



ORIGINAL ARTICLE

Whole-Ecosystem Warming Increases Plant-Available Nitrogen and Phosphorus in an Ombrotrophic Bog

Colleen M. Iversen,^{1,2*} John Latimer,³ Deanne J. Brice,^{1,2}
Joanne Childs,^{1,2} Holly M. Vander Stel,⁴ Camille E. Defrenne,⁵
Jake Graham,⁶ Natalie A. Griffiths,^{1,2} Avni Malhotra,⁷ Richard J. Norby,⁸
Keith C. Oleheiser,^{1,2} Jana R. Phillips,^{1,2} Verity G. Salmon,^{1,2}
Stephen D. Sebestyen,⁹ Xiaojuan Yang,^{1,2} and Paul J. Hanson^{1,2}

¹Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA; ²Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA; ³XCEL Engineering, Oak Ridge, Tennessee, USA; ⁴Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan, USA; ⁵College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan, USA; ⁶School of Civil and Environmental Engineering, Boise State University, Boise, Idaho, USA; ⁷Department of Geography, University of Zurich, Zürich, Switzerland; ⁸University of Tennessee, Knoxville, Tennessee, USA; ⁹Northern Research Station, USDA Forest Service, Grand Rapids, Minnesota, USA

ABSTRACT

Warming is expected to increase the net release of carbon from peatland soils, contributing to future warming. This positive feedback may be moderated by the response of peatland vegetation to rising atmospheric [CO₂] or to increased soil nutrient availability. We asked whether a gradient of whole-ecosystem warming (from + 0 °C to + 9 °C) would increase plant-available nitrogen and phosphorus in an ombrotrophic bog in northern Minnesota, USA, and whether elevated [CO₂] would modify the nutrient response. We tracked changes in

plant-available nutrients across space and through time and in comparison with other nutrient pools, and assessed whether nutrient warming responses were captured by a point version of the land-surface model, ELM-SPRUCED. We found that warming exponentially increased plant-available ammonium and phosphate, but that nutrient dynamics were unaffected by elevated [CO₂]. The warming response increased by an order of magnitude between the first and fourth year of the experimental

Received 1 November 2021; accepted 1 February 2022

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10021-022-00744-x>.

Author Contributions: CMI designed and implemented the ion-exchange resin study, analyzed the data, and wrote the manuscript; JL collected, cleaned, and replaced ion-exchange resins from SPRUCED experimental enclosures; DB, JC, JP, and HVS extracted analyzed ion-exchange resin capsules and/or analyzed extracts for NH₄-N, NO₃-N, and

PO₄-P; NAG, SDS, and KCO designed and implemented the porewater study, and KCO collected porewater and analyzed for nutrient concentrations; AM and JG collected information on resin elevation and depth to water table level; RJN and JC collected data on *Sphagnum* N and P requirement; VGS and CED assisted with the statistical framework and contextualization of available nutrients with plant-nutrient dynamics; XY ran the ELM-SPRUCED model to assess nutrient dynamics; PJH oversees and implements the SPRUCED experimental treatments, as well as the environmental data, above- and belowground. All co-authors read and commented on previous versions of the manuscript.

*Corresponding author; e-mail: iversencm@ornl.gov

manipulation, perhaps because of dramatic mortality of *Sphagnum* mosses in the surface peat of the warmest treatments. However, neither the magnitude nor the temporal dynamics of the responses were captured by ELM-SPRUCÉ. Relative increases in plant-available ammonium and phosphate with warming were similar, but the response varied across raised hummocks and depressed hollows and with peat depth. Plant-available nutrient dynamics were only loosely correlated with inorganic and organic porewater nutrients, likely representing different processes. Future predictions of peatland nutrient availability under climate change scenarios must account for dynamic changes in nutrient acquisition by plants and microbes, as well as microtopography and peat depth.

Key words: warming; elevated [CO₂]; nutrient availability; ombrotrophic bog; SPRUCÉ; peat depth; microtopography; *Sphagnum* moss; nitrogen; phosphorus.

HIGHLIGHTS

- We investigated the nutrient dynamics underpinning peatland responses to changing environmental conditions within the framework of a large-scale warming × CO₂-enrichment experiment in a nutrient-limited ombrotrophic bog at the southern end of the boreal peatland range. Whole-ecosystem warming exponentially increased plant-available ammonium and phosphate, but nutrient dynamics were unaffected by elevated [CO₂].
- The nutrient warming response increased by an order of magnitude between the first and fourth years of warming, perhaps because of dramatic mortality of *Sphagnum* mosses in the surface peat of the warmest treatments. However, this response was not captured by a land surface model parameterized to simulate ecosystem dynamics within the experiment.
- Relative increases in plant-available ammonium and phosphate with warming were similar, but the warming response varied across raised hummocks and depressed hollows and with peat depth.

INTRODUCTION

Peatlands store at least one-third of global soil organic carbon (C) in deep deposits of peat accumulated over millennia due to an imbalance between production and decomposition (Bridgman and others 2006; Gorham 1991; Nichols and others 2019). Warming is expected to increase the net release of C from peatland soils, potentially leading to positive feedback to future warming (Bridgman and others 2008), though these responses could be moderated by elevated [CO₂] or increased peat nutrient availability (Hedwall and others 2017; Milla and others 2006; van der Heijden and others 2000). Here we investigated the nutrient dynamics underpinning peatland responses to changing environmental conditions within the framework of a large-scale warming × CO₂-enrichment experiment in a nutrient-limited ombrotrophic bog at the southern end of the boreal peatland range (that is, the Spruce and Peatland Responses Under Changing Environments, or ‘SPRUCÉ’ experiment; Hanson and others 2017).

Warming has been shown to increase nutrient mineralization rates across a range of upland ecosystems (Rustad and others 2001), and in ecosystems underlain by organic soil (Aerts and others 2006; Munir and others 2017; Salazar and others 2020; Weedon and others 2012). Increased nutrient availability has been found to increase (Bragazza and others 2006; Mack and others 2004) or inhibit (Keller and others 2006; Malhotra and others 2018; Olid and others 2014) peat decomposition rates due to complex interactions among microbial physiology, plant species composition and litter chemistry, and edaphic conditions. Increasing nutrient availability can also change the balance among the fractional cover and biomass of vascular overstory plants and *Sphagnum* mosses, as *Sphagnum* is less competitive at higher levels of nutrient availability (Berendse and others 2001; Vitt and others 1990). Microbial and vegetation responses to increased nutrient availability could be moderated by potential declines in soil moisture and water table levels associated with warming (Weltzin and others 2003).

Nitrogen (N) and phosphorus (P) have different rates of mineralization and immobilization, which are controlled by differing microbial communities, plant-rhizosphere interactions, and edaphic and environmental factors (Richardson and others 2009; Spohn and others 2013; Vitousek and others

1991; Walker and others 1976). Nitrogen and P cycling rates have been shown to respond differently to warming in boreal peatlands (Munir and others 2017) and to freeze–thaw or heatwave events in uplands (Mooshammer and others 2017), with potential implications for shifting plant and microbial communities (Hill and others 2014; Iversen and others 2010; Koerselman and others 1996; Wang and others 2014).

Peatlands are also characterized by small-scale environmental gradients—from undulating surface microtopography, which encompasses raised hummocks and depressed hollows within the span of 1 m (Eppinga and others 2010)—to changes in peat and porewater characteristics, soil moisture and oxygenation, and microbial community abundance and composition with peat depth (Griffiths and others 2017; Griffiths and Sebestyen 2016; Griffiths and others 2019; Tfaily and others 2018; Wang and others 2015; Wilson and others 2021a, 2021b). Microtopographic positions have been shown to have different nutrient availabilities under ambient conditions (Eppinga and others 2010) and to respond differently to small-scale experimental warming (Munir and others 2017). However, how nutrient availability will change with depth throughout the peat profile in response to warming remains an open question, as prior investigations of nutrient response to warming in peatlands have focused on surface peat (Munir and others 2017; Weedon and others 2012). Nutrient availability in ecosystems underlain by organic soils is generally greater within deep peat layers located beyond the reach of plant roots that are often constrained to surface aerobic horizons (Iversen and others 2018; Keuper and others 2012; Murphy and others 2010). Warming in peatlands could therefore lead to increased availability of nutrients in the shallow rooting zone, and in turn, warming-induced drying could also allow roots to access deeper nutrients.

Increases in global mean surface air temperature are projected to be as much as 5.7 °C by 2100, following the rise in atmospheric carbon dioxide concentrations ([CO₂]) and other greenhouse gases due to anthropogenic activities (IPCC, 2021). Thus, any impacts of warming on peatland nutrient cycling must be considered in the context of elevated [CO₂], which might stimulate plant growth and rhizosphere C availability (Walker and others 2021), potentially leading to increased nutrient immobilization in vegetation and microbial communities (de Graaff and others 2006; Finzi and others 2007). However, evidence for changes in ecosystem C and nutrient cycling in response to

elevated [CO₂] is generally based on upland ecosystems (but see Berendse and others 2001; Fenner and others 2007; Milla and others 2006; Toet and others 2006; van der Heijden and others 2000).

Terrestrial biosphere models are a tool that can be used to encode hypotheses about ecosystem responses to changing environmental conditions but must be compared with and validated against observations of changes in ecosystem C and nutrient cycling in response to a range of possible futures (Medlyn and others 2015). ELM-SPRUCED, a point version of the land component of the Energy Exascale Earth System Model (E3SM), has been specifically designed to simulate ecosystem responses to warming and elevated [CO₂] at SPRUCED. ELM-SPRUCED includes coupled C, N and P cycle dynamics (Burrows and others 2020; Yang and others 2019) as well as ombrotrophic bog hydrology, hummock and hollow microtopography, and *Sphagnum* moss as a unique plant functional type (Griffiths and others 2017; Shi and others 2021, 2015).

Here we asked whether a gradient of whole-ecosystem warming would increase plant-available nitrogen and phosphorus in an ombrotrophic bog in northern Minnesota, USA, and whether elevated [CO₂] would modify the nutrient response. We further considered whether nutrient responses to warming varied across space and through time, focusing in particular on the rooting zone (and the surface zone where non-vascular mosses have access to nutrients). We used ion-exchange resins to assess inorganic plant-available nutrients across hummock-hollow microtopography and throughout the peat profile at monthly and cumulative annual time steps (and henceforth refer to these fluxes as ‘resin-available nutrients’). Because bogs are unique ecosystems where vegetation has access to near-surface porewater as a potential source of nutrients, we also compared responses inferred from ion-exchange resins to the dynamics of inorganic and organic nutrients observed in porewater. We compared observed resin-available nutrient dynamics to ELM-SPRUCED model predictions of net nutrient mineralization in the SPRUCED experiment.

MATERIALS AND METHODS

The SPRUCED Experiment

The Spruce and Peatland Responses Under Changing Environments (SPRUCED) experiment is located in the ombrotrophic S1 Bog on the Marcell

Experimental Forest in northern Minnesota, USA (47°30.476' N; 93°27.162' W; 418 m above mean sea level; Sebestyen and others 2011). SPRUCE is located at the southern end of the range of boreal peatlands and is therefore expected to be especially vulnerable to warming conditions. The S1 Bog, similar to other bog basins in the area and region, has accumulated from 2 to 11 m of C-rich peat over the last 11,000 years (McFarlane and others 2018; Parsekian and others 2012). The overstory is dominated by the trees *Picea mariana* (black spruce) and *Larix laricina* (larch), with an understory dominated by ericaceous shrubs (McPartland and others 2020). The bog surface is carpeted by *Sphagnum* mosses, with a minor presence of other mosses (for more information on mosses within the SPRUCE experiment, see Norby and others 2019). The effects of above- and belowground warming and elevated [CO₂] on peatland processes are being assessed in 12.8-m wide by 7-m tall enclosures underlain by belowground corrals (see Figure 1 for enclosure layout and description of treatments and see Hanson and others (2017) and Sebestyen and Griffiths (2016, data citation) for more details). The SPRUCE experimental design is regression-based; two series of five enclosures are warmed at set point levels of either + 0 °C, + 2.25 °C, + 4.5 °C, + 6.75 °C, or + 9 °C above ambient conditions. Aboveground warming is accomplished by introducing warm air generated from propane-fired heat exchangers into the enclosures via forced-air heating distributed around the base of the enclosure. Half of the enclosures also receive elevated [CO₂] via the injection of pure CO₂ into the air circulation ducts to attain a target level of + 500 ppm to replicate conditions predicted for the end of the twenty-first century (Hanson and others 2017). SPRUCE is unique in that it exposes large experimental enclosures to 'whole-ecosystem' warming; belowground warming is accomplished with 3-m deep heating rods that encircle and intersperse each enclosure. The encircling heating rods provide heat from 0 to 3 m depth, while rods within the enclosures only heat from 2–3 m depth to avoid hot spots of direct heating within the rooting zone. This system provides a uniformly warmed volume of peat belowground (Barbier and others 2013).

Beneath each enclosure, the belowground peat volume is encircled by a corral constructed from interlocking piles that reach beneath the peat horizons to the subtending mineral soils. The corral isolates the biogeochemical and hydrological system associated with each enclosure so that each enclosure can be conceptualized as a 'miniature bog' exposed to a future climate. The belowground

corrals also allow quantification of outflow, the shallow lateral flow analogous to runoff via natural passive drainage (data citation: Sebestyen and Griffiths 2016). SPRUCE treatments began with deep-peat warming in 2014 and installation of the corrals in winter 2014–2015; aboveground warming began in August 2015, and elevated [CO₂] additions began in early June 2016 during the first full year of whole-ecosystem warming (Hanson and others 2017).

Although the SPRUCE treatments are applied as differential levels of warming and CO₂ additions, because biological systems respond to actual temperatures we express and evaluate nutrient responses to warming by comparisons to measured peat temperatures at the depth of resin incubations rather than the nominal temperature treatments.

Plant-Available Nutrients Assessed Using Ion-Exchange Resins

Plant-available nutrients were assessed using mixed-bed ion-exchange resin capsules (that is, containing both anion, OH⁻, and cation, H⁺, resins). Ion-exchange resins have been shown to accurately integrate and represent plant-available ammonium (NH₄-N) and phosphate (PO₄-P) across space and through time, including in ecosystems underlain by organic soils (Bridgman and others 2001; Giblin and others 1994; Gu and others 2020), and have been tested at soil temperatures up to 30 °C (Yang and others 1991). The resin capsules at SPRUCE were inserted, incubated, and extracted serially beginning in 2013 and the collections are on-going (data citation: Iversen and others 2017). Data presented here span the full years of 2014 to 2018 and therefore include periods of belowground warming only (2014), above- and belowground warming (2015) and above- and belowground warming with elevated [CO₂] (2016–2018). PVC resin-access tubes (Wecca, Inc., LLC) allowed removal and replacement of the resin capsule without disturbing the peat profile. Access tubes consisted of a 3.2-cm diameter outer tube with a 1.9-cm diameter inner access tube with a resin capsule attached to the base (see Figure S1; as in Iversen and others 2018). Resin-access tubes were installed in June 2013 at a 30° angle from vertical across hummock and hollow microtopography and throughout the shallow peat profile to a depth of 60 cm in hummocks and 30 cm in hollows. Hummock-hollow access-tube arrays were installed in two locations in each of the ten SPRUCE experimental enclosures, as well as two locations in each of two ambient, unenclosed plots (Figure 1).

