding the desired level of warming to the model forcing of ambient air temperature and by representing enclosure effects on shortwave radiation, longwave radiation, and humidity (Hanson, Riggs et al., 2017). We did not attempt to account for observed differences among enclosures in vegetation biomass, composition, or peat properties in these simulations; these ecosystem components were simulated for each treatment combination by the model.

2.8. Measures of Bog Surface Elevation

To evaluate changes in bog elevation that might be correlated with peat mass and C losses from warming, a modified version of the Cahoon et al. (2002) surface elevation table instrument was constructed and renamed the SPRUCED Elevation Transect instrument (SET) for our purposes. The SET instrument was bolted to a permanently installed platform (two per plot anchored in the mineral soils below the peat profile) on a measurement date to obtain a bog surface measurement. The SET instrument can be rotated up to 180° for a maximum of eight individual mini-transect assessments of the bog surface at each location. However, various obstacles at a given location (e.g., dense shrub cover or experimental infrastructure) occasionally limited the use of all eight minitranssects. Along each mini-ransect, nine measurement rods were secured above the bog surface using medium-sized office binder clips. The individual 1.52-m surface measurement rods were constructed from 5-mm diameter fiberglass rods to which a subtending 6.1-mm thick circular acrylic pad (35-mm diameter) was glued. When the minitranssect was secured for measurement at a given compass orientation, the rods were released and allowed to fall under their own mass to the bog surface beneath the shrub canopy. To reach the target bog surface, the rods may have been rotated or tweaked to bypass shrub branches, but they were never pushed into the surface of the bog. Once the rods were in place, the length of the rod remaining above the minitranssect bar was measured to the nearest mm (Figure S8). Initial SET measurements of seasonal change suggested that peak growing season (mid-August) was a stable period for this observation. Because of the porous nature of the bog surface (i.e., a dominant *Sphagnum* moss layer), the SET measurement rods were modified to include a subtending circular acrylic pad designed to sit lightly on the surface of the moss. Realistically, the random nature at which the pad floats or pushes into the surface of the bog makes these measurements accurate only ±5 mm at best. Nevertheless, we record the measured data to the nearest mm at two SET locations per plot every year but report cumulative change (over 3 years) in this paper.

Differences in bog surface elevation between measurement dates may be obtained directly from these measurements (Hanson et al., 2018b), or the absolute elevation can be obtained from the known elevation of the SET permanent platform plate. The respective elevations of the two permanent SET stand platforms (SET =

Stand_Elev, meters amsl) in each experimental plot were obtained from commercial surveys as reported in Griffiths et al. (2016).

3. Results

The ombrotrophic S1 Bog area was a net sink of C ($82 \pm 101 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1} \pm \text{SD}$) in the 3 years before the SPRUCE experimental treatments began (2014 to 2015; Griffiths et al., 2017). After 3 years of experimental manipulation (2016–2018), the SPRUCE team calculated measures of ecosystem NCE from measured NPP C gain and C losses of CO_2 and CH_4 as well as lateral losses of dissolved organic and inorganic C forms. The results (Figure 1 and Table 1) showed all constructed control (nonheated) and warmed plots to be a consistent net source of C. The average C loss per year, based on a linear regression of the data (Figure 1; p value < 0.0001), was $31.3 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1} \cdot ^\circ\text{C}^{-1}$ for the combined years 2016, 2017, and 2018.

Although a large amount of inherent pretreatment variation existed around NCE estimates for the SPRUCE plots due to local spatial and temporal gradients (Griffiths et al., 2017), the magnitude of the C losses from the imposed warming treatments exceeded that range of variation (Figure 1). Through 3 years of warming treatments, the elevated CO_2 treatment plots have not separated from the pattern for all warmed plots for NCE or associated productivity measures.

