Response of boreal peatland ecosystems to global change: A remote sensing approach

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Abstract

Global climate change is expected to result in anywhere from two to four degrees of warming, with consequences for terrestrial ecosystems. The rate of climate change is disproportionally greater at high latitudes, resulting in landscape-scale effects on the composition, structure, and function of arctic and boreal ecology. Remote sensing offers scientists the ability to track large-scale changes through the detection of biophysical processes occurring in terrestrial ecosystems. In this research, I measured the response of boreal peatland ecosystems to a suite of different climate-related drivers including increased temperature, elevated carbon dioxide levels, and hydrologic change. Working within large-scale ecosystem manipulation experiments, I used passive remote sensing to measure the response of two different types of boreal peatlands, a rich fen and an ombrotrophic bog, to simulated climate change. Chapter 1 describes my research on the use of hyperspectral remote sensing to examine changes in the composition and biodiversity of peatlands in response to long-term experimental manipulation. Chapter 2 details my findings on using simple remote sensing techniques to detect changes in peatland ecosystem productivity in response to warming, elevated carbon dioxide, and hydrologic change. Through this work, I demonstrate that remote sensing can be used to characterize the response of a range of different ecosystem properties to global change.

Introduction

Anthropogenic climate change is resulting in wide-spread effects on terrestrial ecosystems with consequences for the carbon cycle, biodiversity, and human health. The most rapid climate change is occurring in the vast and uninhabited regions of the far north. Remote sensing of earth's biophysical processes from near-earth, airborne, and satellite platforms allows scientists to detect changes that are occurring across multiple-spatial scales. Through this research, I investigated the effects of global change on boreal peatland ecosystems, and developed methods for tracking impacts using remote sensing. Peatlands are wetland ecosystems that are characterized by thick organic soils. Although they occur worldwide, most peatlands are distributed across the arctic and boreal regions of the globe where annual productivity outstrips rates of decomposition due to cold, wet conditions. Peatlands contain vast stores of carbon, unique flora, and provide habitat and access to natural resources for northern communities. Changes in temperature, hydrology, and other environmental variables threaten the conditions that have maintained peatlands an atmospheric carbon sink for millennia. Through my Master's research, I worked within two large-scale ecosystem manipulation experiments to characterize the response of peatlands to a suite of different global change factors. I also worked to develop remote sensing methods for tracking impacts to boreal ecosystems over large spatial scales.

This research was conducted at two different sites, one at the Alaska Peatland Experiment (APEX) in central Alaska, and one at the Spruce and Peatland Response Under Climatic and Environmental Change (SPRUCE) experiment in Northern Minnesota. These sites

represent two different types of widely-distributed boreal peatlands. The Alaska site is in a rich fen ecosystem. The experiment was initially designed to examine the effects of hydrology on the ecology and biogeochemistry of peatlands. The northern Minnesota experiment is situated in an ombrotrophic bog, and was designed to test the effects of warming and elevated carbon dioxide levels on peatlands. I examined the effects of experimental manipulation on the ecosystem structure and function at both sites using passive remote sensing techniques.

In Chapter 1, I describe the use of hyperspectral remote sensing methods to detect changes in the biodiversity and community composition of peatland vegetation. I found that long-term experimental manipulation had resulted in a shift in vegetation community composition at both sites. I also found that hyperspectral reflectance data responded strongly to changes in diversity, productivity, and cover of different plant functional types. These results contribute to the growing body of research on using hyperspectral data to examine changes in species diversity and track the cover of different species and plant functional types. In chapter 2, I used remote sensing observations to measure the effects of treatment on ecosystem productivity. My results show a clear effect of treatment on productivity at both sites, and demonstrate the use of simple remote sensing techniques in measuring the response of ecosystems to change. Together, these projects show the direction of response of peatland ecosystems to global change, and further methods in remote sensing of terrestrial ecology.

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Chapter Overview

The Arctic and boreal regions of the northern hemisphere are experiencing rapid environmental change in response to a warming climate. Peatlands, which account for approximately 15% of land surface in northern environments, are experiencing a range of ecosystem changes including increasing temperatures, elevated carbon dioxide levels, and altered hydrology resulting from drought and permafrost thaw. Together, these impacts are leading to shifts in ecosystem structure and community composition that will ultimately affect the productivity, diversity, and carbon balance of peatlands. New remote sensing techniques could offer the ability to complete large-scale analyses of peatland response to climate change. Here, we use near-earth hyperspectral remote sensing to examine peatland community response to a range of experimentally manipulated climate change drivers including elevated carbon dioxide, increased temperatures, and altered hydrology. We found a strong effect of temperature, water table position, and the percent cover of different plant functional types on spectral reflectance. We also found a positive relationship between community-level compositional heterogeneity and variation in the spectral signal from plant canopies. Our results underscore recent advances in using remote sensing for ecological research, and further applications for measuring the effects of global change on far northern ecosystems.

Background

Climate change is having a significant impact on the structure, composition, and biodiversity of ecosystems across the globe (Bellard et al. 2012, Sala et al. 2000). Shifts in the distribution and abundance of species in response to changing environmental conditions affect the function, complexity, and productivity of ecosystems with implications for the global carbon cycle (Cramer et al. 2001, Melillo et al. 1993). Arctic and boreal regions are experiencing climate warming at twice the global average resulting in significant effects on the vegetation composition of arctic tundra and boreal ecosystems (IPCC 2013). Prominent among these effects include the pan-arctic northward expansion of shrubs into tundra and the spread of wetland vegetation as result of permafrost thaw and ground subsidence (Myers-Smith 2008, Tape et al. 2006). Increased fire prevalence is also driving widespread shifts in boreal forest ecosystems from dominance by conifers to deciduous species (Johnstone et al. 2010). These landscape-scale changes are affecting trophic structures, wildlife migration patterns, and human access to natural resources (Chapin et al. 2010, Post et al. 2009).

The relationship between climate and community composition also has important implications for ecosystem-level processes due to the relationship between plant communities and biogeochemical cycles. For example, research indicates that increased temperatures in arctic environments speeds the rate of nitrogen mineralization, promoting the encroachment of woody plants into tundra ecosystems (Weintraub & Schimel 2005). Shifts in arctic and boreal communities also have significant implications for the carbon cycle. Increased shrub cover leads to an increase in the rate of carbon cycling, but with uncertain consequences for the overall arctic carbon budget (Mack et al. 2004, Myers-Smith et al. 2011). Understanding how climate change will affect the carbon cycle is of particular importance in ecosystems that sequester and store large amounts of organic carbon.

Arctic and boreal peatland ecosystems account for approximately 15% of land cover in the northern hemisphere, and are estimated to contain over 30% of all terrestrial soil carbon (Gorham 1991, Yu et al. 2010). Prior research has shown that hydrologic change due to climate-induced permafrost thaw, drought, and extreme flooding have significant effects on carbon cycling in peatlands (Chivers et al. 2009, Olefeldt et al. 2017). Changes in temperature and water table positions in peatlands have also been demonstrated to lead to shifts in species composition, ultimately having effects on ecosystem productivity (Churchill et al. 2014, Weltzin et al. 2000, Weltzin et al. 2003). These studies indicate that drying in peatlands promotes dominance by woody shrubs (Dieleman et al. 2015), where flooding due to increased precipitation or permafrost thaw leads to increased prevalence of graminoid species such as sedges, and increased moss cover (Churchill et al. 2014, Weltzin et al. 2000, Weltzin et al. 2002). Lowered water tables and increased shrub dominance were associated with decreased annual gross primary productivity (GPP) relative to elevated water tables (Churchill et al 2014). Studies have also demonstrated a link between the graminoid cover and methane emissions rates from wetland ecosystems. Sedges are thought to facilitate increased methane emissions rates by allowing methane to escape through aerenchyma, or porous tissues adapted to allow oxygen to diffuse through to the roots of plants growing in anaerobic soils (Ström et al. 2003). Because methane is an extremely potent greenhouse gas, identifying areas that are dominated by species such as sedges that increase the rate of methane emissions is important to predicting future impacts to the climate system (Christensen et al. 2004). Understanding how ecological communities are responding to climate change is particularly significant in arctic and boreal ecosystems, which play a strong role in regulating the global climate system (Chapin et al. 2000).

In addition to characterizing changes in the species composition of terrestrial ecosystems, tracking changes in species diversity across the globe is also of concern for both conservation and ecosystem function. A significant body of research indicates that the diversity of plant functional types in an ecosystem is positively correlated with ecosystem productivity (Díaz & Cabido 2001, Hector 1999, Tilman et al. 1997). This is likely due to a more efficient use of resources achieved by a large variety of plant functional types as opposed to fewer. Biodiversity loss poses a greater threat to productivity in low-diversity ecosystems which lack the species richness necessary to provide a redundancy of functional traits if a species is lost from the system (Reich et al. 2012). Despite the wealth of studies in tropical and temperate ecosystems, few studies have examined changing patterns of species diversity in boreal ecosystems. A number of experimental and observational studies have indicated that species diversity decreases in response to warming in the arctic, but those studies have been mostly limited to arctic tundra ecosystems (Bret-Harte et al. 2001, Pajunen et al. 2011, Walker et al. 2006). The effects of climate change on the biodiversity of ecosystems such as forests and peatlands remains understudied. In peatlands, which have low species richness to begin with, the loss of diversity may be particularly problematic because the loss of a species may also signify the loss of an entire plant functional group. Tracking changes in the biodiversity of peatlands is important for understanding the potential impacts of climate change on the structure and function of these ecosystems.

Most studies that characterize changes in community composition extrapolate field data to a large scale with increasing uncertainty as landscape heterogeneity increases. However, remote sensing is emerging as a powerful tool for understanding shifting patterns in community composition and biodiversity accurately across large spatial extents (Jetz et al. 2016, Pettorelli et al. 2014, Turner 2014, Wang et al. 2016). Many remote sensing instruments and platforms exist that can characterize and monitor a suite of Earth system's processes at varying levels of detail. Sensors range from passive optical imagers that detect reflected solar radiation at various points along the electromagnetic spectrum, to active sensors that send out pulses of electromagnetic radiation at specific wavelengths and then sense their return (Turner et al. 2003). Within optical remote sensing, the collection of spectral information across different regions of the electromagnetic spectrum allows for diverse properties of the Earth's surface to be detected within an image (Jones and Vaughan 2010). Most sensors detect at a few to several broad spectral bands, meaning that larger swaths of the spectrum are aggregated by the detector (Jones and Vaughan 2010). Hyperspectral remote sensing, sometimes called imaging spectroscopy, involves the collection of spectral data across the electromagnetic spectrum at hundreds of narrow bands, ultimately capturing detailed information about Earth's surface (Goetz 2009). Combined high spectral and spatial resolution remote sensing is emerging as one of the most promising new methods for large-scale species distribution and biodiversity mapping (Ustin et al. 2004).

Remote sensing assessments must be based in field studies that characterize the relationships between ecosystem structure and function and reflected solar radiation that can be detected from an aerial platform or satellite (Kerr and Ostrovsky 2003). Current research in optical remote sensing of ecosystems is working to identify how spectral reflectance changes as a function of changes in vegetation community structure. A large body of research has linked photosynthetically active biomass with various remotely-sensed vegetation indices such as the Normalized Difference Vegetation Index (NDVI) that have been invaluable to creating large-scale assessments of changing ecosystem productivity through time (Pettorelli et al. 2005). NDVI has also been used to track the relationship between ecosystem biodiversity and productivity (Wang et al 2016). A number of studies have investigated what plant properties contribute to spectral reflectance signatures to identify the structural and physiological characteristics that determine productivity and visually distinguish between species (Ustin et al. 2004). Species-specific properties can include leaf pigments such as chlorophyll and anthocyanin (Blackburn 2007, Lichtenthaler et al. 1996, Serbin et al. 2014, Sims & Gamon 2002), leaf nitrogen content (Knyazikhin et al. 2013, Martin & Aber 1997), and leaf water content (Peñuelas et al. 1997). Community-level properties that have been demonstrated to have a strong influence on reflectance spectra include leaf area index (Carlson & 1997, Asner et al. 2003), the percent cover of non-photosynthetic vegetation or litter (Asner 1998, Roberts et al. 1993), and the presence of woody material (Asner 1998). The structure and chemistry of different species assembled in a community interact uniquely with incoming solar radiation. Characterizing community structure using aerial imaging spectroscopy involves detecting the unique reflectance properties of different species and plant functional types using high spectral resolution data.

Many different approaches have been used in the analysis of hyperspectral data to characterize community composition and diversity. One method is through the creation of land cover classifications that can detect the crowns of individual organisms from within a canopy (Baldeck & Asner 2014, Clark et al. 2005). This method has been most successfully used in forested ecosystems in which a single tree might occupy several pixels and be therefore able to be distinguished as a unique species (Baldeck et al. 2015, Baldeck and Asner 2013). Classification analysis allows for both the identification of vegetation community types, individual species, as well as functional types, and can also be leveraged to estimate species diversity across a landscape. Mapping species cover in non-forested or mixed ecosystems present the challenge of identifying unique species from within a mixed scene or pixel. In scenes where individual species are present in monocultures across multiple pixels they can be classified in the same manner as individuals from a forest canopy (Pengra et al. 2007). However, species rarely occur in monocultures in natural ecosystems. Despite the challenges inherent to remotely sensing unique species, the use of plant functional type is an effective method of mapping ecosystem structure through the detection of plant physiological characteristics common to different groups of species (Ustin et al. 2004, Ustin & Gamon 2010). In northern boreal and arctic ecosystems where plant functional types play an important role in regulating ecosystem function, mapping their distribution could be an important element of predicting ecosystem responses to environmental change (Chapin et al. 1996).

Remote sensing of species diversity has previously been accomplished by linking spectral heterogeneity among pixels with species richness; a method based on the spectral variation hypothesis (Palmer et al. 2002, Rocchini 2007, Rocchini et al. 2010). Several different statistical approaches have been used in the calculation of spectral heterogeneity. A commonly used method of using spectral heterogeneity from a multi-or-hyperspectral data set as a predictor of species richness is by comparing the coefficient of variation of multiple pixels or scans (Carter et al. 2005, Gould 2000, Levin et al. 2007, Lucas & Carter 2008). Another approach has used Euclidian distances calculated using multivariate eigenvector methods such as principle component analysis. The further a pixel lands from the centroid of the data, the greater the spectral heterogeneity of that pixel (Palmer et al. 2002, Rocchini et al. 2007). This approach has been correlated with alpha diversity metrics that account for both species richness and evenness, such as the Shannon index (Oldeland et al. 2010). More recent research using imaging spectroscopy has also linked variation among spectral scans as well as among pixels, with species diversity (Wang et al. 2016). Together, these studies indicate the ability of multiple different remote sensing approaches to detect the diversity of plant species across a landscape.

In this study, we examined the relationships between community composition, ecosystem structure, and hyperspectral reflectance to further our ability to track climate-induced changes to ecosystems via remote sensing. Our aim was to understand how the impacts of global change on the diversity, composition, and structure of boreal peatland ecosystems can be captured using remote sensing instruments. We addressed the following questions: 1) can the effects of experimental warming, elevated carbon dioxide, and hydrologic change on ecosystem gross GPP be detected via remote sensing, 2) how does the percent cover of different plant functional types influence the reflected spectra, and 3) what is the relationship between species diversity and variation in the spectral signal? We hypothesized that the effects of global change on peatland productivity could be detected using an index such as NDVI that is closely linked with LAI and photosynthetically active biomass (Boleman et al. 2013, Walker et al. 2003). We also hypothesized that the percent cover of plant functional types would predict spectral characteristics, and that the differences would be tied with the foliar chemistry of the dominant species. Finally, we predicted that there would be a positive relationship between species diversity and spectral variation (Wang et al. 2016).

We conducted field sampling in two different peatland communities that are characteristic of northern boreal and arctic regions of the globe. Both sites are located within large-scale ecosystem manipulations examining the effects of a suite of climate change drivers on peatland ecosystem structure and function. Both experiments have resulted in the divergence of vegetation communities due to treatment (Churchill et al. 2014, Montgomery et al. unpublished). We conducted field sampling at both sites to determine which elements of community composition and structure influence the reflectance spectra. Our overarching objective in this research was to improve the ability of remote sensing to characterize and track changes in the communities of far northern environments in response to global change.

Methods

Study Sites

We collected data at two sites that are representative of different northern boreal and arctic peatland communities. The first site was at the Alaska Peatland Experiment (APEX) at the Bonanza Creek Long Term Ecological Research Station, located thirty miles west of Fairbanks, Alaska (64.82°N, 147.87°W). The site is in a sedge-and-shrub-dominated rich fen on the floodplain of the Tanana River. APEX was initiated in 2005 as a long-term manipulation to study the impact of altered hydrology on peatland ecology and biogeochemistry. APEX consists of three water table manipulation treatments: a raised, a lowered, and a control treatment, each 120 m^2 in size. The lowered treatment plot is drained by a trench that borders the plot. Water from the trench is then pumped into the raised water table treatment. The hydrology in the control plot is not manipulated.