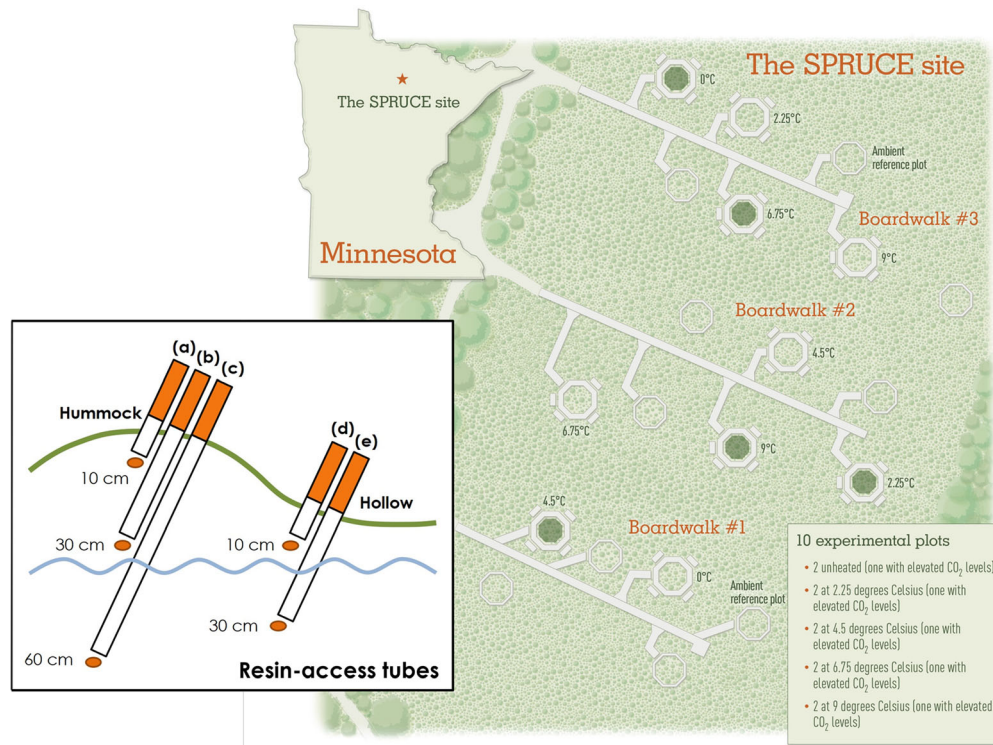


Figure 1. A pictogram of the layout of the SPRUCE experimental enclosures and their associated treatments. The SPRUCE experimental enclosures were warmed above- and belowground in a regression design spanning + 0 °C to + 9 °C; half of the enclosures also received + 500 ppm CO₂ (highlighted in this pictogram with green octagons). There are also two fully-instrumented ambient reference plots without enclosures. Resin-access tubes were installed at multiple depths at two locations (A and B) in each enclosure or ambient plot in paired hummock-hollow microtopography at each location (see inset diagram). SPRUCE site pictogram courtesy of Brett Hopwood, ORNL Graphics, as in Seay (2018).

Locations and elevations of each access-tube array were estimated by terrestrial laser scanning (TLS) using a Riegl VZ-1000 terrestrial laser scanner (Riegl Laser Measurement Systems, Riegl USA, Inc., Winter Garden, FL, USA) as in Graham and others (2020). Briefly, 50-cm tall dowels that had reflectors on their tops were inserted at the peat surface in May 2018, before the TLS scan. The location of the dowel was optimized to reflect the average elevation of the resin-access tube arrays. Elevation was then calculated by subtracting 50 cm. On average, hummocks were about 15 cm higher in elevation than adjacent hollows, with a few exceptions (Table S1).

UNIBEST resin capsules (UNIBEST, Inc., Walla Walla, WA, USA) were placed into contact with the soil at the base of the inner resin-access tube (11.4 cm² of the rounded capsule surface protruded from the base of the tube; Figure S1f) and incubated in situ for approximately 28 days before collection and replacement with a new resin capsule. In cases where resins were frozen into the bog during winter months and unable to be removed, we as-

sumed that the unfrozen time-period was no longer than 28 days (we refer to this collection timeframe as *monthly* below, to differentiate from *annual* nutrient availability). Peat was cleaned from the removed capsules by rinsing with distilled water, and the capsules were air-dried prior to shipment to Oak Ridge National Laboratory (ORNL). At ORNL, the air-dried capsules were serially extracted with 2 M potassium chloride, and the extractant was frozen at -20°C until analysis for nutrient concentrations on a Lachat QuikChem 8500 flow injection analysis autoanalyzer (Hach Company, Loveland, CO, USA) as in Iversen and others (2017, data citation). Nutrient adsorption was blank-corrected based on unincubated resins, standardized per unit of resin capsule surface area, and either standardized per 28 days or summed over a calendar year as a cumulative annual total. Previous studies with these resin capsules indicate they continue to accumulate nutrients over time without saturation (Skogley and others 1996; Yang and others 1991). In the few cases where an observation was lost during sampling or processing,

the value from the second resin array in the same enclosure, at the same microtopographic position and peat depth, was substituted to derive annual cumulative totals. Given that $\text{NO}_3\text{-N}$ adsorbed to resins was negligible and often below detection limits (as might be expected in a saturated, acidic bog ecosystem, Bridgman and others 2001), we focus on resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ for the purposes of this paper.

Resins mimic a plant root, exchanging ions with the surrounding soil system, allowing us to quantify the in situ availability of nutrients for plant acquisition. However, we note that resin-accumulated nutrients are the balance of production (gross nutrient mineralization) and consumption (nutrient immobilization) by surrounding plants, microbes, and soil surfaces. While this is similar to the competitive environment experienced by plant roots, these competing processes must be kept in mind when interpreting observed patterns in resin-available nutrient dynamics. We further compared responses inferred from ion-exchange resins to the dynamics of inorganic nutrients observed in porewater because vegetation has access to near-surface porewater as a potential source of nutrients and porewater is frequently measured across saturated peatland ecosystems (Bourbonniere 2009).

We focused on inorganic nutrient availability given that we were able to capture its accumulation over time and with peat depth using non-destructive ion-exchange resin sampling. However, vegetation in boreal systems has been shown to acquire organic nutrients (Kielland and others 2006), so we also compared the patterns observed in resin-available nutrients to organic nutrients in porewater to gain a broader view of plant-available N and P.

Porewater Nutrients

A nest of six depth-specific (10-cm screened sections) piezometers per enclosure allowed collection of porewater throughout the peat profile (0–3 m) in hollow microtopography. Water samples were collected every 2 weeks using a peristaltic pump and analyzed for nutrients ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and soluble reactive phosphorus, SRP), as well as total N (TN) and total P (TP) at the United States Forest Service laboratory in Grand Rapids, MN, USA. Soluble reactive P concentration (SRP) is largely equivalent to phosphate concentration (PO_4^{3-}) in water, though some condensed phosphate may be measured along with orthophosphate in the colorimetric method that we used to determine SRP (APHA, 2017). Ammonium, $\text{NO}_3\text{-N}$, SRP, TN, and

TP concentrations were quantified via analysis on a Lachat QuikChem autoanalyzer as described in Griffiths and others (2016b, data citation). We focused on the porewater nutrient concentrations at 0–10 cm and 30–40 cm depths to facilitate direct comparison with ion-exchange resins incubated at those depths in adjacent hollows. We averaged the nutrient concentrations for porewater samples that were collected within the dates of the approximately monthly resin incubations, beginning in 2015 and extending through 2018. We calculated ‘organic N’ and ‘organic P’ as the difference between total N and inorganic N and total P and inorganic P, respectively (where organic N was equal to ‘0’ if the difference resulted in a slightly negative number). When porewater nutrients were below detection limits, we used half the detection value as the value for that collection date (the detection limit varied according to methodology described in data citation: Griffiths and others 2016b).

Potential Nutrient Competition

In order to understand the surface dynamics of resin-available nutrients over time, we compared patterns in resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ to patterns in the nutrient requirements of *Sphagnum* mosses given its mortality in response to warming at SPRUCE in later treatment years (Norby and others 2019). *Sphagnum* nutrient requirement was calculated using growth and N and P concentration estimates from each of the dominant *Sphagnum* species measured annually in October 2016, 2017, and 2018 in each experimental enclosure (methods described in Norby and others 2019, and data citations: Norby and others 2018 and 2020). The enclosure-scale N or P requirement for new growth is the concentration of the element in species-specific new growth times the dry matter increment, scaled by fractional cover of each *Sphagnum* species (g N/m^2 or g P/m^2).

While mineral surfaces can immobilize $\text{PO}_4\text{-P}$ (Richardson 1985), the peat in the S1 Bog where the SPRUCE experimental enclosures are located has limited mineral content to a depth of at least 2 m (data citation: Iversen and others 2014). The S1 Bog also has limited bulk and extractable Al and Fe content throughout (Herndon and others 2019; Tfaily and others 2014), though the relationship between P and Fe in surface peat appears to be increasing with warming (Curtinrich and others 2021).

Edaphic and Environmental Conditions in the SPRUCE Enclosures

Peat temperature. We investigated the temperature response of resin-available nutrients, both during the 28-day periods of resin deployment and over the course of each year, using peat temperature measurements collected from multipoint thermistor probes (W.H. Cooke and Co. Inc, Hanover, PA, USA). The probes were installed in each SPRUCE experimental enclosure in 2014 in zone B (that is, the zone in the middle of the SPRUCE experimental enclosures; for more information about probe locations, installation, and calibration, see data citation: Hanson and others 2016). The depth of interest for each soil temperature probe was chosen to most closely match the targeted incubation depth of ion-exchange resin capsules (that is, probes installed in hummocks at ~ 20 cm and 0 cm above the hollow surface, and probes installed in hollows at ~ 10 cm and ~ 30 cm below hollow surface; see Table S2).

Water table. Automated water table elevation measurements and normalization for each enclosure with respect to hollow heights are explained in detail in Hanson and others (2020b, data citation). Briefly, water table elevation measurements collected beginning in 2015 were obtained in stainless steel well casings (Drillers Services, Inc.) centered within each SPRUCE enclosure. The water height within each well was measured with automated sensors (Model WT-VO 2000; TruTrack, Christchurch, New Zealand). Water table absolute elevations in meters were referenced to surveyed elevations of the tops of all wells (data citation: Griffiths and others 2016a), and water level with respect to the mean hollow elevation of an enclosure were normalized to the water height in the well during a uniform post-rainfall, post-drainage period when water tables were just at or below the peat hollows. We only include a water table comparison when the average peat temperature at the depth of each incubated resin was above 0 °C for each incubation period.

Simulated Nutrient Availability Responses to Warming Using ELM-SPRUCES

We used ELM-SPRUCES, a version of the Energy Exascale Earth System Model (E3SM) land model (version 1, ELM v1), to simulate nutrient responses to warming and elevated [CO₂] at SPRUCES. Building on the Community Land Model version 4.5 (CLM4.5), ELM v1 has undergone several ma-

jor developments in recent years. These new developments include the coupling of C, N and P cycle dynamics, the introduction of dynamic storage pools for C, N and P, the improved representation of the effects of nutrient limitation on plant growth, improved phenology for deciduous forests, and various improvements in model parameterization (Burrows and others 2020; Yang and others 2019). Compared to ELM v1, ELM-SPRUCES includes additional processes and plant functional types that are specific to peatland ecosystems (Griffiths and others 2017; Shi and others 2021, 2015). Observational data from the S1 Bog used for model parameterization included leaf- and fine-root N and P concentrations (Salmon and others 2021) and rooting depth for fine roots (Iversen and others 2018). Model evaluation using pretreatment observations of vegetation biomass, growth, and nutrient requirements suggests that ELM-SPRUCES is generally able to capture the observed C and nutrient pools and fluxes (Griffiths and others 2017; Salmon and others 2021).

Model simulations for the current study included three steps: (1) Model spin-up to generate pre-industrial steady-state for C, N and P pools in vegetation and soils, (2) Transient simulations from 1850 to 2014 in which historical atmospheric CO₂ concentrations and N deposition were used as driving data, and (3) Simulations of treatment responses between 2015 and 2018, in which treatment-specific air temperature and atmospheric CO₂ concentrations were used as driving data. In total, there were 11 simulations corresponding to 10 experimental treatments and 1 ambient plot at SPRUCES. We focused here on the outputs of annual cumulative net N and P mineralization from treatment simulations between 2016 and 2018. Net nutrient mineralization per unit peat volume is an imperfect comparison to annual resin-available nutrient accumulation but was the closest nutrient flux available from among the model outputs and integrates similar processes of nutrient mineralization and immobilization (for example, Bridgham and others 2001). Here we compare resin-available nutrients with ELM-SPRUCES simulated net nutrient mineralization responses in a qualitative way with the goal of identifying important gaps in model representation of nutrient cycle dynamics in peatland ecosystems. Gross nutrient mineralization in ELM-SPRUCES is modeled using a Q₁₀ approach (where Q₁₀ = 1.5) and resulting net nutrient mineralization is the remainder after microbial nutrient immobilization.

Statistical Analyses

Resin-Available Nutrient Responses to Warming and Elevated [CO₂]

We used R version 4.0.3 in our statistical analyses (R Core Team 2021) to examine resin-available nutrient responses to warming and elevated [CO₂] in the SPRUCE experimental enclosures from 2014 to 2018. We do not include data from unenclosed, ambient plots in our statistical models (as in Harrison and others 2020a). However, ambient plots were measured to quantify potential experimental artifacts and the data are summarized in Table 1. Peat temperature and the availability of NH₄-N and PO₄-P differed somewhat between the + 0 °C enclosures and the unenclosed, ambient plots, though differences varied by peat depth and among plots (see *Supplementary Statistical Methods* and Table 1).

We assessed responses of resin-available nutrients to warming in the enclosures in two ways: first, we examined the variation in the cumulative annual availability of NH₄-N and PO₄-P, as well as the ratio of the two. We expected that the N/P ratio would provide an assessment of whether resin-available NH₄-N and PO₄-P differed in their response to warming, and also what the implications might be for vegetation N or P limitation (Koerselman and Arthur 1996). To assess these *annual responses*, we compared several potential linear mixed-effect models to consider the effects of warming, elevated [CO₂], microtopography, peat depth, and year on nutrient dynamics using the *lmer* function in the *lme4* package in R (see additional detail in *Supplementary Statistical Methods*; Harrison and others 2018). In these models, both warming and elevated [CO₂] were treated as fixed effects, where warming was a numerical vector of the average annual peat temperature measured at the peat depth closest to that of the resin depth and CO₂ was a discrete variable (for example, ‘ambient’ or ‘elevated’). Peat depth and microtopographic position were combined into a discrete, fixed effect in the models called ‘topodepth’ (for example, hummock at 10 cm, hummock at 30 cm, hollow at 10 cm, and so on). We assumed that year was an important factor given the progression in SPRUCE treatment application, and year was treated as a discrete, fixed effect in the models. In turn, we included enclosure as a random effect in the models (with both a random intercept and a ran-

dom slope) to account for random differences among enclosures and repeated sampling of enclosures that were not explained by our fixed effects. Cumulative annual resin-available nutrients and nutrient ratios were log-transformed prior to statistical analyses to meet model assumptions. We selected a final model based on AIC criteria, as well as standard model selection processes (see *Supplementary Statistical Methods* for more information; Harrison and others 2018). We made pairwise comparisons by topodepth and year using the *pairwise* function in the *emmeans* package in R (Table S3).