Numerical plot data for all components of ecosystem NCE are provided in supporting information Table S1. The detailed breakdown of component fluxes (Figure 2) showed the overall net loss of C from the ecosystem with warming (Figure 1) to be a net combination of various C gains and C losses. Losses in aboveground production by trees (both *Picea* and *Larix* species combined) and the *Sphagnum* moss community were offset by gains in aboveground production by the shrub community and by the belowground production of fine roots of the woody vascular species (Table 1). Therefore, net ecosystem C losses with warming were dominated by warming-enhanced decomposition losses of CO_2 and enhanced net CH_4 production at the warmest temperatures. In particular, net CH_4 losses increased exponentially with increasing temperature. The enhanced CH_4 emissions for the $+6.75^\circ\text{C}$ warming treatment were notably stronger than those for the $+9^\circ\text{C}$ plots (Figure 2). The cause for this deviation from an otherwise consistent nonlinear relationship is not fully evaluated here but is being further investigated by the SPRUCE scientific team.

4. Discussion

The unique SPRUCE in situ, whole-ecosystem warming manipulations enabled us to demonstrate a clear pattern of C loss for ombrotrophic bogs in a hypothetical warmer future. This linearly declining pattern for NCE across a 0°C to 9°C range of warming treatments has never been documented before. The treatments utilized plots (114 m^2 for each enclosure) that enclosed intact examples of ombrotrophic boreal bogs that contained the diversity of the natural system (trees, shrubs, mosses, microbes, and a deep peat soil) and allowed isolated nutrient and water budgets to be evaluated as a part of the experiment. The scope of the SPRUCE effort gives us confidence in the applicability of these ecosystem-scale results for similar extant ombrotrophic bogs. Yet SPRUCE results are specifically for a 45-year successional regrowth stand of *Picea* and *Larix* redeveloping above a largely undisturbed shrub and *Sphagnum* layer in an undrained, “natural” bog. The response and C gain for other bogs, for example, old-growth stand and closed-canopy *Picea* forests, previously drained bogs, or fens are likely to be quantitatively different. For the closed canopy treed bog example, such an ecosystem might have greater ANPP, and therefore, net C gain might still be possible in the face of warming. More minerotrophic peatlands (e.g., along the gradient from poor to rich fens) with higher nutrient availability might also sustain C gain in response to warming, but any speculation about responses in other types of wetlands remains to be tested experimentally.

Past manipulative studies have not approached the scale and complexity of the SPRUCE whole-ecosystem warming experiment. Nevertheless, a few have been done using conceptually analogous approaches. In a long-term manipulation of bog and fen monoliths in mesocosms that included two levels of surface warming from infrared lamp heating combined with water table manipulations, Bridgman et al. (2008) and Chen et al. (2008) found that temperature- and water-table-driven reductions in C accumulation were substantial for fen mesocosms (-400 to $-800 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) but less for bog mesocosms with water table ($-100 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) or temperature (-20 to $-50 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) effects. However, the warming treatments for

these mesocosms with mean annual temperature increases of 0.9 and 1.3°C were much lower than those achieved in the SPRUCE study and in the levels of warming projected from future climate projections (IPCC, 2013). Similar to the SPRUCE results, they concluded that short-term responses to warming were dominated by changes happening in the acrotelm (aerobic surface peat horizons). During midseason periods, their greatest mean monthly warming treatments achieved +4.3°C, but that level of warming was not sustained all year nor did it penetrate beyond several cm below the surface as achieved in the SPRUCE treatments (warming to −2-m depth or greater). Bragazza et al. (2016) reported on a 3-year, high-to-low elevation monolith (0.1 m² × 0.2 m deep) transplant experiment for *Sphagnum*-dominated peatlands that yielded a +5°C warming treatment combined with 60% lower precipitation. They found substantially reduced C accumulation in their transplanted monoliths with warming (approx. −280 g C·m^{−2}·year^{−1}) similar to our in situ ecosystem-scale results. Gerdol et al. (2008) studied an alpine bog from 2002–2005 and found strong effects on NCE during the heatwave of 2003 attributable to enhanced heterotrophic respiration. Pastor et al. (2003) working on both bog and fen mesocosms reported limited temperature effects on dissolved organic C export at levels of export similar to those shown in Figure 2.

