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Key Points:

- In peatlands altered water tables, precipitation, and vegetation affect CH₄ and CO₂ exchange of a large terrestrial CO₂ sink and CH₄ source
- We show that strong proxies of the processes underlying these effects on CO₂ and CH₄ exchange can be detected via remote sensing
- Combining vegetation and peatland mapping with spectral detection of water and photosynthetic capacity will improve our ability to detect greenhouse gas emissions across boreal peatlands

Supporting Information:

Supporting Information may be found in the online version of this article.

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Spectral Indices of Vegetation Condition and Soil Water Content Reflect Controls on CH₄ and CO₂ Exchange in *Sphagnum*-Dominated Northern Peatlands

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Abstract Northern peatlands play an important role in the global C cycle due to their large C stocks and high potential methane (CH₄) emissions. The CH₄ and CO₂ cycles of these systems are closely linked to hydrology, with water table level regulating the balance of oxic and anoxic conditions and the water content of *Sphagnum* mosses that dominate primary production. Previous work has demonstrated that hyperspectral indices well-suited to the detection of altered hydrology in *Sphagnum* peatlands are also highly correlated with GPP. However, little work has been done to extend these findings to CH₄ effluxes. In this study, we evaluate the utility of four hyperspectral indices, two reflecting vegetation photosynthetic function (chlorophyll index (CI); normalized difference vegetation index) and two reflecting water content (wetness index (WI); floating water band index), for detecting effects of altered water table, precipitation, and vegetation community on CH₄ and CO₂ exchange in two peatland mesocosm studies. We found that CI is a good predictor of net CO₂ exchange, and that it captured both drought and vegetation effects consistently across a broad range of vegetation treatments. Further, we demonstrate for the first time that WI combined with CI explained a significant percentage of CH₄ efflux ($R^2 = 0.32\text{--}0.57$). Our results indicate that CI and WI together may be effective tools for detecting effects of altered hydrology and vegetation on northern *Sphagnum*-peatland CH₄ and CO₂ emissions, with implications for detecting and modeling changes in emissions of greenhouse gases at scales ranging from the ecosystem to the Earth system.

Plain Language Summary Peatland ecosystems are important contributors to the global cycles of two major greenhouse gases - methane (CH₄) and carbon dioxide (CO₂). These ecosystems occur where high water tables inhibit decomposition of plant litter and organic matter. The depth of the non-saturated layer regulates uptake of CO₂ via photosynthesis by *Sphagnum* mosses which are often abundant to dominant parts of the ecosystem, as well as emission of CH₄ by microorganisms living deep in the peat and consumption of CH₄ by microorganisms living near the peat surface. Multiple global change factors such as land-use change, warming, and altered precipitation have the potential to lower water tables in peatlands, thereby affecting greenhouse gas exchange with the atmosphere. Remote sensing methods, such as drones and satellites, can be used to evaluate changes in water tables over large scales, which is useful because northern peatlands are distributed across vast stretches of inaccessible boreal regions. In this study, we evaluated the use of hyperspectral remote sensing techniques to detect changes in water tables in an outdoor experimental facility mimicking natural peatlands, and further detect changes in CH₄ and CO₂ cycles associated with altered water tables. We find that hyperspectral methods were effective at detecting the effects of altered water tables on greenhouse gas exchange, which supports further work developing these methods for larger scale applications.

1. Introduction

Northern peatlands act as globally important carbon (C) sinks (Nichols & Peteet, 2019). Changes in climate and large-scale drainage for agriculture and forestry increase the susceptibility of these C sinks to oxidation, which has the potential to shift some peatlands from being net C sinks to sources (Dinsmore et al., 2010; Trettin et al., 2006), although the warming and drying-to-C-loss scenario is far from certain across all boreal peatlands (Charman et al., 2013; Gallego-Sala et al., 2018). Beyond simply acting as net C sinks, peatlands play

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an important role in the balance of two C-containing greenhouse gases, CH₄ and CO₂, which show contrasting responses to altered water tables (Blodau et al., 2004). The balance of CH₄ and CO₂ exchange in peatlands is largely regulated by water table (WT) position, which represents a distinct border between oxic conditions favoring CO₂ production via respiration and CH₄ consumption via methanotrophy, and anoxic conditions favoring CH₄ production via methanogenesis (Nilsson & Öquist, 2013). In short-term predictions of peatland impacts on climate, the balance of CH₄ and CO₂ exchange is arguably more important than the net C balance, because the CH₄ is a more potent greenhouse gas (Collins et al., 2018; Sherwood et al., 2020), despite being a smaller contributor to the net C balance than is CO₂.