After considering the annual accumulation of resin-available nutrients, we examined the variation in accumulated NH₄-N and PO₄-P over the 28-day timeframe (that is, the *monthly* responses). Examining the monthly patterns in resin-available nutrients allowed us to consider the additional factor of depth to the water table, which varied seasonally within a year and therefore could not be analyzed on an annual basis. Given the correlation between peat temperature and depth to water table, we used a principal components analysis to obtain a continuous variable representing the combination of peat temperature and distance to water table and used this variable in a new set of linear mixed-effects models (see details in *Supplementary Statistical Methods*). However, these monthly models were similar to the annual models, and further investigation showed that that water table level—which had not yet changed substantially in response to warming—had little power to explain (less than 10%) observed changes in resin-available nutrients (see *Supplementary Statistical Methods*, Figures WT1 and WT2). Thus, we do not discuss water table results further here.

We did disentangle peat temperature from depth to water table to further explore the temperature sensitivity of monthly nutrient availability. We fit Q₁₀ relationships to the monthly accumulation of resin-available nutrients at a given peat temperature (Lloyd and others 1994). Curves were fit in Sigma Plot (version 14.5, Systat Software, Inpixon HQ, USA) using the equation: Resin-Available Nutrient (μg cm⁻² 28 days⁻¹) = R₁₂ × Q₁₀^{((Peat Temperature-12)/10)}, where R₁₂ is the baseline resin-available nutrient flux during incubation period (targeted at 28 days) at 12 °C, a temperature near the midpoint of the range of peat temperatures across warming treatments, peat depths, and

Table 1. Cumulative Annual Resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$, and Their Annual Ratio, Across Experimental Treatments, Microtopographic Positions, and Peat Depths from 2014 to 2018

Year	Atmospheric [CO_2]	Microtopography	Depth (cm)	Cumulative annual available $\text{NH}_4\text{-N}$ ($\mu\text{g N cm}^{-2} \text{ year}^{-1}$)					
				Amb	0 °C	2.25 °C	4.5 °C	6.75 °C	9 °C
2014	Ambient	Hummock	10	6 ± 2	12	15	11	7	15
			30	38 ± 17	11	35	20	13	18
			60	115 ± 51	25	140	143	152	90
		Hollow	10	20 ± 8	20	23	13	13	31
			30	24 ± 14	12	84	49	26	32
			60	–	11	10	11	4	4
	Elevated	Hummock	10	–	17	21	23	43	17
			30	–	115	49	31	347	33
			60	–	26	13	29	56	18
		Hollow	10	–	77	33	28	179	37
			30	–	7	7	10	11	17
			60	–	25 ± 6	10	23	15	16
2015	Ambient	Hummock	10	7 ± 4	6	7	10	11	17
			30	25 ± 6	10	23	15	16	16
			60	73 ± 24	16	178	106	174	116
		Hollow	10	16 ± 9	18	13	14	20	28
			30	17 ± 4	10	70	32	42	69
			60	–	1	7	7	5	15
	Elevated	Hummock	10	–	21	16	11	32	20
			30	–	50	35	27	407	59
			60	–	19	17	11	77	24
		Hollow	10	–	27	23	26	227	34
			30	–	8	13	5	2	20
			60	–	22 ± 3	22	31	37	31
2016	Ambient	Hummock	10	3 ± 0	8	13	5	2	20
			30	22 ± 3	22	31	37	42	31
			60	78 ± 30	16	157	170	209	173
		Hollow	10	16 ± 5	23	27	12	11	33
			30	17 ± 6	9	78	52	100	122
			60	–	8	6	4	4	9
	Elevated	Hummock	10	–	15	7	63	99	17
			30	–	30	19	54	492	165
			60	–	38	18	44	207	8
		Hollow	10	–	25	30	44	428	97
			30	–	2	5	10	7	10
			60	–	14 ± 2	23	20	98	34
2017	Ambient	Hummock	10	8 ± 5	2	5	10	7	10
			30	14 ± 2	23	20	98	19	34
			60	66 ± 21	17	156	217	273	288
		Hollow	10	14 ± 4	9	16	20	14	25
			30	15 ± 4	9	64	75	127	136
			60	–	3	6	8	8	9
	Elevated	Hummock	10	–	30	10	31	142	49
			30	–	23	20	85	577	281
			60	–	22	13	25	191	7
		Hollow	10	–	20	20	33	484	110
			30	–	6 ± 3	6	13	69	330
			60	–	13 ± 0	17	21	35	85
2018	Ambient	Hummock	10	6 ± 3	6	13	16	69	330
			30	13 ± 0	17	21	35	85	259
			60	63 ± 33	19	159	181	290	409
		Hollow	10	18 ± 0	9	39	16	108	414
			30	9 ± 3	6	118	67	152	501
			60	–	6	6	61	23	14
	Elevated	Hummock	10	–	45	10	49	243	36
			30	–	44	21	109	501	286
			60	–	19	28	113	367	14
		Hollow	10	–	35	24	53	411	104
			30	–	35	24	53	411	104
			60	–	35	24	53	411	104

Table 1. continued

Year	Atmospheric [CO ₂]	Microtopography	Depth (cm)	Cumulative annual available PO ₄ -P (µg P cm ⁻² year ⁻¹)					
				Amb	0 °C	2.25 °C	4.5 °C	6.75 °C	9 °C
2014	Ambient	Hummock	10	1.0 ± 1.3	0.7	3.5	1.3	0.6	2.3
			30	6.1 ± 2.8	1.3	3.2	6.1	4.3	2.3
			60	10.8 ± 1.3	3.9	9.3	25.0	24.1	15.4
		Hollow	10	3.3 ± 1.0	1.9	6.9	3.0	3.1	6.6
			30	2.8 ± 2.8	1.7	13.1	9.1	3.9	4.6
			60	–	–	–	–	–	–
	Elevated	Hummock	10	–	3.3	0.1	1.3	2.6	0.2
			30	–	3.3	2.5	5.0	12.2	2.2
			60	–	25.3	7.9	4.7	56.1	9.8
		Hollow	10	–	5.5	6.9	4.6	10.7	1.9
			30	–	7.0	2.6	2.7	36.1	5.9
			60	–	–	–	–	–	–
2015	Ambient	Hummock	10	1.5 ± 1.2	1.3	0.9	1.4	3.3	3.2
			30	1.6 ± 0.0	1.1	0.9	3.4	9.0	2.2
			60	3.0 ± 1.7	1.4	10.1	8.7	4.6	4.3
		Hollow	10	1.5 ± 0.7	5.3	0.9	2.3	11.0	5.4
			30	1.8 ± 1.3	1.1	1.9	4.7	3.4	3.5
			60	–	–	–	–	–	–
	Elevated	Hummock	10	–	0.6	0.7	2.2	1.4	2.2
			30	–	1.1	1.3	1.9	6.6	3.0
			60	–	3.7	2.1	2.3	54.1	4.5
		Hollow	10	–	4.5	2.5	1.8	31.2	4.2
			30	–	2.6	1.7	2.6	32.5	3.2
			60	–	–	–	–	–	–
2016	Ambient	Hummock	10	0.4 ± 0.1	1.1	1.9	0.7	2.3	4.4
			30	1.1 ± 0.1	2.9	4.3	6.5	29.3	4.7
			60	1.9 ± 0.1	0.7	11.2	15.3	12.1	16.0
		Hollow	10	1.1 ± 0.2	11.1	4.1	1.9	9.1	4.0
			30	0.8 ± 0.2	1.2	7.8	8.5	8.8	13.9
			60	–	–	–	–	–	–
	Elevated	Hummock	10	–	1.7	0.7	1.4	1.7	1.8
			30	–	3.0	1.3	6.8	20.7	2.9
			60	–	3.2	1.9	2.5	46.0	15.4
		Hollow	10	–	11.4	2.8	3.9	33.4	4.4
			30	–	5.8	7.1	3.0	40.3	7.4
			60	–	–	–	–	–	–
2017	Ambient	Hummock	10	1.0 ± 0.7	0.3	0.6	1.7	6.0	2.9
			30	1.0 ± 0.3	1.4	1.9	22.7	4.6	2.2
			60	1.4 ± 0.0	0.5	9.7	21.0	14.4	41.8
		Hollow	10	0.7 ± 0.0	1.1	1.5	2.6	6.9	7.8
			30	0.5 ± 0.2	0.5	7.1	11.8	4.8	17.7
			60	–	–	–	–	–	–
	Elevated	Hummock	10	–	0.5	0.8	2.7	1.8	1.3
			30	–	7.7	0.8	2.1	23.1	5.2
			60	–	2.5	2.1	4.9	60.3	23.6
		Hollow	10	–	7.6	2.1	2.3	33.1	0.6
			30	–	5.9	2.7	1.5	47.5	4.8
			60	–	–	–	–	–	–
2018	Ambient	Hummock	10	1.4 ± 0.8	0.7	6.0	9.1	34.7	78.0
			30	1.8 ± 1.8	0.7	8.3	9.8	41.5	30.0
			60	2.9 ± 2.3	0.6	14.0	14.6	18.0	42.7
		Hollow	10	2.1 ± 1.3	2.7	10.7	5.3	33.5	75.6
			30	1.7 ± 0.1	0.6	5.4	9.9	14.7	73.2
			60	–	–	–	–	–	–
	Elevated	Hummock	10	–	10.3	0.8	25.1	33.4	3.2
			30	–	16.5	1.8	6.7	51.3	5.3
			60	–	8.8	1.8	4.6	72.9	13.9
		Hollow	10	–	17.0	14.9	20.0	85.9	2.2
			30	–	17.0	8.4	7.6	66.9	2.9
			60	–	–	–	–	–	–

Table 1. continued

Year	Atmospheric [CO ₂]	Microtopography	Depth (cm)	Cumulative annual N/P ratio					
				Amb	0 °C	2.25 °C	4.5 °C	6.75 °C	9 °C
2014	Ambient	Hummock	10	31 ± 12	113	4	67	26	8
			30	7 ± 0	8	25	3	4	8
			60	11 ± 6	7	17	5	8	6
		Hollow	10	6 ± 1	11	3	4	44	5
			30	37 ± 42	8	6	6	6	7
			60	—	5	10	6	4	105
	Elevated	Hummock	10	—	8	175	52	2	28
			30	—	5	10	6	4	105
			60	—	5	6	8	6	6
		Hollow	10	—	5	3	6	4	83
			30	—	11	13	39	5	7
			60	—	—	—	—	—	—
2015	Ambient	Hummock	10	5 ± 1	5	7	8	3	6
			30	16 ± 4	9	27	4	2	9
			60	33 ± 29	11	23	10	41	25
		Hollow	10	11 ± 2	4	14	6	2	5
			30	12 ± 5	9	38	6	12	19
			60	—	2	9	5	4	7
	Elevated	Hummock	10	—	19	13	7	5	6
			30	—	13	14	12	9	13
			60	—	8	7	6	2	6
		Hollow	10	—	8	7	6	2	6
			30	—	10	15	8	9	11
			60	—	9	7	11	1	5
2016	Ambient	Hummock	10	13 ± 2	9	7	11	1	5
			30	24 ± 12	12	15	6	2	8
			60	41 ± 11	43	16	16	28	14
		Hollow	10	21 ± 9	3	7	8	4	9
			30	44 ± 32	7	13	7	10	8
			60	—	24	9	3	6	10
	Elevated	Hummock	10	—	5	9	9	5	6
			30	—	9	9	20	11	11
			60	—	9	9	20	11	11
		Hollow	10	—	3	6	11	5	3
			30	—	5	4	16	10	14
			60	—	5	4	16	10	14
2017	Ambient	Hummock	10	9 ± 2	8	7	6	6	3
			30	31 ± 9	17	18	6	18	22
			60	110 ± 99	42	42	17	30	16
		Hollow	10	22 ± 5	23	11	8	18	4
			30	37 ± 15	19	13	16	20	12
			60	—	8	8	3	9	11
	Elevated	Hummock	10	—	4	11	16	6	10
			30	—	36	8	14	9	12
			60	—	3	10	10	5	15
		Hollow	10	—	5	8	20	10	23
			30	—	5	8	20	10	23
			60	—	5	8	20	10	23
2018	Ambient	Hummock	10	6 ± 0	9	2	2	2	4
			30	16 ± 16	28	3	4	3	8
			60	24 ± 8	31	13	15	32	14
		Hollow	10	11 ± 6	3	5	5	3	6
			30	9 ± 4	10	21	8	16	7
			60	—	1	8	2	1	3
	Elevated	Hummock	10	—	3	5	8	5	7
			30	—	5	11	19	7	22
			60	—	5	11	19	7	22
		Hollow	10	—	1	2	7	4	7
			30	—	2	4	12	7	34
			60	—	2	4	12	7	34

We sampled the SPRUCE experimental plots in 2013, but do not include the annual totals here. We sampled only three months in the summer, directly after installation in June 2013, and we expected some disturbance associated with access-tube installation along with a shortened collection timeframe that precluded a full assessment of annual nutrient accumulation. Note that 'cm²' was the surface area of the half of the resin capsule that was in contact with the surrounding peat (that is, Figure S1f). Where an 'A' or 'B' sub-replicate sample was (rarely) missing or lost at a given sampling date, we inserted the value for the other sub-replicate in order to calculate an annual sum; data for each year, depth, and topographic position are averaged across the annual accumulated resin-available nutrients at the A and B location in each enclosure. Note that the NH₄-N and PO₄-P cumulative annual data can also be found in Figure 3, but given the wide range across orders of magnitude of the data, we also include the data here. We also include the data from the ambient plots (that is, 'Amb.', plots without an enclosure that receive no warming or elevated [CO₂]); ambient data for each year, depth, and topographic position are averaged across the annual accumulated resin-available nutrients at the A and B location in each of two ambient plots, which were then averaged ± 1 SD.

microtopographic positions. To obtain a warming response for model comparison, we fit Q_{10} relationships to observations from all enclosures at a given topodepth across all years as well as for the most recent observation year of 2018. For comparison, we also fit Q_{10} response functions to model projections of cumulative annual net N and P mineralization.

Comparisons among resin-available nutrients and other nutrient pools

We examined the relationship between *Sphagnum* annual N and P requirement ($\text{g nutrient m}^{-2} \text{ year}^{-1}$) and surface resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ at 10-cm depth in hummocks and hollows using log-linear regressions. Furthermore, we examined whether resin-available nutrients were correlated with porewater inorganic, organic, and total nutrients. Given that log-transformation did not result in normally distributed data, we used a nonparametric correlation for the porewater comparisons (Spearman's Rho; *stats* package in R).

RESULTS

Cumulative Annual Resin-Available Nutrients Increased With Warming but Varied with Peat Depth and Microtopography

$\text{NH}_4\text{-N}$ was by far the most available N source, with $\text{NO}_3\text{-N}$ making up a negligible fraction; PO_4 availability was intermediate between $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$. Warming increased cumulative annual resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$, but the magnitude of the response varied across microtopographic positions and with peat depth and increased over time. There were no significant effects of elevated $[\text{CO}_2]$ on resin-available nutrients (Table 1). Neither warming nor elevated $[\text{CO}_2]$ had a significant effect on the cumulative annual ratio of resin-available N/P, though resin-available N/P ratio increased with peat depth (Table 1 and Table S3).