The second study site was at the Spruce and Peatland Response Under Climatic and Environmental Change (SPRUCE) project located at the Marcell Experimental Forest in northern Minnesota (47.30°N, 93.29°W). SPRUCE was initiated in 2014 as a climate change experiment to explore the effects of increased temperatures and elevated carbon dioxide levels on the ecological and biogeochemical processes on peatlands on the southern edge of the boreal ecosystem region. The experiment is located within an ombrotophic bog dominated by Sphagnum mosses and black spruce *(Picea mariana)* with an understory of ericaceous shrubs, graminoids, and forbs. The experiment consists of thirteen large treatment plots that create an incomplete factorial design of varying temperature treatments and carbon dioxide levels. In this study, we tracked five control plots and eight treatment plots. Each of the eight treatment plots are surrounded by octagonal enclosures that are 12.8 m in diameter, 7 meters tall, and penetrate through the completely through the peat soils down to mineral soil, which averages 2.5 meters in depth across the site. Of the control plots, 2 of the 5 plots are enclosed with the same chambers as the treatment plots, to account for the chamber effect. Each treatment plot is maintained across a series of increasing temperatures to simulate a range of possible climate change scenarios. Ambient temperatures and CO_2 levels are maintained in one control chamber, and one control chamber has ambient temperatures and elevated CO_2. The remaining eight treatment plots are maintained at +2.25, 4.5 +6.75, and +9 degrees C above ambient temperatures. Carbon dioxide levels are maintained at ambient levels in half of the temperature treatment plots and elevated to between 800 and 900 parts per million in the other half of the plots. The SPRUCE experimental design is designed as a regression-based design in which ecological change could be measured in response to a broad range of temperatures (Hanson et al. 2017).

Vegetation Cover Sampling

Percent cover of plant species and functional types were measured at APEX along two transects positioned across 4-5 replicate plots in each treatment via a point-intercept sampling method. A metal frame was positioned above the canopy 1 m above the surface of the peat. A laser pointer was inserted into ten evenly-spaced holes in the metal frame along the transect. At each point, whatever the laser illuminated was recorded. Species, height above the ground, and whether at least half of the laser beam was illuminating the target were recorded. If the laser was completely or mostly on the target, it was recorded as a "good hit," and if it was less than half hitting the target it was recorded as a "bad hit." This was repeated for each "hit" from the canopy to the surface of the peat. If the target was not photosynthetic it was recorded as either "standing dead," indicating that it was non-photosynthetic biomass but was still standing, or as "litter," indicating that it was part of the thatch forming at the surface of the peat. For the lowered and raised treatments, four replicate plots were sampled, and in the control treatment five replicates were sampled.

Vegetation cover at SPRUCE was sampled in mid-July in thirteen chambers across the factorial of temperature and carbon dioxide treatments. In each chamber, plots three 2 m^2 in size were sampled using a 1 x 2 m frame that was set onto PVC pipes installed in the experiment to facilitate repeated data collection in the exact same area. The frame was divided into 50 cells that 20 x 20 cm in size. Species presence and absence of all graminoids, forbs, low shrubs, and small trees were recorded within each cell of the grid. If a species was present in half of the cells, it was considered to occupy 50% of the plot.

Functional Trait Data

Plant functional trait data were collected via destructive sampling techniques at APEX. Ten individuals of each of four dominant species, *Carex utriculata, Equisetum fluviatile, Potentilla palustris,* and *Calamagrostis canadensis* were collected at each water table treatment for a total of thirty replicates for each species across the experiment. Rare species were not harvested due to concerns regarding destructive sampling within the experiment. For each species, either several leaves or all aboveground biomass was harvested. In the case of *P. palustris* and *C. canadensis,* several leaves were harvested from each indvidual. For the other two species, all aboveground biomass of the plant was harvested. This was due to the size of the plant, and our desire to minimize destructive sampling in the treatments. The samples were scanned using a high-resolution scanner and leaf area was calculated using the ImageJ software (Schneider et al. 2012). The samples were then rinsed in deionized water, dried, and weighed. The leaf tissue samples were then ground into a

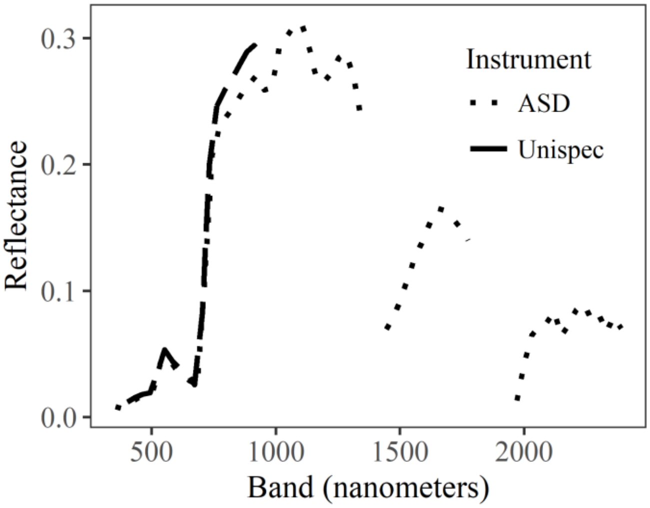

Figure 1: Bands included in SPRUCE and APEX spectral sampling. Dashed line indicates SPRUCE data and dotted lines indicate APEX data.

fine powder in a ball grinder, measured into tin cups, and analyzed for carbon and nitrogen content using a Costech ECS, Model 4010 Elemental Analyzer.

Spectral Sampling

To link spectral reflectance with community composition and species diversity, sampling of spectral reflectance was performed at both APEX and SPRUCE in the same plots where vegetation cover data were collected. Spectral reflectance measurements were taken at APEX using an Analytical Spectral Devices Fieldspec Pro that measured reflectance in one-nanometer bandwidths between 300 and 2500 nanometers (Figure 1). Reflectance was measured relative to a white Spectralon reference panel that reflected 100 percent of incoming solar 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 five minutes. Scans were performed at one-meter above ground surface at nadir with a 25 degree foreoptic field of view, resulting in a ground field of view that was 47 cm in diameter:

$$GFOV = 2\frac{height * tan(25°)}{2} \tag{1}$$

A level was used to ensure that the fiber optic cable was positioned at nadir. Data were collected during peak growing season, on June 29th, 2016. Scans were performed in a one hour window on each side of solar noon, which occurred at approximately 12:30 pm. Three scans were performed within at each vegetation plot and then averaged. For each scan, water and atmospheric absorption bands that had a relative reflectance of greater than one or less than zero were automatically excluded, as well as areas that presented with noise from the instrument. This resulted in three regions of the electromagnetic spectrum included in the analysis (Figure 1). Thirteen plots were sampled for both vegetation and spectral reflectance between the three APEX water table manipulation treatments, five plots in the control treatment, and four plots each in both the lowered and raised plots.

Spectral sampling at SPRUCE was done using a PP Systems UniSpec-DC spectroradiometer that detected incoming and reflected solar radiation in 3-4 nm bandwidths between 310 and 1100 nm. The instrument includes both an upward looking, cosine corrected sensor (to measure downwelling radiation) and downward looking pointing to measure reflected (i.e., upwelling) electromagnetic radiation. The fiber optic cable on the Unispec was fitted with a field-of-view restrictor that limited the field of view 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 m^2. Dark current and white reference scans were performed between each treatment chamber. Scans were performed inside the chambers to account for potential differences in light conditions due to the chamber walls. Three scans were performed above each vegetation plot and averaged. Reflectance was calculated for the average of the three scans following the methods of Harris et al. (2014) and Wang et al. (2016), which included both downwelling and white reference values in calculating reflectance. Incorporating values from both the upwelling and downwelling sensors was done to correct for potential differences in the sensors themselves. Corrected reflectance was calculated using the following equation.

$$\frac{R_{target}/I_{downwelling}}{R_{panel}/I_{downwelling}} \qquad (2)$$

In this equation R_{target} is the reflectance of the ground surface, R_{panel} refers to the reflectance of the panel, and $I_{downwelling}$ refers to the upward-pointing sensor measuring the downwelling radiation. Data were cleaned to eliminate noisy bands particularly at the beginning and end of the spectrum, resulting in a data range from 400-1000 nm used in the analysis (Figure 1). Data for chamber number 4 were also excluded, because reflectance data for the plot presented as a significant outlier from the other plots, indicating that the sensor may have captured reflectance from an unintended target, or that sky conditions had changed during the time of measurement. Data were collected in late season on September 22, 2016 under clear sky conditions beginning at 1:00 pm. Although it was past peak growing season, senescence had only just begun at the site. We hypothesized that collecting data in the early fall might improve our ability to detect species richness because of carotenoids and anthocyanins present in leaf tissues around senescence increasing the optical diversity and allowing for better species distinctions. Thirty-nine plots were sampled across the thirteen SPRUCE treatments.

Data Analysis

Vegetation cover data were converted to percent cover estimates and several different community-level vegetation metrics were derived. The Shannon diversity, which incorporates both species richness and evenness into a single measure of diversity:

$$H' = -\sum_{i=1}^{s} p_i \log(p_i) \tag{3}$$

In this equation, Shannon diversity (H') is calculated at the plot-level, in which p_i represents the proportion of the population represented by species i (Gotelli & Ellison 2014). Shannon diversity was calculated for each plot using the R Vegan package for community ecology (Oksenan et al. 2016). Leaf area index for APEX was calculated at each sampling point along the transect as the density of vegetation from the canopy to the soil surface. We calculated two separate LAI values for each plot, one including non-photosynthetic biomass and one only including hits on living plant tissues. Specific leaf area and carbon to nitrogen ratios were calculated and analyzed to determine whether there was a treatment effect of hydrologic change on plant functional traits at APEX. Average trait values were calculated for each of the four species. Community weighted mean (CWM) values for SLA and C:N ratio were calculated using methods described in prior literature on functional traits in which the CWM trait value for each plot was calculated as the sum of the mean trait values of each species weighted by its' relative abundance in that plot (Ackerly et al. 2007, Díaz et al. 2007, Violle et al. 2007). We determined whether species diversity and CWM trait values differed significantly by treatment using a one-way ANOVA with a Bonferroni correction, with treatment added to the model as a factor. Significant differences were assigned at an alpha-level of 0.05.

We examined dissimilarities in community composition at both sites using non-metric multidimensional scaling (NMDS) ordination. We performed NMDS for the compositional data at both SPRUCE and APEX datasets, and then fit treatment to the model to determine the relationship between treatment and composition. This tested whether the treatment was significantly correlated with the variance within the dataset, and indicated the strength and direction of the relationship. At APEX, treatment was added to the model as a factor, and at SPRUCE, temperature was analyzed as a continuous variable and carbon dioxide level as a factor.

We calculated the Normalized Difference Vegetation Index (NDVI) for each plot from the spectral measurements. NDVI has been widely demonstrated to correlate strongly with ecosystem GPP and photosynthetic biomass, something that we were unable to directly measure in either of these experiments (Boelman et al. 2003, Walker et al. 2003). Therefore, by using NDVI as a proxy for productivity, we are able to further describe treatment effects on peatland ecosystem structure and productivity. NDVI was calculated as the normalized ratio of the a visible and a near-infrared band.

$$NDVI = \frac{800\,nm - 630\,nm}{800\,nm\ + 630\,nm} \tag{4}$$

We also performed significance testing to determine between treatment differences in NDVI using a one-way ANOVA at APEX, and a two-way ANOVA at SPRUCE with temperature added to the model as a continuous variable and carbon dioxide as a factor. In both cases, a Bonferroni correction was applied to the ANOVA model to examine significant differences among treatments and significance was assigned at an alpha-level of 0.05.

We performed principle components analyses on the spectral reflectance data to determine which community properties (percent cover of different species and functional types, community weighted trait values, LAI) contributed most strongly to variation among spectral scans. We performed the analyses using the R vegan package (Oksenan et al. 2016). We determined the significance of effects of different community variables on spectra by fitting community data to the spectral PCA results. This modeled the relationship between the PCA axes of the spectral data and the community vector as a linear relationship. By this method, significance values are assigned by automatically comparing the sample data with a randomly permuted dataset. Community drivers of spectral variation were statistically significant at an alpha-value of less than or equal to 0.05.

We also explicitly examined the relationship between diversity and spectral variation through several measures of both community and spectral heterogeneity following similar methods to those used by Wang et al. (2016), who found a positive relationship between plot-level species diversity and the coefficient of variation of the associated spectral scans. Based on their findings, we predicted that greater coefficients of variation among plot-level spectral reflectance scans would correlate with higher Shannon diversity. We also performed a similar analysis based on research done by Rocchini et al. (2010), which theorized that greater community heterogeneity would be correlated with greater spectral heterogeneity. In this analysis, we used measured heterogeneity as centroid distances derived from a principal components analysis, where heterogeneity was measured as distance from the center point of the PCA (Li & Reynolds 1995, Rocchini et al. 2010). Basic linear regression was used to determine the relationship between diversity and spectral coefficient of variation, as well as between spectral heterogeneity and community heterogeneity. Diagnostic plots were used to confirm that the data were normally distributed with equal variances.

Results

1) *Community composition and functional trait data*

We found significant differences in community composition and species diversity among the water table treatments at APEX. We found greater biodiversity in the raised and control treatments as compared to the drained plot ($P < 0.05$, method = Bonferroni). We also found significantly higher relative cover of litter in the lowered water-table plot ($P < 0.05$, method = Bonferroni). Although we did not find a significant treatment effect on sedge or shrub cover, our data do point to a trend towards greater sedge cover in the control and raised water-table plots as compared to the lowered water-table plot. No statistically significant differences were found for community weighted mean values of either SLA or C:N ratios across the treatments at APEX when data were analyzed via the one-way ANOVA with a Bonferroni correction.

Our multivariate analysis of community composition indicated that water table treatment was significantly associated with differences in community composition. The percent cover of grasses and shrubs accounted for the strongest sources of variation in the NMDS. The lowered water-table treatment was also associated with a greater litter cover relative to either of the other treatments plots. The raised water-table plot was similar to the control plot, but was associated with a greater cover of forbs and mosses as compared to the control plot (Figure 2). Results from the ordination indicate a stress of 0.149 for two dimensions, with treatment a significant source of variation within the dataset (p=0.012)

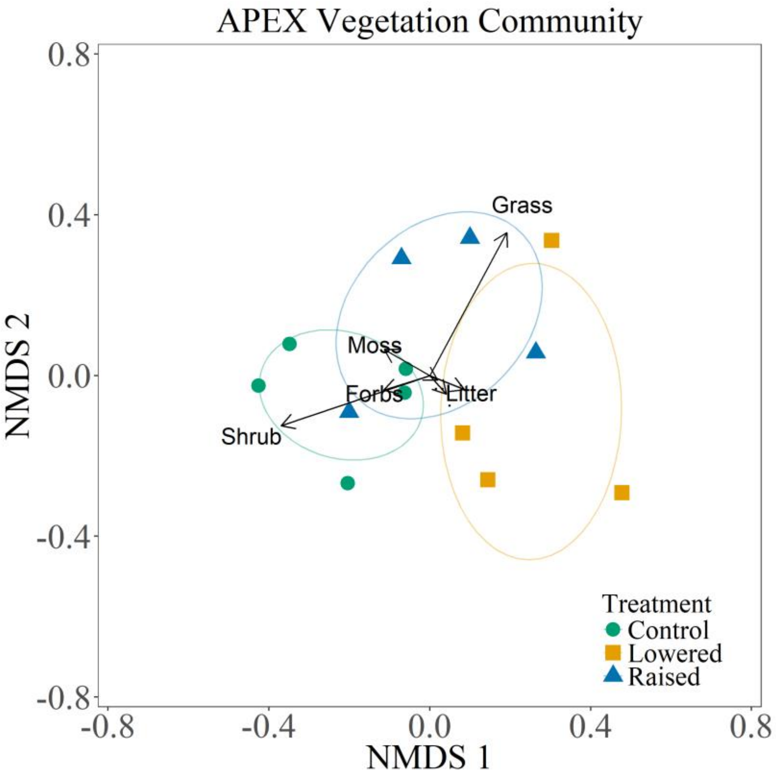

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Figure 2: NMDS for APEX community composition

We found no difference in species diversity among treatments at SPRUCE. However, the NMDS results of the community data indicated that the temperature treatment was a significant vector within the community dataset. Warmed plots were associated with an increase in shrub cover. Ambient plots were associated with a greater cover of forbs (Figure 3). NDMS model results showed a stressed of 0.033 for two dimensions. Heat and chamber were significantly correlated with the variation in community composition (p<0.01).

