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The response of boreal peatland community composition and NDVI to hydrologic change, warming, and elevated carbon dioxide

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Abstract

Widespread changes in arctic and boreal Normalized Difference Vegetation Index (NDVI) values captured by satellite platforms indicate that northern ecosystems are experiencing rapid ecological change in response to climate warming. Increasing temperatures and altered hydrology are driving shifts in ecosystem biophysical properties that, observed by satellites, manifest as long-term changes in regional NDVI. In an effort to examine the underlying ecological drivers of these changes, we used field-scale remote sensing of NDVI to track peatland vegetation in experiments that manipulated hydrology, temperature, and carbon dioxide (CO_2) levels. In addition to NDVI, we measured percent cover by species and leaf area index (LAI). We monitored two peatland types broadly representative of the boreal region. One site was a rich fen located near Fairbanks, Alaska, at the Alaska Peatland Experiment (APEX), and the second site was a nutrient-poor bog located in Northern Minnesota within the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment. We found that NDVI decreased with long-term reductions in soil moisture at the APEX site, coincident with a decrease in photosynthetic leaf area and the relative abundance of sedges. We observed increasing NDVI with elevated temperature at the SPRUCE site, associated with an increase in the relative abundance of shrubs and a decrease in forb cover. Warming treatments at the SPRUCE site also led to increases in the LAI of the shrub layer. We found no strong effects of elevated CO_2 on community composition. Our findings support recent studies suggesting that changes in NDVI observed from satellite platforms may be the result of changes in community composition and ecosystem structure in response to climate warming.

KEYWORDS
boreal peatlands, carbon dioxide, climate change, community composition, NDVI, remote sensing, soil moisture, warming

1 | INTRODUCTION

An increase in vegetation greenness, as measured via the Normalized Difference Vegetation Index (NDVI), has been observed across the Northern Hemisphere in recent decades. A number of studies have linked this change to climate warming. Substantial evidence suggests that shorter, less severe winters are resulting in warmer spring

temperatures and extended growing seasons leading to changes in peak values and timing of NDVI (Delbart et al., 2008; Karlsen et al., 2009; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997; Tucker et al., 2001). Northern regions are also experiencing an increase in mean annual precipitation in both winter and summer seasons that may contribute to the changes observed in NDVI (Bintanja & Selten, 2014; Hinzman et al., 2005; Post et al., 2009; Walsh, Overland, Groisman, & Rudolf, 2011). The shift in greenness has been particularly pronounced in the high arctic and has been linked with an increase in shrub cover (Beck & Goetz, 2011; Goetz, Bunn, Fiske, & Houghton, 2005; Myers-Smith et al., 2011, 2015; Tape, Sturm, & Racine, 2006). Remote sensing studies of the boreal region have yielded mixed results compared to those in the arctic. Although previously consistent with arctic greening, trends in the boreal region reversed in the late twentieth century showing a decrease in NDVI ("browning"), likely resulting from moisture limitation (Beck & Goetz, 2011; Buermann et al., 2014; Myneni et al., 1997; Park et al., 2016; Phoenix & Bjerke, 2017; Piao et al., 2011; Verbyla, 2015). These findings highlight the complex spatiotemporal relationships among climate, vegetation change, and NDVI at regional scales.

Although there is strong indication that NDVI is changing across the boreal region, there is limited research describing what may be driving the observed trends. Given the low spatial resolution of many satellite products, combined with a limited number of field studies that manipulate global change drivers, it is unclear whether shifts in NDVI are the result of impacts on vegetation biophysical parameters (e.g., LAI), vegetation community composition, or other processes. The studies that have used NDVI as a monitoring technique in peatlands have found relationships with water table position (Meingast et al., 2014), standing biomass and rates of ecosystem production (Boelman, Stieglitz, Griffin, & Shaver, 2005; Boelman et al., 2003; Hope, Kimball, & Stow, 1993; La Puma, Philippi, & Oberbauer, 2007), and vegetation cover, particularly of shrubs (Hope et al., 1993; Meingast et al., 2014; Riedel, Epstein, & Walker, 2005; Walker et al., 2003). In this research, we sought to provide context to observed trends in NDVI through analysis of field-scale experiments that manipulate various global change drivers of peatland vegetation.

Peatlands are widely distributed across the circumpolar north. They account for approximately 19% of soil area in the northern permafrost region (Tarnocai et al., 2009). Because of their large carbon stores (Bridgham, Patrick Megonigal, Keller, Bliss, & Trettin, 2006; Gorham, 1991; Yu, Loisel, Brosseau, Beilman, & Hunt, 2010), peatlands are crucial to regulating the global climate system (Chapin et al., 2000). Furthermore, peatland ecosystems are particularly vulnerable to climate change because of the combined risk they face from rising temperatures and changing hydrologic conditions. Experimental manipulation of peatland hydrology has demonstrated that decreasing moisture availability results in peatlands becoming a source of CO_2 due to lower gross primary productivity (GPP) relative to ecosystem respiration (ER) rates in rich and poor fens, (Chivers, Turetsky, Waddington, Harden, & McGuire, 2009; Olefeldt et al., 2017; Radu & Duval, 2018; Strack, Waddington, Lucchese, &

Cagampan, 2009) and bogs (Weltzin, Harth, Bridgham, Pastor, & Vonderharr, 2001; Weltzin et al., 2000). Changes in hydrology also affect peat temperature (cf. Waddington et al., 2015). While increases in temperature have generally been shown to stimulate microbial activity and increase ER in peat (Moore & Dalva, 1993; Silvola, Alm, Ahlholm, Nykanen, & Martikainen, 1996), assessments of interactive effects among temperature, soil moisture, and vegetation production are difficult in field settings (Johnson, Pypker, Hribljan, & Chimner, 2013) and likely change over time (Chivers et al., 2009; Olefeldt et al., 2017). Yet, there are few long-term manipulation studies assessing the role of multiple climate drivers on bog and fen biophysical properties simultaneously (Dieleman, Branfireun, McLaughlin, & Lindo, 2015; Weltzin, Bridgham, Pastor, Chen, & Harth, 2003; Weltzin et al., 2000). Further understanding of the relationship between multiple global change drivers (e.g., warming, altered hydrology, and elevated CO_2), peatland ecosystem structure (i.e., LAI and community composition), and NDVI will elucidate recent trends in satellite observations across large areas of the boreal region.

Temperature and hydrology are strong controls on peatland community composition, which contributes to the carbon sequestration and storage potential of peatlands (Breeuwer et al., 2009; Dieleman et al., 2015; Goud, Moore, & Roulet, 2017; Olefeldt et al., 2017; Radu & Duval, 2018; Ward, Bardgett, McNamara, & Ostle, 2009; Weltzin et al., 2000). However, exactly how changes in climate affect vegetation community composition and function are likely to be different in bogs and fens, owing to differences in water residence time and nutrient status. For example, studies have shown that drying in nutrient-rich fen peatlands leads to an increase in shrub cover, a decrease in graminoid cover, and a decrease in annual GPP (Churchill, Turetsky, McGuire, & Hollingsworth, 2014). In nutrient-poor bog and nutrient-poor fen systems, drying can also lead to increases in shrub cover and decreases in graminoid and moss cover (Breeuwer et al., 2009; Potvin, Kane, Chimner, Kolka, & Lilleskov, 2015; Radu & Duval, 2018; Weltzin et al., 2000, 2003). However, effects of drying on productivity are mixed. Some studies have indicated that drying decreases GPP, while others have indicated that a shift from graminoid to shrub dominance could be associated with an increase in GPP, potentially offsetting increases in plant and soil respiration (Radu & Duval, 2018; Weltzin et al., 2000).

Several studies have found a significant effect of increasing temperature on peatland community composition and GPP. However, previous research has yielded a range of results depending on peatland hydrologic connectivity and nutrient status. For example, studies have indicated that warming in hydrologically connected fen peatlands leads to shifts in dominance from non-vascular *Sphagnum* mosses to vascular plants such as graminoids (Dieleman et al., 2015; Weltzin et al., 2003). However, in nutrient-poor bog peatlands that lack connectivity with groundwater, warming also could lead to drying, potentially favoring shrub cover over graminoids (Weltzin et al., 2000, 2003). Although shrub cover is correlated with GPP, it is less clear how the potential increase in aboveground

productivity will affect overall rates of ecosystem carbon exchange (Weltzin et al., 2000). These studies indicate that peatland above-ground productivity is determined by a series of complex and poorly resolved interactions among plant species, temperature, and hydrology.

While there is a developing literature on the effects of changing temperature and soil moisture on peatland ecosystem function, far fewer studies have investigated the effects of elevated CO_2 in peatlands. Peatland mesocosm experiments have yielded conflicting results that underscore the complexity of ecological responses to elevated CO_2. Some studies have shown that elevated CO_2 increases the productivity of peatland vascular plants, in particular graminoids (Dieleman et al., 2015; Grulke, Riechers, Oechel, Hjelm, & Jaeger, 1990). Others have indicated no changes in vascular plant growth resulting from CO_2 fertilization alone, but have documented that the combined effects of nitrogen and CO_2 enrichment led to increases in the growth of both graminoids and shrubs (Berendse et al., 2001; Heijmans et al., 2001). These studies found no significant effect of elevated CO_2 on non-vascular productivity (Berendse et al., 2001; Dieleman et al., 2015). Ombrotrophic bog peatlands are by definition nutrient-poor and typically dominated by *Sphagnum* mosses. This could indicate a relatively small effect of elevated CO_2 on the productivity of bogs as compared to fens. These studies suggest that bogs and fens might exhibit different responses to elevated CO_2 levels due to the unique responses of vascular versus non-vascular plant functional types (PFTs).