Because peatland hydrology, and more specifically surface moisture and WT position, can be the primary drivers of landscape to regional greenhouse gas exchange, remote sensing techniques that are used to infer peatland hydrology may be advantageous for evaluating peatland CH₄ and CO₂ exchange. State-of-the-art remote sensing techniques have emerged as a means to characterize aspects of peatland hydrology, namely vegetation inundation extent, surface moisture content and WT position, over large spatial extents via both passive (Banskota et al., 2017; De Vries et al., 2017; Mazziotta et al., 2019; Meingast et al., 2014) and active (Battaglia et al., 2021; Bechtold et al., 2018; Bourgeau-Chavez, Endres, Powell, et al., 2017; Bourgeau-Chavez et al., 2013, 2005; Huang et al., 2017) sensing systems. Spectral indices of vegetation condition and water content have shown to correlate consistently to CO₂ fluxes in *Sphagnum* peatlands (Lees et al., 2019, 2020; Letendre et al., 2008). In contrast, there has been limited work on extending these analyses to CH₄ emissions from peatlands (Lees et al., 2018), despite the significant climate change potential associated with CH₄. At present, it remains unclear what remote sensing methods can effectively be used to evaluate changes in CH₄ and CO₂ cycling in response to altered hydrology across northern peatlands. This represents a critical gap in our ability to detect global-scale changes in greenhouse gas emissions which may feed back to ongoing and accelerating climate changes (Henderson et al., 2015).

One of the primary remote sensing targets in peatlands is *Sphagnum* mosses, because they are key players in regulating the hydrology and CH₄ and CO₂ exchange of northern peatland ecosystems. *Sphagnum* photosynthesis and resulting C sequestration are dependent on peat moisture and the level of the water table because *Sphagnum* mosses acquire water primarily through capillary transport (Strack et al., 2009; Thompson & Waddington, 2008; Titus & Wagner, 1984), rather than having roots which can exploit deeper soil moisture. In turn, peat is insulated by the accumulation of *Sphagnum* litter – which is intrinsically resistant to decomposition due to its chemistry (Bengtsson et al., 2018; Dorrepaal et al., 2005) and also tends to decompose slowly because it grows in cold, acidic, and water-saturated environments – thereby reducing water temperatures and loss of water via evapotranspiration. While all *Sphagnum* species rely on capillary transport to access water from the WT, and utilize hyaline cells to retain water, different species form distinct functional groupings related to where they grow in relation to the WT level. Landforms such as hollows and lawns contain mosses that tend to grow at or just above the surface of the water table (i.e., within 5–10 cm), and exhibit low tolerance to alteration of WT level, while hummock mosses grow further above the WT, and are more resilient to periods of lowered WT (Jassey & Signarbieux, 2019; Nijp et al., 2014; Rydin & McDonald, 1985). Hollow mosses tend to dry and bleach rapidly as WT is lowered, while hummock mosses dry more slowly because their longer stems, smaller capitula and denser growth forms promote capillary transport and water retention (Mazziotta et al., 2019; McCarter & Price, 2014; Titus & Wagner, 1984). These features result in differences in *Sphagnum* water content and bleaching that reflect WT level, potential CH₄ and CO₂ exchange, and landform. Because *Sphagnum* are poikilohydric, with highly variable tissue water content driving easily visible differences in spectral characteristics (Figure 1), *Sphagnum* mosses may serve as useful remote sensing indicators of the hydrology of peatlands (A. Harris, 2008; A. Harris & Bryant, 2009). Further, the ability to remotely sense these specific features of *Sphagnum* (water content and greenness), which are proxies that are closely related to environmental and biotic controls on CO₂ and CH₄ fluxes, may provide a window into the C cycle of peatlands (J. L. Bubier et al., 1995; A. Harris & Dash, 2011). Indeed, hyperspectral wetness and photosynthesis indices have been used in concert with empirical models to infer WT level and gross photosynthesis at the landscape scale at the Mer Bleue ombrotrophic peatland (Arroyo-Mora et al., 2018; Kalacska et al., 2018), however, CH₄ fluxes were not addressed in the aforementioned studies.