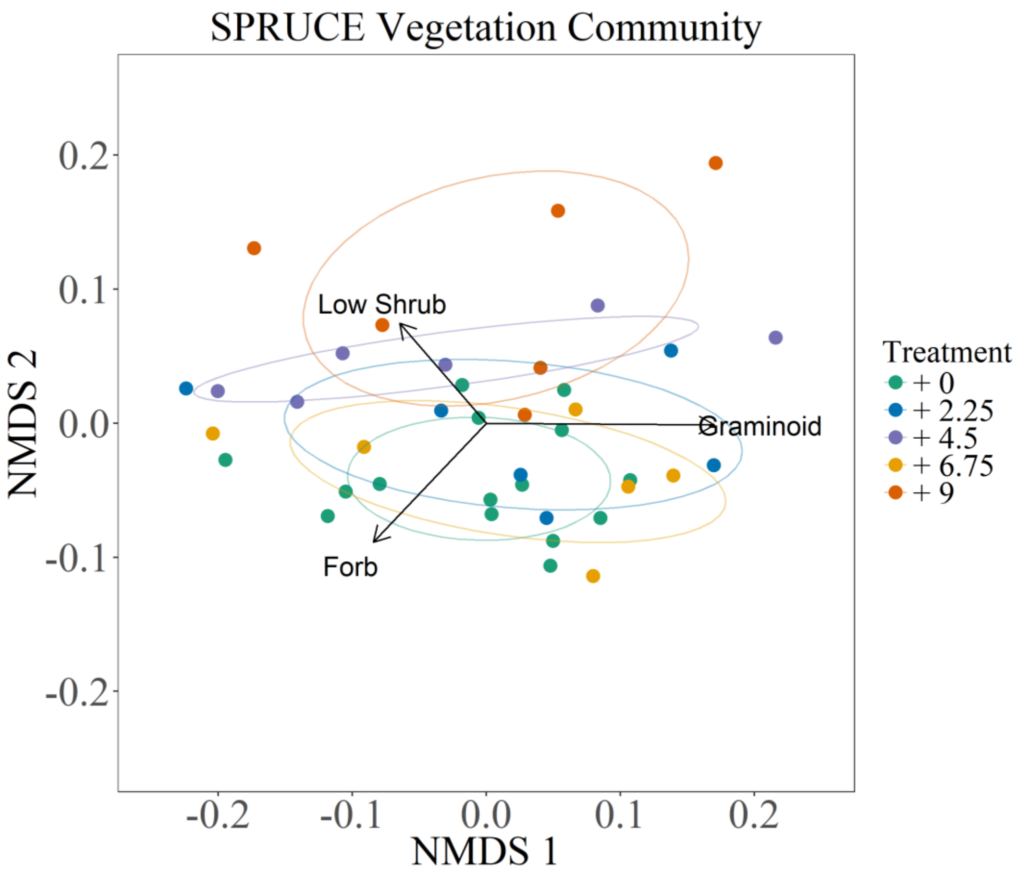

Figure 3: NMDS for SPRUCE community composition

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2) NDVI

We observed an effect of treatment on NDVI at both sites. At APEX, we found significantly higher NDVI values in the control plot as compared to the raised and lowered water-table plots, likely due to the greater fraction of litter to photosynthetic leaf area in the lowered plot relative to the other plots (Figure 4). We found a strong effect of warming on NDVI at SPRUCE, with greater warming leading to much higher observed NDVI values. The results of our two-factor ANOVA indicate a significant effect of warming on NDVI; however, CO_2 did not effect on NDVI values (Table 1).

Effect	Df	F-value	P
temp	1	38.90	**<0.001**
CO_2	1	1.11	0.300
temp:CO_2	1	0.804	0.377

Table 1: ANOVA results for SPRUCE on effect of treatment on NDVI

There was also a trend indicating an effect of CO_2 level on NDVI at SPRUCE at +6.75 and +9 degrees C of warming, with elevated CO_2 leading to higher NDVI values (Figure 5). However, these results were not significant.

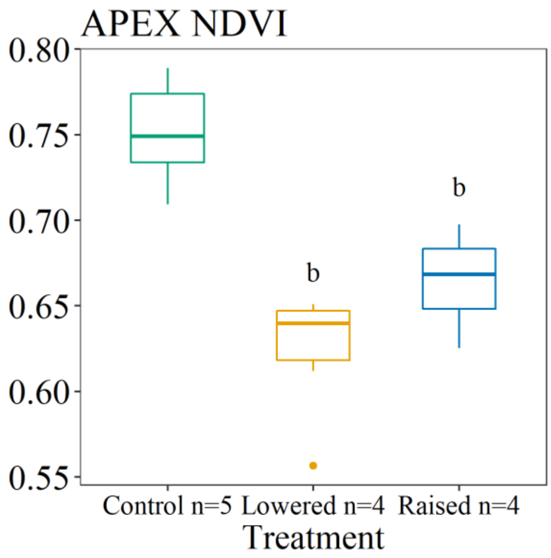

Figure 4: NDVI for APEX vegetation plots. Treatments with the same letters are not significantly different from each other at a significance level of $P < 0.05$.

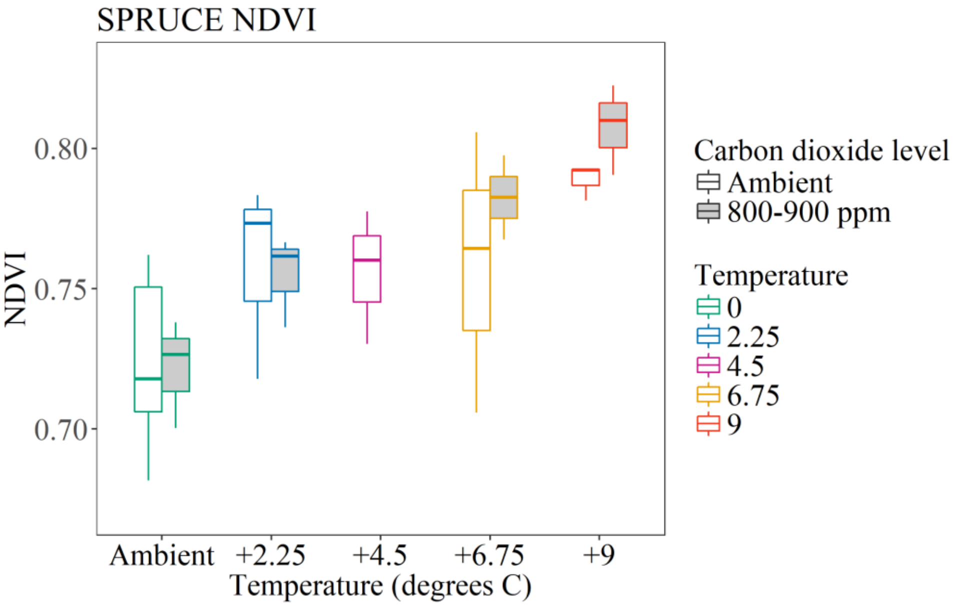

Figure 5: NDVI for SPRUCE by heating and CO_2 treatment.

3) Community drivers of spectral response

The results of the principle components analysis of our spectral sampling reflect the same community-level differences described above. Data from the spectral sensors at both sites indicate significant differences in 2016 across treatments. At APEX, spectral reflectance varied as a function of the species diversity and the percent cover of litter within the treatment plots. Species diversity at APEX was closely associated with the percent cover of mosses and forbs, both of which were relatively rare across the site. Mosses and forbs together accounted for less than ten percent on average of the cover at APEX, yet had a strong effect on spectral reflectance, particularly in the control and raised water table treatment plots. Overall, the first principle component explained 79% of the variation in the dataset, largely driven by differences in diversity and the percent cover of photosynthetic biomass (Figure 6).

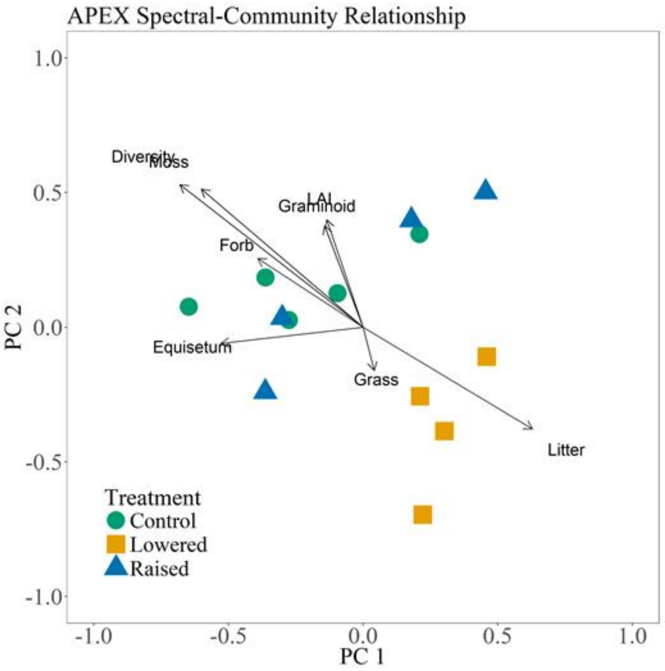

Figure 6: PCA for APEX spectral data demonstrating distribution of treatment plots with community variables mapped on. The length of the arrow represents the strength of the gradient.

PCA results from the reflectance data at SPRUCE show significant spectral differences across temperature and CO_2 treatments (Figure 7). Like APEX, reflectance spectra responded strongly to differences in forb cover. Shrub cover also emerged as a significant vector in the SPRUCE data. Since we did not find any strong differences in diversity among treatments, diversity did not emerge as a significant vector in the analysis. These results suggest that the relative cover of shrubs versus forbs is a key driver of spectral differences among treatments.

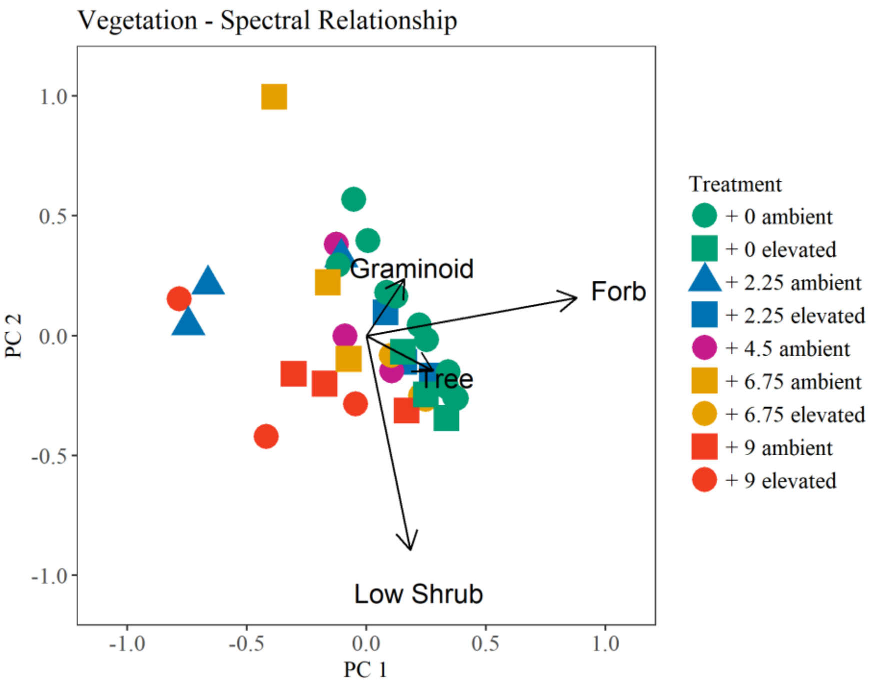

Figure 7: PCA for spectral data at SPRUCE experiment demonstrating the distribution of treatments with community variables mapped on. The length of the arrow represents the strength of the gradient.

4) Community-spectral variation relationships

We also explicitly examined the relationship between species diversity and spectral diversity. We only used APEX data for this analysis because we didn't find significant differences in biodiversity or species composition at SPRUCE. We performed two analyses that quantified both community and spectral variation according to different approaches found in the literature (Rocchini et al. 2013, Wang et al. 2016; Figure 8). We performed one analysis exploring the relationship between Shannon diversity and spectral coefficient of variation calculated for an entire spectral scan and compared among plots. In the second analysis, we calculated heterogeneity for both community and spectral data using a multi-variate analysis in which heterogeneity was measured as distance from the global centroid of both the spectral and community datasets. The relationship between Shannon diversity and spectral CV showed a significant positive relationship (R^2_{adj}=0.36, F_{11}=7.77, p=0.02, RMSE=0.24). The relationship between community and spectral heterogeneity showed a slightly weaker relationship but also positive relationship (R^2_{adj}=0.25, F_{11}=4.93, p=0.05, RMSE=0.78). It should be explicitly noted that

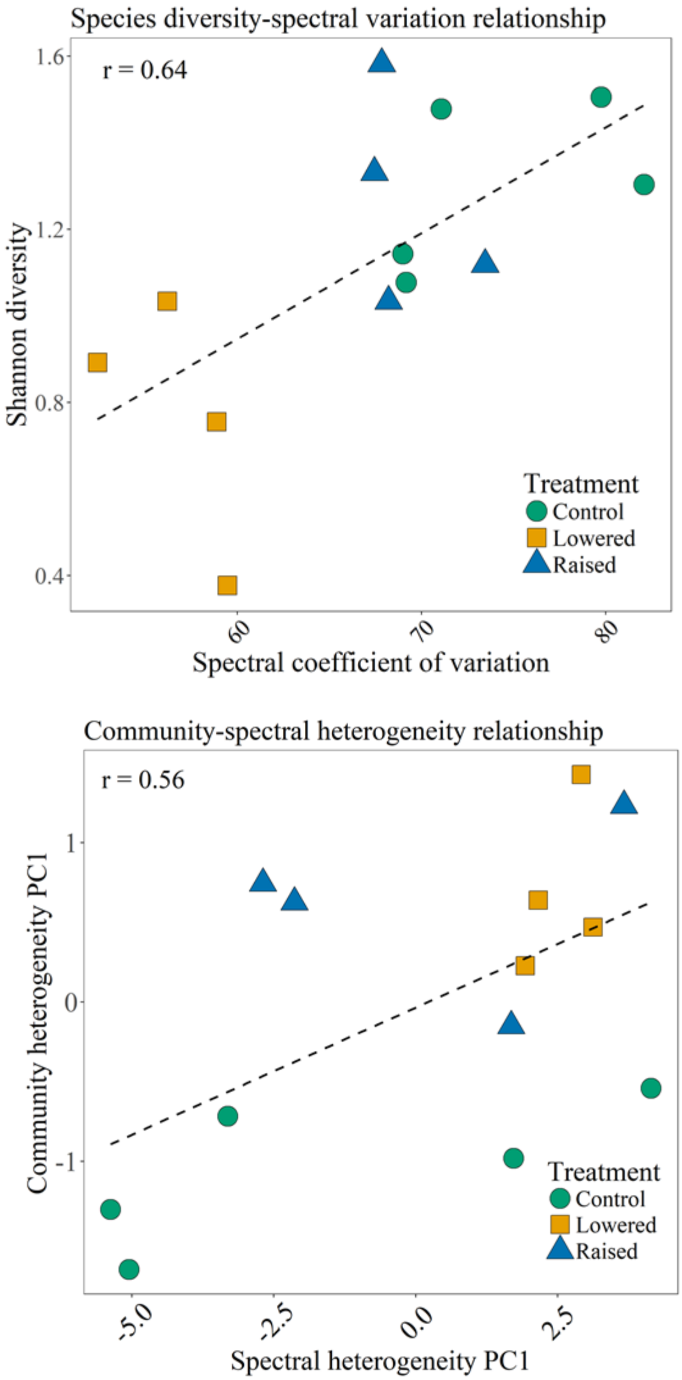

Figure 8: Linear relationship between spectral and community variation. Top: Shannon diversity and spectral coefficient of variation. Bottom: Spectral heterogeneity and community heterogeneity measured as Euclidian distance for a global centroid calculated using a PCA.

differences in heterogeneity are relative to a global mean value, and are therefore relative. Points closest to zero along both axes are less heterogenous than those further from the global mean. (Figure 8, bottom figure).