The objective of this research was to examine the effects of a variety of global change drivers on peatland community composition and NDVI. We leveraged two different peatland ecosystem manipulation experiments; one located in a nutrient-rich fen and one in a nutrient-poor bog to test the effects of altered hydrology, increased temperature, and elevated CO_2, on plant community composition, LAI, and NDVI. The Alaska Peatland Experiment (APEX) at the Bonanza Creek Long Term Ecological Station manipulates water table in a nutrient-rich fen. The Spruce and Peatland Responses Under Changing Environments (SPRUCE) project at the Marcell Experimental Forest, Minnesota, USA, manipulates temperature and CO_2 in a nutrient-poor bog. We predicted that drought would decrease NDVI at the rich fen site, coincident with a decrease in graminoid cover and an associated decrease in total leaf area. We predicted that warming and CO_2 fertilization would increase NDVI in the bog study system, coincident with a decrease in sedge cover and an increase in shrub cover, driving an overall increase in leaf area. Specifically, we predicted an increase in shrub cover with increasing temperature and elevated CO_2, and a decrease in graminoid cover coincident with drying. We hypothesized that NDVI would be highly sensitive to changes in vegetation composition, and in particular the abundance of woody shrubs. We measured the direct effects of changing climate drivers on biophysical and compositional properties of peatland vegetation, in order to further remote sensing applications in the area of global change ecology.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted at two large-scale experiments representative of two types of common northern boreal peatlands—bogs and fens. Here, we examined the effects of altered hydrology in a fen ecosystem, which naturally have fluctuating water tables, while the effects of altered temperature and atmospheric CO_2 were examined in a bog ecosystem lacking groundwater connectivity. The first site was at the APEX at the Bonanza Creek Long Term Ecological Research Station, located forty kilometers west of Fairbanks, Alaska (64.82°N, 147.87°W). The experiment is located in a sedge-and-shrub-dominated rich fen on the floodplain of the Tanana River (See Table 2 for species list). APEX was initiated in 2005 to assess the long-term effects of altered hydrology on peatland ecology and biogeochemistry (Kane, Turetsky, Harden, McGuire, & Waddington, 2010; Kane et al., 2013; Olefeldt et al., 2017; Turetsky et al., 2008). APEX consists of three water table manipulation plots, a raised, lowered, and control treatment, each 120 m² in size. The lowered treatment plot is drained by a trench (~40 cm wide, ~1 m deep) into the peat, which ranges in depth from 1 to 1.5 m. Water from the trench is then pumped into the raised water table treatment to keep it consistently flooded near the peat surface. The hydrology in the control plot is not manipulated, and its water table typically falls somewhere between the raised and lowered treatment plots. Target separation among water table treatments is approximately 20 cm during the growing season; however, there has been considerable inter- and intra-annual variability in water table position over the last decade, consistent with variable hydrology in fen ecosystems (Olefeldt et al., 2017).

The second study site was at the SPRUCE project located at the Marcell Experimental Forest in northern Minnesota, USA (47.30°N, 93.29°W). The SPRUCE experiment was designed following a regression-based model in which ecological change could be measured in response to a broad range of increasing temperature treatments (Hanson et al., 2017). SPRUCE treatments were initiated in 2014 to explore the effects of increased above- and belowground temperatures and elevated CO_2 on ecological and biogeochemical processes at the southern edge of the boreal biome (Tfaily et al., 2014). The experiment is located within an ombrotrophic bog dominated by *Sphagnum* mosses, black spruce (*Picea mariana*) and tamarack (*Larix laricina*), with an understory of ericaceous shrubs, graminoids, and forbs. The experimental design consists of ten enclosed treatment plots with five temperature treatments (0, 2.25, 4.5, 6.75, and 9°C) with and without elevated CO_2 (~900 ppm). The above- and belowground temperature treatments are implemented by maintaining a fixed differential from actual temperatures in the two reference plots. The plots consist of octagonal enclosures that are 12.8 m in diameter (114.8 m² in area), 8 m tall, with a belowground corral that penetrates through the peat to glacial material below, which averages 2.5 m deep across the site. The enclosures are maintained at a series of increasing temperatures by forced air and deep peat

heating across a range of possible climate change scenarios (Hanson et al., 2017).

2.2 | Vegetation cover sampling and measurement of LAI

To determine the effects of experimental manipulation on community composition, surveys of species presence were conducted at both experiments. Slightly different sampling strategies were followed at each site, according to the protocols associated with each experiment (Table 1). At APEX, species cover was recorded using a Point Bar Vegetation Survey method (Bonanza Creek LTER; Jonasson, 1988). At the lowered and raised treatments, four replicate plots were sampled, and in the control treatment, five replicates were sampled. Two transects were established perpendicular to each other across each of the 4–5 replicate 1 × 1 m vegetation plots. A laser pointer was inserted into 10 evenly spaced holes in a meter-long metal frame positioned at 1 m above soil surface for each of the two transects, for a total of 20 points sampled per 1 × 1 m vegetation plot. In total, 80 or 100 points were sampled across the water table treatments. At each interception of the laser, species and height above the ground were recorded from the canopy to the surface of the peat. All live biomass was identified to species, and dead biomass was marked as "litter," indicating that it was part of the thatch forming at the surface of the peat. Species were then categorized into PFT (Table 2), and percent cover of each PFT was calculated for each plot based on the number of hits of each PFT relative to the entire sample.

Leaf area index at APEX was calculated as the number of layers of photosynthetic vegetation between the canopy and the soil surface. The fractional cover of photosynthetic vegetation to non-photosynthetic vegetation (PV/NPV) was also calculated in each plot by taking the ratio between measured green leaf area and litter cover. Along with LAI, fractional cover of green leaf area to bare soil or litter has been shown to relate to NDVI due to the absorption of infrared light by non-photosynthetic biomass and exposed earth (Carlson & Ripley, 1997). Thus, both LAI and the PV/NPV ratio were examined as potential drivers of NDVI.

Vegetation composition at SPRUCE was sampled at peak growing season in the 12 chambers spanning the full range of temperature and CO_2 treatments, plus the unchambered references. In each chamber, three plots 2 m^2 in size were sampled using a gridded frame of 1 × 2 m that was set onto fixed PVC pipes installed at each plot corner to facilitate repeated data collection over the same area. Each frame was divided into 50 – 20 × 20 cm cells. The presence and absence of all species were recorded for each cell of the grid. Species were categorized into PFT's for analysis according to the SPRUCE protocol (Table 2). We determined frequency of each PFT (as a surrogate for percent cover) as the number of cells where at PFT is present divided by the total number of cells sampled.

Leaf area index was measured at SPRUCE using an LI-COR LAI 2200 (Lincoln, NE) instrument that estimated leaf area per unit ground area as the amount of incoming light available below a canopy (Gower & Norman, 1991). LAI measurements were taken in late June of 2017, at peak growing season. Measurements were done near mid-day on a cloud-free day. The reference sensor was positioned on a tripod in an open meadow with no nearby tree cover. Sensors were matched at the beginning of the field campaign. Light diffusing lenses were used on both sensors to create uniform light conditions. Measurements were taken at two central sampling locations in each of the three vegetation community plots in each chamber. At each sampling location, two scans were taken each at 1 m above the shrub canopy and beneath the shrub canopy at the surface of the peat. The measurements taken above the shrubs represented the LAI of the tree canopy, which were then subtracted from the LAI values for the shrub layer to examine the effect of treatment on the shrub layer.

2.3 | NDVI time series data collection

Both sites were instrumented with Decagon Inc. (Pullman, WA) NDVI sensors (Gamon, Kovalchuck, Wong, Harris, & Garrity, 2015) at the beginning of the 2016 growing season. They consisted of two sensors that measured irradiance at 630 and 800 nm, one upward looking to measure incoming light and the other downward looking to measure reflected light. The hemispherical (incoming) sensor is cosine corrected to account for sun angle. The downward-pointing sensor has a field of view (FOV) of 36°, and each sensor was installed at a height of 150 cm above the peat surface at both sites, which results in an instantaneous FOV of approximately 53 cm in diameter. Data were stored on Em50G data loggers with measurements collected every 10 min throughout the growing season. NDVI was automatically calculated as the normalized ratio of a visible and a near-infrared band.

$$NDVI = \frac{810\,nm - 650\,nm}{810\,nm + 650\,nm}. \tag{1}$$

Three NDVI sensors were installed at APEX, one in each water table manipulation plot. The NDVI sensors at APEX were installed above an instrument-free area of the plot to avoid disturbance from manual measurement or interference by other objects. Six sensors were installed at SPRUCE, in the +0°C, +4.5°C, and +9°C chambers, with one sensor each in an ambient and elevated CO_2 chamber at each temperature. Sensors were installed above undisturbed community composition plots that are not instrumented or destructively sampled in any way. At both experiments, care was taken to ensure that the location above which sensors were installed was representative of the treatment as a whole. At both sites, the vegetation canopies had largely homogenous species cover, and the results from vegetation surveys indicated no statistically significant differences in cover among plots within treatments (see Results, Section 10).

During processing of the APEX field data, only NDVI values between 11:00 a.m. and 2:00 p.m. were included in the analysis, or approximately 2 hr on each side of solar noon (Gamon et al., 2015).

TABLE 1 Description of two study sites, data types, and differing data collection methods between sites

	APEX	SPRUCE
Peatland type	Rich fen	Ombrotrophic bog
Location	Alaska, USA	Minnesota, USA
Experimental design	Water table manipulation with 120 m² control, lowered and raised treatments	Regression-based factorial between increasing temperature and CO_2 level
Vegetation sampling	Point bar laser survey method	2 m² sampling frame method
LAI	Point bar laser survey method	LI-COR LAI 2200
Spectral reflectance	ASD FieldSpec Pro	Unispec-DC
Decagon NDVI sensors	One each located in the control, lowered and raised WT treatments (3 total)	Two each located in the +0, +4.5, and +9°C chambers, one each n an ambient and elevated CO_2 chamber (6 total)

Note. APEX: Alaska Peatland Experiment; LAI: leaf area index; NDVI: Normalized Difference Vegetation Index; SPRUCE: Spruce and Peatland Responses Under Changing Environments.