In the present study, our objective was to extend these previous efforts, by evaluating the efficacy of multiple spectral indices at detecting changes in environmental drivers of both CH₄ and CO₂ exchange in two *Sphagnum*-peatland mesocosm experiments subjected to altered hydrological conditions including lowered WT and

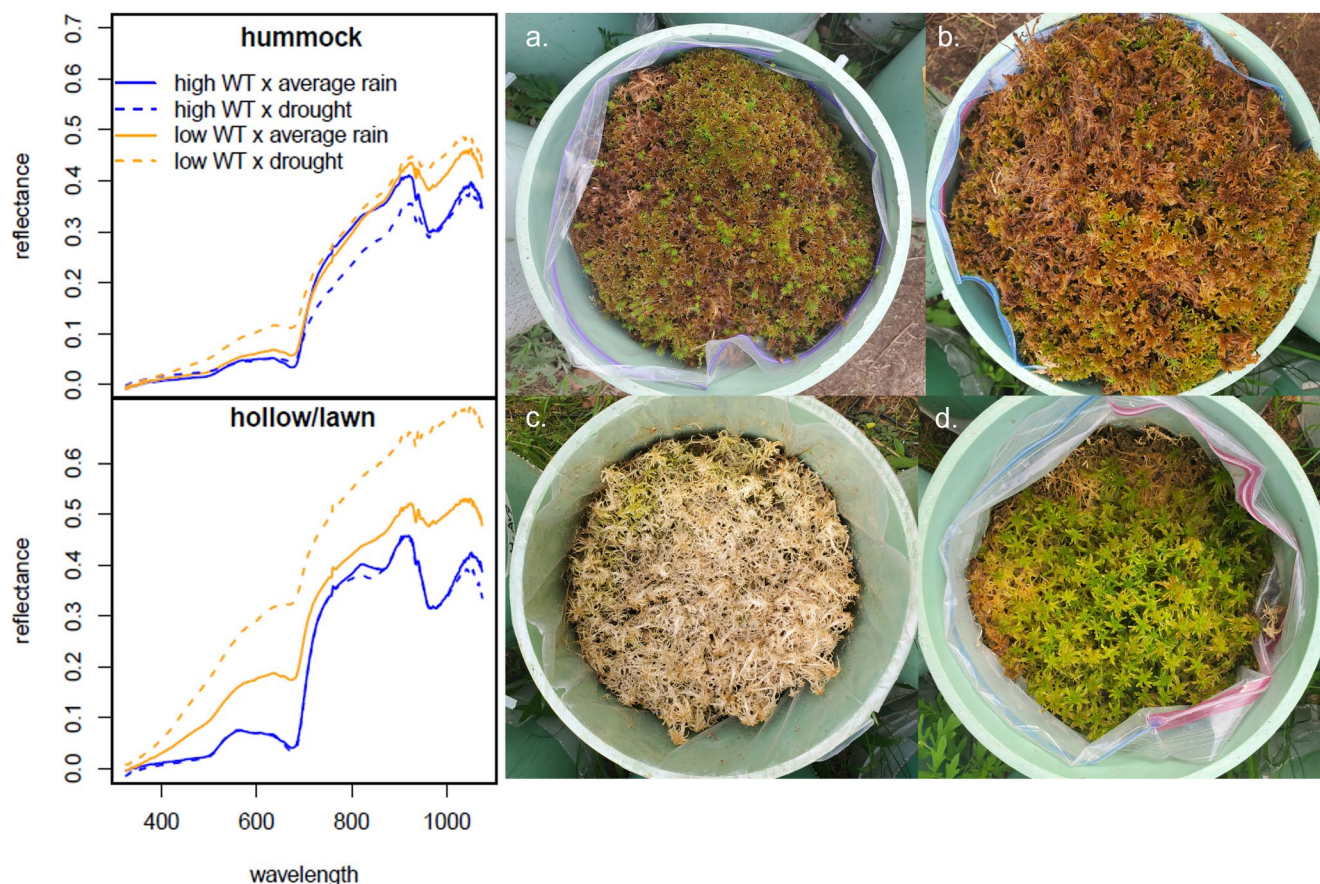


Figure 1. (Left panel) Waveform for each Sphagnocosm treatment (WT = water table), averaging 4 bins per treatment, across two dates. The bleaching driven by lowered water tables in the hollow/lawn is clearly visible in the waveform. *photos*) (a) Low water table hummock, (b) High water table hummock, (c) Low water table-drought hollow/lawn, (d) High water table-drought hollow/lawn.