Samson et al. (2018) reported on a warming study of a nutrient-poor fen operated in 2013–2014 using passive open-top chambers (2.4-m base width) that had maximum daily differential air temperatures of 1.1°C to 1.8°C. Notwithstanding the low level of warming, Samson et al. (2018) found enhanced CO₂ losses with warming and a reduced water table. They did not calculate an annual C budget estimate that could be compared with the SPRUCE results. The SPRUCE results include and expand on the range and type of warming studies previously reported.

4.1. How Do Our NCE Results Across a Wide Range of Warming Contrast With Other Important Known Environmental Drivers of Peatland Change?

A key driver for changing peatland C dynamics is the water table level (Moore et al., 1998; Trettin et al., 2006). In general, lower water tables decrease CH₄ production while increasing CO₂ production (Kolka et al., 2018). Long-term changes in C stocks would depend on the balance of those losses against vegetation production changes. In the SPRUCE study, water table was influenced by the warming treatments in a dynamic manner depending on the balance between enhanced evapotranspiration from warming and the timing of precipitation events. Water levels were drawn down to lower levels and for longer durations in the warmest plots during midsummer dry periods with warming (−10 to 30 cm; Figure S6). Nevertheless, precipitation inputs from snow melt and summer events kept water near the bog hollow surface throughout much of the 2016 through 2018 study period. In related studies, Munir et al. (2015) contrasted unmanipulated control peatland sites with recently drained and long-term drained sites (10 years old) for their effects on C cycle processes. They embedded passive, solar-driven, open-top chambers within these sites that produced annual warming treatments of approximately +1°C (with instantaneous midday warming as high as +6°C). Munir et al. (2015) found sustained C uptake for warmed plots without water table manipulations but immediate C losses for warmed and recently drained plots. If the plots were previously drained (i.e., 10 years earlier), the responses were attenuated. Following 80 years of lowered water tables (~15 cm lower) as a result of levees at the Seney National Wildlife in Upper Michigan, researchers observed increases in CO₂ fluxes and decreases in CH₄ fluxes when compared to hydrologically unaltered reference fen sites (Ballantyne et al., 2014; Chimner et al., 2017). Fens and bogs have also been shown to have opposite responses to an increasing water table with fens showing lower and bogs higher production and respiration, respectively (Sulman et al., 2010). If during the remaining planned operation of SPRUCE (through 2025) the experimental warming treatments were to overlap with less precipitation or less frequent precipitation events, we may see a gradient of reduced water table levels with warming. Such changes would be expected to enhance CO₂ production and decomposition from newly aerated surface peat layers and reduce CH₄ emissions. The net effect on the peatland C budget would depend on these changes and a potentially strong interaction with vegetation responses to additional nutrient releases from the decomposition of surface peat.

The eCO₂ treatments used in SPRUCE to assess the effects of CO₂ on NPP are relatively large (+500 ppmv) and indicative of a potential future global atmosphere beyond the year 2100. Through 3 years of manipulation, we have yet to find consistent eCO₂ responses evident above the dominant temperature effects for community-level NPP gains. Norby et al. (2019) did report reduced *Sphagnum* NPP with eCO₂ for 2018. Leaf-level responses to eCO₂ in the woody plants were evident as increased nonstructural carbohydrates