The best overall model fit to explain the variability in $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ and their ratio (that is, the model with the lowest AIC) included the average annual peat temperature at the depth closest to that of the resin, as well as combined hummock-hollow microtopographic position and depth (that is, the 'topodepth' term), and year, with enclosure as a random factor (conditional $R^2 = 0.77, 0.71$, and 0.43 for $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and N/P ratio models, respectively; Figure 2). A model including elevated $[\text{CO}_2]$ did not provide a better fit

to any of the resin-available nutrient data (See *Supplementary Statistical Methods*). Within the best-fit model for $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$, we also observed significant interactions between warming and topodepth, as well as warming and year, and we observed an increase in the strength of the warming $\times$ year interaction over time (Figure 2, *Supplementary Statistical Methods*). In turn, the best-fit linear mixed-effect model for cumulative annual N/P ratio also included a significant interaction between topodepth and year (Figure S2, *Supplementary Statistical Methods*).

Given the significant interactions with warming, we also fit separate log-linear models to average annual peat temperature at a given topodepth and log-transformed cumulative available $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and the ratio of the two at each microtopographic position and peat depth, across all years (Figure 3) and within a single year (Table S4). The only significant log-linear models between peat temperature and resin-available $\text{NH}_4\text{-N}$ or $\text{PO}_4\text{-P}$ indicated an exponential increase in resin-available nutrients with increasing peat temperature at deeper peat depths (Figure 3) and in more recent years (Table S4). We saw no significant relationships between annual N/P ratio and warming at any topodepth position either within or across years (Table S4, with the exception of an extremely weak relationship at 60-cm peat depth).

Within a given treatment year, resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ tended to be least in shallow peat and less in raised hummocks compared with depressed hollows (Tables 1 and S3, Figure 3). Averaged across all enclosures, resin-available $\text{NH}_4\text{-N}$ to $\text{PO}_4\text{-P}$ were significantly greater in 2018 than in previous years (Figure 2; Table S3). In turn, the ratio of cumulative annual available $\text{NH}_4\text{-N}$ to $\text{PO}_4\text{-P}$ ranged from about 1:1 to 175:1 across all years, microtopographic positions, and peat depths (Table 1).

ELM-SPRUCE Predicted Increases in Annual Net Nutrient Mineralization with Warming

Across all topodepths, ELM-SPRUCE predicted increases in annual cumulative net N and P mineralization with warming (Figure 4), but the magnitudes of the warming responses in model simulations (assessed by Q_{10} response functions) were much lower than the warming responses observed in the resin-available nutrient data, especially in surface soils (Table S5). As with observed resin-available nutrient dynamics (Table 1), model prediction of net N and P mineralization was

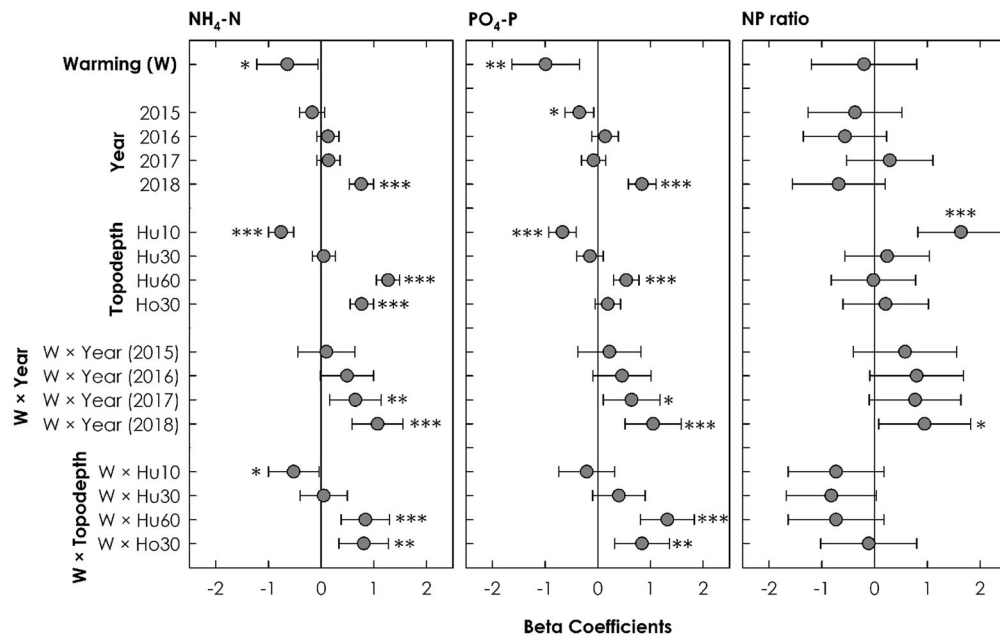


Figure 2. Linear mixed-effects model beta coefficients and their 95% confidence intervals. The coefficients correspond to the factors in the final linear mixed-effect models for the effects of warming, microtopography and depth (as ‘topodepth’, which treats each microtopographic position and depth as discrete locations), and year, and the interactive effects of warming $\times$ topodepth and warming $\times$ year on resin-available $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$ and the ratio of $\text{NH}_4\text{-N}$ to $\text{PO}_4\text{-P}$ (see *Supplementary Statistical Methods* for selection of final models). The beta coefficients for warming, year, and topodepth were added for reference but cannot be interpreted in isolation because of significant interactions. For each factor and interaction, the beta coefficients represent the difference between a baseline (alphabetically or numerically the first level) and the other levels of each factor or interactions. For example, for years, the baseline is the year 2014 and for topodepth, the baseline is Ho10 (‘hollow, 10 cm peat depth’). The final model was different for the N/P ratio, as it included an additional topodepth $\times$ year interaction term; the full range of beta coefficients for all of the interactions in the N/P ratio model are included in Figure S2. Asterisks indicate level of significance at $P < 0.001$ ***; $P < 0.01$ ** and $P < 0.05$ *.

greater in the hollows than in the hummocks, but in contrast to the observations, model-predicted net nutrient mineralization tended to decrease with peat depth (Figure 4).

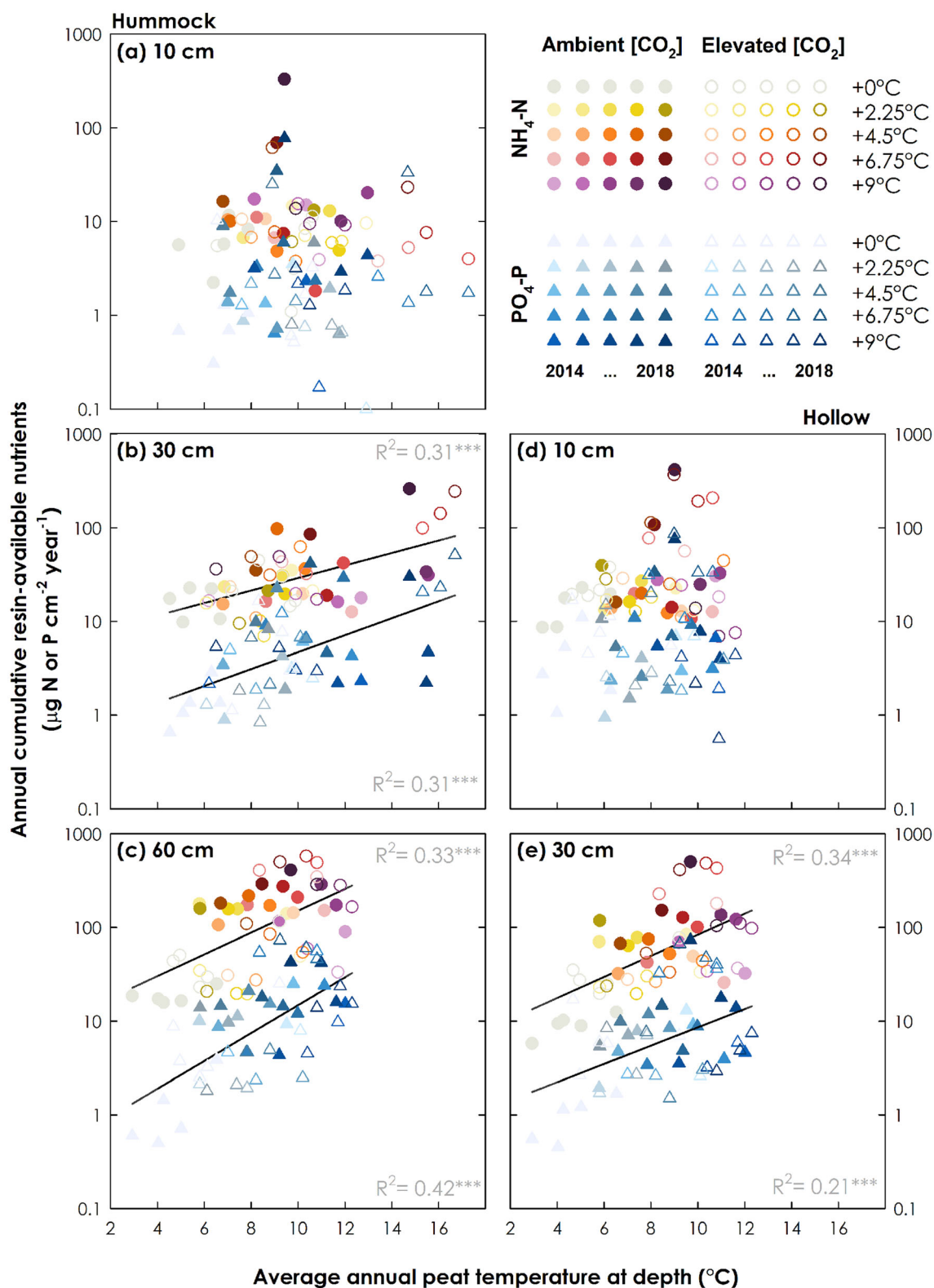
Large Increases in Shallow Peat Resin-Available Nutrients were Correlated with Mortality of *Sphagnum* Mosses in Warmest Enclosures

The increase in cumulative annual resin-available nutrients with warming had initially been much greater below the rooting zone (that is, at 60- and 30-cm depths in hummocks and hollows, respectively, Table 1, Figs. 2, 3), but this changed in later treatment years, where we saw large increases in both $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ at 10-cm peat depth in both hummocks and hollows (Table 1, Figure 3). During the same time period (that is, between 2016 and 2018), we observed a steep decline in *Sphagnum* N and P requirement (that is, the N or P content of

new tissue in g nutrient per m^2 per year; Figure S3), in conjunction with *Sphagnum* mortality in the warmest treatments (Norby and others 2019). The observed increase in shallow resin-available nutrients was related ($R^2 = 0.24$ for $\text{NH}_4\text{-N}$ and 0.09 for $\text{PO}_4\text{-P}$) to the decline in *Sphagnum* nutrient requirements in the warmest treatments (Figure 5).

Monthly Resin-Available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ Increased Exponentially in Response to Warming

Given that nutrient response to warming was most notable in later treatment years, we individually examined the Q_{10} dynamics in the last year of available data (2018, after 4 years of whole-ecosystem warming, Figs. 6 and S4, as well as across all treatment years, Table S5; see Figures S5 and S6 for all data across all years). We found that a Q_{10} function explained the warming response of



◀**Figure 3.** Annual, cumulative $\text{NH}_4\text{-N}$ or $\text{PO}_4\text{-P}$ adsorbed to ion-exchange resins regressed against annual average peat temperature at a depth closest to the depth of resin incubation. The panels represent multiple peat depths in hummock and hollow microtopography, and the observations span a gradient of whole-ecosystem warming and warming combined with elevated $[\text{CO}_2]$. Each data point is one enclosure, in years 2014 to 2018. Closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$; all data shown were included in log-linear regressions. More intense colors correspond with more recent years. The full range of colors and symbols are listed here; henceforth figure legends include colors for 2018 only. Letter insets correspond to depth of resin incubation (a, b, and c are 10, 30, and 60-cm depths in hummocks and d and e are 10 and 30-cm depths in hollows, respectively, see inset in Figure 1). Asterisks indicate level of significance corresponding to log-linear regression at $P < 0.001^{***}$, $P < 0.01^{**}$ and $P < 0.05^*$, and R^2 is the adjusted R^2 of $\text{NH}_4\text{-N}$ regression (upper right of each panel) or $\text{PO}_4\text{-P}$ regression (lower right of each panel); note the log-scale of the y-axis. See Table S4 for regression parameters (predicted resin-available nutrients were back-transformed for the purposes of the lines presented in this figure).

$\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ to increasing peat temperatures when observations from across all warming and $[\text{CO}_2]$ treatments were examined within a given microtopography and peat depth, especially in deeper soil (Figs. 6 and S4, respectively; observations from 2018 only). Significant Q_{10} values for increases in monthly resin-available nutrients with peat temperature across all treatments ranged from ~ 3 to as much as ~ 9 in 2018, and higher when all years were combined (Table S5); in turn, R_{12} values—the baseline amount of resin-available nutrient at 12°C —tended to increase with peat depth (Table S5). While the ratio between monthly resin-available N and P did not change significantly in response to warming, it did tend to increase with peat depth (Figure 7).

Monthly Resin-Available Nutrients and Porewater Nutrients were only Somewhat Correlated

Cumulative monthly resin-available inorganic nutrients in hollows were somewhat correlated with porewater inorganic nutrients in hollows across all enclosures and years 2015–2018 in both shallower (Spearman's $Rho = 0.30$ and 0.32 , for N and P, respectively, $P < 0.001$ for each) and deeper peat (Spearman's $Rho = 0.69$ and 0.52 for N and P,