At SPRUCE, only values between 11:00 a.m. and 1:00 p.m. were included in the analysis. We used a slightly narrower window at SPRUCE given the differences in day length between the two sites. In addition, a threshold of 0.5 was applied at both sites to exclude NDVI measurements that may have occurred during very overcast days. The exclusion of observations taken when the sun was not directly overhead at both was done to minimize the potential for shading. At APEX, this was less of an issue since the site is open, hence the larger window of usable data, whereas SPRUCE has an intermittent canopy of spruce and tamarack trees, as well as a greater amount of instrumentation and interference by the chamber walls. For both sites, a daily average NDVI value was calculated for each measurement location.

2.4 | Plot-level measurement of NDVI

To make a direct comparison of the relationship between community composition and NDVI, we also collected one-time plot-level measurements of NDVI using handheld spectroradiometers above all of the vegetation plots at both study sites. At APEX, we used an Analytical Spectral Devices FieldSpec Pro (Boulder, CO). Incoming solar reflectance was measured relative to a white Spectralon reference panel that reflected 100% of incoming radiation. Measurements were recorded under clear sky conditions, and white reference scans were performed between spectral data collection at each water table treatment plot, or approximately every 5 min. Scans were performed at one meter above ground surface at nadir with a 25 degree foreoptic, resulting in a ground FOV that was 47 cm in diameter:

$$GFOV = 2\frac{\text{height} \times \tan(25°)}{2}. \tag{2}$$

Data were collected during peak growing season, on June 29, 2016. Scans were performed within a 1-hr window on each side of solar noon, which occurred at approximately 12:30 p.m. Reflectance was calculated "on the fly" by the instrument against a white reference scan that was performed immediately prior to data collection using a Spectralon panel (North Sutton, NH). White reference scans were performed between plots, or approximately every minute.

Three scans were recorded above each vegetation plot and then averaged. NDVI was calculated using the same bands as the Decagon sensors (see Equation 1).

Sampling at SPRUCE was done using a PP Systems UniSpec-DC (Amesbury, MA) spectroradiometer. The fiber-optic cable on the Unispec was fitted with a FOV restrictor that limited the FOV to approximately 15°. The instrument foreoptic was leveled at 1 m above the ground capturing an area of approximately 35 cm in diameter or 0.1 m². Three scans were performed above each vegetation plot and averaged. White references scans were performed between each treatment. Reflectance was calculated for the average of the three scans following the methods of Harris, Gamon, Pastorello, and Wong (2014) and Wang et al. (2016).

$$\frac{R_{\text{target}}/I_{\text{downwelling}}}{R_{\text{panel}}/I_{\text{downwelling}}}. \tag{3}$$

In this equation, R_{target} is the light reflected from the vegetation canopy, R_{panel} refers to the reflectance of the white reference panel, and $I_{\text{downwelling}}$ refers to the upward-pointing sensor measuring the incoming solar radiation. Data were collected in late season on September 22, 2016, under clear sky conditions beginning at 1:00 p.m. Data from the Decagon NDVI time series indicated that the growing season was just past peak greenness at this time (Figure 2), and showed strong separation among treatments. NDVI was calculated for each plot following Equation 1. We also performed a spectral resampling method to the ASD and Unispec data to account for differences in the spectral resolution and spectral response among instruments used in data collection (Supporting Information Appendix S1). Finally, we compared the NDVI values collected using the handheld spectral sensors with the NDVI values captured on the same day by the Decagon sensors to determine whether there was agreement among instrument types. We found a high level of agreement between NDVI values captured across platforms (see Supporting Information Figure S1).

2.5 | Data analysis

Vegetation cover data were analyzed for differences in PFT cover among the treatments at each site. Data were analyzed using a

TABLE 2 List of species present at both peatland sites and plant functional groupings used in analysis

SPRUCE		APEX	
Plant functional type	Species	Plant functional type	Species
Forb	*Drosera rotundifolia*	Equisetum	*Equisetum fluviatile*
Forb	*Maianthemum trifolium*	Forb	*Galium trifidum*
Graminoid	*Carex magellanica*	Forb	*Potamogeton gramineus*
Graminoid	*Carex oligosperma*	Graminoid	*Calamagrostis canadensis*
Graminoid	*Carex trisperma*	Graminoid	*Carex loliacea*
Graminoid	*Eriophorum vaginatum*	Graminoid	*Carex utriculata*
Graminoid	*Eriophorum virginicum*	Moss	*Sphagnum spp.*
Shrub	*Andromeda polifolia*	Shrub	*Potentilla palustris*
Shrub	*Chamaedaphne calyculata*		
Shrub	*Kalmia polifolia*		
Shrub	*Rhododendron groenlandicum*		
Shrub	*Vaccinium angustifolium*		
Shrub	*Vaccinium oxycoccos*		

Note. APEX: Alaska Peatland Experiment; SPRUCE: Spruce and Peatland Responses Under Changing Environments.

multi-variate non-metric multidimensional scaling ordination using a Bray–Curtis dissimilarity index to assess community-level differences among treatments. Permutation tests were used in both cases to determine whether statistically significant differences existed in composition among treatments and to determine the strength of the relationship between NDVI and community composition. Stress plots were used to diagnose the goodness of fit of the model. An alpha level of 0.05 was used to determine whether treatment was a statistically significant predictor of variation within the community ordination. The same method was used to determine whether plot-level NDVI values were significantly correlated with variation in community composition. R-Vegan was used for all multi-variate analyses (Oksanen et al., 2017).

We tested the effects of treatments on LAI and the ratio of photosynthetic to non-photosynthetic cover at APEX using a one-way ANOVA with an alpha level of 0.05, with a Bonferroni post hoc comparison of means to examine differences among treatments. LAI for SPRUCE was analyzed using a linear regression model with temperature as a continuous variable and CO_2 level included as a factor (Hanson et al., 2017).

Responses of NDVI to treatment at both sites were analyzed using ANOVA with date as a random effect. At SPRUCE, a two-factor ANOVA was used, with temperature included as a continuous variable and CO_2 level as a categorical variable. At APEX, a one-way ANOVA was used, with water table treatment included as a categorical variable. We also fit the processed daily time series data with seasonal curves to determine how treatment affected the timing of green-up, senescence, and peak NDVI. We fit the models using Gaussian parameters following the methods outlined in Chivers et al. (2009) and Wilson et al. (2007) for modeling seasonal vegetation dynamics in peatlands. Our model assumed that seasonal development of NDVI was unimodal and normally distributed. In our model:

$$\text{Daily NDVI}_i = 1e\left(-0.5\left(\frac{\text{JD} - \text{NDVI}_{max}}{b}\right)^2\right) \quad (4)$$

where Daily NDVI_i is daily NDVI in treatment i, NDVI_{max} is the maximum NDVI value for the season, JD is the Julian day, and b describes the shape of the Gaussian curve, estimated as one standard deviation on each side of NDVI_{max}.

3 | RESULTS

3.1 | Response of NDVI to hydrologic change, warming, and elevated CO_2

Model results show a highly significant effect of long-term hydrologic change at APEX on NDVI (ANOVA, $F_{2,156}$ = 7.54, $p < 0.001$). Values were significantly higher in the control and raised plots as compared to the lowered plot, which had lower NDVI values throughout the entire growing season (Figure 1). The lowered plot also peaked at a lower value compared to the control and raised treatments (Table 3). NDVI was highest in the control plot during the early part of the growing season and showed greater peak values than either of the other treatments (Table 3). However, in the second half of the growing season, the raised plot had the greatest NDVI, which peaked at a somewhat later date (Figure 1, Table 3).

Normalized Difference Vegetation Index at SPRUCE showed a clear positive response to warming (Figure 2), but a mixed response to CO_2 level (Figure 3). Statistical analysis indicated a significant temperature effect and an effect of the interaction between temperature and CO_2 level, but a non-significant effect for CO_2 on its own (Table 4). The chamber with the highest NDVI throughout the growing season was the +9°C treatment with elevated CO_2 (Figure 2, Table 3).

Overall, NDVI at both sites responded strongly to treatment, and at both sites, the effect was evident early in the spring and was persistent throughout the entire growing season. Warming appeared to extend the growing season, and drought appeared to result in a decreasing trend in NDVI. Both sites exhibited strong seasonal trends in NDVI, but had very different seasonal curves. At APEX, NDVI was already at above 0.5 when the sensors were installed, but by late August, vegetation senescence resulted in a rapid drop off in NDVI, whereas at SPRUCE, NDVI remained high (i.e., above 0.8) into late fall. These site differences may be attributed to differences in both experimental design and plant community type, as well as the differences in growing season length in Minnesota versus Alaska (Table 2).

3.2 | Vegetation cover and LAI in response to hydrologic change, warming, and elevated CO_2 and relationship to NDVI

We found differences in community composition by treatment at APEX. We found a higher average percent cover of graminoids in the raised and control plots (30% and 24%, respectively), as compared with the lowered plot (21%). We also found a 5%–10% greater cover of shrubs, equisetum, and mosses in the control plot over either of the other two plots. The lowered plot had a 10%–20% greater litter cover than the raised or control plots. Results from the community ordination indicate a stress of 0.08 for two dimensions, and the permutation test indicated that water table treatment was significantly correlated with variation in community composition ($R^2 = 0.41$, $p = 0.025$). NDVI was also correlated with variation in community composition ($R^2 = 0.50$, $p = 0.040$). The percent cover of forbs and shrubs accounted for the largest sources of variation in the non-metric multidimensional ordination (NMDS). The raised water-table treatment was associated with greater cover of forbs as compared to the control (Figure 4a). The control was associated with

the greatest cover of shrubs and mosses compared to other treatments. Both the raised and control plots were associated with higher NDVI compared to the lowered plot, which was associated with greater litter cover relative to either of the other treatments. We did not observe any differences in community composition among replicate plots within water-table treatments indicating a homogenous canopy within each treatment.