Discussion

The northern boreal region of the globe is vast and has very low population density. Of the roughly twelve million square kilometers that constitutes the boreal region, 30 % of that area is covered by peatlands (Gorham 1991). Climate in this region is changing rapidly, and given the large spatial extent and low population density, examining changes to the landscape must largely be achieved using remote sensing. In our research, we investigated the relationships between hyperspectral reflectance and community structure and composition. These results reinforce previous studies that have used hyperspectral remote sensing as a tool for mapping biodiversity and ecological community composition. We have also shown that remote sensing data can capture the response of peatland community composition and biodiversity to a range of different global change drivers, including hydrologic change, increasing temperatures, and increasing atmospheric CO_2. Prior research has already demonstrated that hydrology, temperature, and CO_2 affect peatland ecosystem structure and function (Boleman et al. 2003, Chivers et al. 2009, Churchill et al. 2014, Olefeldt et al. 2017). However, no study has used remote sensing to track peatland ecological response to such a diverse suite of global change drivers. These results highlight the potential to use hyperspectral data to identify and track a range of different climate change-induced impacts to northern boreal ecosystems.

The results of our field study indicate that hyperspectral datasets can be used to identify the changes in ecosystem structure and function associated with climate change. Through our research, we found that hydrology, temperature, and CO_2 alter NDVI and long-term community composition in two different types of boreal peatland ecosystems. Our field results from APEX indicate that long-term hydrologic change in sedge-dominated systems lead to shifts in community composition and ecosystem productivity. Our results corroborated those of Churchill et al. (2014) who found a significantly higher cover of sedges in the raised water-table plot. The dominant source of variation within the principle components analysis of APEX spectral data appeared largely driven by the greater diversity and overall cover associated with the control and raised plots, and a higher percent cover of litter associated with the lowered plots, which likely describes a gradient of ecosystem GPP (Figure 6). At the SPRUCE experiment, we found that community composition, but not diversity, varied significantly among treatments. In our results, shrub and forb cover were significantly different among the chambers in 2016, and both emerged as significant vectors within the multi-variate analysis of the reflectance spectra. These results indicate both the possibility that global change could shift the composition of ombrotrophic bog ecosystems with potential impacts on bog productivity, and points to a potential method of tracking these changes using remote sensing.

The differences in NDVI that we observed in this experiment indicate that ecosystem productivity is influenced by the global change drivers in both study systems. Prior research by Boelman et al. (2003) found that NDVI in an Alaskan graminoid fen was strongly tied to aboveground annual net primary production (NPP), with higher NDVI values indicated greater annual NPP. Although destructive sampling in either experiment was impossible, the main correlate of NDVI at APEX appeared to be the strong differences in diversity and the relative percent cover of litter among the treatments (Figure 4). However, NDVI has also been shown to correlate with several metrics of productivity including GPP, NPP, and leaf area index (Boelman et al. 2003, La Puma et al. 2007). Therefore, it is unclear whether the NDVI signal is being driven by greater instantaneous photosynthetic production, or by a greater amount of biomass present within the field-of-view or pixel. Because we found no differences in percent cover of photosynthetic versus non-photosynthetic vegetation at SPRUCE, it is also unclear in this case whether the differences in NDVI were a result of greater GPP or changes in overall leaf area or standing biomass. Further research is needed to examine the relationship between NDVI, photosynthesis, and NPP, particularly in response to changes in temperature and CO_2 level.

Our results also support the growing body of research on remote sensing of biodiversity. We have demonstrated that drought in peatlands negatively affects biodiversity, particularly of mosses and herbaceous species. This was captured by the spectral data. Specifically, variation and heterogeneity in spectral reflectance increased with increasing vegetation diversity among plots. Increasing spectral heterogeneity has been used as a proxy for diversity in several studies that have attempted to map diversity using remote sensing (Carter et al.2005, Gould 2000, Rochinni et al. 2010). These studies have been based on the species-area relationship in which species richness increases with scale across a heterogeneous landscape (Whittaker 1972). These studies have extrapolated species richness by calculating indices such as NDVI, and then calculating heterogeneity for pixel aggregates of varying spatial scales. Where these approaches model diversity as a function of area, our approach captures diversity directly by comparing the spectral heterogeneity among plots with varying levels of diversity. Alternative approaches have attempted to map diversity through the identification of unique species (Baldeck et al. 2015, Baldeck and Asner 2013, Carlson et al. 2007, Féret and Asner 2014). However, this approach is challenging in non-forested systems in which individual organisms do not occupy an entire pixel. Our results indicate that remote sensing may be used to estimate relative level of diversity directly by comparing the spectral heterogeneity of pixels within an image. This relies on the assumption that diversity is a key factor in determining the heterogeneity of an image pixel, rather than other factors such as canopy structure or bare soil. We suggest that these results may be best applied in systems with relatively homogenous canopies such as grasslands or, as in our study system, open wetlands. Given that most recent attempts to directly estimate diversity using hyperspectral data have occurred in forested areas, these results provide a novel approach to mapping diversity in a non-forested ecosystem.

In arctic and boreal ecosystems where the environment is undergoing rapid change, the methods we have described could prove invaluable to developing assessments of shifts in community composition over time. The use of hyperspectral imagery is integral to this approach because of the ability to select the spectral bands that best capture the variation across community types. The high spatial resolution of aerial over satellite data is also key to this approach because it allows for fine-scale distinctions among cover classes. There are multiple research programs that collect hyperspectral data and make it publicly available to scientists. NASA’s Airborne Visible/Infrared Imaging Spectrometer has collected hyperspectral imagery of research areas of interest for nearly two decades (Goetz et al. 1985). However, no data collected in northern arctic or boreal ecosystems are currently available to the public. The National Ecological Observatory Network recently launched its hyperspectral Aerial Observation Platform with a mission of “…bridging scale from organisms and individual stands to satellite based remote sensing” (Kampe et al. 2010). Our results set the stage for future studies that could use publicly-available hyperspsectral data to identify and track community and ecosystem level changes in arctic and boreal regions.

Conclusion

The results from the manipulation experiments presented herein clearly demonstrate that changing climate drivers have significant impacts on peatlands, ultimately leading to changes in their community composition, species diversity, and ecosystem productivity. We further demonstrate the utility and efficacy of leveraging remotely sensed data to characterize and track such changes through time. Indeed, remote sensing is emerging as an effect tool supporting ecological research given its growing ability to characterize key elements of ecosystem structure and function such as leaf area, foliar chemistry, species diversity, and, more recently, the cover of different species and plant functional types. In this research, we demonstrated that remote sensing can be used to detect the effects of a range of global change drivers on the productivity and community composition of two types of peatland ecosystems representative of extensive areas of the northern boreal environment. We also showed the feasibility of using hyperspectral remote sensing to map the distribution of plant functional types over large spatial extents. These findings could be applied to future studies examining changes in the distributions of plant functional types, biodiversity, and ecosystem productivity. In light of rapid global change, these studies could provide valuable insight into the changing ecology of the far north.

Chapter 2: Temperature, carbon dioxide, and hydrologic controls on peatland NDVI

Chapter Overview

Northern boreal peatlands play a significant role in the global carbon cycle. Global change is expected to have significant impacts on the community composition and productivity of peatlands ecosystems as hydrologic change, warming temperatures, and elevated carbon dioxide (CO_2) levels alter the conditions that have historically maintained peatlands as a sink for carbon from the atmosphere. Given their vast stores of soil organic carbon, understanding how peatland vegetation will respond to climate change is important for predicting the future of the boreal carbon cycle. We used passive remote sensing techniques to non-invasively estimate ecosystem gross primary production (GPP) in response to experimental manipulation of hydrology, temperature, and CO2 levels. We installed Normalized Difference Vegetation Index (NDVI) sensors in two large-scale peatland ecosystem manipulation experiments, one in a rich fen ecosystem in Alaska and one in an ombrotrophic bog in northern Minnesota. Our fen site is located within a hydrologic manipulation called the Alaska Peatland Experiment (APEX), which was established to study the effects of water table position and soil moisture contents on peatland ecology and biogeochemistry. Our bog site is located at the Spruce and Peatland Response Under Climatic and Environmental Change (SPRUCE) project. SPRUCE is a large-scale experiment examining the effects of warming and CO_2 enrichment on boreal peatlands. We also measured the percent cover of different species and plant functional types at both sites, and measured flux rates of CO_2 at APEX. We found a significant effect of long-term drought on peatland NDVI at APEX although we did not observe strong relationships between CO_2 flux rates and NDVI values. We also observed a significant positive interaction between warming and elevated CO^2 at the SPRUCE site. We found that vegetation communities had responded to the effects of treatment at both sites. Drought led to an overall decrease in photosynthetic biomass, and warming was associated with an increase in the relative abundance of shrubs and graminoids. Our findings suggest that global change could substantially alter the productivity and community structure of boreal peatland communities throughout the northern hemisphere.

Background

Climate change is occurring at a disproportionate rate in the arctic and boreal regions of the globe, with implications for the structure, function, and productivity of northern ecosystems. Shorter and less severe winters are resulting in warmer spring temperatures and extended growing seasons (Delbart et al. 2008, Karlsen et al. 2009, Myneni et al. 1997, Tucker et al. 2001). Northern regions are also experiencing an increase in mean annual precipitation, which has increased winter snowfall in the arctic and increased summer rainfall across the boreal region (Bintanja and Seltan 2014, Hinzman et al. 2005, Post et al. 2009, Walsh et al. 2011). Research suggests that changing patterns of temperature and precipitation are having significant effects on the ecology and carbon cycling of arctic and boreal ecosystems (McGuire et al. 2009). Northern ecosystems account for a significant flux of carbon out of the atmosphere, and therefore understanding their response to global change is crucial to predicting future impacts to the carbon cycle. Prior research has documented an increase in the annual photosynthetic productivity of arctic ecosystems observed via satellites (Beck and Goetz 2011, Goetz 2005, Tape et al. 2006). The trend in arctic productivity is driven by an extension in the growing season, as well as by the expansion of shrubs and trees into areas where they were previously restricted by a variety of abiotic and biotic factors including temperature, nutrient availability, and interactions among species (Chapin et al. 1995, Tape et al. 2006, Strum et al. 2005). However, less is known about how boreal ecosystem productivity is responding to climate change. Some studies have documented a decrease in photosynthetic activity measured from satellites in boreal forests (Beck and Goetz 2011), while others show an increase in photosynthetic area across the boreal, as well as in the arctic (Park et al. 2016). Still poorly understood is how complex interactions among species, climate, and disturbance will affect the long-term carbon balance of the boreal region (Kurz et al. 2008). However, given the evidence that significant changes will likely occur to the boreal carbon cycle, understanding how ecosystem productivity will respond to changing climate is important to making future climate change predictions.

Peatland ecosystems are particularly vulnerable to carbon loss induced by climate change because of the combined risk they face from increasing temperature and changing hydroclimate. Peatlands cover 1-5% of earth’s surface, predominantly at high latitudes, yet contain nearly one-third of the global store of soil carbon (Bridgham et al. 2006, Gorham et al. 1991, Yu et al. 2010). Peatlands are highly sensitive to warming temperatures, which increase rates of microbial respiration, allowing stored carbon from peat soils to be released into the atmosphere (Davidson and Janssens 2006). The peatland carbon cycle is also strongly tied to water table position and soil moisture content.

Experimental manipulation of peatland hydrology has shown that lowering water tables to simulate drought results in peatlands becoming a source of CO_2 due to lower gross primary productivity (GPP) and greater ecosystem respiration rates (Chivers et al. 2009, Olefeldt et al. 2017). Conversely, keeping water tables at or above the soil surface maintains peatlands CO_2 sinks because GPP outstrips respiration rates (Chivers et al. 2009, Olefeldt et al. 2017). Long-term changes in temperature and hydrology have been shown to have lasting effects on peatland community composition, with possible implications for overall ecosystem productivity (Breeuwer et al. 2009, Dieleman et al. 2014, Olefeldt et al. 2017). Research has found that plant functional types are important predictors of carbon flux in and out of peatlands (Goud et al. 2017). Changes in soil moisture content may have particularly negative effects on the *Sphagnum* mosses that dominate peatlands. Research has shown that drought can lead to desiccation of *Sphagnum* tissues, effectively eliminating photosynthesis for the duration of the drought (Strack et al. 2009). Because the *Sphagnum* mosses that form peat soils grow very slowly and sequester most of the carbon in peat, determining how this vegetation type will respond to increased temperature and changing hydroclimate is important to calculating whether peatlands can remain a sink for CO_2 in the future (Clymo 1970).

Increased levels of atmospheric CO_2 have also been shown to affect the productivity and function of terrestrial ecosystems. Studies published on this topic have yielded complex results that highlight the importance of interactions among a suite of biotic and abiotic factors. A series of CO_2 enrichment experiments performed on mid-latitude and northern hardwood forests demonstrate an increase in net primary production (NPP) with elevated

CO_2 (DeLucia et al. 1999, Norby et al. 2002, Norby et al. 2005). However, other research has shown little or no increase in productivity in response to elevated CO_2 levels in nutrient-limited systems, or indicate that the effects of CO_2 fertilization may be constrained by nutrient availability over the long term (Duursma et al. 2016, Ellsworth et al. 2017, Oren et al. 2001). Similarly, research in grasslands has indicated that elevated CO_2 levels allow plants to maintain high levels of productivity by increasing water use efficiency despite higher temperatures, but that the effects diminish under nutrient limitation (Morgan et al. 2011, Mueller et al. 2016, Parton et al. 2007, Reich et al. 2006, Reich and Hobbie 2013, Roy et al. 2015). *Sphagnum* dominated bog ecosystems are very nutrient poor, so one might predict a relatively small effect of elevated CO_2 on the productivity of ombrotrophic bog peatlands. These studies also indicate that different species respond uniquely to elevated CO_2 resulting in shifts in community composition over time, with additional consequences for ecosystem productivity (Mueller et al. 2016, Owensby et al. 1999). In peatlands, which have a variety of vascular and non-vascular plants, we would anticipate that the response to CO_2 would be highly species-specific and dependent on nutrient availability and soil moisture contents.

Despite the wealth of research on the effects of elevated CO_2 on ecosystem productivity in temperate forests and grasslands, arctic and boreal ecosystems have received very little attention even though they are experiencing climate change at an accelerated pace relative to the rest of the world. Mesocosm experiments that have examined the effect of elevated CO_2 on *Sphagnum* dominated ecosystems have yielded conflicting results. Some studies have shown that elevated CO_2 may increase the productivity of vascular plants at the expense of *Sphagnum* growth (Berendse et al. 2001), while other have indicated a positive response of *Sphagnum* to elevated CO_2 when combined with nitrogen fertilization (Heijmans et al. 2001, Jauhiainen et al. 2013). A study by Mueller et al. (2016) found that elevated CO_2 led to an increase in graminoid cover at the expense of moss cover. Additional research in graminoid-dominated systems found positive effects of elevated CO_2 on ecosystem GPP (Grulke et al. 1989). The Spruce and Peatland Response Under Environmental and Climatic Change (SPRUCE) project at the Marcell Experimental Forest in northern Minnesota, USA is the first large-scale experiment to examine the effects of CO_2 enrichment on boreal peatland ecosystems.

Productivity has historically been estimated though a combination of direct and indirect methods. The most direct method of estimating aboveground productivity is through the destructive sampling of annual growth following experimental manipulation. Destructive sampling is typically done at the end of an experiment because it irrevocably alters the study system. Therefore, it is prohibitive in long-term experiments where year-to-year measurements are necessary (Gower et al. 1999). Ecosystem CO_2 flux measurement is another widely-used method for estimating productivity. Gas exchange analysis combines light and darkened measurements of a whole ecosystem, either sealed within a chamber or through constant measurement of ambient CO_2 levels using eddy covariance towers (Baldocchi 2001, Baldocchi 2003, Goulden & Crill 1997, Livingston & Hutchinson 1995, Running et al. 1999). Both rely on the same set of assumptions to calculate productivity. The light or daytime measurement captures the net ecosystem exchange (NEE) of carbon between ecosystems and the atmosphere. NEE integrates ecosystem respiration (ER), or the combination of root respiration and microbial respiration, and gross primary productivity (GPP), which represents the uptake by photosynthesis (Baldocchi 2003, Livingston & Hutchinson 1995). The dark or nighttime measurement captures ecosystem respiration in the absence photosynthesis. The difference between ER and NEE measurements represents the GPP of the system (Saigusa et al. 2002). If the NEE flux rate is positive, then the system is a source for carbon at the time of measurement. If negative, it represents a sink for carbon because GPP is greater than ER. Measuring rates of CO_2 flux between ecosystems and the atmosphere has been widely accomplished using chambers that are sealed over the ecosystem for a time during which CO_2 levels are continuously monitored using infrared gas analysis (Livingston & Hutchinson 1995). The drawback of the chamber method is that, while it can control for wind and other factors, it can only be done on a relatively small scale since the ecosystem must be fully sealed in the chamber (Livingston & Hutchinson 1995, Goulden & Crill 1997). Although eddy covariance towers can aggregate CO_2 exchange rates across larger footprints, the area sampled can change depending on wind speed and direction to reflect the productivity of a variety of ecosystems across the landscape. Therefore, they cannot reliably capture the productivity of a specific ecosystem when they exist within a heterogeneous landscape (Baldocchi et al. 2001). For this reason, eddy covariance measurements have frequently been paired with satellite-based estimates of productivity that can help tie flux measurements to specific areas with greater accuracy (Churkina et al. 2005, Running et al. 1999, Turner et al. 2006, Zhao et al. 2005).