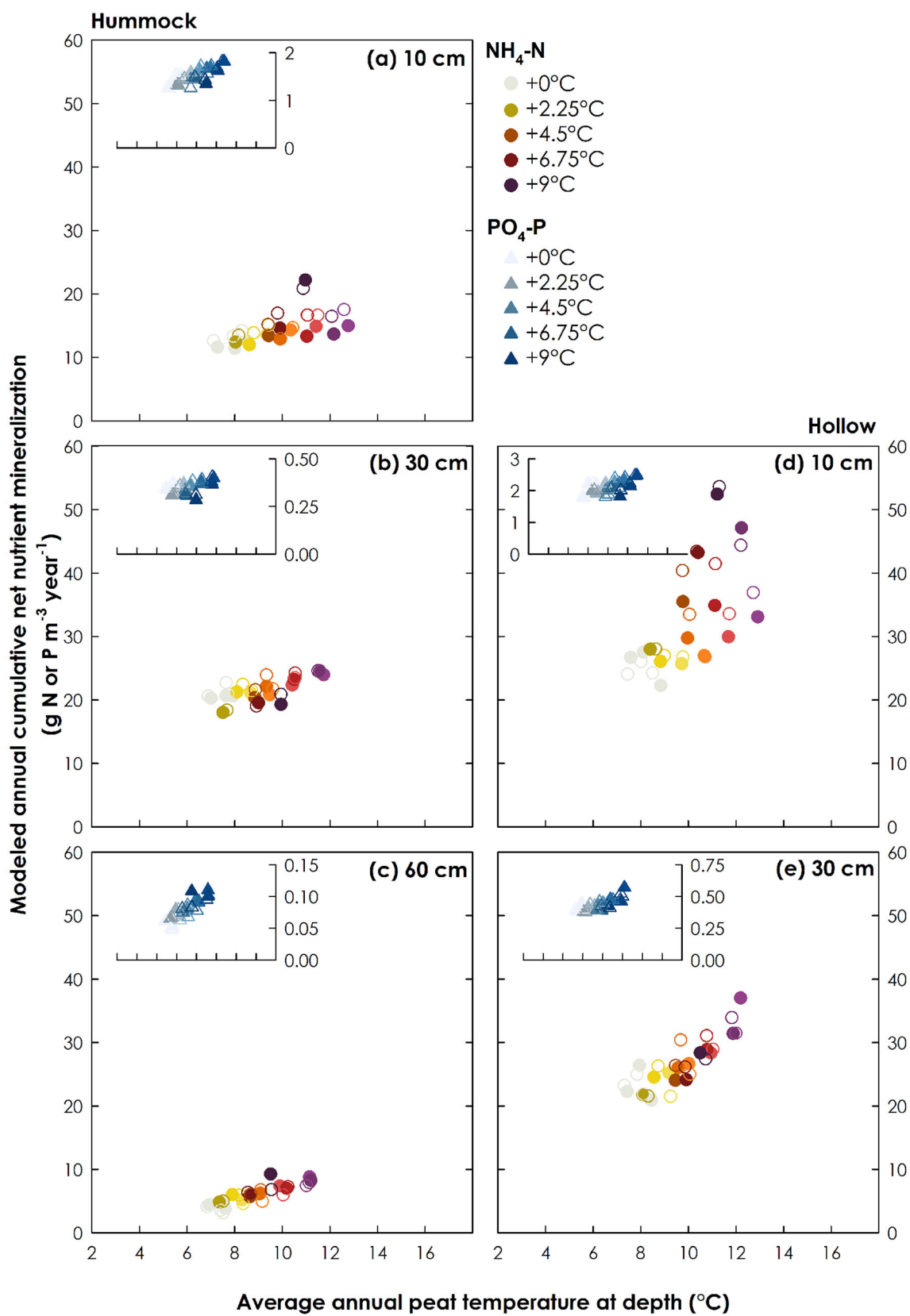
respectively, $P < 0.0001$ for both N and P; Figs. 8, S7). Resin-available inorganic nutrients were somewhat correlated with porewater organic nutrients (that is, the difference between total N or P and inorganic N or P) in shallower peat (Spearman's $Rho = 0.34$ and 0.30 for ON and OP respectively, $P < 0.0001$, for both N and P) and in deeper peat (Spearman's $Rho = 0.38$ and 0.18 , $P < 0.0001$ and $P = 0.004$, for N and P, respectively; Figs. 8, S7). Resin-available inorganic nutrients and total porewater nutrients were also somewhat correlated, both in shallower peat (Spearman's $Rho = 0.42$ and 0.38 for TN and TP respectively, $P < 0.0001$, for both N and P) as well as in deeper peat (Spearman's $Rho = 0.66$ and 0.52 , $P < 0.0001$ for both N and P; Figs. 8, S7).

DISCUSSION

The controls over peatland C balance range from the environmental constraints of cold, acidic, waterlogged peat to the interplay between C production and decomposition as mediated by nutrient-limited plants and microbes (Bridgman and others 1998; Limpens and others 2008). Many of these responses are underpinned by, or will affect, nutrient dynamics throughout the peat profile. Here we found that after 4 years of whole-ecosystem warming and elevated $[\text{CO}_2]$ treatments: (1) Warming exponentially increased resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$, and the magnitude of the response increased over time and varied across the microtopography of the bog surface and with peat depth; (2) these dynamics were generally unaffected by elevated $[\text{CO}_2]$; and (3) relative increases in resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ with warming were similar, though resin-available N/P ratios increased with peat depth.

Warming Increased Resin-Available Nutrients, but Responses Depended on Microtopography and Peat Depth

Warming exponentially increased resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$. The strength of this response increased by an order of magnitude between the first and fourth years of whole-ecosystem warming, and the increase in resin-available nutrients with warming was greatest in deeper peat, at least early in the progression of experimental warming (Tables 1, Figs. 2 and 3). However, we did not observe any significant effects of elevated $[\text{CO}_2]$ on resin-available $\text{NH}_4\text{-N}$ or $\text{PO}_4\text{-P}$ (Table 1; Figure 3). While evidence for peatland responses to elevated $[\text{CO}_2]$ is mixed, others have shown previously that



◀ **Figure 4.** ELM-SPRUC model prediction of net N mineralization and net P mineralization (inset). Each data point is one SPRUCE enclosure, in years 2016 to 2018. More intense colors correspond with more recent years (see full year-color array in Figure 3); closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$. Letter insets correspond to depth of resin incubation (a, b, and c are 10, 30, and 60-cm depths in hummocks and d and e are 10 and 30-cm depths in hollows, see inset in Figure 1). Note that model output data are in units of g nutrient per unit soil volume per year; also note the differences in the y-axis for the net P mineralization figures, as model-predicted net P mineralization was quite low at some peat depths.

elevated $[\text{CO}_2]$ may not necessarily increase plant production in nutrient-limited and *Sphagnum*-dominated bogs (Berendse and others 2001), including the SPRUCE experimental enclosures (McPartland and others 2020, but see Norby and others 2019). Thus, we may not expect an impact of elevated $[\text{CO}_2]$ on nutrient cycling, or in turn, nutrient responses may be weak or delayed. And while depth to water table almost certainly plays a role in controlling resin-available nutrient dynamics throughout the peat profile, especially given controls over rooting depth distribution and

microbial activity, we saw little warming-induced effects of water table level on resin-available nutrients (see *Supplementary Statistical Methods*).

Diminished competition at depth from shallowly rooted vascular plant species, microbial communities, and *Sphagnum* mosses could explain the relatively stronger initial increases in resin-available nutrients with warming at deeper peat depths relative to shallower peat depths (Table 1; Figs. 3, S5, S6). For example, prior to the initiation of warming, we found that the fine roots of the ericaceous shrubs and tree species in the S1 Bog were extremely shallowly distributed above the average summer water table level (Iversen and others 2018). And given that vertical transport of dissolved organic matter has been observed in the S1 Bog and in the SPRUCE experimental enclosures (Tfaily and others 2014, 2018; Wilson and others 2021b), nutrients not acquired by plants in surface peat could accumulate at deeper peat depths (Griffiths and Sebestyen 2016; Griffiths and others 2019). In turn, warming may lead to the destabilization and subsequent decomposition of organic matter at depth (for example, Tfaily and others 2018; Wilson and others 2021a; AminiTabrizi and others 2022). Perhaps most importantly, prior to warming, the surface of the S1 Bog was carpeted by a layer of *Sphagnum* mosses (Norby and others

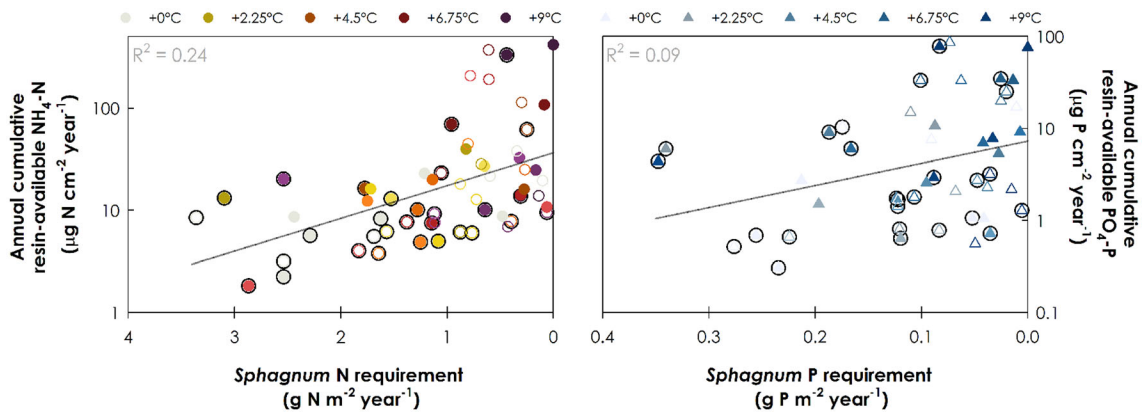
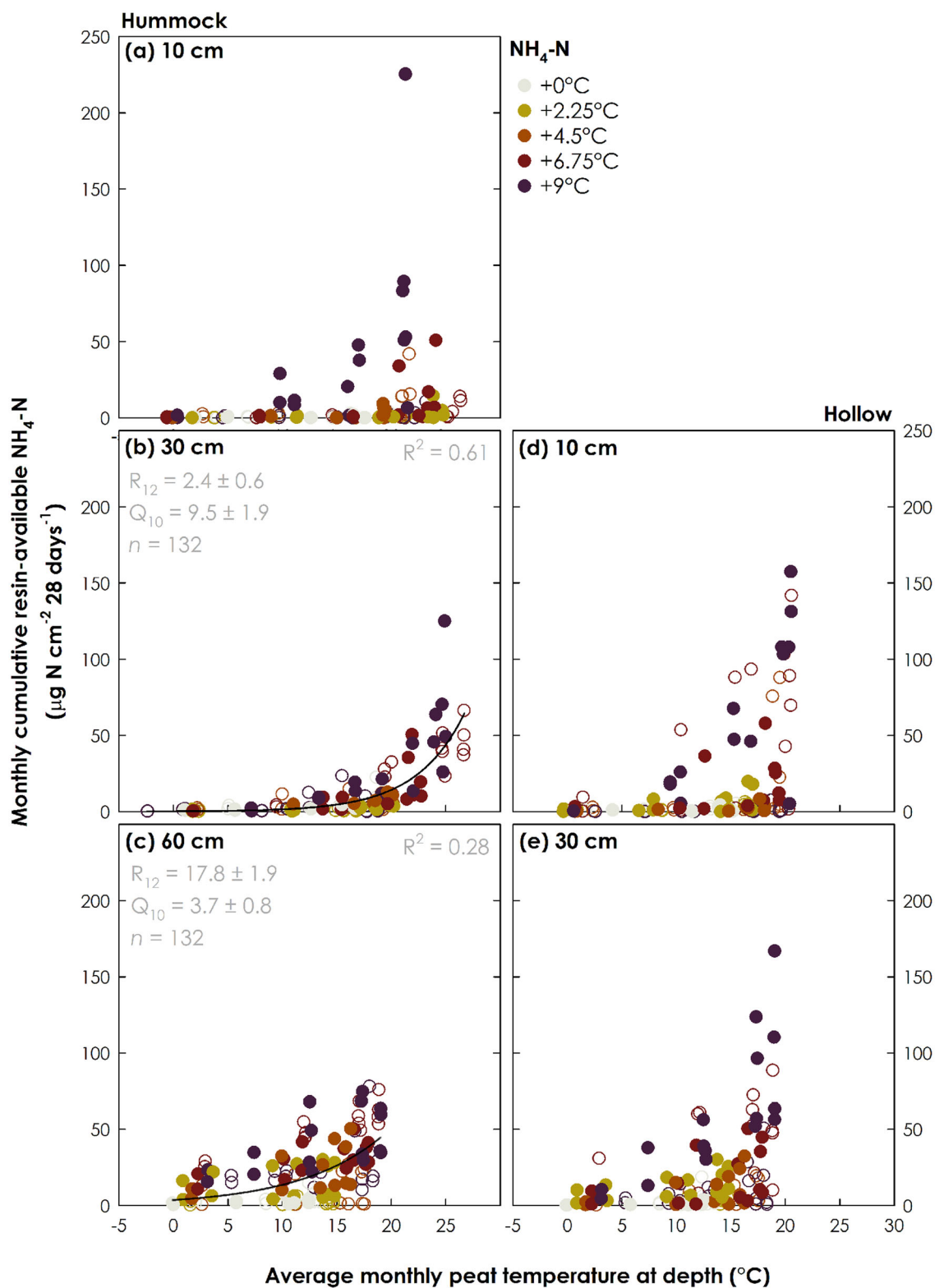


Figure 5. Relationship between *Sphagnum* moss N and P requirements and annual cumulative resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$. Declining *Sphagnum* N and P requirement with warming from 2016 to 2018 (see Figure S3) could have been a causal factor in the large increases in resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ at 10-cm peat depth in more recent years in both hummocks and hollows (hummock microtopography is designated with black circle outline in both panels; note differences in y-axes between $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$). Cumulative annual nutrient predictions were back-transformed to fit to data on graph; R^2 shown are adjusted R^2 . More intense colors represent more recent years (see full year-color array in Figure 3); closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$. Note that the x-axis is plotted from greatest to least *Sphagnum* N and P requirement to highlight the relationship between declining *Sphagnum* nutrient requirement and increasing resin-available N and P. The log-linear relationships between log-transformed cumulative annual $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ and *Sphagnum* N or P requirement over the years 2016 – 2018 were as follows: $\log_{10}(\text{NH}_4\text{-N}) = -0.32^{***} (\pm 0.07 \text{ SE}) \times \text{Sphagnum } N_{\text{req}} + 1.56^{***} (\pm 0.10 \text{ SE})$ and $\log_{10}(\text{PO}_4\text{-P}) = -2.46^* (\pm 1.04 \text{ SE}) \times \text{Sphagnum } P_{\text{req}} + 0.86^{***} (\pm 0.14 \text{ SE})$, respectively (asterisks indicate level of significance for intercept and slope, where * is $P < 0.05$ and *** is $P < 0.0001$).



◀ **Figure 6.** Temperature response functions for $\text{NH}_4\text{-N}$ for approximately 28-day resin collections in 2018. Gray text indicates parameters from a significant Q_{10} response function ± 1 SE ($P \leq 0.05$), where R_{12} is the baseline amount of $\text{NH}_4\text{-N}$ available at $12^\circ\text{C} \pm 1$ SE, n is the number of observations from monthly $\text{NH}_4\text{-N}$ accumulation on resins sampled for ~ 28 days across all enclosures over 9 sampling periods in 2018 for A and B subplots within each enclosure, and R^2 is the adjusted R^2 . Peat temperature at depth was the average temperature at the depth at which the resin was incubated (see Table S2) during the incubation period. $\text{PO}_4\text{-P}$ data from 2018 only are in Figure S4 and all resin-available nutrient data for both $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ from 2014 to 2018 are in Figures S5 and S6, respectively, and have been appended to Iversen and others (2017, data citation). Closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$. Letter insets correspond to depth of resin incubation (a, b, and c are 10, 30, and 60-cm depths in hummocks and d and e are 10 and 30-cm depths in hollows, see inset in Figure 1).

2019) which compete for and intercept nutrients at the peat surface from microbial mineralization, throughfall, and precipitation (Bähring and others 2017; Wang and others 2014).