We did not find significant differences in LAI among treatments at APEX (Figure 4b). However, in our analysis of fractional cover we found that the ratio of photosynthetic to non-photosynthetic leaf area was significantly higher in the raised and control plots than the lowered plot ($F_{2,10} = 6.72$, $p = 0.014$). The overall percent cover of litter was marginally greater in the lowered water table plot relative to either the control or raised plots ($F_{2,10} = 4.16$, $p = 0.049$). We attribute the lack of significant difference in LAI among treatments to the generally low LAI found at APEX (typically less than 2).

Results from the community composition sampling at SPRUCE indicated that the warmest treatments had approximately 10% greater shrub cover on average than the control plots, which had an 8% greater cover of forbs. The NMDS results of the community data at SPRUCE indicated that the temperature treatment was a strong correlate with community composition (stress, 0.33; permutation test $R^2 = 0.33$, $p = 0.004$). Warmed plots were associated with greater shrub cover, whereas ambient plots were associated with a greater cover of forbs (Figure 5a). LAI at SPRUCE showed a clear positive effect of warming (Figure 5b; $R^2 = 0.68$, $F_{3,34} = 23.8$, $p < 0.001$, RMSE = 0.93). NDVI was positively associated with temperature treatment (Figure 5a panel; $R^2 = 0.26$, $p = 0.037$), and thus by proxy shrub cover and LAI. We found no strong effects of elevated CO_2 on community composition. We also did not observe any differences in community cover among plots within temperature treatment.

Altogether, the results indicate that temperature (SPRUCE) and water table position (APEX) are strong controls on functional group

FIGURE 1 Normalized Difference Vegetation Index (NDVI) response to long-term water table manipulation at Alaska Peatland Experiment. Weekly values are pictured for clarity. Daily NDVI values are fitted with a seasonal curve derived using a non-linear least-squares regression model. Error bars represent standard deviation of the mean
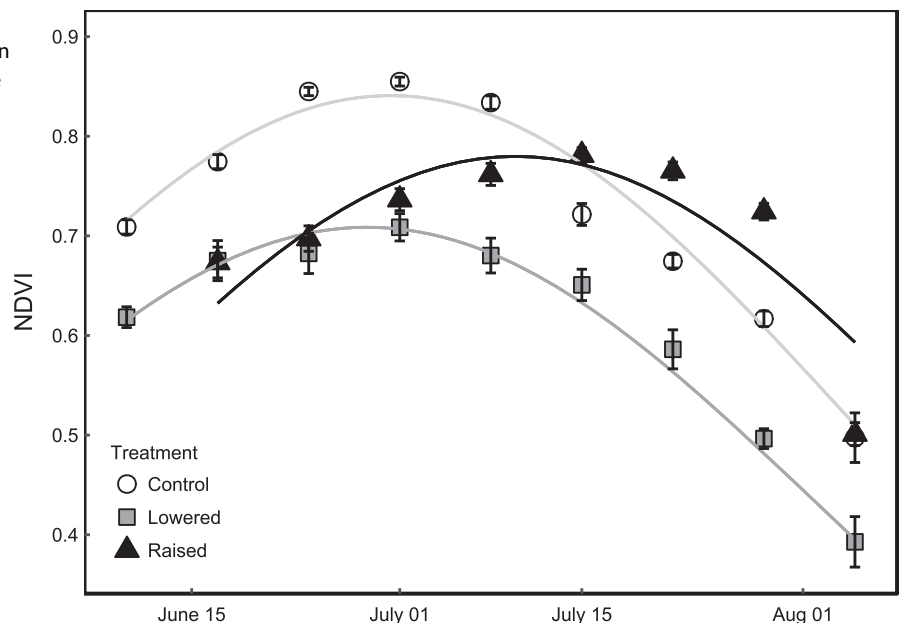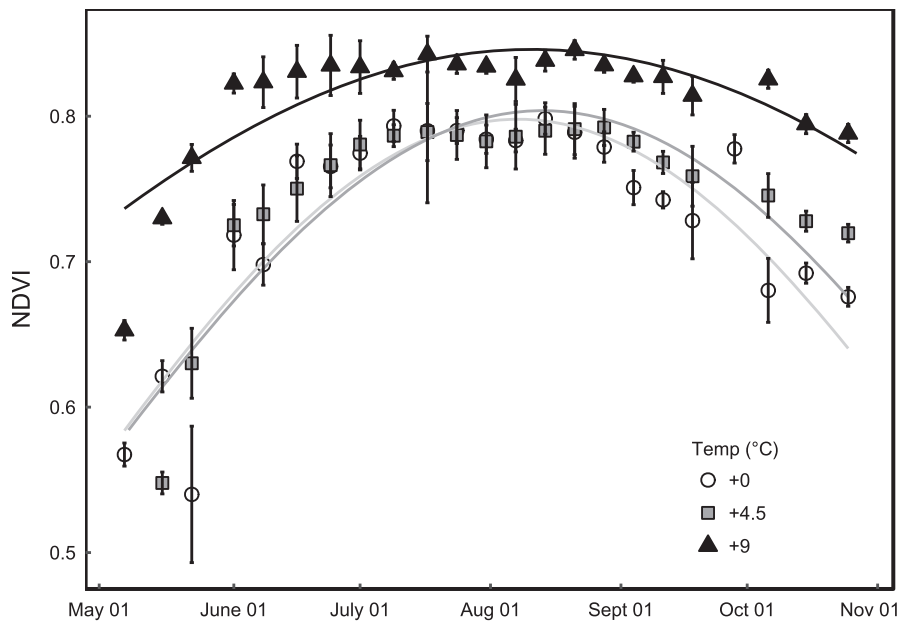
FIGURE 2 Spruce and Peatland Responses Under Changing Environments (SPRUCE) Normalized Difference Vegetation Index (NDVI) in response to warming at SPRUCE. Weekly values are pictured for clarity. Daily NDVI values are fitted with a seasonal curve derived using a non-linear least-squares regression model. Error bars represent standard deviation of the mean

composition and overall leaf area across different peatland ecosystems. These results also demonstrate that variation in community composition induced by warming and altered hydrology has significant effects on NDVI.

4 | DISCUSSION

We observed significant effects of experimental manipulation on community composition, LAI, and NDVI associated with warming and hydrologic change. We discerned strong differentiation in composition at both sites, largely resulting from differences in the relative percent cover of shrubs, and changes in overall vascular leaf area. Changes in composition and LAI resulted in a strong effect on NDVI at both sites, indicating that the productivity and stature of vegetation in peatland ecosystems responded strongly to simulated climate change. These results are consistent with previous studies that have found positive relationships between NDVI and peatland ecosystem productivity (Boelman et al., 2003, 2005). The effects of treatment on NDVI manifested as changes in peak NDVI values and in the timing of senescence in the manipulated ecosystems. These results highlight the role that shifting vegetation communities will play in determining ecosystem productivity in response to climate change in boreal peatlands.

4.1 | Response of NDVI to long-term hydrologic change

We observed strong responses in both community composition and NDVI to long-term hydrologic change. The response of NDVI observed at the APEX site is consistent with prior research that found an overall decrease in GPP with long-term drought (Churchill et al., 2014; Olefeldt et al., 2017). We found that the fraction of photosynthetic to non-photosynthetic leaf area was significantly

higher in the raised and control water-table treatments as compared to the lowered water-table treatment. This indicates that, even if overall LAI showed only a non-significant trend toward being lower in the lowered water-table plot, the greater relative cover of litter to photosynthetic leaf area is likely driving this trend in NDVI. Many studies have found that the relative cover of photosynthetic biomass is related to NDVI due to differences in the reflectance properties of living versus dead vegetation in both the visible and infrared regions of the electromagnetic spectrum (Gamon et al., 1995; Walker et al., 2003). In the case of APEX, differences in NDVI can most likely be attributed to differences in fractional cover, as well as decrease in graminoid cover in the lowered plot (Churchill et al., 2014). We also saw greater cover of shrubs, forbs, and mosses in the control plot, which were correlated with NDVI in our community ordination. Overall, low photosynthetic cover contributed to low NDVI values in the lowered plot, while higher leaf area and a greater cover of a variety of PFTs contributed to higher NDVI values in the control plot.