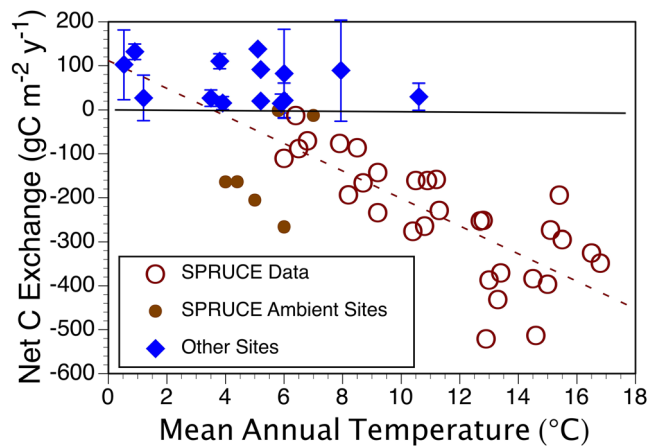


Figure 3. A comparison showing net C exchange results from the SPRUCE warming manipulations plotted against mean annual air temperatures, contrasted with observational data \pm SD for other peatland studies. Comparisons were limited to other temperate peatlands (some bogs and some fens) for which similar calculations could be made (Table S2; Dinsmore et al., 2010; Griffiths et al., 2017; Golovatskaya & Dyukarev, 2009; Koehler et al., 2011; Nilsson et al., 2008; Olson et al., 2013; Roulet et al., 2007; Turunen et al., 2004; Worrall et al., 2009). The methods used to estimate NCE varied across the various studies. Here we included studies that were based on estimates of net CO_2 exchange (NPP based or eddy covariance minus methane losses and minor TOC losses and a few based on ^{210}Pb tracers).

and differential biochemical acclimation, and there is evidence that the unique isotopic label of the eCO_2 is showing up in the heterotrophic soil community (Hopple et al., 2020). However, the net impact on allocation to growth has yet to develop. This is perhaps due to the nutrient-limited conditions in ombrotrophic bogs (e.g., N; Urban & Eisenreich, 1988), which have been shown to limit eCO_2 responses for upland forest ecosystems (De Graaff et al., 2006; Norby et al., 2010). Enhanced decomposition was, however, expected to eliminate such a nutrient limitation (N and P) for rooted vegetation in the warmed plots and is confirmed by increasing N and P availability in the warmed plots (C. Iversen, personal communication, 15 January 2020). We are continuing to investigate the balance among microbially mediated increases in nutrient availability and vegetation productivity. Vegetation C gain will depend in part on differing peatland plant strategies for nutrient acquisition and use (e.g., Iversen et al., 2010), how nutrient availability and rooting depth distributions change throughout the peat profile in response to changing environmental conditions (e.g., Iversen et al., 2011), and competition within and among mosses and vascular plant species (Jassey et al., 2013; Norby et al., 2019).

Prior studies of eCO_2 impact on peatland vegetation and ecosystem processes have produced mixed results. Hoosbeek et al. (2001) found limited responses to eCO_2 for ombrotrophic bog vegetation, and Girardin et al. (2016) conducting an analysis across all type of boreal forest vegetation could not demonstrate eCO_2 changes over the past century of monotonically increasing atmospheric CO_2 . In a monolith study based on a

mesotrophic fen in Wales, UK (Fenner et al., 2007), eCO_2 studies showed both evidence of the incorporation of eCO_2 ^{13}C -isotopic signatures in plant material and in enhanced biomass. In another Welsh U.K. ombrotrophic bog with greater nutrient limitation, Ellis et al. (2009) found enhanced CO_2 and CH_4 flux from eCO_2 treatments ($\sim +150$ ppmv) but reduced dissolved organic C losses. In the Ellis et al. study, the eCO_2 effects were overwhelmed or masked by water table drawdown responses leading to C losses from all treatments after 12 weeks.

4.2. Do “Climate Space-for-Temperature Gradients” Produce Similar Results?

Griffiths et al. (2017) compared pretreatment C exchange data for the S1 Bog site (a northern Minnesota temperate ombrotrophic bog) with four other similar peatland systems having comparable methods for NCE determination (Dinsmore et al., 2010; Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007), and the SPRUCE manipulation results have been added to that list for comparison (Figure 3 and Table S2). Even though these studies represent a range of peatland types, they also cover a climate space spanning a wide range of mean annual air temperatures (0.5°C to 10.6°C) similar to the range of manipulated temperatures in SPRUCE ($+0^\circ\text{C}$ to $+9^\circ\text{C}$).