Remote sensing techniques are increasingly being used to examine the productivity of ecosystems in a manner that is non-destructive, not overly sensitive to landscape and climate heterogeneity, and can be to be aggregated over large spatial extents using airborne or satellite data (Running et al. 2004, Schloss et al. 1999, Turner et al. 2006). Remotely-sensed data can be collected by active sensors such as radar or lidar detectors, or passive sensors that measure solar radiation reflected off Earth's surface. Satellite imaging is the most common form of passive remote sensing. Most satellite imagers detect reflectance across a variety of visible and infrared spectral bands, which can yield valuable insight into Earth's biophysical properties (Jones & Vaughan 2010). Numerous data products exist that model NPP using visible and near-infrared spectral information combined with modeled estimates of plant respiration (Hunt 1994, Running et al. 2004). Products based on the ratio of absorbed photosynthetically active radiation (APAR) by the canopy over the total amount photosynthetically active radiation present (PAR) are commonly used to create global models of GPP (Running 2004, Tucker & Sellers 1986, Turner et al. 2006). Remotely-sensed measurements of NPP combine remote measurements of photosynthesis with estimates of plant light-use efficiency, which vary widely across vegetation types (Running et al. 2004). However prior research has demonstrated strong correlations between peatland PAR levels and measurements of productivity across ecosystems, including in both fen and bog peatlands (Boleman et al. 2003, Frolking et al. 1998). The conceptual relationship between NPP and PAR forms the basis for the widely-used Normalized Difference Vegetation Index (NDVI), which is calculated using a visible and an infrared band (Jones & Vaughan 2010). The visible band is strongly absorbed during photosynthesis, and is therefore synonymous with APAR, and the infrared band is strongly reflected, and so is thought of as equivalent to PAR. The fraction of absorbed photosynthetically active radiation (FPAR) is therefore equivalent to NDVI (Field et al. 1995, Prince & Goward 1995, Running et al. 2004).

$$\frac{NIR - VIS}{NIR + VIS} = NDVI \qquad \frac{APAR}{PAR} = FPAR \approx NDVI \tag{1}$$

NDVI has been widely used in both ecology and remote sensing to estimate ecosystem productivity at a variety of scales from the plot-level in response to experimental manipulation (Boleman et al. 2003, Goodin & Henebry 1997, Wang et al. 2016), to the global scale in the creation of terrestrial estimates of NPP (Nemani et al. 2003, Pettorelli et al. 2005).

Our objective in this research was to examine the effects of global change factors on peatland ecosystems using remote sensing. Working within two ecosystem manipulation experiments, we measured the effects of altered hydrology, increased temperature, and elevated CO_2 levels on peatland productivity, which we inferred through plot-level measurements of NDVI. We predicted that remotely-sensed estimates of peatland productivity would respond to global change drivers, specifically, we predicted that drought would negatively affect productivity at our rich fen site, and that warming and CO_2 fertilization would lead to an increase in peatland productivity in our bog study system. In this research, we consider NDVI to be a measurement of GPP. We believe that this is appropriate, because both LAI and rate of photosynthesis have been shown to correlate strongly with NDVI (Boelman et al. 2003, Gamon et al. 1995, Sellers 1987, Walker et al. 2003). Therefore, we also predict that GPP will be positively correlated with NDVI. Through this research, we aim to measure the direct effects of changing climate drivers on peatland vegetation, as well as to further remote sensing applications in northern boreal ecosystems.

Methods

Site Description

We conducted this study at two large-scale ecosystem experiments representative of two types of common northern boreal peatlands. The first site was at the Alaska Peatland Experiment (APEX) at the Bonanza Creek Long Term Ecological Research Station, located thirty miles west of Fairbanks, Alaska (64.82°N, 147.87°W). The experiment is situated in a sedge-and-shrub-dominated rich fen on the floodplain of the Tanana River. Fen peatlands are characterized by hydrologic connectivity with groundwater, indicating a higher nutrient status relative to bogs, which are fed primarily by rainwater (Wright et al. 1992). APEX was initiated in 2005 as a long-term experimental manipulation looking at the impact of hydrology on peatland ecology and biogeochemistry. APEX consists of three water table manipulation plots, a raised, lowered, and control treatment, each 120 m^2 in size. The lowered treatment plot is drained passively by a trench that borders the plot to reduce the water table level significantly below the surface of the peat. Water from the trench is then pumped into the raised water table treatment to keep it consistently flooded several centimeters above 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. Water table position and soil moisture content are measured manually at six wells in each water table treatment (Chivers et al. 2009).

The second study site included in this experiment was at the Spruce and Peatland Response Under Climatic and Environmental Change (SPRUCE) project located at the Marcell Experimental Forest in northern Minnesota, USA (47.30°N, 93.29°W). SPRUCE was initiated in 2014 as a climate change experiment to explore the effects of increased temperatures and elevated CO_2 levels on the ecological and biogeochemical processes at the southern edge of the boreal biome. The experiment is located within an ombrotophic bog dominated by Sphagnum mosses and black spruce (*Picea mariana*) with an understory of ericaceous shrubs, graminoids, and forbs. The experimental design consists of thirteen treatment plots with an incomplete factorial between temperature and CO_2 levels. The plots consist of octagonal enclosures the are 12.8 m in diameter (114.8 m^2 in area), 7 m tall, and penetrate through the peat to mineral soil, which averages 2.5 m deep across the site. The enclosures are maintained at a series of increasing temperatures to simulate a range of possible climate change scenarios. An additional five plots are monitored as controls. Two control plots are also enclosed by chambers. One chambered control has ambient temperature and CO_2 levels, and the other chambered control has ambient temperatures and elevated CO_2. The remaining eight treatment plots are maintained at +2.25, +4.5 +6.75, and +9 degrees C above ambient temperatures. Parts per million of CO_2 reflect ambient levels in half of the temperature treatment plots, and are elevated to between 800 and 900 ppm in the other half. The SPRUCE experimental design was conceived as a regression-based design in which ecological change could be measured in response to a broad range of increasing temperature treatments (Hanson et al. 2017).

NDVI Data Collection

Both sites were instrumented with Decagon Inc. NDVI sensors at the beginning of the 2016 growing season (Gamon 2015). They consisted of two sensors that measured irradiance at 630 and 800 nm for both incoming and reflected light. The hemispherical (incoming) sensor is cosine corrected to account for sun angle. The field stop (downward) sensor captured reflected solar radiation. The downward pointing sensors had fields of view of 36°, and were installed at a height of 150 cm above the peat surface at both sites, capturing an area of approximately 53 cm in diameter. Data were captured on Em50G data loggers every ten minutes throughout the growing season. 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. Sensors were installed above undisturbed community composition plots, which are not instrumented or destructively sampled in any way.

Processing the data occurred slightly differently for the two sites due to the differing light conditions at each experiment. In interior Alaska, the sun is out nearly twenty-four hours every day during summer months, whereas northern Minnesota experiences darkness during summer nights. For the APEX field site, NDVI values of less than 0.5 were excluded from the data set. These values occurred exclusively during the few hours on either side of midnight when the sun was below the horizon. At SPRUCE, only values between 11:00 AM and 1:00 PM were included in the analysis, which approximates solar noon. In addition, a threshold of 0.5 was applied to exclude NDVI measurements that may have occurred during very overcast days. The exclusion of observations taken when the sun was not overhead was done to minimize the potential for shading of the sensors by trees or other instruments. At APEX, this was not an issue since the site is very open and so there was no risk of shading whereas SPRUCE has an intermittent canopy of tamarack and spruce trees. For both sites, a daily average NDVI value was calculated for each plot.

Vegetation Cover Sampling and Measurement of LAI

To account for potential community compositional differences among the treatments, we measured the percent cover of all species present at both experiments. Percent cover of each species was measured at APEX using a point-intercept sampling method. At each plot, two transects were established perpendicularly to each other across a series of replicate 1x1 meter vegetation plots. For the lowered and raised treatments, four replicate plots were sampled, and in the control treatment five replicates were sampled. A metal transect was positioned above the canopy at one meter above the surface of the peat. A laser pointer was inserted into ten evenly-spaced holes in the metal frame along the transect. At each point, whatever the laser touched was recorded. Species and height above the ground were recorded at each interception from the canopy to the surface of the peat. If the target was not able to be identified, it was recorded as either “standing dead,” indicating that it was non-photosynthetic biomass but was still standing, or as “litter,” indicating that it was part of the thatch forming at the surface of the peat. Leaf area index (LAI) was calculated as the number of layers of photosynthetic vegetation between the canopy and the soil surface. It excluded any litter or standing dead materials.

Vegetation cover at SPRUCE was sampled in mid-July in thirteen chambers across the factorial of temperature and CO_2 treatments. In each chamber, 3 plots 2 m^2 in size were sampled using a gridded frame of 1 x 2 m, which was set onto PVC pipes installed in the experiment to facilitate repeated data collection over the exact same area. The frame was divided into 50 – 20 x 20 cm cells. Presence and absence of all graminoids, forbs, low shrubs, and small trees were recorded for each cell of the grid. If a species was present in half of cells, it was considered to occupy 50% of the plot.

LAI was measured at SPRUCE using an LI-COR LAI 2200 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 clear day with no cloud cover. 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 of LAI were done at all three each vegetation community plots in each treatment chamber. Measurements were taken in the center of both halves of the 1x2 meter plots, or at two sampling locations in each plot. At each sampling location, two scans were taken at 1 meter 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.

Carbon Dioxide Flux Measurements

CO_2 flux measurements were collected seven times throughout the growing season at APEX using 60 cm^3 clear chambers. The chambers were constructed using an aluminum frame and plexiglass walls, and sealed to prevent leaks. The chambers were set on 60 cm^2 metal collars that were permanently installed in the peatland. CO_2 levels were measured using an EGM-4 Portable Photosynthesis System. Flux rate was measured under ambient light conditions to record NEE rates for 120 seconds. The chamber was then shrouded using a heavy cloth, and ecosystem respiration rates were measured under darkened conditions for 120 seconds. The chamber was flushed between ambient and darkened fluxes back to ambient levels. GPP was estimated as the difference between the ambient flux and the darkened flux at the time of measurement. We followed the convention that negative flux rates represented carbon being lost from the atmosphere and sequestered in biomass, and positive fluxes represented carbon being released into the atmosphere from the ecosystem (Olefeldt et al. 2017). Therefore, greater GPP values are represented by more negative flux rates.

Data Analysis

Vegetation cover data were analyzed to see whether significant differences existed in species percent cover between the treatments at both sites. Data were analyzed using a multi-variate non-metric multidimensional scaling ordination using a Bray-Curtis dissimilarity index to look at community-level differences among plots, and treatment was fit to the model to determine whether statistically significant differences existed in composition among treatments. 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 vector within the ordination. R-Vegan was used for all multi-variate analyses (Oakensen et al. 2016). LAI was compared between treatments at APEX using significance testing at an alpha level of 0.05, with a Bonferroni post-hoc comparison of means to examine differences among treatments. LAI for SPRUCE were analyzed using a linear regression model with heat as a continuous variable. NDVI data for both sites were analyzed using an analysis of variance with date as a random effect to isolate the effect of treatment. At SPRUCE, a two-factor ANOVA was used, with temperature included as a continuous variable and CO_2 level as a factor. At APEX, water table treatment was analyzed as a factor. The relationship between NDVI and the CO_2 flux measurements for the APEX site was analyzed using basic linear regression with a Pearson’s correlation analysis.

Results

1) *Response of vegetation community composition, NDVI and CO_2 flux to experimental water table manipulation*

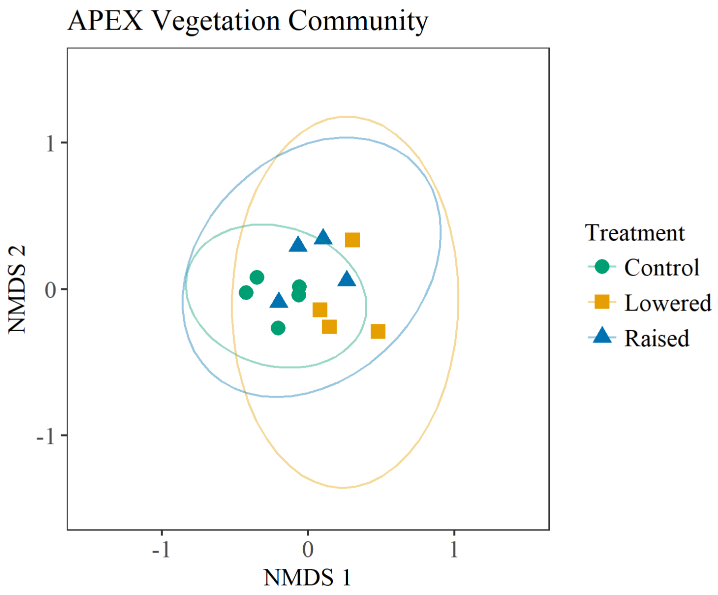

Figure 9: NMDS of APEX vegetation community.

APEX community data indicate significant differences in cover between the three treatments. Results from the NMDS indicated a good model fit with a non-metric R^2 value of 0.99 for the relationship between the observed dissimilarity and the ordination distance. The stress of the model was 0.14, with two dimensions. We found significant relationships between community composition and treatment vectors, primarily resulting from differences in shrub and grass cover ($r^2 = 0.45$, $p = 0.01$) (Figure 9). Grasses were associated with cover in the raised plots, and shrubs were associated with cover in the control plots. The lowered plot was associated with a higher but not significantly greater cover of litter.

APEX NDVI values were significantly higher in the control and raised plots than the lowered plot, which had lower NDVI values throughout the entire growing season (Figure 10). There was a trend towards greater LAI in the raised and control plots as compared to the lowered plot, although the results were not significant. However, the fractional cover of photosynthetic LAI to non-photosynthetic LAI was found to be significantly greater in the control and raised treatments relative to the lowered treatment (ANOVA $F_{2,\text{ error df}}$ =6.71, $P < 0.05$). Model results show a highly significant effect of long-term hydrologic change on NDVI (ANOVA, $F_{2,\text{ error df}}$=7.76, $P < 0.001$). NDVI in the lowered water table treatment was consistently lowest throughout the growing season, and peaked at a lower level as compared to the control and raised treatments. NDVI was highest in the control plot for the early part of the growing season, and peaked at a higher level than either of the other treatments. However, in the second half of the growing season, the raised plot had the greatest NDVI, which peaked at a substantially later date (Figure 10).