We saw differences in NDVI even though the summer of 2016 was extremely rainy in central Alaska, and so achieving separation of water tables proved to be impossible late in the growing season (See Supporting Information Figure S2). Adding to this complexity, the peat surface has actually been subsiding at the lowered plot relative to the control and raised plots over time (Olefeldt et al., 2017), meaning that height of the water table above peat surface is actually greater over the lowered plot than that of the other treatments during flooded conditions (Supporting Information Figure S2). It is possible that this unequal pattern of flooding led to further decreases in NDVI as high water differentially occluded the signal from the vegetation (Figure 1). However, since NDVI had already peaked and begun to decrease in the lowered and control plots well before the major flooding occurred, the results from APEX should be interpreted primarily as the result of long-term hydrologic changes rather than the result of seasonal differences in water table position.
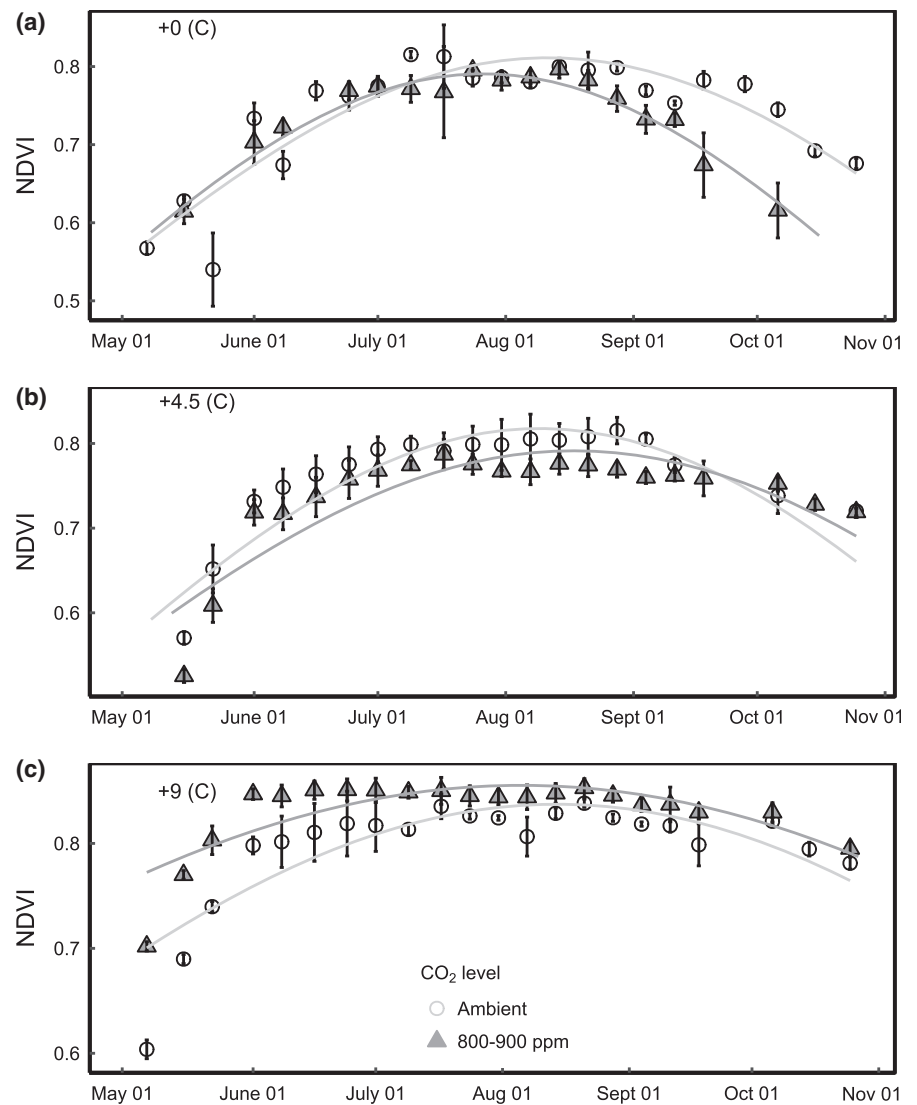
FIGURE 3 Effects of CO_2 on Normalized Difference Vegetation Index at Spruce and Peatland Responses Under Changing Environments experiment. Top: +0°C; middle: +4.5°C; bottom: +9°C temperature treatments

Unlike in the lowered water-table plot, we did not find strong differences in PFT cover between the control and raised water-table treatments. Therefore, the differences observed in NDVI between the control and raised water-table plots are more difficult to explain, particularly the seasonal dynamic in which NDVI in the raised plot peaked nearly a month later than the control plot (Figure 1). Given the results of our analysis of community composition, variation in NDVI may reflect differences in phenology resulting from subtle variation in species cover. For example, the control plot has a greater cover of one sedge species, *Carex utriculata*, whereas the raised plot has greater number of different sedge species, as well as a higher cover of mosses and forbs. Because sedges have been shown to begin senescing earlier than herbs or ericaceous shrubs, the differing NDVI seasonal curves could be attributed to the phenology of these plant functional groups (Leppälä, Kukko-Oja, Laine, & Tuittila, 2008). An additional unexplored attribute of GPP that was not addressed through this study was the possibility of algal production during periods of inundation (DeColibus et al., 2017; Wyatt et al., 2012). Given the flooding that occurred in 2016, particularly later in the growing

season, it is possible that algal growth masked some changes in vascular plant NDVI late in the growing season when water tables were high (Supporting Information Figure S2). The high water table also changes the relative stature of the vegetation, increasing the importance of open water reflectance and associated effects of chlorophyll-producing microorganisms. Further research on this topic could be particularly relevant in employing remote sensing data to track vegetation changes resulting from inundation or drainage across the northern region (Osterkamp & Romanovsky, 1999; Riordan, Verbyla, & McGuire, 2006).

4.2 | Response of NDVI to warming and elevated CO_2

We observed a particularly strong effect of warming on all aspects of vegetation community composition and biophysical properties measured at SPRUCE. Results indicate a strong positive effect of warming on NDVI, consistent with prior research findings (Boelman et al., 2003). This was particularly pronounced for the +9°C

TABLE 3 Model coefficients generated using non-linear least-squares regression analysis

Treatment	Model results					
	NDVI$_{Max}$ (k)	NDVI$_{Max}$ JD	b (σ)	n days	RSS	RMSE
APEX						
Control	0.841	182	35.721	57	0.026	0.022
Lowered	0.709	180	34.739	57	0.069	0.035
Raised	0.780	192	35.333	50	0.071	0.038
SPRUCE						
+0	0.798	221	118.333	150	0.115	0.028
+4.5	0.804	226	123.170	151	0.113	0.027
+9	0.846	224	183.814	149	0.046	0.018
+0 Ambient	0.811	224	117.443	150	0.137	0.030
+0 Elevated	0.791	209	104.554	122	0.045	0.019
+4.5 Ambient	0.818	222	117.396	139	0.108	0.028
+4.5 Elevated	0.791	231	131.007	146	0.114	0.028
+9 Ambient	0.837	227	167.963	144	0.062	0.021
+9 Elevated	0.855	219	202.688	147	0.037	0.016

Notes. Models were fit by transforming date into Julian day values and then using peak NDVI values and standard deviation on either side of the peak to fit Gaussian curves to seasonal trends in NDVI. NDVI$_{Max}$ refers to peak NDVI (i.e., k in a Gaussian distribution), NDVI$_{Max}$JD refers to the date of NDVI$_{Max}$, b denotes the shape of the curve (i.e., σ in a Gaussian distribution), and n denotes the number of days of observations used to fit the model. RSS is the model residual sum of squares, and RMSE is the model root mean square error.
APEX: Alaska Peatland Experiment; NDVI: Normalized Difference Vegetation Index; SPRUCE: Spruce and Peatland Responses Under Changing Environments.

TABLE 4 SPRUCE model of NDVI in response to experimental manipulation of temperature and elevated CO_2

SPRUCE	df	SS	MS	F value	p
Temp	2	1.033	0.517	179.850	**<0.001**
CO_2	1	0.001	0.001	0.02	0.655
Temp:CO_2	1	0.003	0.046	16.116	**<0.001**
Residuals	841	2.415	0.003		

Notes. Temperature was a continuous variable, and CO_2 was a factor (NDVI ~ temp * CO_2 + Error (Date). Bold p-values indicate statistically significant difference among treatments at a 95% confidence level.
MS: mean of squares; NDVI: Normalized Difference Vegetation Index; SPRUCE: Spruce and Peatland Responses Under Changing Environments; SS: sum of squares.

treatment, which had greater NDVI throughout the growing season. The +4.5°C treatment had similar NDVI values to the control treatments in the early and middle part of the growing season, but appeared higher than the control plots in the fall. An extension in growing season length with warming is to be expected, and these results are consistent with previous studies that have examined changing phenology across the Northern Hemisphere (Menzel et al., 2006; Peñuelas & Filella, 2001). Shrub layer LAI also showed a strong positive linear response to warming. Warming is the probable driver of changes in LAI and increases in NDVI. Because the results of our NMDS analysis indicate a shift in the relative abundance of forbs and shrubs associated with warming, it is likely that the increase in both LAI and NDVI is resulting from an increased

abundance of shrubs with warming. Because LAI is highly correlated with GPP, this result, along with our NDVI data, points to an overall increase in aboveground GPP of this vegetation layer, coincident with an increase in shrub cover.

These results support several of the central hypotheses of the SPRUCE experiment. The original SPRUCE hypotheses predicted that annual net primary production (NPP) would not increase with warming overall, but that GPP would increase in some species and decrease in others. Shifts in GPP will be due primarily to the effects of warming on peat soil moisture content and water table position which will favor vascular plants over mosses (Weltzin et al., 2003). An increase in the GPP of vascular plants and a decrease in the productivity of *Sphagnum* and other bryophytes resulting from interactions between temperature, soil moisture content, and nutrient availability are also predicted. Although our findings suggest an increase in GPP, NDVI is unsuited to examine belowground responses to warming. Pairing NDVI measurements with ecosystem CO_2 flux measurements would help to further elucidate the relationship between apparent increases in productivity and potential changes in the rate of ER.