reduced rainfall (Table 1). We focused on two indicators of vegetation greenness (normalized difference vegetation index NDVI; chlorophyll index CI) and two indicators of water content (floating water band index FWBI; wetness index WI) that previous work has indicated are closely related to *Sphagnum* primary productivity and water content (Table 2) (A. Harris, 2008; Lees et al., 2020; Meingast et al., 2014). We measured CO₂ and CH₄ fluxes using static chambers, and paired these with spectral measurements using a handheld spectroradiometer in both mesocosm experiments. We hypothesized that CH₄ emissions would be closely linked to spectral indices reflecting WT level, while CO₂ emissions would reflect the interaction between vegetation “greenness” indices and spectral water content indices. Furthermore, we hypothesized that these relationships would be stronger in vegetation and *Sphagnum* landform types that are less resistant to drought and lowered WT. While previous work has examined these relationships with respect to CO₂ fluxes in similar peatland ecosystems (Arroyo-Mora et al., 2018; Lees et al., 2020), to our knowledge this is the first study to carefully evaluate the utility of the

Table 1
Summary of the Treatments Imposed in Each Experiment

Experiment	Treatments	Levels
PEATcosm	Water table	2—High and low
	Vegetation (via clipping)	3—Ericaceous shrubs, sedges, control
Sphagnocosm	Water table	2—High and low
	Rainfall	2—Average and drought
	<i>Sphagnum</i> landform	2—Hummock and hollow

Table 2

Spectral Indices Used for Vegetation Water Content (Wetness Index, Floating Water Band Index) and Greenness (Chlorophyll Index, Normalized Difference Vegetation Index)

Index	Equation	Reference
WI	R_{900}/R_{970}	Peñuelas et al., 1993
FWBI	$R_{920}/\min(R_{960-1000})$	Peñuelas et al., 1993
CI	$(R_{750-800}/R_{695-740}) - 1$	A. Harris, 2008
NDVI	$(R_{850} - R_{680})/(R_{850} + R_{680})$	A. Harris, 2008

aforementioned spectral indices at detecting changes in CH₄ exchange in northern peatlands.

2. Methods

Spectral reflectance measurements were paired with measurements of net ecosystem exchange of CO₂ (NEE) and CH₄ efflux in two mesocosm studies conducted at the USDA Forest Service Northern Research Station in Houghton, Michigan in 2012 and 2020. For both NEE and CH₄ fluxes, we use the sign convention that efflux to the atmosphere is a positive flux, while ecosystem uptake is a negative flux. Both studies used mesocosms assembled from *Sphagnum*-dominated northern peatlands, and focused on inter-related vegetation and altered hydrological treatments as described below. The

PEATcosm experiment focused on the complete peat-*Sphagnum*-vascular plant ecosystem, while the Sphagnocosm experiment focused only on the peat-*Sphagnum* ecosystem, excluding vascular plants.

2.1. PEATcosm Study Site and Experimental Facility

Research was conducted at the US Forest Service's Houghton, MI outdoor experimental mesocosm facility (Potvin et al., 2014) consisting of 24 intact monoliths (1 m³, 1 m depth) of peat originating from an extensive oligotrophic peatland in Meadowlands, MN USA (N47.07278°, W92.73167°). Vegetation was dominated by the sedge *Carex oligosperma* Michx.; ericaceous shrubs *Chamaedaphne calyculata* L., Moench., *Kalmia polifolia* Wangenh., and *Vaccinium oxycoccos* L.; and the mosses *Sphagnum rubellum* Wilson, *S. magellanicum* Brid., *S. fuscum* (Schimp.) Klinggr., and *Polytrichum strictum* Brid. The full factorial experiment comprised 2 water table (WT) x 3 plant functional group (PFG) treatments in a randomized block design with four replicates, which resulted in a total of 24 mesocosm bins. The WT treatment consisted of two levels, average (“high”) and low (“low”), which were manipulated during the growing season using a combination of artificial rainwater addition, rainout shelters, and regulated outflow via draining. The PFG treatment had three levels: Ericaceae only (E), sedge only (S), untreated PFG controls (C). From the S bins, the dominant Ericaceae were removed by manually clipping aboveground biomass; likewise, from the E bins, the dominant sedges were removed by clipping. For further details on the experimental setup and species composition see Potvin et al. (2014). Mean WT level below the moss surface in the mesocosms was measured using submersible pressure transducers (Grainger 2HMC7) situated at the bottom of perforated 5 cm diameter PVC wells installed in one corner of each bin, with weekly manual checks to ensure sensor accuracy.