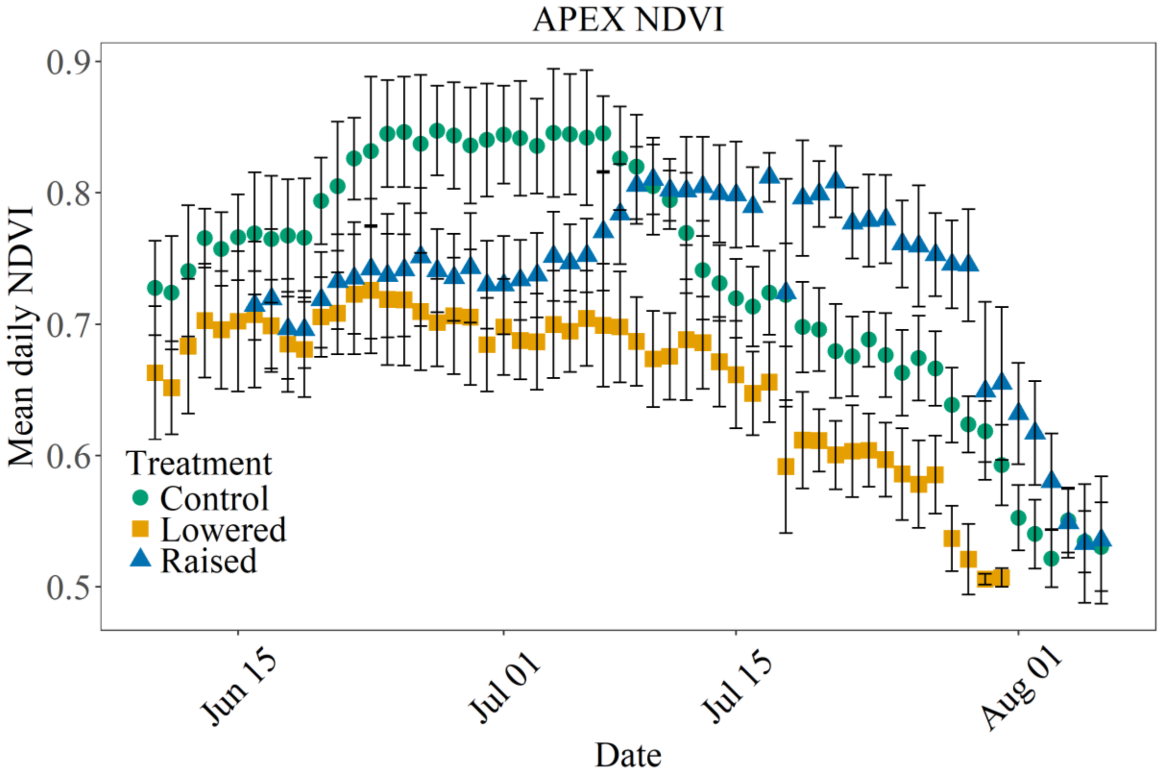

Figure 10: APEX NDVI for the 2016 growing season. Error bars are standard deviation of the mean (N≈80 per day at 10 minute intervals).

Carbon dioxide flux – NDVI relationship

We did not find statistically significant relationships between NDVI and any of the gas flux measurements when we subjected the data to a basic linear regression analysis (Figure 11). There were weak trends towards greater NDVI with more negative GPP and NEE fluxes, and lower NDVI with more positive ER fluxes, but the relationships were not strong enough to be conclusive. We further analyzed differences in flux rates among treatments using a one-way Analysis of Variance with a Bonferroni pairwise comparison. We found no differences in either ER or GPP, and only marginally significant differences in NEE. However, this result is called into question because NEE is a product of both

GPP and ER and no differences were found in either of those cases.

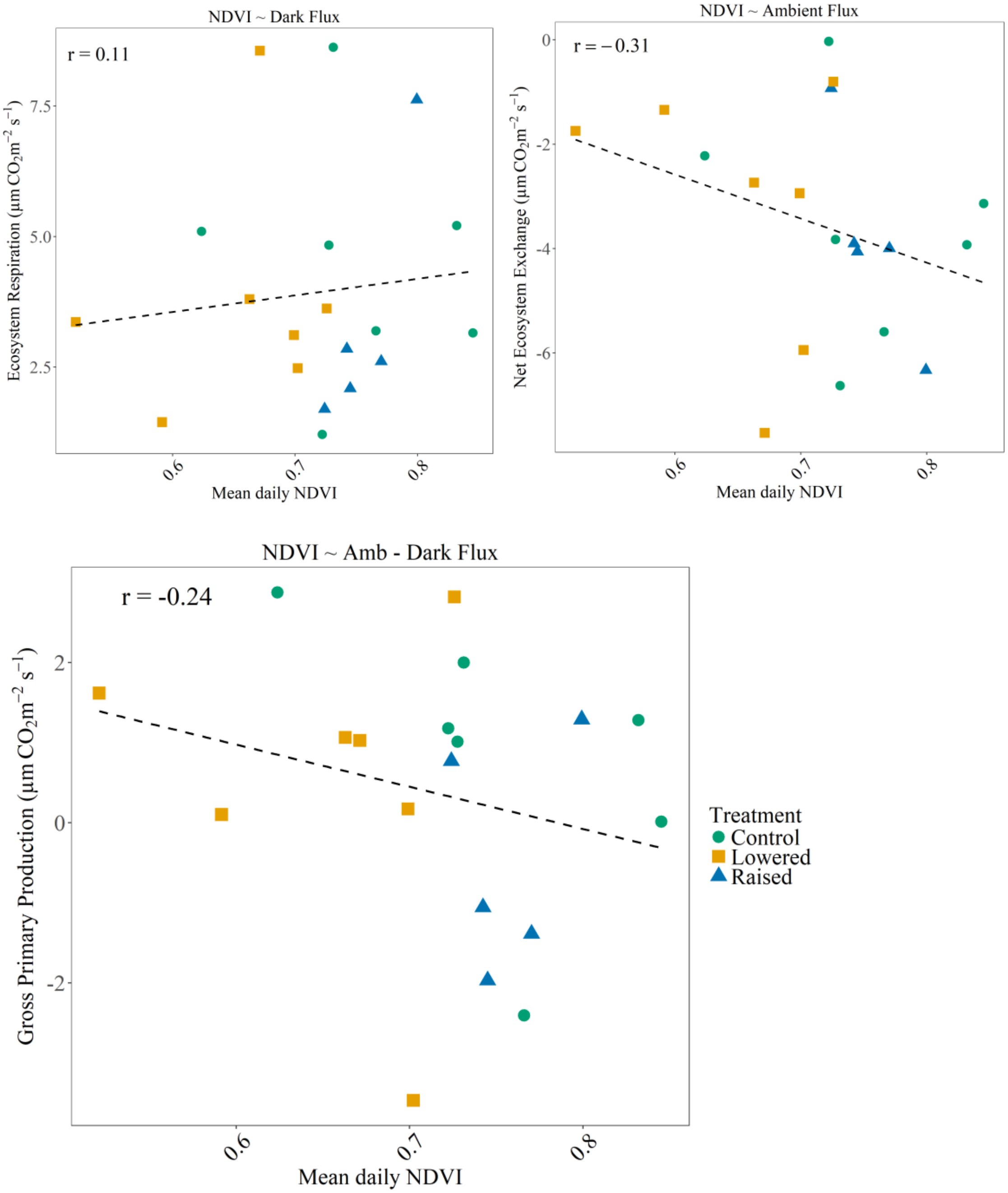

Figure 11: NDVI- CO2 flux relationships for APEX with Pearson Correlation coefficients for each relationship.

2) Response of vegetation community composition, LAI, and NDVI to experimental warming and elevated CO_2

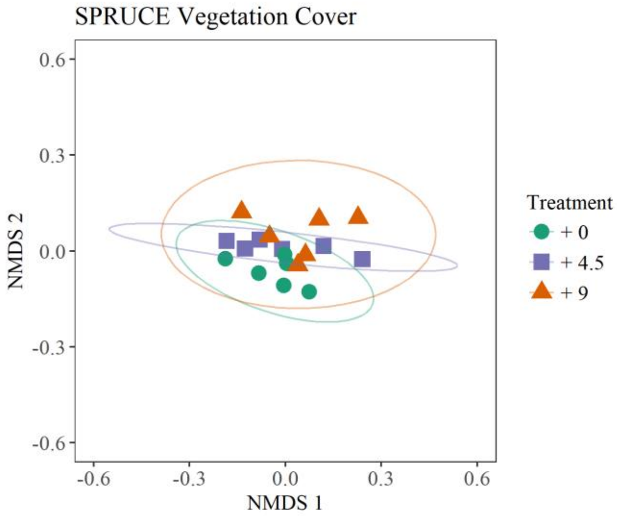

Figure 12: NMDS of SPRUCE vegetation community. Ellipses are standard deviation of the mean.

SPRUCE NMDS model results had a stress of 0.03 for two dimensions with a non-metric R^2 value of 0.99 for the relationship between the observed dissimilarity between the plots and the ordination distances. The results from fitting treatment to the model indicate that warming was a significant vector in the NMDS, but not CO_2 level (r^2 = 0.58, p = 0.001) (Figure 12).

SPRUCE showed a clear positive response in NDVI to warming, but a mixed response to increased CO_2 level (Figure 13). 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 2). The chamber with the highest NDVI throughout the growing season was the +9° C treatment with elevated CO_2.

SPRUCE	***DF***	***F value***	***P***
temp	*1*	*264.5*	***<0.001***
co2	*1*	*0.025*	*0.875*
temp:co2	*1*	*23.6*	***<0.001***

*Table 2: SPRUCE model contained temperature as a continuous variable, and CO2 as a factor (NDVI ~ temp * CO2 + Error(Date).*

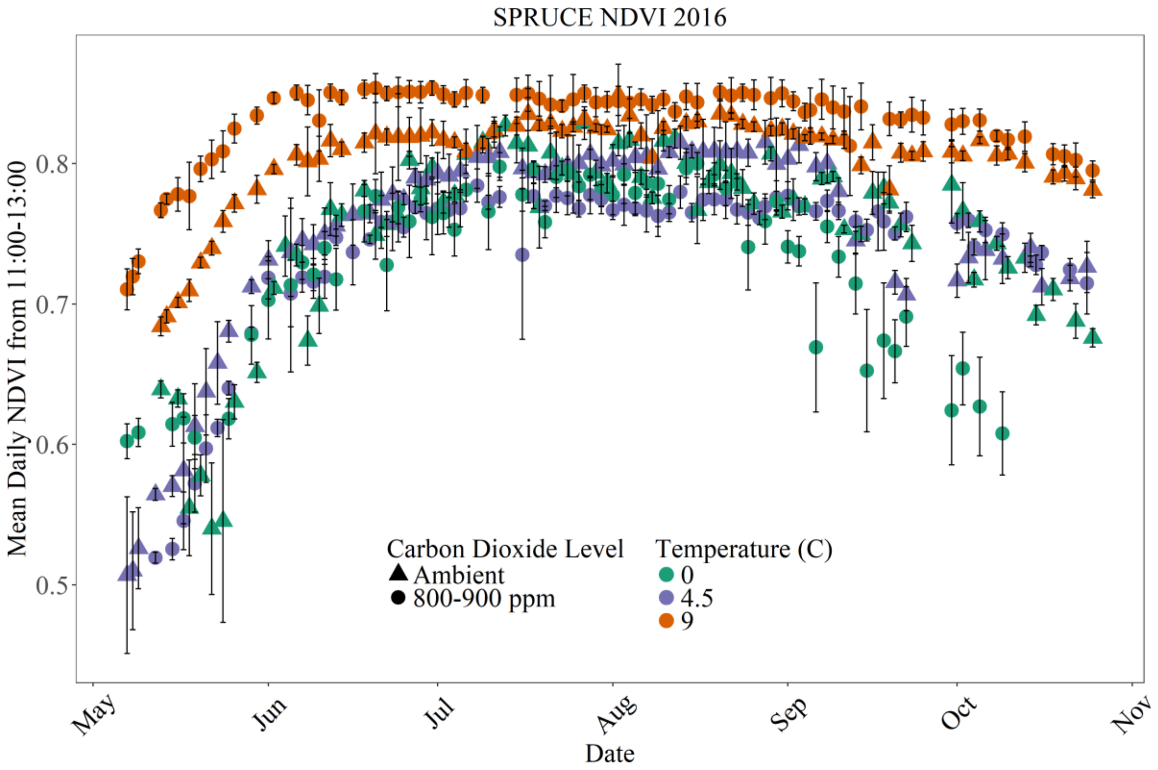

Figure 13: SPRUCE NDVI for 2016 growing season. Shown are NDVI values for every other day. Error bars are standard deviation of the mean (N=12 per day at 10 min. intervals).

Overall, NDVI at both sites responded strongly to treatments, and at both sites the effect began early in the spring and was apparent throughout the growing season. Warming appeared to extend the growing season and drought appeared to negatively affect NDVI. Seasonality at both sites led to strong trends in the NDVI data. At APEX, NDVI was already at above 0.5 when the sensors were installed, but by late August senescence was clear, whereas at SPRUCE NDVI remained high into early winter. These site differences may be attributed both to differences in community type, as well as the differences in growing season length in Minnesota versus Alaska.

LAI at SPRUCE showed a clear positive effect of warming (Figure 14). We analyzed the data using a linear model, with temperature as a continuous variable. Our results indicate that LAI responded strongly to increased temperature ($R^2 = 0.64$, $F_{36}=66.0$, $P < 0.001$, RMSE = 0.97).

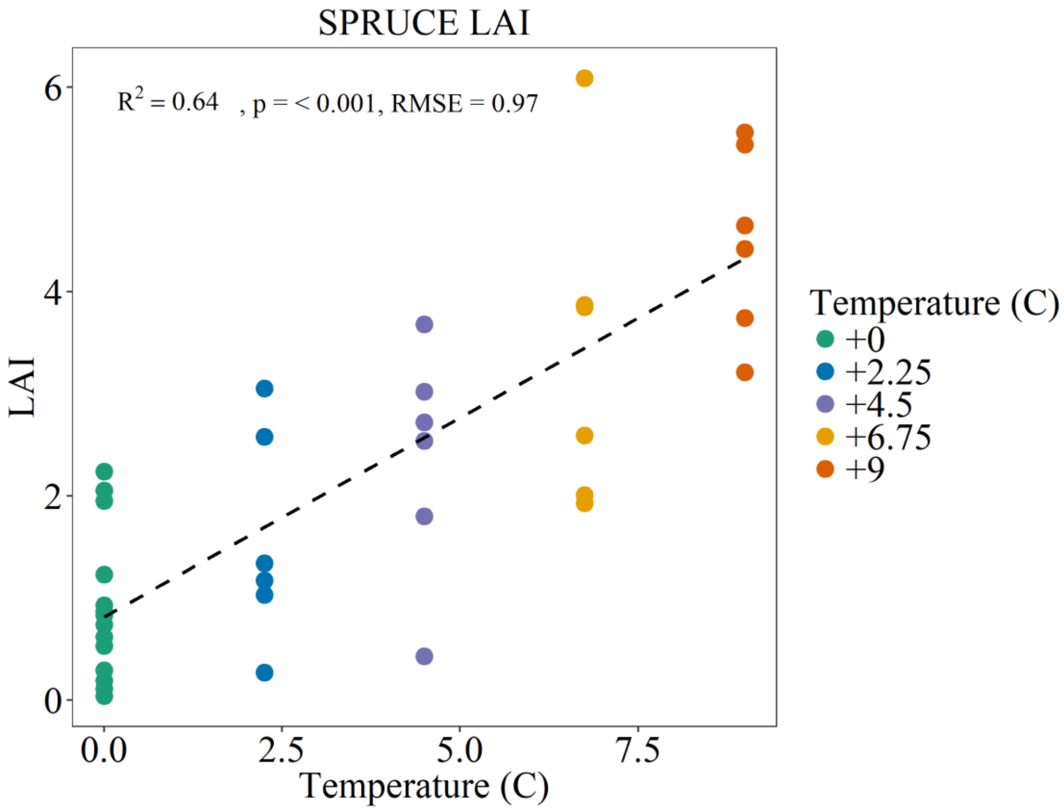

Figure 14: Response of LAI to increased temperature at SPRUCE.

Discussion

Understanding how northern boreal ecosystems will respond to global change will aid researchers in predicting future changes to the terrestrial carbon cycle. In this study, we observed the response of two widely-distributed types of boreal peatland vegetation communities to simulated changes in hydrology, temperature, and levels of atmospheric CO_2. NDVI at both peatland study sites showed clear responses to treatments, which we interpret as indicative of changes in ecosystem GPP. The effects of treatment on productivity manifested as changes in peak NDVI values and growing season length of the manipulated ecosystems. We observed a strong effect of warming on NDVI at SPRUCE, and of drought at APEX. Results from APEX should be interpreted as the result of long-term hydrologic changes rather than the result of annual differences in water table position. In a typical year at APEX, water table separation between the lowered and raised plots would reach an annual average of over twenty centimeters, and of up to forty centimeters in the late season (Olefeldt et al. 2017). However, the summer of 2016 was extremely rainy in central Alaska, and so achieving a meaningful separation of water tables proved to be impossible (Figure 14).