Our results also support the hypothesis of the SPRUCE project postulating that elevated CO_2 will have a greater effect on GPP at higher temperatures. Elevated CO_2 levels did not have a clear effect on NDVI in the ambient or +4.5°C treatments, but appeared to have an interactive effect at +9°C, as supported by our model result indicating a significant interaction between CO_2 and warming (Table 2). Our results are also supported by research that suggests that the positive effects of elevated CO_2 on photosynthesis increase with
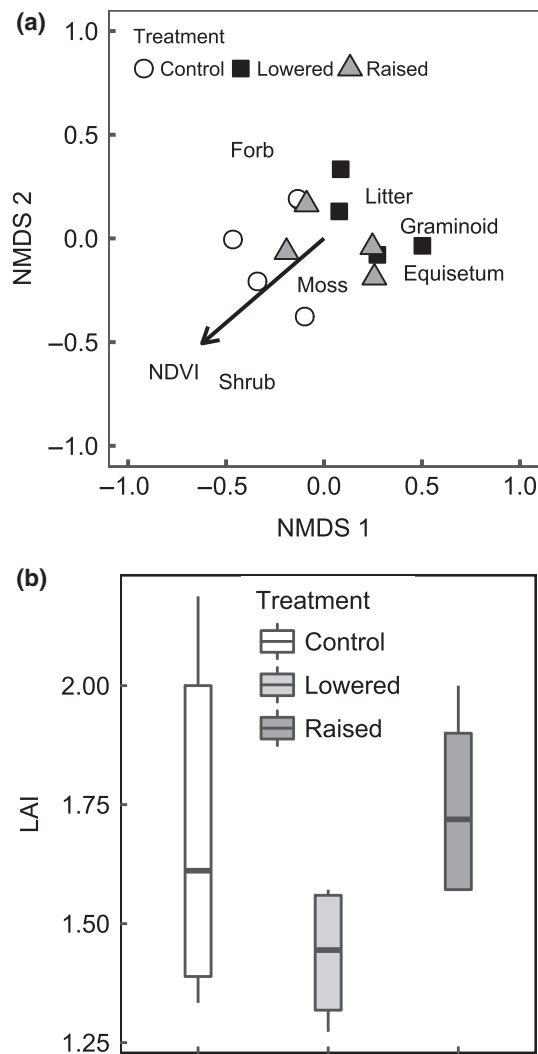
FIGURE 4 NMDS and leaf area index (LAI) results for Alaska Peatland Experiment (APEX) 2016 community composition. (a) APEX community results with treatment indicated by shape and Normalized Difference Vegetation Index mapped on to denote relationship to variation within community composition. (b) LAI in response to water table manipulation at APEX in which water table treatment is analyzed as a factor

warming (Long, 1991; Luo et al., 2008). As is the case with warming alone, this result may also be due to interactions between changing species composition and increases in leaf area and biomass in existing species. Research on the effects of carbon enrichment on *Sphagnum* has yielded contradictory findings; some studies have indicated that moss growth increases in response to elevated CO_2, and others have shown no effect (Berendse et al., 2001; Heijmans et al., 2001). However, a number of studies have shown that the productivity of vascular plants, particularly graminoids, increases in response to elevated CO_2 (Morgan et al., 2011; Norby et al., 2002; Nowak, Ellsworth, & Smith, 2004; Owensby, Ham, Knapp, & Auen, 1999). Although we cannot say definitively to which PFTs the apparent effects of elevated CO_2 in the +9°C treatment may be attributed, we would expect the positive effects of CO_2 enrichment to primarily

affect vascular PFTs. Because peatlands are characterized by a variety of vascular and non-vascular plants depending on their nutrient availability, we predict that future response of peatland vegetation to elevated CO_2 will be highly species-specific and dependent on nutrient status of the peatland (e.g., bog vs. fen).

4.3 | Relationship of NDVI to ecosystem GPP

Research has shown that NDVI correlates with aboveground NPP (Boelman et al., 2003), GPP (La Puma et al., 2007), and LAI (Carlson & Ripley, 1997; Walker et al., 2003) and can therefore be thought of as combining multiple ecological responses to experimental manipulation into one measurement. Since NDVI responds to a variety of plant and community-level processes, it is difficult to identify the locus of the treatment effect, whether changes in species composition, leaf area, or leaf-level processes. In the case of APEX, differences in NDVI were due to the long-term effects of a decade worth of hydrologic manipulation on community composition and photosynthetic biomass. As discussed above, in high water years such as 2016 algal production could also have contributed photosynthetic capacity to the NDVI signal, because algal production is influenced by water table history at this site (DeColibus et al., 2017; Wyatt et al., 2012). At SPRUCE, warming affected the species composition and leaf area of the vegetation community, which in turn had a strong effect on NDVI. Further measurement of leaf and ecosystem-level gas exchange and biomass measurements would strengthen our understanding of how unique peatland taxa are responding to global change.

Despite the demonstrated relationship between NDVI and GPP, recent literature on NDVI in moss-dominated systems has revealed limitations that should be considered when extrapolating these results to satellite observations of arctic and boreal change (May, Parker, Unger, & Oberbauer, 2018). Studies have shown that the unique moisture-holding capacity of non-vascular plants leads to poor relationships between GPP and NDVI due to the potential for large changes in spectral reflectance characteristics following the desiccation or re-wetting of moss communities (Bubier, Rock, & Crill, 1997; May et al., 2018). Further, it has been shown that light-use efficiency, which forms the basis for the NDVI-GPP relationship, varies significantly in response to warming and drying in non-vascular plants as compared with vascular species (Huemmrich et al., 2010; Kross, Seaquist, & Roulet, 2016). At APEX, which is dominated by tall graminoid species, mosses accounted for <10% of total cover on average in 2016. However, SPRUCE has significant moss cover, which has been negatively affected by the warming treatments. Although an examination of the role of moss decline on NDVI at SPRUCE was outside of the purview of this research, future remote sensing of peatlands should certainly take the role of non-vascular responses to climate change into account. Some studies have suggested that alternative indices that are more sensitive to foliar moisture content may aid in evaluating the response of moss-dominated communities to warming and hydrologic change (Harris, 2008; Meingast et al., 2014; Van Gaalen, Flanagan, & Peddle, 2007).
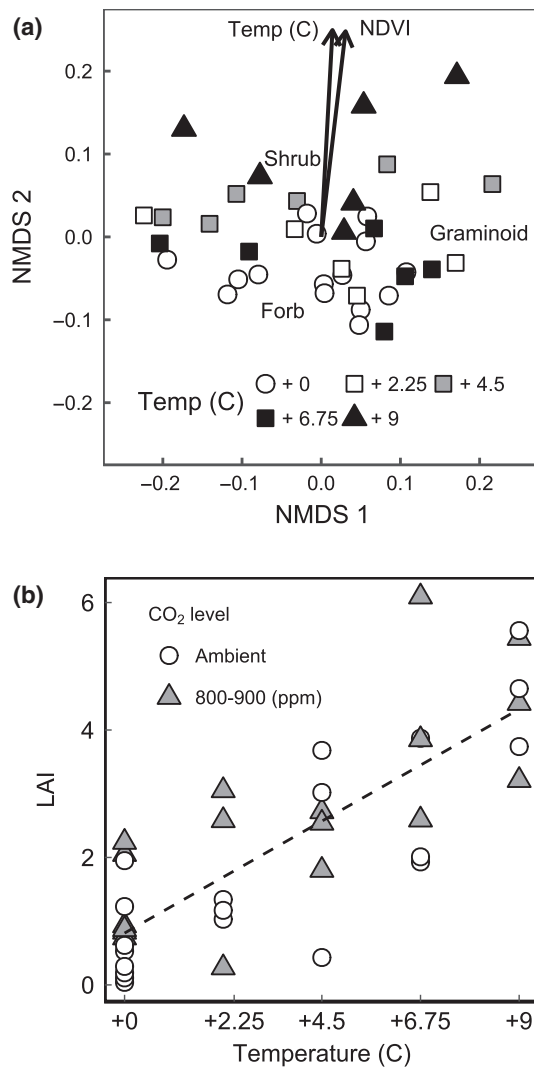
(a)

(b)

FIGURE 5 Spruce and Peatland Responses Under Changing Environments (SPRUCE) NMDS and leaf area index (LAI) results. (a) Community response to experimental manipulation of temperature and CO_2, with Normalized Difference Vegetation Index (NDVI) relationship to community composition. (b) LAI response to warming and elevated CO_2 at SPRUCE. The SPRUCE experiment is a regression-based design in which temperature is analyzed as a continuous variable. Temperature is indicated by symbol. CO_2 did not emerge as a significant vector, and so is not included in the graph. NDVI and temperatures are mapped on as correlated vectors to demonstrate the relationship between composition and temperature and NDVI. Note: n values differ among treatments at SPRUCE due to the greater number of control chambers relative to heated chambers

4.4 | Implications for northern boreal and arctic ecosystems

Widespread shifts in NDVI have been observed across the circumpolar region over the past three decades. Arctic greening has been well documented through both field and remote sensing studies (Ackerman, Griffin, Hobbie, & Finlay, 2017; Myers-Smith et al., 2011, 2015; Tape et al., 2006). However, studies of the boreal have been less consistent: Some have documented greening, while others have

indicated a browning trend (Myneni et al., 1997; Park et al., 2016; Phoenix & Bjerke, 2017; Piao et al., 2011). Through this research, we studied the effects of a range of global change drivers on the biophysical properties and NDVI of two types of common northern boreal peatlands. These results point to changes in aboveground leaf area and changes in community composition, and shrub cover in particular, as potential drivers of satellite observed trends in boreal NDVI. We found a positive response of NDVI to warming, coincident with the increase in shrub cover, and a negative response of NDVI to long-term drought. We show here that state factors such as temperature and hydrology are drivers of plant community composition and NDVI. Previous studies have shown the effects of climate drivers on NDVI, but their relationship to community composition and structure has previously not been well resolved. Further research is needed to investigate the interactive effects of warming and hydrologic change across different types of peatland ecosystems, and to relate the findings of this research to satellite datasets to understand further how warming and changes in hydrology are affecting ecological function across arctic and boreal regions.

CONFLICT OF INTEREST

The authors claim no conflict of interests.