A range of observational studies are available for comparison to the SPRUCE results. Olson et al. (2013) provide similar NCE estimates for a fen near the SPRUCE experimental site over 3 years (2009–2011) that had mean annual temperatures from 3.5°C to 5.9°C . Turunen et al. (2004) reported recent (i.e., 50 year) C changes from C stocks and ^{210}Pb dating approaches and also found a range of C gains from 5 to 131 $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ over a mean annual temperature range from 0.9°C to 5.1°C . Worrall et al. (2009) reported a range of C gains from 20 to 92 $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ for a low-lying ombrotrophic peatland in Northern England with a mean annual temperature of 5.2°C . Long-term eddy covariance observations in a temperate ombrotrophic peatland in Scotland over 11 years (Helfter et al., 2015) showed mean C uptake of 64.1 $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ at a site with a mean annual temperature of 8.3°C . From an observation period in Siberia from 1999–2007, Golovatskaya and Dyukarev (2009) found C gain for a sedge-*Sphagnum* fen (102.3 ± 79.1 $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$). Combining these data into a climate space for temperature relationship analogous to the imposed SPRUCE treatments, Figure 3 shows that the unmanipulated sites have consistent net positive C gains ranging from 14 to over 100 $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ with little to no relationship with temperature.

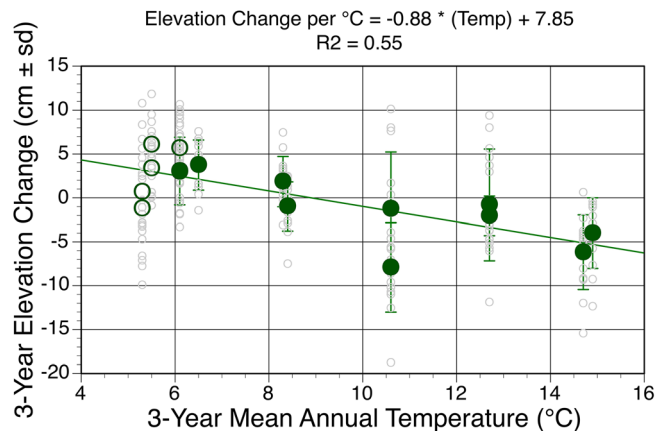


Figure 4. Cumulative 3-year elevation change for the S1 Bog ambient plots (large open symbols) and the SPRUCE treatment plots within the S1 Bog (large filled symbols \pm SD) as a function of the 3-year average mean annual air temperatures of the site or treatment plots. Small open gray symbols are individual minitransect data shown to illustrate full variation of these data.

Lindroth et al. (2007) reported a “positive but weak correlation” between NCE and mean annual temperatures for nine northern European and Canadian peatlands. Ultimately, site- and latitude-specific differences in vegetation composition and peat recalcitrance will play an important role in controlling peatland responses to a warmer future (Hodgkins et al., 2018).

The disparity between the strong C losses in the manipulated experiment for a raised bog over a 0°C to +9°C range and with no or limited changes for a similar mean annual temperature gradient for a range of peatland types raises a question about the use of climate space-for-time interpretations when scaling climate warming assumptions. Conversely, experimental treatments with a rapid change to a “future” warming climate as described for SPRUCE may also produce a result unique to the manipulation that may or may not be representative of future climates that might take decades to centuries to develop. A 26-year study by Melillo et al. (2017) of a soil-only warming manipulation in an upland midlatitude hardwood forest found dramatic undulations in their systems’ C efflux response through time. The SPRUCE study is planned to extend through a full decade of manipulations, allowing us to observe changes in the strength of the warming response through time. Throughout this observation period,

we will be examining the mechanisms responsible for changing NPP and variation in the strength of subsurface microbial C losses to better inform mechanistic models that will be an effective method for scaling peatland responses across space and time.