Dynamics of Resin-Available Nutrients in Response to Other Nutrient Pools

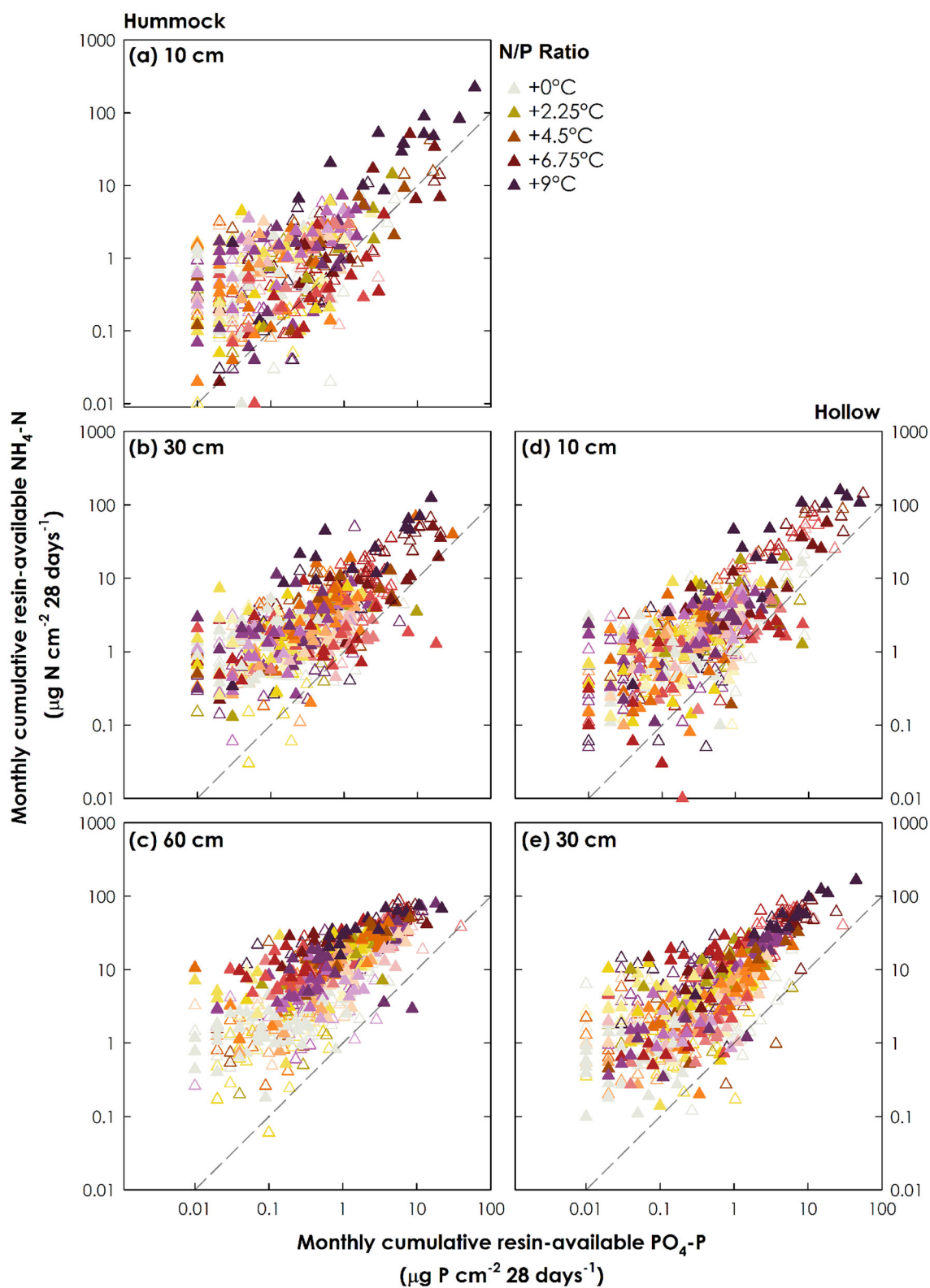
We saw a marked increase in $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ in the surface peat of the warmest treatments in recent years—especially in 2018 (Table 1, Figs. 2, 3). This was unexpected given observed increases in above- and belowground production of ericaceous shrubs as well as in ectomycorrhizal fungal rhizomorphs in response to warming that would ostensibly increase nutrient acquisition by bog vascular plant species (Defrenne and others 2021; Malhotra and others 2020; McPartland and others 2020).

We hypothesize that the increase in nutrient availability in surface peat in the warmest plots in later treatment years was linked to the mortality of *Sphagnum* mosses with warming at SPRUCE. By 2018, the mosses were essentially decimated in the warmest enclosures from either peat drying or shading from the strong growth response of ericaceous shrubs (Norby and others 2019). In particular, the largest increases in resin-available nutrients we observed were in the warmest enclosures with the least *Sphagnum* nutrient demand (Figure 5). Furthermore, this large increase in resin-available nutrients could also be related to the loss of *Sphagnum* capture of atmospherically derived

nutrients (for example, van der Heijden and others 2000; Wang and others 2018), which could explain the relatively greater relationship with resin-available N, which has higher deposition rates than P (Salmon and others 2021). In turn, there may have been an increase in nutrients released from dead and decaying *Sphagnum* necromass (Gerdol and others 2007). While not significant in the overall statistical model, there is some evidence that the strong increase in surface nutrients with warming in more recent years was suppressed under elevated $[\text{CO}_2]$ (Table 1). We continue to monitor whether this pattern develops over time.

The relationship between nutrient availability and *Sphagnum* growth is bi-directional; while the increase in inorganic nutrient availability in the surface peat of the warmest SPRUCE treatments could be driven by the loss of *Sphagnum*, it could also be contributing to and potentially accelerating *Sphagnum* loss. The detrimental impacts of increased nutrient availability on *Sphagnum* growth and ground cover have been observed in a number of long-term nutrient fertilization or nutrient deposition experiments in nutrient-poor peatlands (for example, Limpens and others 2011; Larmola and others 2013; Juutinen and others 2016; Levy and others 2019). Shifting peatland vegetation composition with increased nutrient availability has implications for peatland ecosystem function, including increased peat subsidence and decreased capacity for peatland carbon storage (Franzén 2006; Limpens and others 2011; Larmola and others 2013; Kiheri and others 2020), and we are beginning to observe some of these impacts in the SPRUCE experimental treatments (Norby and others 2019; Hanson and others 2020a).

Given that bogs are water-saturated ecosystems where much of the belowground peat environment tends to be perennially inundated with porewater, we compared resin-available nutrient dynamics to porewater nutrient dynamics. We found that resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ were only somewhat correlated with porewater inorganic N and P (Figs. 8 and S7, respectively), likely indicating that these metrics of nutrient dynamics represent different spatial and temporal components of the bog nutrient cycles. In contrast to the ‘root-like’ acquisition of ion-exchange resins, porewater, similar to one-time soil extractions, represents a snapshot, or pool, of residual nutrients that are not currently immobilized in plant or microbial biomass (Bourbonniere 2009; Bridgham and others 2001; Griffiths and others 2019). Furthermore, previous work has shown that ion-exchange resins may be good integrators of nutrient ‘hot moments’



◀**Figure 7.** The relationship between resin-available $\text{PO}_4\text{-P}$ and $\text{NH}_4\text{-N}$ (that is, the N/P ratio) across SPRUCE experimental treatments. The data span all enclosures, sub-replicates, peat depths, and sampling dates from 2014 to 2018, standardized to a 28-day sampling interval; the dashed lines are the 1:1 line. Given the log scale, any $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ observations that were determined to be '0' after blank correction are not shown. More intense colors represent more recent years (see full year-color array in Figure 3); closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$ (note that the color scheme has been used previously for $\text{NH}_4\text{-N}$ data only, but we also use here for the N/P ratio to avoid introducing yet another color array). Letter insets correspond to depth of resin incubation (a, b, and c are 10, 30, and 60-cm depths in hummocks and d and e are 10 and 30-cm depths in hollows, respectively, see inset in Figure 1).

that occur over time (Darrouzet-Nardi and Bowman 2011), while these dynamic fluxes could either be missed with periodic sampling or assigned outsized importance. On the other hand, lateral outflow could be a good integrator of nutrient 'hot spots' across the plot (for example, Sebestyen and Griffiths 2016; Curtinrich and others 2021). We did observe stronger correlations between resin-available and porewater nutrients in deeper peat (Figs. 8, S7), potentially due to the accumulation of nutrients transported downward through the peat profile (for example, Griffiths and Sebestyen, 2016) or the destabilization of organic matter at depth with warmer temperatures (for example, Tfaily and others 2018; Wilson and others 2021a; AminiTabrizi and others 2022).

Organic nutrients have been hypothesized to be a potential nutrient source in cold, nutrient-limited ecosystems (Kielland 1994; Kielland and others 2006; Raab and others 1999; Schimel and others 2004), including in the S1 Bog (Salmon and others 2021). However, ion-exchange resins do not allow us to make any conclusions with regard to plant-available organic nutrients, as inorganic resin-available nutrients were not well-correlated with porewater organic N and P (Figure 8). Although porewater organic N and P were a large fraction of the total dissolved nutrient pools ($\sim 81\% \pm 19$ SD for N and $46\% \pm 29$ SD for P across all collection dates and depths), much of this porewater organic nutrient pool likely represents polymers too large for plants to directly uptake (Schimel and Bennett 2004). Furthermore, increasing mineral N can lead to decreasing preference for organic N acquisition (Cott and others 2020), though mycorrhizal part-

nerships can change this dynamic (Defrenne and others 2021).

In addition to N and P, other macronutrients limit plant growth in peatlands (for example, Hoosbeek and others 2002; Larmola and others 2013; Wang and others 2018; Levy and others 2019), and the dynamics of multiple nutrient cations in porewater are being quantified over space and time at the S1 Bog as well as in the SPRUCE experimental enclosures (for example, Griffiths and Sebestyen 2016; Griffiths and others 2019). Preliminary evidence indicates that the outflow of nutrients such as Ca and Fe have increased with warming in the SPRUCE experimental treatments (Curtinrich and others 2021).

Warming Increased the Availability of $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ at Similar Rates

We did not find any significant differences in the relative responses of resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ to warming (Table 1; Figs. 2, 3, and 7). The ratio of cumulative annual available $\text{NH}_4\text{-N}$ to $\text{PO}_4\text{-P}$ was highly variable, but averaged $12.6 (\pm 17.2$ SD) across all depths and years, close to the average N/P ratio of plant biomass at the S1 Bog (~ 12 ; Salmon and others 2021). The cumulative annual resin-available N/P ratio tended to be slightly lower than the average N/P ratio of peat measured in the S1 Bog (0 to 30 cm peat depth, averaged across hummocks and hollows, 18 ± 4 SD; Salmon and others 2021) and in a recent review spanning a range of boreal bogs (0 – 50 cm peat depth, 24.5 ± 0.8 ; Wang and others 2015). This could indicate that there was a relatively more limited $\text{NH}_4\text{-N}$ supply compared to $\text{PO}_4\text{-P}$ in the pool of nutrients that were mineralized from peat and became resin-available between 2014 and 2018 (potentially due to low activation energy of N-acquiring enzymes compared to P observed in the S1 Bog; Steinweg and others 2018). In turn, it could be that $\text{NH}_4\text{-N}$ tended to be more limiting for plant and microbial growth in the SPRUCE enclosures (Cleveland and others 2007; Salmon and others 2021), and thus there was more competition from plants and microbes with the ion-exchange resins for $\text{NH}_4\text{-N}$ compared to $\text{PO}_4\text{-P}$. Although the cumulative annual resin-available N/P ratio did not change significantly in response to warming, resin-available N/P ratio did tend to increase with peat depth (Tables 1 and S3; Figure 7), indicating an increase in P limitation in deeper peat. This increasing N/P ratio with depth has been observed in the peat profile in the SPRUCE bog (Salmon and others 2021) as well as in other bogs (Wang and

others 2015). One theory regarding these depth dynamics is that P is strongly limiting to microbial growth in peatlands and is tightly cycled at the peat surface, whereas N is buried and accumulates with peat depth (Bridgman and others 1998; Hill and others 2014; Steinweg and others 2018; Tfaily and others 2014; Wang and others 2015).

Nutrient Availability Increased Exponentially with Peat Temperature

In addition to examining the response of $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ to warming and elevated $[\text{CO}_2]$ at an annual level, we were also able to look at the more highly-resolved resin-available nutrient dynamics at a $\sim$ monthly (28-day) timestep. We fit Q_{10} temperature response functions to consider the temperature cues of monthly nutrient availability (similar to soil CO_2 efflux, as in Hanson and others 2000) and to provide an important model parameter that may be used to simulate or benchmark nutrient availability in land surface models (for example, Shi and others 2021). A Q_{10} function explained a large fraction of variation in resin-available $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ with increasing peat temperature in deeper peat, where the Q_{10} parameter was quite large (ranging from 2.5 to 51.4 across all years, microtopographic positions, and peat depths; Figs. 6 and S4, Table S5). However, the Q_{10} function was a poor fit in surface soils, potentially due to the influence of competition from plants and microbes on nutrient accumulation on ion-exchange resins or potential loss of nutrients to deeper peat.

Implications for Understanding and Modeling Peatland Responses to Warming

A hypothesized indirect response of ecosystems to warming is an increase in microbial nutrient mineralization, and therefore plant-available nutrients, that leads to increased plant growth and changing plant community composition, with follow-on impacts on ecosystem C storage (Bragazza and others 2013; Liu and others 2020; Rustad and others 2001; Salazar and others 2020). We use terrestrial biosphere models such as ELM-SPRUCED to conceptualize and test these hypotheses—along with other mechanisms such as plant physiology and nutrient requirements—but models must be compared with and validated against experimental observations. Annual cumulative net nutrient mineralization predicted by ELM-SPRUCED reflects nutrient availability on an annual time scale and is

a foundation for modeled plant and soil responses to warming. We compared model-predicted net nutrient mineralization with our long-term and highly resolved observations of resin-available nutrient dynamics; these fluxes have been qualitatively compared previously across a number of peatland ecosystems to inform understanding of peatland nutrient dynamics (as in Bridgman and others 2001).

Similar to the patterns observed in resin-available nutrients, ELM-SPRUCED projected a sustained and exponential increase in net N and P mineralization in response to warming, with no discernable effects of elevated $[\text{CO}_2]$ (Figure 4). However, the magnitudes of the modeled increases in net N and P mineralization with increasing peat temperature were much lower than the responses observed in resin-available nutrients (for example, the calculated Q_{10} responses for model output of net nutrient mineralization ranged between ~ 1.5 and 5 across peat depths and microtopographic positions, compared to the much higher observed Q_{10} responses in resin-available nutrients; Figs. 6 and S4, Table S5). This could be because the Q_{10} warming response of microbial decomposition is underestimated by the model, or in turn because models do not incorporate potential ‘hot moments’ that are integrated by ion-exchange resins over time (for example, Darrouzet-Nardi and Bowman 2011).

Model predictions of increases in annual cumulative net N and P mineralization with warming were greater in depressed hollows, likely due to model-predicted drying in the hollows with warming (a response not observed at SPRUCED between 2014 and 2018), which increases organic matter decomposition. ELM-SPRUCED also predicted greater net nutrient mineralization in hollows on average, similar to the observed patterns in resin-available nutrients, though the mechanism for this was less clear and may be related to relatively less root activity in the hollows than hummocks (for example, Iversen and others 2018).

ELM-SPRUCED predicted a decrease in net N and P mineralization with depth (Figure 4), in contrast to observations of increasing resin-available nutrients with depth, across all treatments (Table 1, Figure 3). ELM-SPRUCED encodes a decline in microbial activity with peat depth, but we hypothesize that the model is either not capturing the potential transport of dissolved organic matter (and associated nutrients) downward through the peat profile (for example, Griffiths and Sebestyen 2016) or not capturing the destabilization and subsequent decomposition of organic matter at depth with warmer temperatures (for example,

Tfaily and others 2018; Wilson and others 2021a; AminiTabrizi and others 2022). The absence of either mechanism could explain why the model does not predict an accumulation of nutrients in deeper peat. Continued iteration between experimental observations and model predictions, which are based on underlying model parameterization and process conceptualization, can help to improve our projections of peatland responses to climate change across the world.