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REFERENCES

Ackerman, D., Griffin, D., Hobbie, S. E., & Finlay, J. C. (2017). Arctic shrub growth trajectories differ across soil moisture levels. *Global Change Biology*, 23(10), 4294–4302. https://doi.org/10.1111/gcb.13677

Beck, P. S. A., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters*, 6(4), 045501. https://doi.org/10.1088/1748-9326/6/4/045501

Berendse, F., Van Breemen, N., Rydin, Hå., Buttler, A., Heijmans, M., Hoosbeek, M. R., … Wallén, B. (2001). Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biology*, 7(5), 591–598. https://doi.org/10.1046/j.1365-2486.2001.00433.x

Bintanja, R., & Selten, F. M. (2014). Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature*, 509 (7501), 479–482. https://doi.org/10.1038/nature13259

Boelman, N. T., Stieglitz, M., Griffin, K. L., & Shaver, G. R. (2005). Interannual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. *Oecologia*, 143(4), 588–597. https://doi.org/10.1007/s00442-005-0012-9

Boelman, N. T., Stieglitz, M., Rueth, H. M., Sommerkorn, M., Griffin, K. L., Shaver, G. R., & Gamon, J. A. (2003). Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia*, 135(3), 414–421. https://doi.org/10.1007/s00442-003-1198-3

Breeuwer, A., Robroek, B. J. M., Limpens, J., Heijmans, M. M. P. D., Schouten, M. G. C., & Berendse, F. (2009). Decreased summer water table depth affects peatland vegetation. *Basic and Applied Ecology*, 10 (4), 330–339. https://doi.org/10.1016/j.baae.2008.05.005

Bridgham, S. D., Patrick Megonigal, J., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon balance of North American wetlands. *Wetlands*, 26(4), 889–916. https://doi.org/10.1672/0277-5212(2006) 26[889:TCBONA]2.0.CO;2

Bubier, J. L., Rock, B. N., & Crill, P. M. (1997). Spectral reflectance measurements of boreal wetland and forest mosses. *Journal of Geophysical Research: Atmospheres*, 102(D24), 29483–29494. https://doi.org/10.1029/97JD02316

Buermann, W., Parida, B., Jung, M., MacDonald, G. M., Tucker, C. J., & Reichstein, M. (2014). Recent shift in Eurasian boreal forest greening response may be associated with warmer and drier summers. *Geophysical Research Letters*, 41(6), 1995–2002. https://doi.org/10.1002/2014GL059450

Carlson, T. N., & Ripley, D. A. (1997). On the relation between NDVI, fractional vegetation cover, and leaf area index. *Remote Sensing of Environment*, 62(3), 241–252. https://doi.org/10.1016/S0034-4257(97)00104-1

Chapin, F. S., Mcguire, A. D., Randerson, J., Pielke, R., Baldocchi, D., Hobbie, S. E., … Running, S. W. (2000). Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, 6(S1), 211–223. https://doi.org/10.1046/j.1365-2486.2000.06022.x

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan Rich Fen. *Ecosystems*, 12(8), 1329–1342. https://doi.org/10.1007/s10021-009-9292-y

Churchill, A. C., Turetsky, M. R., McGuire, A. D., & Hollingsworth, T. N. (2014). Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen. *Canadian Journal of Forest Research*, 45(2), 185–193. https://doi.org/10.1139/cjfr-2014-0100

DeColibus, D. T., Rober, A. R., Sampson, A. M., Shurzinske, A. C., Walls, J. T., Turetsky, M. R., & Wyatt, K. H. (2017). Legacy effects of drought alters the aquatic food web of a northern boreal peatland. *Freshwater Biology*, 62(8), 1377–1388. https://doi.org/10.1111/fwb.12950

Delbart, N., Picard, G., Le Toans, T., Kergoat, L., Quegan, S., Woodward, I., … Fedotova, V. (2008). Spring phenology in boreal Eurasia over a nearly century time scale. *Global Change Biology*, 14(3), 603–614. https://doi.org/10.1111/j.1365-2486.2007.01505.x

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., & Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology*, 21(1), 388–395. https://doi.org/10.1111/gcb.12643

Gamon, J. A., Field, C. B., Goulden, M. L., Griffin, K. L., Hartley, A. E., Joel, G., … Valentini, R. (1995). Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological Applications*, 5(1), 28–41. https://doi.org/10.2307/1942049

Gamon, J. A., Kovalchuck, O., Wong, C. Y. S., Harris, A., & Garrity, S. R. (2015). Monitoring seasonal and diurnal changes in photosynthetic pigments with automated PRI and NDVI sensors. *Biogeosciences*, 12 (13), 4149–4159. https://doi.org/10.5194/bg-12-4149-2015

Goetz, S. J., Bunn, A. G., Fiske, G. J., & Houghton, R. A. (2005). Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America*, 102(38), 13521–13525. https://doi.org/10.1073/pnas.0506179102

Gorham, E. (1991). Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1(2), 182–195. https://doi.org/10.2307/1941811

Goud, E. M., Moore, T. R., & Roulet, N. T. (2017). Predicting peatland carbon fluxes from non-destructive plant traits. *Functional Ecology*, 31, 1824–1833. https://doi.org/10.1111/1365-2435.12891

Gower, S. T., & Norman, J. M. (1991). Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology*, 72(5), 1896–1900. https://doi.org/10.2307/1940988

Grulke, N. E., Riechers, G. H., Oechel, W. C., Hjelm, U., & Jaeger, C. (1990). Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. *Oecologia*, 83(4), 485–494. https://doi.org/10.1007/BF00317199

Hanson, P. J., Riggs, J. S., Nettles, W. R., Phillips, J. R., Krassovski, M. B., Hook, L. A., … Barbier, C. (2017). Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated CO_2 atmosphere. *Biogeosciences*, 14(4), 861–883. https://doi.org/10.5194/bg-14-861-2017

Harris, A. (2008). Spectral reflectance and photosynthetic properties of *Sphagnum* mosses exposed to progressive drought. *Ecohydrology*, 1(1), 35–42. https://doi.org/10.1002/eco.5

Harris, A., Gamon, J. A., Pastorello, G. Z., & Wong, C. Y. S. (2014). Retrieval of the photochemical reflectance index for assessing xanthophyll cycle activity: A comparison of near-surface optical sensors. *Biogeosciences; Katlenburg-Lindau*, 11(22), 6277. https://doi.org/doi.org.ezp1.lib.umn.edu/10.5194/bg-11-6277-2014

Heijmans, M. M. P. D., Berendse, F., Arp, W. J., Masselink, A. K., Klees, H., De Visser, W., & Van Breemen, N. (2001). Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. *Journal of Ecology*, 89(2), 268–279. https://doi.org/10.1046/j.1365-2745.2001.00547.x

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., Dyurgerov, M. B., Fastie, C. L., … Yoshikawa, K. (2005). Evidence and implications of recent climate change in Northern Alaska and other Arctic Regions. *Climatic Change*, 72(3), 251–298. https://doi.org/10.1007/s10584-005-5352-2

Hope, A. S., Kimball, J. S., & Stow, D. A. (1993). The relationship between tussock tundra spectral reflectance properties and biomass and vegetation composition. *International Journal of Remote Sensing*, 14(10), 1861–1874. https://doi.org/10.1080/01431169308954008

Huemmrich, K. F., Gamon, J. A., Tweedie, C. E., Oberbauer, S. F., Kinoshita, G., Houston, S., … Oechel, W. C. (2010). Remote sensing of tundra gross ecosystem productivity and light use efficiency under varying temperature and moisture conditions. *Remote Sensing of Environment*, 114(3), 481–489. https://doi.org/10.1016/j.rse.2009.10.003

Johnson, C. P., Pypker, T. G., Hribljan, J. A., & Chimner, R. A. (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO_2/CH_4 dynamics in a Northern Michigan Peatland. *Ecosystems*, 16(5), 736–748. https://doi.org/10.1007/s10021-013-9646-3

Jonasson, S. (1988). Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, 52(1), 101–106. https://doi.org/10.2307/3565988

Kane, E. S., Chivers, M. R., Turetsky, M. R., Treat, C. C., Petersen, D. G., Waldrop, M., … McGuire, A. D. (2013). Response of anaerobic carbon cycling to water table manipulation in an Alaskan rich fen. *Soil Biology and Biochemistry*, 58, 50–60. https://doi.org/10.1016/j.soilbio.2012.10.032

Kane, E. S., Turetsky, M. R., Harden, J. W., McGuire, A. D., & Waddington, J. M. (2010). Seasonal ice and hydrologic controls on dissolved organic carbon and nitrogen concentrations in a boreal-rich fen. *Journal of Geophysical Research: Biogeosciences*, 115(G4). https://doi.org/10.1029/2010JG001366

Karlsen, S. R., Hogda, K. A., Wielgolaski, F. E., Tolvanen, A., Tommervik, H., Poikolainen, J., & Kubin, E. (2009). Growing-season trends in Fennoscandia 1982–2006, determined from satellite and phenology data. *Climate Research*, 39(3), 275–286. https://doi.org/10.3354/cr00828

Kross, A., Seaquist, J. W., & Roulet, N. T. (2016). Light use efficiency of peatlands: Variability and suitability for modeling ecosystem production. *Remote Sensing of Environment*, 183, 239–249. https://doi.org/10.1016/j.rse.2016.05.004

La Puma, I. P., Philippi, T. E., & Oberbauer, S. F. (2007). Relating NDVI to ecosystem CO_2 exchange patterns in response to season length and soil warming manipulations in arctic Alaska. *Remote Sensing of Environment*, 109(2), 225–236. https://doi.org/10.1016/j.rse.2007.01.001