4.3. Are There Independent Data that Support the Calculated C Loss Rates?

The measures of NCE loss reported here result from an integration of various measures of C gain or loss based on growth or flux observations. A typical method for confirmation of such results would be whole-ecosystem flux observations using eddy covariance methods (Helfter et al., 2015), but such approaches are not available to the SPRUCE project given the constraints of the enclosure air warming method. However, surface elevation change of the SPRUCE bog can provide insights into large changes in volume that may be driven by mass and thus C loss. Over the 3-year warming period, the S1 Bog had a 0.88-cm loss of elevation for every degree of warming to which the ecosystem was exposed (Figure 4). If such elevation changes are converted to volume changes within the biologically active surface layers of the bog (Hopple et al., 2020; Wilson et al., 2016) and all volume loss is assumed to come from the loss of mass and associated C, we estimate the 3-year loss of C from the warmest treatment (+9°C) to be 1,400 g C m⁻² (calculation assumptions are in the supporting information). Such a rate of change translates to an annual loss of -467 g C m⁻² year⁻¹, which is in line with the prior rates for the warming treatments of -389 g C m⁻² year⁻¹ from our manipulation data in Figure 1 (calculated assuming 16°C as the mean annual temperature for a +9°C treatment). Unaccounted for C losses in the SPRUCE elevation transect instrument (SET), data may also arise from the collapse of the *Sphagnum* community layer (Norby et al., 2019), loss of water volume from desiccation (Schothorst, 1977; Wösten et al., 1997), or a loss of root structural volume beneath the surface. While our data show enhanced fine-root production and thus do not support a root mechanism elevation loss, we cannot discount the contribution of the other mechanisms. Microtopography is known to vary widely across peatland types due to geomorphology, legacy and extant conditions, and community composition. Changes in water table depth and decomposition rates can greatly affect peat microform, density, and deformation and thus lead to various ecohydrological feedbacks to the system over time (Waddington et al., 2010). Over the course of the SPRUCE experiment, such feedbacks could reduce or alleviate the current rate of C loss under the warming manipulations, for example, if decomposition and the elevation loss eventually lead to a reduction in water table depth and greater surface water availability.

4.4. Can ELM-SPRUCE Capture the Nature of the Experimental Results?

As a part of the SPRUCE effort the ELM-SPRUCE model is being developed for peatland land cover types and being evaluated against SPRUCE empirical data. The ELM-SPRUCE model with appropriate

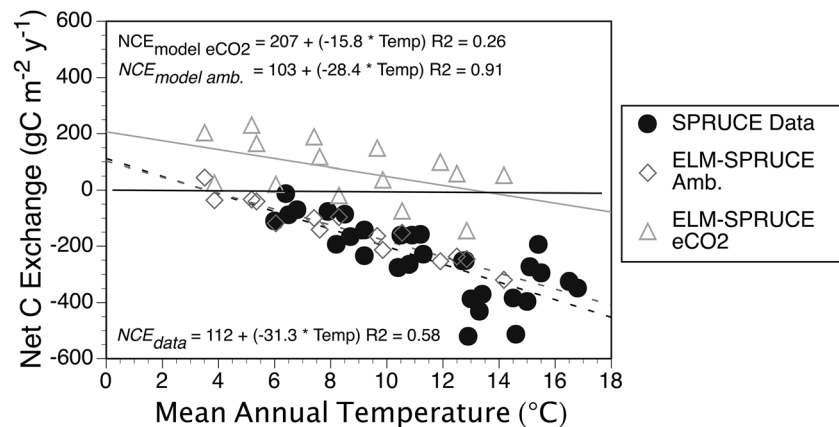


Figure 5. A comparison of the SPRUCE warming treatment measured changes in net C exchange (NCE; $\text{g C m}^{-2} \text{ year}^{-1}$) from the S1 ombrotrophic bog for data from 2016, 2017, and 2018 with ELM-SPRUCE modeled NCE estimates plotted against mean annual air temperatures for the respective sites. Measured data are solid symbols (dashed black line), and model estimates are from the ELM-SPRUCE model runs using ambient (open diamonds; dashed gray line) or elevated CO_2 data (open triangles; solid gray line).

representation of peatland microtopography and subsurface biogeochemistry is capable of projecting net C flux for the S1 Bog with a C loss rate of $28.4 \text{ g C m}^{-2} \text{ year}^{-1} \text{ } ^\circ\text{C}^{-1}$ in response to warming under ambient CO_2 that overlaps the SPRUCE measured data for 2016 through 2018 (Figure 5).

Similar to the empirical results, the largest component contributing to simulated C loss is increased heterotrophic respiration. Beyond the empirical surface observations, ELM-SPRUCE simulations predicted decreased heterotrophic respiration near the surface (see supporting information Figure S10) and strongly increased values 30–70 cm below the hummock tops. These model results suggest that modest declines in water table may be having large impacts in addition to the temperature changes.