CONCLUSIONS

The SPRUCE experimental warming by elevated $[\text{CO}_2]$ manipulation is the largest of its kind, allowing us to examine the whole-ecosystem im-

pacts of a gradient of warming and potential interaction with rising atmospheric $[\text{CO}_2]$ in a peatland ecosystem. We found that warming exponentially increased plant-available nutrients, but that the magnitude of the response varied over time and across the microtopography of the bog surface and with peat depth. To-date these patterns remained generally unaffected by elevated $[\text{CO}_2]$. Furthermore, complex interactions are suggested by the simultaneous long-term loss of the *Sphagnum* community and the relatively sudden increase in the availability of nutrients in surface peat, likely driven by both biotic and abiotic factors. Predictions of peatland nutrient availability in land surface models under climate change scenarios must account for dynamic changes in nutrient acquisition

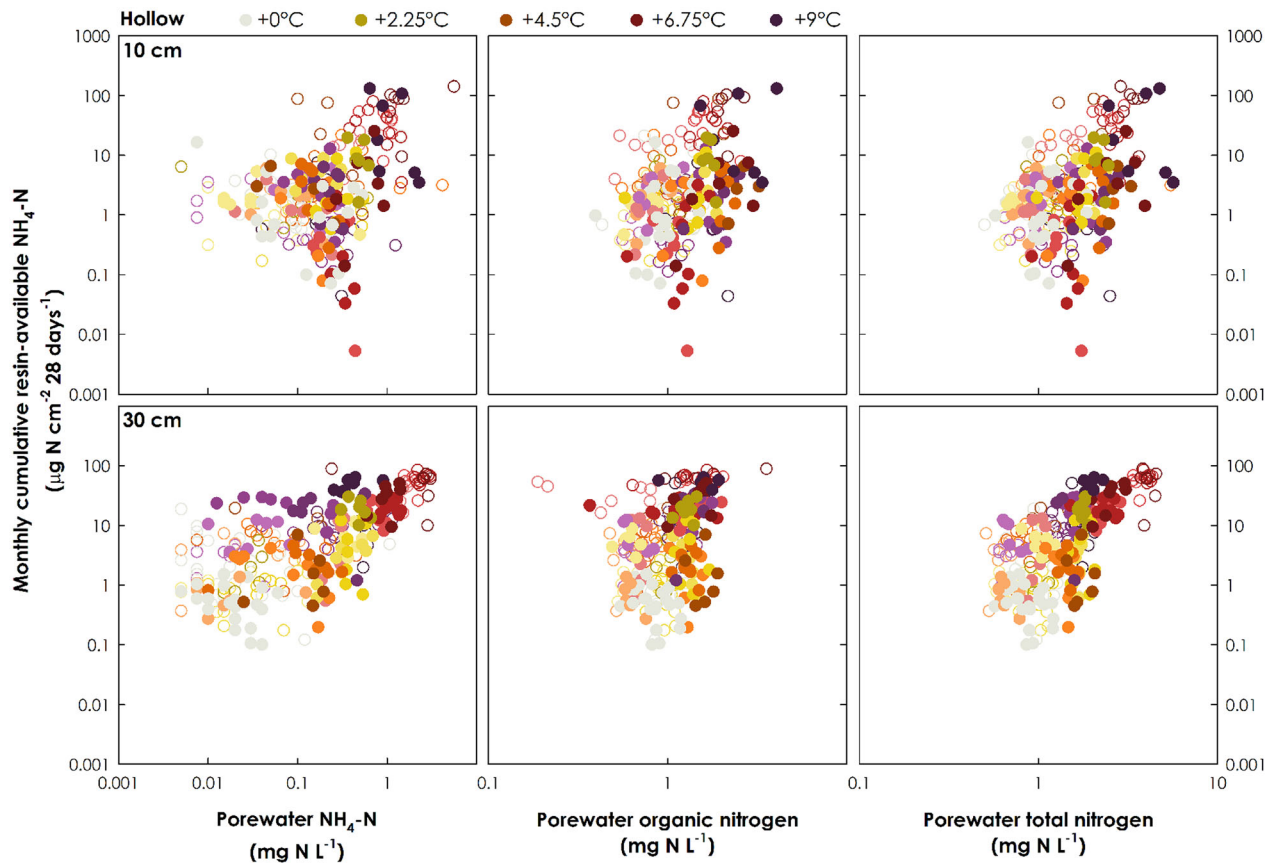


Figure 8. Comparisons of resin-available $\text{NH}_4\text{-N}$ with inorganic, organic, and total N concentrations in porewater. Data span 2015 – 2018, at 10 cm or 30 cm depth in the hollows only, and nutrient data from discrete $\sim$ biweekly porewater collections were averaged within the dates of the $\sim$ monthly resin incubations. More intense colors represent more recent years (see full year-color array in Figure 3); closed symbols are ambient $[\text{CO}_2]$ while open symbols are elevated $[\text{CO}_2]$. For the purposes of this analysis, we focused on the porewater nutrient concentrations at 0–10 cm and 30–40 cm piezometer depths to facilitate direct comparison with ion-exchange resins incubated at those depths in adjacent hollows (that is, from only one, adjacent resin array per enclosure). Note that the units for porewater nutrients are g nutrient per L of porewater, while the units for resin-available nutrients have been standardized to the resin surface area. Comparisons of resin-available $\text{PO}_4\text{-P}$ with porewater P concentrations are in Figure S7.

by plants and microbes, as well as microtopography and peat depth.

ACKNOWLEDGEMENTS

The SPRUCE experiment is supported by the Biological and Environmental Research program in the United States Department of Energy's Office of Science. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the United States Department of Energy under contract DE-AC05-00OR22725. We thank Sarah Bellaire, Alana Burnham, Kelsey Carter, Ingrid Slette, and Nathan Stenson for their help in the field or laboratory. We also thank the editorial staff and anonymous reviewers for their helpful feedback. The contributions of SDS and funding for the Marcell Experimental Forest and laboratory analysis by the Forest Service were provided by the Northern Research Station of the United States Department of Agriculture Forest Service.

FUNDING

United States Department of Energy, Office of Science, Biological and Environmental Research program. *This manuscript has been authored in part by UT-Battelle, LLC, under contract DE-AC05-00OR22725 with the US Department of Energy (DOE). The publisher acknowledges the US government license to provide public access under the DOE Public Access Plan (<http://energy.gov/downloads/doe-public-access-plan>).*

DATA AVAILABILITY

Data presented in this manuscript have been appended to: Iversen CM, Latimer J, Burnham A, Brice DJ, Childs J, Vander Stel HM. 2017. SPRUCE plant-available nutrients assessed with ion-exchange resins in experimental plots, beginning in 2013. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. Data set accessed at <http://dx.doi.org/10.3334/CDIAC/spruce.036>

Declarations

Conflicts of interest The authors declare no competing interest.

REFERENCES

Aerts R, Cornelissen JHC, Dorrepaal E. 2006. Plant performance in a warmer world: General responses of plants from cold,

northern biomes and the importance of winter and spring events. *Plant Ecology* 182:65–77.

- AminiTabrizi R, Dontsova K, Graf Gracheta N, Tfaily MM. 2022. Elevated temperatures drive abiotic and biotic degradation of organic matter in a peat bog under oxic conditions. *Science of the Total Environment* 804:150045.
- APHA. 2017. Standard methods for the examination of water and wastewater, 23rd edn. DC: Washington.
- Bähring A, Fichtner A, Friedrich U, von Oheimb G, Härdtle W. 2017. Bryophytes and organic layers control uptake of airborne nitrogen in low-N environments. *Frontiers in Plant Science* 8:2080.
- Barbier C, Hanson PJ, Todd DE, Belcher D, Jekabson EW, Thomas WK, Riggs J. 2013. Air flow and heat transfer in a temperature-controlled open top enclosure. *American Society of Mechanical Engineers* 7:9780791845233.
- Berendse F, Van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B. 2001. Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biology* 7:591–598.
- Bourbonniere RA. 2009. Review of water chemistry research in natural and disturbed peatlands. *Canadian Water Resources Journal* 34:393–414.
- Bragazza L, Freeman C, Jones T, Rydin H, Limpens J, Fenner N, Ellis T, Gerdol R, Hájek M, Hájek T, Iacumin P, Kutnar L, Tahvanainen T, Toberman H. 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proceedings of the National Academy of Sciences of the United States of America* 103:19386–19389.
- Bragazza L, Parisod J, Buttler A, Bardgett RD. 2013. Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change* 3:273–277.
- Bridgman SD, Updegraff K, Pastor J. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79:1545–1561.
- Bridgman SD, Updegraff K, Pastor J. 2001. A comparison of nutrient availability indices along an ombrotrophic-minerotrophic gradient in Minnesota wetlands. *Soil Science Society of America Journal* 65:259–269.
- Bridgman SD, Megonigal JP, Keller JK, Bliss NB, Trettin C. 2006. The carbon balance of North American wetlands. *Wetlands* 26:889–916.
- Bridgman SD, Pastor J, Dewey B, Weltzin JF, Updegraff K. 2008. Rapid carbon response of peatlands to climate change. *Ecology* 89:3041–3048.
- Burrows SM, Maltrud M, Yang X, Zhu Q, Jeffery N, Shi X, Ricciuto D, Wang S, Bisht G, Tang J, Wolfe J, Harrop BE, Singh B, Brent S, Baldwin S, Zhou T, Cameron-Smith P, Keen N, Collier N, Xu M, Hunke EC, Elliott SM, Turner AK, Li H, Wang H, Golaz J-C, Bond-Lamberty B, Hoffman FM, Riley WJ, Thornton PE, Calvin K, Leung LR. 2020. The DOE E3SM v1.1 Biogeochemistry configuration: Description and simulated ecosystem-climate responses to historical changes in forcing. *Journal of Advances in Modeling Earth Systems* 12: e2019MS001766.
- Cleveland CC, Liptzin D. 2007. C:N: P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85:235–252.

- Cott GM, Jansen MAK, Megonigal JP. 2020. Uptake of organic nitrogen by coastal wetland plants under elevated CO₂. *Plant and Soil* 450:521–535.
- Curtinrich HJ, Sebestyen SD, Griffiths NA, Hall SJ. 2021. Warming stimulates iron-mediated carbon and nutrient cycling in mineral-poor peatlands. *Ecosystems*.
- Darrouzet-Nardi A, Bowman WD. 2011. Hot spots of inorganic nitrogen availability in an alpine-subalpine ecosystem, Colorado Front Range. *Ecosystems* 14:848–863.
- Defrenne CE, Childs J, Fernandez CW, Taggart M, Nettles WR, Allen MF, Hanson PJ, Iversen CM. 2021. High-resolution minirhizotrons advance our understanding of root-fungal dynamics in an experimentally warmed peatland. *Plants, People, Planet* 3:640–652.
- de Graaff MA, van Groenigen KJ, Six J, Hungate B, van Kessel C. 2006. Interactions between plant growth and soil nutrient cycling under elevated CO₂: a meta-analysis. *Global Change Biology* 12:2077–2091.
- Eppinga MB, Rietkerk M, Belyea LR, Nilsson MB, De Ruiter PC, Wassen MJ. 2010. Resource contrast in patterned peatlands increases along a climatic gradient. *Ecology* 91:2344–2355.
- Fenner N, Ostle NJ, McNamara N, Sparks T, Harmens H, Reynolds B, Freeman C. 2007. Elevated CO₂ effects on peatland plant community carbon dynamics and DOC production. *Ecosystems* 10:635–647.
- Finzi AC, Norby RJ, Calafapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME, Ledford J, Liberloo M, Oren R, Polle A, Pritchard S, Zak DR, Schlesinger WH, Ceulemans R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences* 104:14014–14019.
- Franzén LG. 2006. Increased decomposition of subsurface peat in Swedish raised bogs: Are temperate peatlands still net sinks of carbon? *Mires and Peat* 1:03.
- Gerdol R, Petraglia A, Bragazza L, Iacumin P, Brancaleoni L. 2007. Nitrogen deposition interacts with climate in affecting production and decomposition rates in *Sphagnum* mosses. *Global Change Biology* 13:1810–1821.
- Giblin AE, Laundre JA, Nadelhoffer KJ, Shaver GR. 1994. Measuring nutrient availability in arctic soils using ion exchange resins: A field test. *Soil Science Society of America Journal* 58:1154–1162.
- Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probably responses to climatic warming. *Ecological Applications* 1:182–195.
- Graham JD, Glenn NF, Spaete LP, Hanson PJ. 2020. Characterizing peatland microtopography using gradient and microform-based approaches. *Ecosystems* 23:1464–1480.
- Griffiths NA, Sebestyen SD. 2016. Dynamic vertical profiles of peat porewater chemistry in a northern peatland. *Wetlands* 36:1119–1130.
- Griffiths NA, Hook LA, Hanson PJ. 2016a. SPRUCE S1 Bog and SPRUCE experiment location survey results, 2015 and 2020. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.015>
- Griffiths NA, Sebestyen SD, Oleheiser KC, Stelling JM, Pierce CE, Nater EA, Toner BM, Kolka RK. 2016b. SPRUCE Porewater Chemistry Data for Experimental Plots Beginning in 2013, 3rd edition. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.028>
- Griffiths NA, Hanson PJ, Ricciuto DM, Iversen CM, Jensen AM, Malhotra A, McFarlane KJ, Norby RJ, Sargsyan K, Sebestyen SD, Shi X, Walker AP, Ward EJ, Warren JM, Weston DJ. 2017. Temporal and spatial variation in peatland carbon cycling and implications for interpreting responses of an ecosystem-scale warming experiment. *Soil Science Society of America Journal* 81:1668–1688.
- Griffiths NA, Sebestyen SD, Oleheiser KC. 2019. Variation in peatland porewater chemistry over time and space along a bog to fen gradient. *Science of the Total Environment* 697:14.
- Gu Q, Grogan P. 2020. Nutrient availability measurement techniques in arctic tundra soils: in situ ion exchange membranes compared to direct extraction. *Plant and Soil* 454:359–378.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48:115–146.
- Hanson PJ, Riggs JS, Nettles WR, Krassovski MB, Hook LA. 2016. SPRUCE whole ecosystems warming (WEW) environmental data beginning August 2015. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.032>
- Hanson PJ, Riggs JS, Nettles WR, Phillips JR, Krassovski MB, Hook LA, Gu L, Richardson AD, Aubrecht DM, Ricciuto DM, Warren JM, Barbier C. 2017. Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated CO₂ atmosphere. *Biogeosciences* 14:861–883.
- Hanson PJ, Griffiths NA, Iversen CM, Norby RJ, Sebestyen SD, Phillips JR, Chanton JP, Kolka RK, Malhotra A, Oleheiser KC, Warren JM, Shi X, Yang X, Mao J, Ricciuto DM. 2020a. Rapid net carbon loss from a whole-ecosystem warmed peatland. *AGU Advances* 1: e2020aAV000163.
- Hanson PJ, Phillips JR, Nettles WR, Pearson KJ, Hook LA. 2020b. SPRUCE plot-level water table data assessments for absolute elevations and height with respect to mean hollows beginning in 2015. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.25581/spruce.079/1608615>
- Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794.
- Hedwall P-O, Brunet J, Rydin H. 2017. Peatland plant communities under global change: negative feedback loops counteract shifts in species composition. *Ecology* 98:150–161.
- Herndon EM, Kinsman-Costello L, Duroe KA, Mills J, Kane ES, Sebestyen SD, Thompson AA, Wulfschlegel SD. 2019. Iron (Oxyhydr)Oxides serve as phosphate traps in tundra and boreal peat soils. *Journal of Geophysical Research: Biogeosciences* 124:227–246.
- Hill BH, Elonen CM, Jicha TM, Kolka RK, Lehto LLP, Sebestyen SD, Seifert-Monson LR. 2014. Ecoenzymatic stoichiometry and microbial processing of organic matter in northern bogs and fens reveals a common P-limitation between peatland types. *Biogeochemistry* 120:203–224.
- Hoosbeek MR, Van Breemen N, Vasander H, Buttler A, Berendse F. 2002. Potassium limits potential growth of bog vegetation under elevated atmospheric CO₂ and N deposition. *Global Change Biology* 8:1130–1138.