2.2. Sphagnocosm Study Site and Experimental Facility

In June 2020, a second mesocosm study was established at the Houghton mesocosm facility focused specifically on *Sphagnum* peatlands (Sphagnocosm) using a completely random full factorial design with 2 WT treatments x 2 rainfall treatment x 2 *Sphagnum* landform treatments with 4 replicates. Thirty-two intact monoliths (9,400 cm³, 30 cm depth) of peat were extracted from an oligotrophic peatland in Nestoria, MI (46°34'22.66" N, 088°16'44.85" W) and transported to the mesocosm facility, where they were maintained under wet conditions for 2 weeks prior to implementation of the WT and precipitation treatments. Peat monoliths were contained in doubled 1 gallon plastic bags left open at the top, and installed into 35 cm tall x 20 cm diameter PVC tubes (see images in Figure 1). Monoliths represented either topographically elevated hummocks dominated by *Sphagnum fuscum*, or lawns/hollows dominated by *Sphagnum fallax*. After 2 weeks under fully wet conditions, a “high” and “low” WT treatment were implemented by drilling a drain hole in the side of each mesocosm, and allowing water to drain freely to that level (either 5 or 25 cm below the peat surface). Regular visual assessment indicated that WT stayed very near the level of the drain hole over the course of the experiment, and variation of WT level throughout the study was mostly driven by growth or subsidence of peat monoliths driving increases or decreases in surface elevation ranging between approximately +1 to −4 cm. At the same time an “average” and “drought” rainfall treatment was implemented, representing either the average summer rainfall (16.3 cm per month), or a 50% reduction in average rainfall, respectively. All natural rainfall was excluded from the mesocosms using clear plastic rainout shelters sitting ~40 cm above the mesocosm surface, and artificial rainwater (see Potvin

et al. (2014) for rainwater chemistry) was added manually 3 times per week over the course of 11 weeks. *Sphagnum* percent cover was measured via point-intercept on 23 October 2020. Temperature at the surface of moss in each mesocosm was not significantly different between the “average” and “drought” groups ($p = 0.91$, temperature = 26.16 and 26.08°C for “average” and “drought” respectively).

2.3. CH₄ and CO₂ Flux Measurements

The static chamber technique was used to measure CH₄ and CO₂ fluxes from both PEATcosm and Sphagnocosm. In PEATcosm, CH₄ measurements were made using opaque chambers (400 l volume) constructed to fit tightly to the mesocosm bins. Chambers were sealed for approximately 40 min, during which time headspace CH₄ concentrations were measured 5 times using a field portable flame ionization detector (FID; Inficon-Photovac MicroFID, New York, USA), which was directly plumbed to each chamber (Sánchez et al., 2017). The MicroFID would pull a small volume of air (~60 ml) directly from the chamber and provide a stabilized concentration reading. This method was validated using comparison with the more standard approach of collecting gas samples using a syringe and then injecting the sample into a gas chromatograph, which indicated the MicroFID method exhibited less variability and gave more linear fits, but showed the same trend and magnitude as the GC based method (cf., Sánchez et al., 2017). In PEATcosm, CO₂ measurements were conducted using a clear acrylic chamber (620 l volume) constructed to fit tightly to the edge of the mesocosm bins, with closed cell foam around the bottom edge creating an air-tight seal. A hatch was built into the top of the chamber to allow ventilation between sequential measurements on the same bin. Two computer CPU fans mixed the air in the chamber during measurements. The change in CO₂ concentration in the chamber was measured for 2 min using a portable infrared gas analyzer (IRGA; PP Systems EGM-4, Amesbury, Massachusetts, USA). All CO₂ measurements were conducted between 9 a.m. and 3 p.m. during sunny conditions to ensure maximum sunlight conditions (PAR during measurements was 1519 ± 416). Both CH₄ and CO₂ flux estimates were based on the change in gas concentration in the chamber per unit time and converted to an areal basis.