Leppälä, M., Kukko-Oja, K., Laine, J., & Tuittila, E.-S. (2008). Seasonal dynamics of CO_2 exchange during primary succession of boreal mires as controlled by phenology of plants. *Écoscience*, 15(4), 460–471. https://doi.org/10.2980/15-4-3142

Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant, Cell & Environment*, 14(8), 729–739. https://doi.org/10.1111/j.1365-3040.1991.tb01439.x

Luo, Y., Gerten, D., Le Maire, G., Parton, W. J., Weng, E., Zhou, X., … Rustad, L. (2008). Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, 14(9), 1986–1999. https://doi.org/10.1111/j.1365-2486.2008.01629.x

May, J. L., Parker, T., Unger, S., & Oberbauer, S. F. (2018). Short term changes in moisture content drive strong changes in Normalized Difference Vegetation Index and gross primary productivity in four Arctic moss communities. *Remote Sensing of Environment*, 212, 114–120. https://doi.org/10.1016/j.rse.2018.04.041

Meingast, K. M., Falkowski, M. J., Kane, E. S., Potvin, L. R., Benscoter, B. W., Smith, A. M. S., … Miller, M. E. (2014). Spectral detection of near-surface moisture content and water-table position in northern peatland ecosystems. *Remote Sensing of Environment*, 152, 536–546. https://doi.org/10.1016/j.rse.2014.07.014

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), 1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Moore, T. R., & Dalva, M. (1993). The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *European Journal of Soil Science*, 44(4), 651–664. https://doi.org/10.1111/j.1365-2389.1993.tb02330.x

Morgan, J. A., LeCain, D. R., Pendall, E., Blumenthal, D. M., Kimball, B. A., Carrillo, Y., … West, M. (2011). C4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature*, 476(7359), 202–205. https://doi.org/10.1038/nature10274

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., … Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, 5(9), 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386(6626), 698–702. https://doi.org/10.1038/386698a0

Norby, R. J., Hanson, P. J., O'Neill, E. G., Tschaplinski, T. J., Weltzin, J. F., Hansen, R. A., … Johnson, D. W. (2002). Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, 12(5), 1261–1266. https://doi.org/10.1890/1051-0761(2002) 012[1261:NPPOAC]2.0.CO;2

Nowak, R. S., Ellsworth, D. S., & Smith, S. D. (2004). Functional responses of plants to elevated atmospheric CO_2 – Do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist*, 162(2), 253–280. https://doi.org/10.1111/j.1469-8137.2004.01033.x

Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2017). vegan: Community Ecology Package. R package version 2.4-4. Retrieved from https://CRAN.RURLHYPHEN;

Olefeldt, D., Euskirchen, E. S., Harden, J., Kane, E., McGuire, A. D., Waldrop, M. P., & Turetsky, M. R. (2017). A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability. *Global Change Biology*, 23, 2428–2440. https://doi.org/10.1111/gcb.13612

Osterkamp, T. E., & Romanovsky, V. E. (1999). Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes*, 10(1), 17–37. https://doi.org/10.1002/(SICI)1099-1530(199901/03)10:1<17:AID-PPP303>3.0.CO;2-4

Owensby, C. E., Ham, J. M., Knapp, A. K., & Auen, L. M. (1999). Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology*, 5(5), 497–506. https://doi.org/10.1046/j.1365-2486.1999.00245.x

Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E. S., Høgda, K.-A., Karlsen, S. R., … Myneni, R. B. (2016). Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, 11(8), 084001. https://doi.org/10.1088/1748-9326/11/8/084001

Peñuelas, J., & Filella, I. (2001). Responses to a warming world. *Science*, 294(5543), 793–795. https://doi.org/10.1126/science.1066860

Phoenix, G. K., & Bjerke, J. W. (2017). Arctic browning: Extreme events and trends reversing Arctic greening. *Global Change Biology*, 22(9), 2960–2962. https://doi.org/10.1111/gcb.13261

Piao, S., Wang, X., Ciais, P., Zhu, B., Wang, T., & Liu, J. (2011). Changes in satellite-derived vegetation growth trend in temperate and boreal Eurasia from 1982 to 2006. *Global Change Biology*, 17(10), 3228–3239. https://doi.org/10.1111/j.1365-2486.2011.02419.x

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., … Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325(5946), 1355–1358. https://doi.org/10.1126/science.1173113

Potvin, L. R., Kane, E. S., Chimner, R. A., Kolka, R. K., & Lilleskov, E. A. (2015). Effects of water table position and plant functional group on plant community, aboveground production, and peat properties in a peatland mesocosm experiment (PEATcosm). *Plant and Soil*, 387(1–2), 277–294. https://doi.org/10.1007/s11104-014-2301-8

Radu, D. D., & Duval, T. P. (2018). Precipitation frequency alters peatland ecosystem structure and CO_2 exchange: Contrasting effects on moss, sedge, and shrub communities. *Global Change Biology*, 24, 2051–2065. https://doi.org/10.1111/gcb.14057

Riedel, S. M., Epstein, H. E., & Walker, D. A. (2005). Biotic controls over spectral reflectance of arctic tundra vegetation. *International Journal of Remote Sensing*, 26(11), 2391–2405. https://doi.org/10.1080/01431160512331337754

Riordan, B., Verbyla, D., & McGuire, A. D. (2006). Shrinking ponds in sub-arctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research: Biogeosciences*, 111(G4), G04002. https://doi.org/10.1029/2005JG000150

Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., & Martikainen, P. J. (1996). CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. *Journal of Ecology*, 84(2), 219–228. https://doi.org/10.2307/2261357

Strack, M., Waddington, J. M., Lucchese, M. C., & Cagampan, J. P. (2009). Moisture controls on CO2 exchange in a *Sphagnum*-dominated peatland: Results from an extreme drought field experiment. *Ecohydrology*, 2(4), 454–461. https://doi.org/10.1002/eco.68

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686–702. https://doi.org/10.1111/j.1365-2486.2006.01128.x

Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23(2), GB2023. https://doi.org/10.1029/2008gb003327

Tfaily, M. M., Cooper, W. T., Kostka, J. E., Chanton, P. R., Schadt, C. W., Hanson, P. J., … Chanton, J. P. (2014). Organic matter transformation in the peat column at Marcell Experimental Forest: Humification and vertical stratification. *Journal of Geophysical Research: Biogeosciences*, 119(4), 661–675. https://doi.org/10.1002/2013JG002492

Tucker, C. J., Slayback, D. A., Pinzon, J. E., Los, S. O., Myneni, R. B., & Taylor, M. G. (2001). Higher northern latitude normalized difference vegetation index and growing season trends from 1982 to 1999. *International Journal of Biometeorology*, 45(4), 184–190. https://doi.org/10.1007/s00484-001-0109-8

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*, 113(G3). https://doi.org/10.1029/2007JG000496

Van Gaalen, K. E., Flanagan, L. B., & Peddle, D. R. (2007). Photosynthesis, chlorophyll fluorescence and spectral reflectance in *Sphagnum* moss at varying water contents. *Oecologia*, 153(1), 19–28. https://doi.org/10.1007/s00442-007-0718-y

Verbyla, D. (2015). Remote sensing of interannual boreal forest NDVI in relation to climatic conditions in interior Alaska. *Environmental Research Letters*, 10(12), 125016. https://doi.org/10.1088/1748-9326/10/12/125016

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8(1), 113–127. https://doi.org/10.1002/eco.1493

Walker, D. A., Epstein, H. E., Jia, G. J., Balser, A., Copass, C., Edwards, E. J., … Raynolds, M. K. (2003). Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research: Atmospheres*, 108(D2), 8169. https://doi.org/10.1029/2001JD000986

Walsh, J. E., Overland, J. E., Groisman, P. Y., & Rudolf, B. (2011). Ongoing climate change in the Arctic. *Ambio*, 40(1), 6–16. https://doi.org/10.1007/s13280-011-0211-z

Wang, R., Gamon, J. A., Montgomery, R. A., Townsend, P. A., Zygielbaum, A. I., Bitan, K., … Cavender-Bares, J. (2016). Seasonal variation in the NDVI–species richness relationship in a Prairie Grassland experiment (Cedar Creek). *Remote Sensing*, 8(2), 128. https://doi.org/10.3390/rs8020128

Ward, S. E., Bardgett, R. D., McNamara, N. P., & Ostle, N. J. (2009). Plant functional group identity influences short-term peatland ecosystem carbon flux: Evidence from a plant removal experiment. *Functional Ecology*, 23(2), 454–462. https://doi.org/10.1111/j.1365-2435.2008.01521.x

Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J., & Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, 9(2), 141–151. https://doi.org/10.1046/j.1365-2486.2003.00571.x

Weltzin, J. F., Harth, C., Bridgham, S. D., Pastor, J., & Vonderharr, M. (2001). Production and microtopography of bog bryophytes: Response to warming and water-table manipulations. *Oecologia*, 128(4), 557–565. https://doi.org/10.1007/s004420100691

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., & Chapin, C. T. (2000). Response of Bog and Fen plant communities to warming and water-table manipulations. *Ecology*, 81(12), 3464–3478. https://doi.org/10.1890/0012-9658(2000) 081[3464:ROBAFP]2.0.CO;2

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K. A., Farrell, E. P., & Tuittila, E.-S. (2007). A high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in peatland vascular plant communities. *Plant Ecology*, 190(1), 37–51. https://doi.org/10.1007/s11258-006-9189-1

Wyatt, K. H., Turetsky, M. R., Rober, A. R., Giroldo, D., Kane, E. S., & Stevenson, R. J. (2012). Contributions of algae to GPP and DOC production in an Alaskan fen: Effects of historical water table manipulations on ecosystem responses to a natural flood. *Oecologia*, 169(3), 821–832. https://doi.org/10.1007/s00442-011-2233-4

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., & Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters*, 37(13), L13402. https://doi.org/10.1029/2010GL043584

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