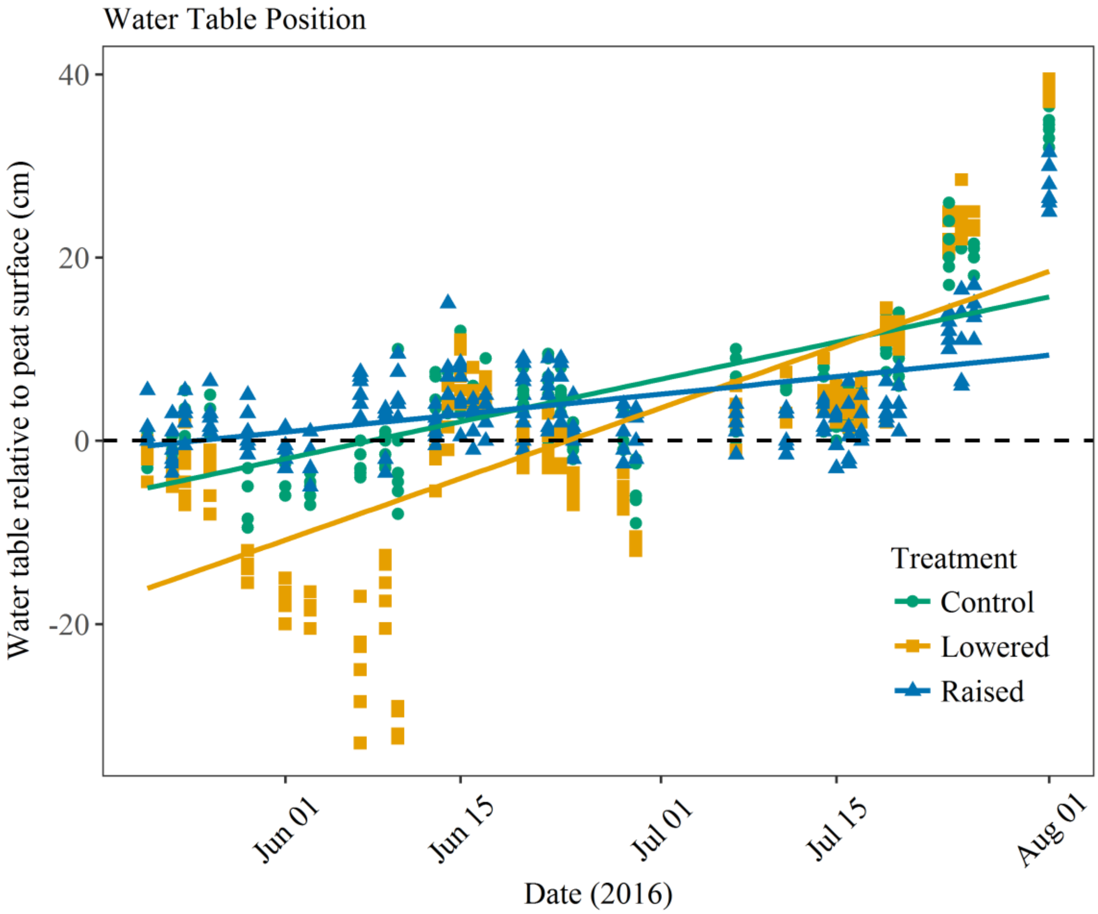

Figure 15: Plot of water table position at APEX in the summer of 2016. Water tables were successfully separated for the early part of the growing season, but meaningful separation ended in mid-June following heavy rainfall that continued for the duration of the summer.

The lack of annual water table difference is also implicated in the lack of significant difference in the rate of CO_2 flux, which is controlled almost entirely by annual variation in soil moisture contents and water table position (Chivers et al. 2009, Churchill et al. 2014, Olefeldt et al. 2017). Therefore, all differences in NDVI found at APEX in this experiment must be attributed to the legacy effects of long-term hydrologic change rather than the effects of active manipulation. These results are consistent with prior research at the site and elsewhere that found an overall decrease in GPP with long-term drought

(Churchill et al. 2013, Olefeldt et al. 2017). We found that the fraction of photosynthetic to non-photosynthetic leaf area was significantly higher in the raised and control treatments. This indicates that, even if photosynthetic leaf area showed only a non-significant trend towards being lower in the lowered plot, the greater relative cover of litter to photosynthetic leaf area is likely driving the trend in NDVI. Many studies have found that the relative cover of photosynthetic biomass is strongly 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 the fraction of photosynthetic to non-photosynthetic biomass.

Although this explains the trend observed in NDVI in the lowered plot, we did not find any differences in fractional cover between the control and raised treatments. Therefore, the differences observed in NDVI between the control and raised APEX plots is 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 10). Given the results of our analysis of community composition, variation in NDVI may reflect differences in phenology resulting from 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 cover of mosses, grasses, and forbs. The raised plot is also more species rich than the control plot. It may have been that *C. utriculata* experienced senescence earlier than other species present at the site and that the differences in NDVI may result from variation in the phenology of the species present in each treatment.

Results from SPRUCE indicate a strong positive effect of warming on NDVI, again suggesting increased productivity. This was particularly pronounced for the +9º C treatment, which had greater NDVI throughout the growing season. The +4.5º C treatment had similar NDVI values to the control treatments in the early and middle part of the growing season, but appeared higher than ambient in the fall. An extension in growing season length with warming is to be expected, and these results are consistent with many previous studies that have published similar findings (Peñuelas & Filella 2001). However, these results are some of the first to examine changes in the phenology of boreal peatland species in response to global change.

Leaf area index of the shrub layer at SPRUCE also showed a strong positive linear response to heat treatment. The changes in LAI observed in the heat treatments are the probable cause for the increases in NDVI with observed warming. Because we also found a shift in the relative abundance of forbs and shrubs, it is likely that the increase in both LAI and NDVI are resulting from an increased abundance of shrubs with warming (Montgomery et al. unpublished). Because LAI is highly correlated with GPP, this result, along with our NDVI data points to an overall increase in aboveground productivity with warming.

These results support several of the central hypotheses of the SPRUCE experiment. SPRUCE hypothesis H2 states that annual NPP will not increase with warming overall, but that GPP will increase in some species and decrease in others (Hanson et al. 2009). Shifts in GPP will be due primarily to the negative effects of warming on peat soil moisture content and water table position which will favor vascular plants over mosses (Weltzin et al. 2003). H2 predicts 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. Our results show an increase in overall GPP with warming, coincident with an apparent increase in graminoid and shrub cover which broadly supports H2. Our findings and could also indicate an overall increase in productivity, even accounting for the shift in community composition. It is unclear from our data to which plant functional types we may attribute the increase in GPP, and whether or not those increases are outstripping losses from due to ER. Pairing NDVI measurements with ecosystem CO_2 flux, as we did at APEX, would help to further elucidate the relationship between apparent increases in productivity and potential changes in the rate of ER.

Our results also support H6 of the SPRUCE project that elevated CO_2 will positively influence NPP at higher temperatures (Hanson et al. 2009). Elevated CO_2 levels did not have a clear effect on the ambient or +4.5° C treatments, but appeared to have an interactive effect at +9º C. This trend is also supported by our model result that indicated a significant effect for the interaction between CO_2 and warming. This result is also supported by research that suggests that the positive effects of elevated CO_2 on photosynthesis increase with warming (Long 1991, Luo 2008). As is the case with temperature, this result may also be due to interactions between changing species composition and overall ecosystem productivity. Prior research examining the response of boreal peatland species to elevated CO_2 has yielded mixed results, and no study has yet examined the combined effects of warming and elevated CO_2 on *Sphagnum* dominated ecosystems. Research on the effects of carbon enrichment on *Sphagnum* has yielded contradictory findings; some studies have indicated that moss growth responds positively to elevated CO_2, and others showed no effect (Berendse et al. 2001, Heijmans et al. 2001). However, vascular plants have broadly been shown to respond positively to elevated CO_2 in numerous studies (Nowak et al. 2004). Although we cannot say definitively to which plant functional types the apparent effects of elevated CO^2 in the +9° C treatment may be attributed, it is likely that the increase in NDVI observed is due to the greater abundance of shrubs and graminoid species in those plots.

While the results of our research indicate that hydrology, temperature and CO_2 levels affect peatland ecosystem productivity, it is difficult to pinpoint the exact effect that these treatments have on ecosystem structure or function. Because NDVI is correlated with a variety of plant and community-level processes, which are, in turn, correlated with each other, it is difficult to identify the locus of the treatment effect. In the case of APEX, we were unable to manipulate the water tables in the summer of 2016, which means that any effects on NDVI must be due to the long-term effects of a decade worth of treatment on the vegetation community. Despite the difficulty of being unable to manipulate the water tables due to unusual amounts of rainfall, in some ways the lack of water table difference makes it easier to eliminate potential explanations for the signal we did observe. At SPRUCE, warming and elevated CO_2 levels are affecting the phenology, species composition, and plant physiology of the vegetation community. These combined effects are resulting in an increase in NDVI, but whether that is because of increased LAI, NPP, or increased photosynthesis is unclear. Given that these factors are all correlated, it is likely that they are all occurring, although we predict that the responses are species-specific. Further measurement of leaf and ecosystem-level gas exchange would strengthen our understanding of how unique peatland taxa are responding to global change.

In future research, additional spatial and temporal replication would also allow us to better understand how variation in ecosystem structure and community composition effects NDVI. At both APEX and SPRUCE, one sensor was installed in each treatment, so spatial replication was low even though temporal resolution was very high. Increasing the number of sensors installed in each treatment would increase the power of the data by ensuring that differences in NDVI were not simply a result of variation in community composition but an effect of the treatment. Adding additional years of data to the experiment would also strengthen these results by increasing certainty in the effects of treatment on NDVI, and by allowing us to observe the long-term effects of treatment on productivity.

Despite the limitations of using NDVI as a metric of productivity, we can consider it to be an independent observation that combines multiple elements of community structure and function into a synthetic measurement. Because it has been shown to correlate with aboveground NPP (Boleman et al. 2003), GPP (La Puma et al. 2007), and leaf area index (Carlson & Ripley 1997, Walker et al. 2003), it can be thought of as combining multiple responses to treatment into one measurement. Additionally, NDVI can be passively observed at high temporal resolution capturing the effects of treatment on phenology; another important corollary to productivity in boreal peatlands (Kross et al. 2014). Therefore, it provides valuable insight into the response of peatland ecology to a suite of different treatment effects and should be thought of as a standalone measurement of ecosystem function.

The results of this research show the effects of multiple potential global change drivers on peatland ecosystem productivity. Warming had a strong positive effect on NDVI, and long-term drought had a strong negative effect. Flooding and elevated CO_2 yielded mixed responses. These findings indicate that global change will have a significant effect on northern boreal peatlands, and gives some sense as to the direction of these changes. In a warmer and more CO_2-rich world, the GPP of northern boreal peatlands may increase in conjunction with shifts in species composition and an overall increase in photosynthetic activity. However, if warming also leads to a reduction in peatland soil moisture, it may counter the effects of warming through water limitation. Although looking at the interactions between warming and water table position and soil moisture contents is beyond the scope of this research, it is to be expected that there would be an interaction as higher temperatures lead to greater evapotranspiration from peatland vegetation and soils (Hanson et al. 2009). In boreal regions that are underlain with permafrost, warming in peatlands is also expected to effect hydrology through the thawing of previously frozen soils (O’Donnell et al. 2012). Future research should incorporate hydrology in an analysis of the effects of warming and elevated CO_2 on peatland NDVI to account for the likely interactions among them.

Conclusion

How climate change will affect the ecology and subsequently the carbon cycle of northern boreal ecosystems is an extremely important question in global change research. In this study, we investigated how a suite of controls on ecosystem function alters the vegetation composition and GPP of peatlands using proximal remote sensing methods. Remote sensing in ecological science is a growing research area that seeks to apply the findings of field observations to satellite data to track changes across multiple spatial and temporal scales. In our study, we found significant effects of warming, elevated CO_2, and hydrologic change on peatland ecosystem structure and function. Because they cover a large amount of land at high latitudes and contain approximately one-third of the global pool of soil carbon, understanding how peatlands will respond to climate change is important to understanding future impacts to the carbon cycle. NDVI correlates with the productivity of an ecological community, which can help researchers determine what the net balance of carbon in peatlands will be under climate change. Future research is needed to investigate the interactive effects of the different global change drivers explored here, as well as to capitalize on widely available time-series satellite datasets to look at effects of changing climate on boreal peatlands across the landscape, and through time.

Final Thoughts

We are living in an era of rapid global change that is unprecedented in human history. The extent of human-induced global warming is still unknown, but Earth's ecosystems are already showing the effects. The rate of climate warming has been most dramatic in the far northern reaches of the globe, and through my Master's research, I have had the opportunity to observe some of its impacts firsthand. Climate has played an integral role in the formation of my study system, peatlands, which became widespread throughout the north after the retreat of the glaciers over 10,000 years ago. The cold, wet conditions that allow peatlands to form may become more limited in the future, particularly in the southernmost reaches of the boreal biome. Through my research, I have looked in various ways at the climate controls on peatland ecological function. And, although my research has centered on peatlands, the remote sensing methods that I used can be applied to answering similar questions across many different types of ecosystems. It is my hope that this body of research will help further scientific understanding of how the ecosystems of the far north will respond to climate change.

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Appendix I: Mapping boreal peatland plant functional types using hyperspectral remote sensing

Overview

In recent years, spectral remote sensing has successfully been used to conduct large-scale analyses of ecosystem structure and function. Remote sensing has been used to detect differences in ecosystem net primary production (NPP) (Field et. al 1995), leaf nitrogen and chlorophyll content (Aber and Martin 1997, Sims and Gamon 2002) and water stress (Gao 1996). Spectral indices have been developed that are sensitive to elements of ecosystem structure such as leaf area index and canopy cover (Carlson and Ripley 1997). Satellites with frequent return visits have also been used to map changes in phenology, or the timing of annual flowering and tree senescence (Turner et al. 2003). Together, these tools provide a powerful approach for examining ecosystem changes at landscape, regional, and global scales. Although these tools have been broadly applied to addressing questions regarding ecosystem structure and function, current research in ecology seeks to apply remote sensing techniques to mapping the distribution of unique species over large areas (Ker and Ostrovsky 2003, Turner et al. 2003, Turner 2014). The use of remote sensing as a tool for looking at species' distributions could give ecologists the ability to track and species' responses to climate change (Turner et al. 2003). These large-scale analyses will help to inform management strategies and environmental policy approaches for conservation and management in the face of global climate and land-use change.

High-resolution hyperspectral imagery is emerging as a promising method of performing accurate large-scale analyses of species' distributions using remote sensing (Turner 2014). The benefit of using hyperspectral data over three band or multi-spectral data is that leveraging a greater number of spectral bands in order to perform landscape classification allows for the differentiation of cover types based on subtler spectral differences that distinguish species from each other. Doing this allows for species' leaf area index, the presence of specific photosynthetic pigments, leaf water status, and other leaf-level characteristics to be analyzed simultaneously. Hyperspectral imagery, paired with high spatial resolution or "hyperspatial" imagery (less than one-meter ground resolution) has been used to quantify populations of mammals and birds, as well as to map the distribution of invasive plant species (Barbosa et al. 2016, Turner et al. 2003).

However, even with high spatial resolution, the feasibility of mapping individual organisms using remotely sensed data is dependent on how structurally and spectrally distinct they are within a scene or image. For example, species in tropical forests may be more difficult to distinguish from each other than species in a savannah due to the high level of species richness and heterogeneity present in rainforests (Baldeck and Asner 2014). Recent research in this area has been working to employ hyperspectral imagery to differentiate plant functional types from within complex, landscapes such as forests and prairies by using subtle differences in spectral reflectance detectable by using many spectral bands (Jetz et al. 2016, Féret & Asner 2014). Together, these studies indicate a significant interest in using remote sensing to map the composition of ecological communities at the landscape scale.

This project explored the use of high-resolution hyperspectral imagery in detecting fine-scale patterns of plant functional types across a landscape. My study will further research in the field of remote sensing in ecology, and help to better understand the distribution of different vegetation cover types.

Methods

1) *Site Description*

I used a dataset that was collected at the Bonanza Creek Long Term Ecological Research Station. The landscape is composed of peatland soils overlain by several different vegetation community types. Included in the study area are black spruce and tamarack forests, sedge meadows, tussock grasslands, *Sphagnum* moss bogs, and shrub/birch communities. The study area is located within a section of the Tanana River floodplain.

2) *Aerial hyperspectral data acquisition*

Airborne hyperspectral data were collected across a 3 km^2 in June of 2015 by the remote sensing company SpecTir above the Bonanza Creek Long-Term Experimental Research Forest in central Alaska. The area encompassed a number of different eco-types including spruce bog, open fen peatlands, tussock meadows and areas of ericaceous shrub cover. The instrument used in the data collection was a ProSpecTir push broom imaging spectrometer that collected data at 360 spectral bands from approximately 400 to 2450 nanometers with a one-nanometer bandwidth at a spectral resolution of approximately 5 nm. The imagery was collected approximately 200 meters above the ground surface, resulting in a spatial resolution of 1 m^2. The study area is approximately three square kilometers in size.