The model simulations for an elevated CO_2 atmosphere (+500 ppmv) showed reduced temperature sensitivity compared with ambient CO_2 ($-15.8 \text{ g C m}^{-2} \text{ year}^{-1} \text{ } ^\circ\text{C}^{-1}$; Figure 5). They revealed that while the model captures the temperature response well under ambient CO_2 , it fails to predict the general lack of response to elevated CO_2 concentrations. Processes such as biogeochemical nutrient limitations or shifts in allocation patterns in the real world that limit eCO_2 responses may be represented incompletely or incorrectly in the virtual world of ELM-SPRUCE leading to this discrepancy. ELM-SPRUCE does include a detailed treatment of nitrogen and phosphorus cycle dynamics and C-N-P interactions. In the model N and P availability is simulated as a result of complex interactions between plant, microbes, and soils, as well as external nutrient inputs and outputs such as N and P deposition and leaching. Where possible, data collected at the site were used to parameterize the model. For example, observed N and P concentrations of plants and fresh litter were used for model parameterization. Site measured N and P deposition rates were also used as model inputs. In ELM-SPRUCE warming levels above 2.25°C lead to strong increases in N and P mineralization reducing the effects of nutrient limitation compared to ambient conditions under eCO_2 . In the actual experiment as describe in section 4.1, enhanced decomposition and associated nutrient mineralization appear to be rapidly recaptured by plot vegetation and microbial activity. If the expansion of microbial biomass is dominating this recapture, the *Sphagnum* and higher plants would not benefit from its release and therefore would not result in a strong C gain under simulated eCO_2 atmospheres. Discrepancies between model simulations and data under eCO_2 conditions suggest that we need to look more closely at carbon allocation and nutrient limitation within the model and collect additional observations to validate associated hypotheses. Follow-on papers will assess the model's ability to capture observed vegetation and CH_4 cycle responses.

4.5. Relevance of ELM-SPRUCE Results for Other Sites and Models

While we have not yet attempted to simulate other sites using ELM-SPRUCE, other modeling studies indicate broadly similar responses to manipulations at other peatland ecosystems. Waddington et al. (1998) modeled a fen ecosystem response to 3°C warming with and without water table decreases and found that both

warming and water table decreases reduced C gain. These responses were compounded when the treatments were combined. They did not calculate annual NCE data that could be quantitatively compared to SPRUCE results (Figures 1 and 2). Nevertheless, SPRUCE results also demonstrate C losses with warming and associated water table reductions (Figure S6). Empirically, we cannot explicitly separate the warming from the limited drying effect, though ELM-SPRUCE results show a high sensitivity of heterotrophic respiration to water table changes, and future modeling may help isolate these effects. Other modeling work has produced similar results. Ise et al. (2008) simulated peatland changes for 4°C warming and associated water table changes and projected a 40% loss of soil organic C from shallow peat and 86% loss from deep peat. Interpretation of the source of SPRUCE net C losses throughout the peat layers was not yet quantitatively defined, but the underlying mechanisms have been evaluated (Hopple et al., 2020; Wilson et al., 2016). Heijmans et al. (2008) ran an ecosystem model for a bog including vegetation types, C, nitrogen, and water dynamics. They concluded that the effects of temperature, precipitation, N-deposition, and atmospheric CO₂ would all play a role in defining future net C flux. Their model projected decreased C accumulation only for high N-deposition sites. Sulman et al. (2012) evaluated the ability of seven ecosystem models to simulate C fluxes from three peatland sites in Canada and the northern United States (two fens and one *Sphagnum*-dominated bog). Their comparison of model results to local eddy covariance data showed variable capacity to capture measured daily data, but they did not integrate annual totals that we could compare directly with the SPRUCE measured or modeled data (Figure 5). Further model development and model-data synthesis are needed to quantify the contributions from different mechanisms behind C losses in the SPRUCE experiment that cannot be measured directly, including the application of additional models at SPRUCE and an evaluation of ELM-SPRUCE at additional sites such as those described above. Such efforts may also inform how these contributions will change over time and will allow an assessment of the broader relevance of our SPRUCE manipulation that will be necessary for spatial scaling these results.