- IPCC (2021). Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte V, P Zhai, A Pirani, SL Connors, C Péan, S Berger, N Caud, Y Chen, L Goldfarb, MI Gomis, M Huang, K Leitzell, E Lonnoy, JBR Matthews, TK Maycock, T Waterfield, O Yelekçi, R Yu, B Zhou (eds.)]. Cambridge University Press. In Press.
- Iversen CM, Bridgman SD, Kellogg LE. 2010. Scaling plant nitrogen use and uptake efficiencies in response to nutrient addition in peatlands. *Ecology* 91:693–707.
- Iversen CM, Hanson PJ, Brice DJ, Phillips JR, McFarlane KJ, Hobbie EA, Kolka RK. 2014. SPRUCE peat physical and chemical characteristics from experimental plot cores, 2012. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.005>
- Iversen CM, Latimer J, Burnham A, Brice DJ, Childs J, Vander Stel HM. 2017. SPRUCE Plant-Available Nutrients Assessed with Ion-Exchange Resins in Experimental Plots, Beginning in 2013. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.036>.
- Iversen CM, Childs J, Norby RJ, Ontl TA, Kolka RK, Brice DJ, McFarlane K, Hanson PJ. 2018. Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat. *Plant and Soil* 424:123–143.
- Juutinen S, Moore TR, Laine AM, Bubier JL, Tuittila E-S, De Young A, Chong M. 2016. Responses of the mosses *Sphagnum capillifolium* and *Polytrichum strictum* to nitrogen deposition in a bog: Growth, ground cover, and CO₂ exchange. *Botany* 94:127–138.
- Keller JK, Bauers AK, Bridgman SD, Kellogg LE, Iversen CM. 2006. Nutrient control of microbial carbon cycling along an ombrotrophic-minerotrophic peatland gradient. *Journal of Geophysical Research: Biogeosciences* 111:G3.
- Keuper F, van Bodegom PM, Dorrepaal E, Weedon JT, van Hal J, van Logtestijn RSP, Aerts R. 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology* 18:1998–2007.
- Kielland K. 1994. Amino-acid absorption by arctic plants—Implications for plant nutrition and nitrogen cycling. *Ecology* 75:2373–2383.
- Kielland K, McFarland J, Olson K. 2006. Amino acid uptake in deciduous and coniferous taiga ecosystems. *Plant and Soil* 288:297–307.
- Kiheri H, Velmala S, Pennanen T, Timonen S, Sietiö O-M, Fritze H, Heinonsalo J, van Dijk N, Dise N, Larmola T. 2020. Fungal colonization patterns and enzymatic activities of peatland ericaceous plants following long-term nutrient addition. *Soil Biology and Biochemistry* 147:107833.
- Koerselman W, Arthur FMM. 1996. The Vegetation N: P Ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33:1441–1450.
- Larmola T, Bubier JL, Kobyljanec C, Basiliko N, Juutinen S, Humphreys E, Preston M, Moore TR. 2013. Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. *Global Change Biology* 19:3729–3739.
- Levy P, van Dijk N, Gray A, Sutton M, Jones M, Leeson S, Dise N, Leith I, Sheppard L. 2019. Response of a peat bog vegetation community to long-term experimental addition of nitrogen. *Journal of Ecology* 107:1167–1186.
- Limpens J, Berendse F, Blodau C, Canadell JG, Freeman C, Holden J, Roulet N, Rydin H, Schaepman-Strub G. 2008. Peatlands and the carbon cycle: from local processes to global implications – a synthesis. *Biogeosciences* 5:1475–1491.
- Limpens J, Granath G, Gunnarsson U, Aerts R, Bayley S, Bragazza L, Bubier J, Buttler A, van den Ber LJJ, Francez A-J, Gerdol R, Grosvernier P, Heijmans MMPD, Hoosbeek MR, Hotes S, Ilomets M, Leith I, Mitchell EAD, Moore T, Nilsson MB, Nordbakken J-F, Rochefort L, Rydin H, Sheppard LJ, Thormann M, Wiedermann MM, Williams BL, Xu B. 2011. Climatic modifiers of the response to N deposition in peat-forming *Sphagnum* mosses: a meta-analysis. *New Phytologist* 191:496–507.
- Liu H, Xu X, Zhou C, Zhao J, Li B, Nie M. 2020. Geographic linkages of plot traits to salt marsh productivity. *Ecosystems*.
- Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8:315–323.
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin FS. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–443.
- Malhotra A, Moore TR, Limpens J, Roulet NT. 2018. Post-thaw variability in litter decomposition best explained by microtopography at an ice-rich permafrost peatland. *Arctic, Antarctic, and Alpine Research* 50:e1415622.
- Malhotra A, Brice DJ, Childs J, Graham JD, Hobbie EA, Vander Stel H, Feron SC, Hanson PJ, Iversen CM. 2020. Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences* 117:17627–17634.
- McFarlane KJ, Hanson PJ, Iversen CM, Phillips JR, Brice DJ. 2018. Local spatial heterogeneity of Holocene carbon accumulation throughout the peat profile of an ombrotrophic northern Minnesota bog. *Radiocarbon* 60:941–962.
- McPartland MY, Montgomery RA, Hanson PJ, Phillips JR, Kolka R, Palik B. 2020. Vascular plant species response to warming and elevated carbon dioxide in a boreal peatland. *Environmental Research Letters* 15:12.
- Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler R, Jain AK, Luo Y, Parton W, Prentice IC, Thornton PE, Wang S, Wang Y-P, Weng E, Iversen CM, McCarthy HR, Warren JM, Oren R, Norby RJ. 2015. Using ecosystem experiments to improve vegetation models. *Nature Climate Change* 5:528–534.
- Milla R, Cornelissen JHC, van Logtestijn RSP, Toet S, Aerts R. 2006. Vascular plant responses to elevated CO₂ in a temperate lowland *Sphagnum* peatland. *Plant Ecology* 182:13–24.
- Mooshammer M, Hofhansl F, Frank AH, Wanek W, Hämmerle I, Leitner S, Schneckner J, Wild B, Watzka M, Keiblinger KM, Zechmeister-Boltenstern S, Richter A. 2017. Decoupling of microbial carbon, nitrogen, and phosphorus cycling in response to extreme temperature events. *Science Advances* 3:e1602781.
- Munir TM, Khadka B, Xu B, Strack M. 2017. Mineral nitrogen and phosphorus pools affected by water table lowering and warming in a boreal forested peatland. *Ecohydrology* 10:15.
- Murphy MT, Moore TR. 2010. Linking root production to aboveground plant characteristics and water table in a temperate bog. *Plant and Soil* 336:219–231.
- Nichols JE, Peteet DM. 2019. Rapid expansion of northern peatlands and doubled estimate of carbon storage. *Nature Geoscience* 12:917–921.
- Norby RJ, Childs J. 2018. SPRUCE: Sphagnum productivity and community composition in the SPRUCE experimental Plots.

- Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.25581/spruce.049/1426474>
- Norby RJ, Childs J, Hanson PJ, Warren JM. 2019. Rapid loss of an ecosystem engineer: *Sphagnum* decline in an experimentally warmed bog. *Ecology and Evolution* 9:12571–12585.
- Norby RJ, Childs J, Brice DJ. 2020. SPRUCE: Sphagnum carbon, nitrogen and phosphorus concentrations in the SPRUCE experimental plots. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.25581/spruce.084/1647361>
- Olid C, Nilsson MB, Eriksson T, Klaminder J. 2014. The effects of temperature and nitrogen and sulfur additions on carbon accumulation in a nutrient-poor boreal mire: Decadal effects assessed using 210Pb peat chronologies. *Journal of Geophysical Research: Biogeosciences* 119:392–403.
- Parsekian AD, Slater L, Ntarlagiannis D, Nolan J, Sebestyen SD, Kolka RK, Hanson PJ. 2012. Uncertainty in peat volume and soil carbon estimated using ground-penetrating radar and probing. *Soil Science Society of America Journal* 76:1911–1918.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Raab TK, Lipson DA, Monson RK. 1999. Soil amino acid utilization among species of the Cyperaceae: Plant and soil processes. *Ecology* 80:2408–2419.
- Richardson CJ. 1985. Mechanisms controlling phosphorus retention capacity in freshwater wetlands. *Science* 228:1424–1427.
- Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C. 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil* 321:305–339.
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen J, Gurevitch J, GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562.
- Salazar A, Rousk K, Jónsdóttir IS, Bellenger J-P, Andr sson  S. 2020. Faster nitrogen cycling and more fungal and root biomass in cold ecosystems under experimental warming: a meta-analysis. *Ecology* 101:e02938.
- Salmon VG, Brice DJ, Brigham S, Childs J, Graham JD, Griffiths NA, Hofmockel K, Iversen CM, Jicha TM, Kolka RK, Kostka JE, Malhotra A, Norby RJ, Phillips JR, Ricciuto D, Schadt CW, Sebestyen SD, Shi X, Walker AP, Warren JM, Weston DJ, Yang X, Hanson PJ. 2021. Nitrogen and phosphorus cycling in an ombrotrophic peatland: A benchmark for assessing change. *Plant and Soil* 466:649–674.
- Schimel JP, Bennett J. 2004. Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85:591–602.
- Seay S. 2018. Peatlands hold carbon even in warming environment. Oak Ridge National Laboratory Review 51:20–23.
- Sebestyen SD, Griffiths NA. 2016. SPRUCE enclosure corral and sump system: Description, operation, and calibration. Climate Change Science Institute, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. <https://doi.org/10.3334/CDIAC/spruce.015>
- Sebestyen SD, Dorrance C, Olson DM, Verry ES, Kolka RK, Elling AE, Kyllander R. 2011. Long-term monitoring sites and trends at the Marcell Experimental Forest. In R. K. Kolka, S. D. Sebestyen, a. E. S. Verry, and K. N. Brooks (Eds.), *Peatland Biogeochemistry and Watershed Hydrology at the Marcell Experimental Forest* (pp. 15–72). New York, NY: CRC Press, Inc.
- Shi X, Thornton PE, Ricciuto DM, Hanson PJ, Mao J, Sebestyen SD, Griffiths NA, Bisht G. 2015. Representing northern peatland microtopography and hydrology within the Community Land Model. *Biogeosciences* 12:6463–6477.
- Shi X, Ricciuto DM, Thornton PE, Xu X, Yuan F, Norby RJ, Walker AP, Warren JM, Mao J, Hanson PJ, Meng L, Weston D, Griffiths NA. 2021. Extending a land-surface model with Sphagnum moss to simulate responses of a northern temperate bog to whole ecosystem warming and elevated CO₂. *Biogeosciences* 18:467–486.
- Skogley EO, Dobermann A. 1996. Synthetic ion-exchange resins: Soil and environmental studies. *Journal of Environmental Quality* 25:13–24.
- Spohn M, Kuzyakov Y. 2013. Phosphorus mineralization can be driven by microbial need for carbon. *Soil Biology and Biochemistry* 61:69–75.
- Steinweg JM, Kostka JE, Hanson PJ, Schadt CW. 2018. Temperature sensitivity of extracellular enzymes differs with peat depth but not with season in an ombrotrophic bog. *Soil Biology and Biochemistry* 125:244–250.
- Tfaily MM, Cooper WT, Kostka JE, Chanton PR, Schadt CW, Hanson PJ, Iversen CM, Chanton JP. 2014. Organic matter transformation in the peat column at Marcell Experimental Forest: Humification and vertical stratification. *Journal of Geophysical Research-Biogeosciences* 119:661–675.
- Tfaily MM, Wilson RM, Cooper WT, Kostka JE, Hanson P, Chanton JP. 2018. Vertical stratification of peat pore water dissolved organic matter composition in a peat bog in northern Minnesota. *Journal of Geophysical Research: Biogeosciences* 123:479–494.
- Toet S, Cornelissen JHC, Aerts R, van Logtestijn RSP, de Beus M, Stoevelaar R. 2006. Moss responses to elevated CO₂ and variation in hydrology in a temperate lowland peatland. *Plant Ecology* 182:27–40.
- van der Heijden E, Verbeek SK, Kuiper PJC. 2000. Elevated atmospheric CO₂ and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. var. *mucronatum* (Russ.) Warnst. *Global Change Biology* 6:201–212.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87–115.
- Vitt DH, Chee W-L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106.
- Walker TW, Syers JK. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.
- Walker AP, De Kauwe MG, Bastos A, Belmecheri S, Georgiou K, Keeling RF, Zuidema PA. 2021. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂. *New Phytologist* 229:2413–2445.
- Wang M, Moore TR. 2014. Carbon, nitrogen, phosphorus, and potassium stoichiometry in an ombrotrophic peatland reflects plant functional type. *Ecosystems* 17:673–684.
- Wang J, Shi F, Xu B, Wang Q, Wu Y, Wu N. 2014. Uptake and recovery of soil nitrogen by bryophytes and vascular plants in an alpine meadow. *Journal of Mountain Science* 11:475–484.
- Wang M, Moore TR, Talbot J, Riley JL. 2015. The stoichiometry of carbon and nutrients in peat formation. *Global Biogeochemical Cycles* 29:113–121.

- Wang M, Talbot J, Moore TR. 2018. Drainage and fertilization effects on nutrient availability in an ombrotrophic peatland. *Science of the Total Environment* 621:1255–1263.
- Weedon JT, Kowalchuk GA, Aerts R, van Hal J, van Logtestijn R, Taş N, Röling WFM, van Bodegom PM. 2012. Summer warming accelerates sub-arctic peatland nitrogen cycling without changing enzyme pools or microbial community structure. *Global Change Biology* 18:138–150.
- Weltzin JF, Bridgham SD, Pastor J, Chen J, Harth C. 2003. Potential effects of warming and drying on peatland plant community composition. *Global Change Biology* 9:141–151.
- Wilson RM, Griffiths NA, Visser A, McFarlane KJ, Sebestyen SD, Oleheiser KC, Bosman S, Hoppie AM, Tfaily MM, Kolka RK, Hanson PJ, Kostka JE, Bridgham SD, Keller JK, Chanton JP. 2021a. Radiocarbon analyses quantify peat carbon losses with increasing temperature in a whole ecosystem warming experiment, *Journal of Geophysical Research: Biogeosciences* 126: e2021aJG006511.
- Wilson RM, Tfaily MM, Kolton M, Johnston ER, Petro C, Zalman CA, Hanson PJ, Heyman HM, Kyle JE, Hoyt DW, Eder EK, Purvine SO, Kolka RK, Sebestyen SD, Griffiths NA, Schadt CW, Keller JK, Bridgham SD, Chanton JP, Kostka JE. 2021b. Soil metabolome response to whole-ecosystem warming at the Spruce and Peatland Responses under Changing Environments experiment. *Proceedings of the National Academy of Sciences* 118:e2004192118.
- Yang JE, Skogley EO, Georgitis SJ, Schaff BE, Ferguson AH. 1991. Phytoavailability soil test: Development and verification of theory. *Soil Science Society of America Journal* 55:1358–1365.
- Yang X, Ricciuto DM, Thornton PE, Shi X, Xu M, Hoffman F, Norby RJ. 2019. The effects of phosphorus cycle dynamics on carbon sources and sinks in the Amazon region: A modeling study using ELM v1. *Journal of Geophysical Research: Biogeosciences* 124:3686–3698.