3) *Data analysis*

We used the aerial imagery to perform an unsupervised classification analysis of plant functional types across the landscape. We used a principle components analysis to determine which three spectral bands within the hyperspectral data were associated with the greatest variation among the pixels that composed the scene. We designated five different classes representative of dominant plant functional types. The classes were coniferous forests, shrub, tussock meadow, graminoid fen, and open *Sphagnum* bog. Before performing the analysis, we identified fifty points within each class using a high-resolution base map in order to determine the accuracy of the final product. We then performed an unsupervised classification analysis using a k-means clustering algorithm of plant functional type using three spectral bands. The classification analysis was completed using the rgdal package, and Quantum GIS was used for all map making (QGIS 2017, Bivand et al. 2016). We determined the accuracy of the final product by comparing the classes generated in the classification analysis with our pre-defined points.

Results

1) *Selection of spectral bands*

To select the most relevant spectral bands to use in the classification analysis, I extracted the loadings from the PCA for the first three principle components. I sorted them to determine which spectral band correlated with the greatest amount of variance within the data set. The bands that I ended up using were 1780, 885, and 720 nanometers, determined by components 1-3. I used this information to create a raster layer of those three bands, and used that raster layer run a classification analysis (Figure 15).

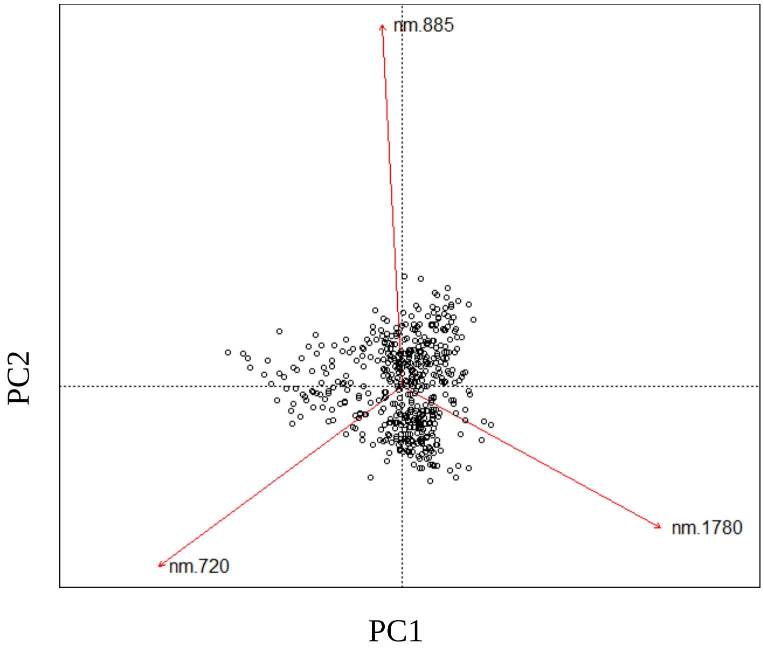

Figure 16: PCA plots for bands used in classification analysis

2) *Classification of plant functional types*

The results of the mapping project indicate that the unsupervised classification analysis was very successful at distinguishing between cover types (Figure 16). The classification analysis separated cover into five classes based on the bands that best described the variance within the dataset. The model success was determined by how many of the previously identified points fell into the same class (Table 3). Tussock grass and shrub cover were each very successfully classified, with over 90% of the points falling into one category. Graminoid fen was not very successfully classified, with pre-identified points distributed throughout categories. Forested points were also split between multiple categories. The lack of congruence between our identified points and the model result may be due to heterogeneous nature of ecological communities, and the crude validation technique employed here.

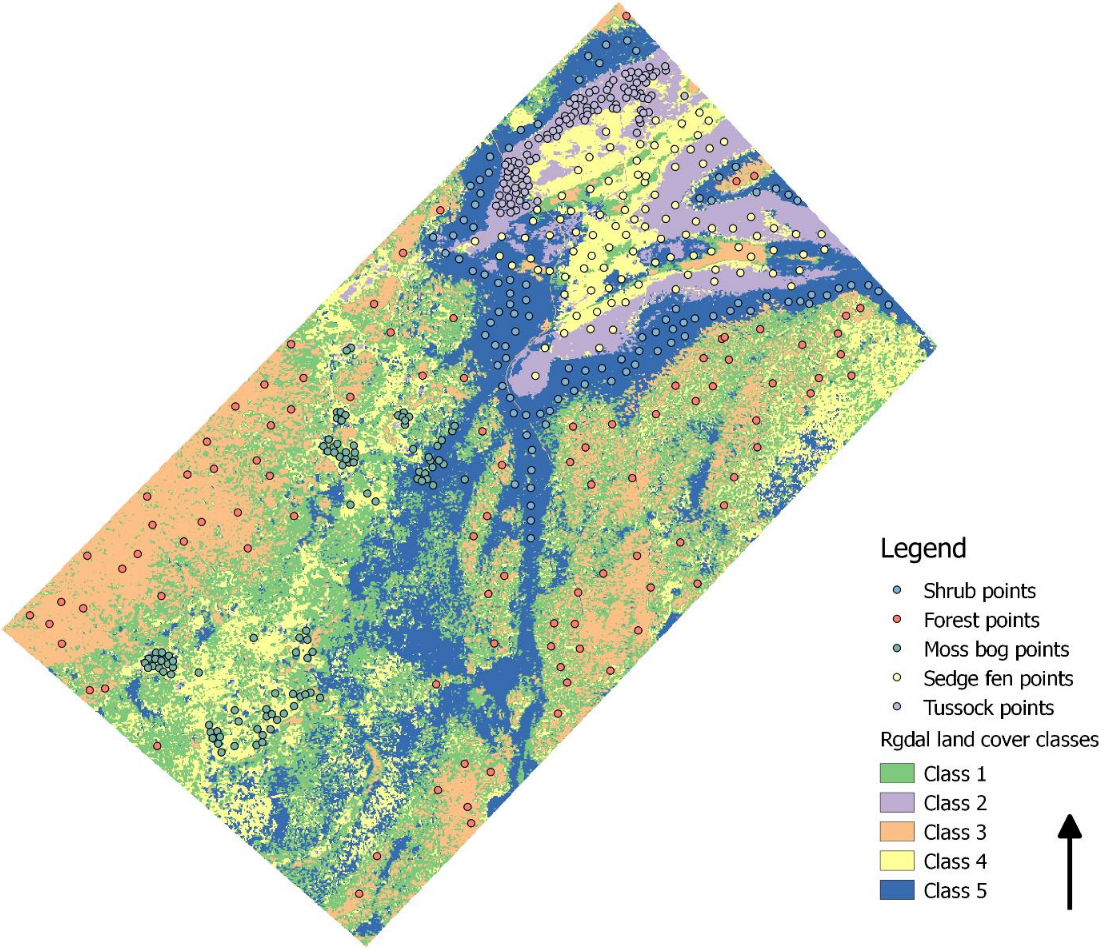

Figure 17: Map of plant functional types at APEX and surrounding area.

	Class 1	*Class 2*	*Class 3*	*Class 4*	*Class 5*
Forest >70%	*41*	*0*	*50*	*7*	*1*
Graminoid fen	*11*	*40*	*3*	*28*	*17*
Shrub	***0***	***0***	***2***	***2***	***95***
Forest < 30%	*16*	*2*	*5*	*54*	*22*
Tussock Grass	***1***	***91***	***1***	***4***	***2***

Table 3: Results of unsupervised classification analysis in Rgdal. Shown in bold are the classes for which there was >90% correspondence between a single class and one known cover type. Shown in italics are classes for which there was ≥50% overlap between a single class and one cover type

Conclusion

Remote sensing is a burgeoning area in ecological research because of its potential to provide information about the status of ecosystems over large spatial scales. Central to research in remote sensing ecology is the use of high-resolution hyperspectral imagery that can detect fine-scale distinctions in land surface cover (Féret, J.-B. & Asner, G.P. 2014, Kerr and Ostrovsky 2003, Turner et al. 2003, Turner 2003). Hyperspectral imagery can provide detailed surface information that can be customized to specific ecosystems depending on which spectral bands best explain the variance among pixels in an image (Kampe et al. 2010). In this study, I used one-meter resolution hyperspectral imagery to detect the cover of different ecotypes in an Alaskan boreal ecosystem. Through use of principle components analysis, I determined which of 360 spectral bands best described the variance among the pixels in my study area. I used this information to create a land cover classification, hoping to capture the distribution of plant functional types across the landscape. My results demonstrate the potential to use remote sensing to detect patterns of ecological diversity over a large spatial scale.

Appendix II: Measuring the effects of hydrologic change on leaf-level photosynthesis in a rich fen ecosystem

Overview

As part my thesis work on the effects of water table manipulation on the productivity of peatlands, I also measured rates of photosynthesis on four plant species common in northern boreal rich fen ecosystems. I was initially interested in both the basic question of how drought or flooding influences rates of photosynthesis in rich fen species, but also in using leaf-level photosynthesis as an explanatory variable in a larger study that asked how remote sensing could be used to measure changes in the structure and function of peatlands. Because leaf-level photosynthesis is linked with the ways in which plant tissues reflect incoming solar radiation, I had hoped to use differences in the foliar chemistry and photosynthetic capacity of species within the study system to explain potential differences in spectral reflectance signatures collected over the canopy (Sims & Gamon 2002, Sellers 1987).

Prior research has shown that NPP is affected by changes in hydrology. Experimental manipulation of water tables has shown that drought in peatlands leads to an overall decrease in NPP, and that long term hydrologic change can lead to shifts in community composition (Chivers et al. 2009, Churchil et al. 2014, Olefeldt et al. 2017). Long-term flooding has been shown to lead to a greater abundance of sedges, and drought has been shown to decrease sedge cover and increase the cover of woody shrubs (Churchill et al. 2014). Therefore, I predicted that drought would lead to a decrease in the rate of photosynthesis, particularly among sedges, and that flooding would lead to higher rates of photosynthesis in sedges, and lower rates of photosynthesis in shrubs.

Methods

Site description

We conducted this study at the Alaska Peatland Experiment (APEX) at the Bonanza Creek Long-Term Ecological Research station located thirty miles west of Fairbanks, Alaska. The site is situated in a sedge and shrub dominated rich fen on the floodplain of the Tanana River. The site consists of three large water table manipulation plots designed to test the effect of hydrologic change on the ecology and biogeochemistry of peatlands. The lowered water table plot is drained by gravity into a trench surrounding the plot on three sides. The raised water table treatment is flooded using water that is pumped in from the trench surrounding the lowered plot. The control plot is left unmanipulated. In a usual field season water table separation would reach up to forty centimeters between the lowered and raised plots. However, due to unusually high levels of rainfall, we were unable to successfully manipulate the water tables.

Photosynthesis measurements

Photosynthesis was measured during two weeks in mid-late July. Measurements were done at or shortly passed peak growing season. Photosynthesis was characterized the four most common species present across the three water table treatment plots. The species were *Carex utriculata, Equisetum faluviatile, Potentilla palustris,* and *Calamagrostis* *canadensis*. Ten individuals of each species were measured at each plot. Photosynthesis was measured using a LI-COR 6400XT. Chamber conditions were controlled so that temperature was kept at 20° C, and photosynthetically active radiation levels were set at 1500 µm. CO_2 was maintained at the slightly elevated level of 400 ppm in the chamber; up from approximately 390 at ambient. Flow rate was kept at 250 µm per second. Relative humidity within the chamber was allowed to fluctuate somewhat, but was generally maintained at between 40 and 60%. The leaf was placed in the chamber and allowed to acclimate to the chamber conditions for as long as necessary to maintain stable leaf-level stomatal conductance of CO_2 and H_2O. Once the leaf had acclimated to the conditions within the chamber, which typically took around five minutes, the reference chamber was matched to the sample chamber, and then allowed to return to the designated reference conditions (400 ppm CO_2, ~40-60% RH). Once the reference chamber had returned to its original levels, three measurements were recorded on each leaf thirty seconds apart from each other. The LICOR 6400 XT automatically calculates a rate of photosynthesis in micromoles of CO_2 per m^2 per second.

After recording the final photosynthesis measurement, the leaf was marked around the edge of the chamber to record the exact area sampled by the leaf chamber. Because the leaves were all smaller than the 3x2 cm chamber, and were variable in size and shape, the photosynthesis measurements had to be corrected to leaf area. To do that, the leaf or entire plant were harvested, and the sections of the leaves that were inside the chamber were measured using the image processing software ImageJ. All photosynthesis measurements were corrected for leaf area.

The three measurements recorded of each leaf were averaged into one value for each of the ten individuals of each species included in the experiment. Differences in rate of photosynthesis were analyzed using a one-way analysis of variance with a Bonferroni correction to examine significant differences among treatments

Results

The only significant difference occurred for *Equisetum fluviatile*, which had significantly higher rates of photosynthesis in the control plot (Figure 17; ANOVA $_{Df = 2, F = 4.5}$ p = 0.02) . However, there was a consistent with a trend in the data towards higher rates of photosynthesis in the control plots, and lower rates of photosynthesis in the lowered plot.

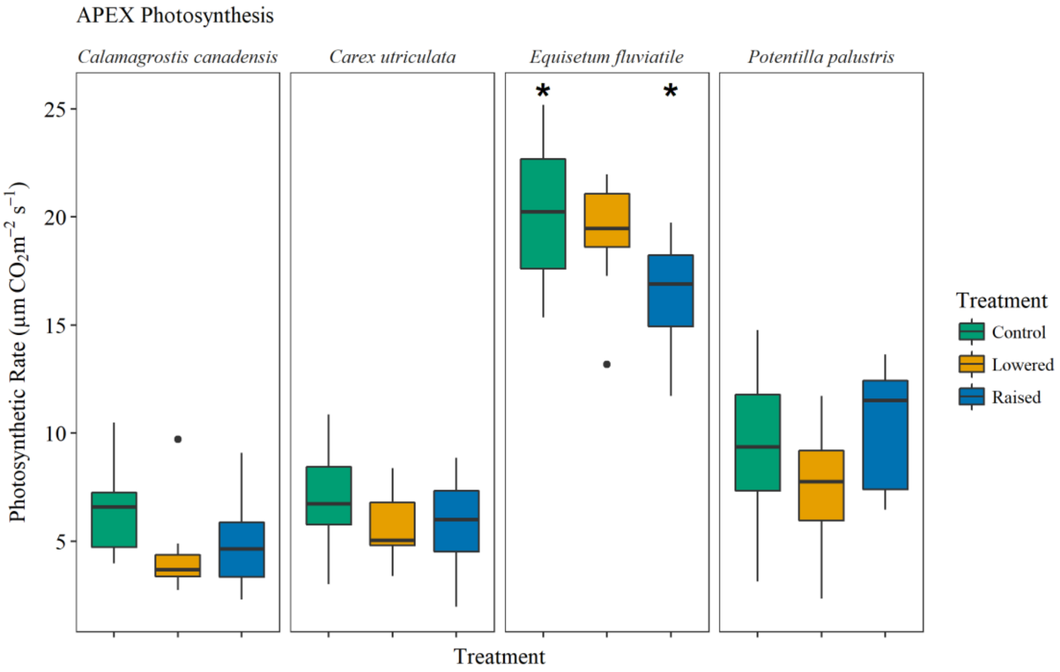

Figure 18: Rates of photosynthesis for the four most dominant plant species at APEX.

Conclusion

The photosynthesis did not show strong differences by treatment, although there was a non-significant trend towards greater photosynthesis in the control plot and decreased photosynthesis with long-term decreases in water table position in soil moisture contents. These results are consistent with the findings of previous studies at APEX which have found that long-term drought leads to a decrease in peatland productivity (Churchill et al. 2014, Chivers et al. 2009, Olefeldt et al. 2017). The lack of difference in rates of photosynthesis in the year 2016 could be attributed to the difficulties that we had in successfully manipulating the water tables due to unusually high levels of rainfall. At the time when photosynthesis measurements were collected, the water tables for all three treatment plots were at least ten centimeters above the surface. Therefore, the trends in the data cannot be attributed to active water table manipulation, but rather the long-term effects of change on the ecosystem.

The challenge with integrating these results into my thesis work, other than the lack of significant findings, was the problem of scaling. I had initially wanted to use these results to explain differences in spectral reflectance collected at the canopy level. However, the spectral sensors I used in my study integrated a measurement over the entire ecosystem, including soil, water, non-photosynthetic biomass, woody stems, and living plant tissues. Many studies have linked leaf-level physiology with spectral reflectance measured directly at the leaf surface using an artificial light source rather than the light from the sun (Sims & Gamon 2002). While this can yield valuable information about plant physiology and genetics, it is challenging to integrate this information over heterogeneous canopies. One way that I thought to do this was by calculating community weighted mean values for photosynthesis rates that would reflect the composition of the species within each plot (Ackerly et al. 2007, Díaz et al. 2007, Violle et al. 2007). However, due to the lack of statistically significant differences in photosynthetic rates, I did not believe that the addition of this data would strengthen my thesis results.