4.6. What Are Implications for the Future of Temperate Raised Bog Peatlands?

McFarlane et al. (2018) quantified the peat age distribution and long-term accumulation rates for the S1 Bog from C stocks and ¹⁴C isotopic characteristics by depth. They found that the peat profile has accumulated since the last glacial retreat from Minnesota 11,000 years ago leaving behind a total C stock of around 176 kg C m⁻² to a calculated depth of 2.25 m (actual peat depths can be much greater; Parsekian et al., 2012). Of this total pool, the uppermost stocks to a depth of 0.5 m associated with peat accumulation over 2,000 years before present represent a C stock of 31.3 kg C m⁻². If the C loss rates with warming reported here (31.3 g C·m⁻²·year⁻¹·°C⁻¹ from Figure 1) were associated with mass and C loss and sustained through time for the +2.25°C, +4.5°C, +6.75°C, and +9°C treatments (70, 141, 211, and 282 g C·m⁻²·year⁻¹, respectively), the total pool of C in the upper 0.5 m of peat would be released back to the atmosphere in 447, 222, 148, and 110 years, respectively. Such rates of loss would be 4.5 to 18 times faster than the rate of historical accumulation for the ombrotrophic bog. Of course, such rates of C loss measured in the first 3 years of the SPRUCE study could be attenuated with time. Yet even if these early data are faster than long-term rates of C loss from bogs under “real” rates of climate change, the results would likely exceed the C accumulation rates of the past. One might also expect changes in the elevation and associated vegetation composition of these ecosystems. Loss of the ecosystem engineer *Sphagnum* from the SPRUCE plots (Norby et al., 2019), with its known recalcitrance to and impacts on decomposition (Jassey et al., 2013), could exacerbate C losses as decomposition of non-*Sphagnum* tissues becomes a more prominent source of annual litterfall. Over the next few centuries, the studied ombrotrophic or raised bog system might eventually return to the elevation status of a fen if precipitation levels in this region remain high. This would be an important transition of the ombrotrophic system (rain fed) to one with flowing nutrient supplies from the surrounding watershed (minerotrophic fen) and would likely result in a further increase in CH₄ emissions (Hodgkins et al., 2014; McCalley et al., 2014).

These SPRUCE results from an initial 3 years of warming suggest a potentially dramatic response of extant ombrotrophic bogs to future warming and significant greenhouse gas feedback to the atmosphere for both CO₂ and CH₄ that are not quantified from available climate space-for-time data. Plant functional types (trees, shrubs, and mosses) had variable NPP responses, and despite strong increases in shrub NPP above-ground and root NPP belowground, warming caused the bog to switch from a net ambient sink to a consistent net source of C. A lowering of the water table and decreased abundance of *Sphagnum* within the bog

surface layer (Norby et al., 2019) are likely an important factor in these ecosystem changes. From our unique whole-ecosystem experiment, we are able to provide net rates of change in the bog C balance as a function of temperature as well as elucidate plant functional type responses that may contribute to this response.

SPRUCE is nevertheless still a single, albeit comprehensive, study on one ombrotrophic bog. While the results may have merit for the development of general conclusions with respect to many peatlands, the results have much greater value through their interpretation within models for the development of new hypotheses for peatlands with alternate characteristics (e.g., minerotrophic fens, pocosins, or tropical peatlands). By studying the key processes impacted under warming and eCO₂ manipulations and their relationships with water table depth, we can improve the mechanistic representation of those processes within peatland models and their application in Earth system models. Future manipulations in other peatland or upland ecosystems using appropriately scaled whole-ecosystem warming approaches would be needed to demonstrate the universal nature of such responses. Since it would not be possible for the science community to accomplish empirical data collections or manipulations for all important ecosystems, models capable of capturing the essence of such work will be critical to the temporal, spatial, and prognostic scaling of climate change impacts.

Data Availability Statement

Data sets pertaining to this study are in the online project archive at <http://mnspruce.ornl.gov> and for long-term storage in the U.S. Department of Energy's (DOE) Environmental Systems Science Data Infrastructure for a Virtual Ecosystem (ESS-DIVE; <http://ess-dive.lbl.gov/>).

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