In Sphagnocosm, CH₄ and CO₂ fluxes were measured simultaneously in a clear acrylic chamber (6,280 cm³) constructed to have an air-tight seal to the surface of the bins, first in full sunlight, and immediately after under dark conditions underneath a blackout shroud. CO₂ fluxes are presented for light conditions (i.e., net ecosystem exchange), while CH₄ fluxes are presented for dark conditions to match the PEATcosm design, although light and dark fluxes were not statistically different. Gas concentrations were measured within the chamber over two minutes using a cavity ring-down spectroscopy gas concentration analyzer (CRDS; Picarro GasScouter G4301, Santa Clara, CA). Air within the relatively small chamber was mixed by perforating the outlet tube from the gas analyzer, and coiling the perforated tube around the inner wall of the chamber. All gas exchange measurements were conducted between 9 a.m. and 3 p.m. to ensure maximum sunlight conditions. For PEATcosm and Sphagnocosm, respectively, 60 and 64 paired measurements of CH₄ and CO₂ effluxes were analyzed for the present paper. It is important to note that these data sets represent restricted subsets (<10%) of the total gas flux measurements for both studies, because we are specifically focusing on those samples that were paired closely in time with spectral measurements. As such, we do not emphasize an overall analysis of the treatment effects on the CH₄ and CO₂ fluxes in the current paper, but rather focus specifically on the relation of these fluxes, spectral indices of greenness and water content, and the drought treatments.

2.4. Reflectance Measurements

In PEATcosm, spectral measurements were taken using an ASD Fieldspec 3 portable spectroradiometer (Analytical Spectral Devices, Boulder, CO) between 11:00 and 15:00 EDT under clear and low haze conditions (Meingast et al., 2014). This spectroradiometer has a nominal spectral range spanning 350–2500 nm. It is comprised of three sensors (visual and near-infrared (VNIR), shortwave infrared 1 (SWIR1), and shortwave infrared 2 (SWIR2)) and has a spectral resolution of 3 nm between 350 and 1,000 nm and 10 nm for wavelengths from 1,000 to 2500 nm. Each recorded reflectance measurement is an average of 10 samples. Prior to calculation of the spectral indices, a linear interpolation routine was applied to produce reflectance measurements every 1 nm; this interpolation is completed within the ASD software. Measurements were taken immediately prior to moisture and water-table measurements. The spectroradiometer was attached to a steel sampling frame placed around the peat bin to allow repeated measurement of the same locations throughout the study season (between 3 July and 10 August of 2012 and 2013). For Sphagnocosm, spectral measurements

were taken on 6 and 7 August 2020, using an ASD FSP HH 325 portable spectroradiometer, with a nominal spectral range spanning 325–1,075 nm, using the same protocol as above. In Sphagnocosm, the spectroradiometer was held 30 cm above the surface of the center of the bin on both sampling dates. In both studies, the spectroradiometer was white referenced every 10 min to account for changes in sun angle and sky conditions by multiplying relative reflectance by known reflectance of a Labsphere certified reflectance standards spectralon disk (Labsphere, North Sutton, NH), to arrive at absolute reflectance. The spectral signatures were processed into spectral indices CI, NDVI, WI and FWBI using equations provided in the literature (Table 2) using the statistical software package R v3.0.1 (R Core Team, 2019). For further details on the reflectance measurements see Meingast et al. (2014).

2.5. Statistical Analyses

Analyses of variance were conducted to evaluate treatment level-effects of drought (water table treatment in PEATcosm, and water table treatment and rainfall in Sphagnocosm) and vegetation treatments (Ericaceous shrub and Sedge removal in PEATcosm, *Sphagnum* landform – hummock or hollow – in Sphagnocosm) on spectral indices (CI, NDVI, WI, FWBI) and CH₄ and CO₂ effluxes. CH₄ data were log-transformed for Sphagnocosm but not PEATcosm. Linear mixed effects modeling was used to evaluate the response of spectral indices CI and WI, and NEE and CH₄ exchange, to the fixed effects in PEATcosm of WT level, air temperature, vegetation treatment (Ericaceous shrub-only and Sedge-only treatment, where sedges were excluded due to their high negative correlation with Ericaceous shrub cover which precluded independently analyzing the two factors), and living *Sphagnum* cover; and, in Sphagnocosm, the fixed effects of WT level, rainfall, air temperature, *Sphagnum* landform (hollow or hummock), and living *Sphagnum* cover. Linear mixed effects models were also used to evaluate the fixed effects of CI and WI on NEE and CH₄ exchange in both studies. In all models, date and mesocosm were included as random effects to account for repeated sampling on the same mesocosms across multiple dates. NDVI and FWBI were excluded from this analysis due to the high correlation of NDVI with CI, and FWBI with WI ($R^2 = 0.82$ and 0.98 respectively). In each case, three models were compared, (a) a model with all interaction terms included, (b) a model with all additive terms along with interaction terms for *Sphagnum* landform (in Sphagnocosm) or *Sphagnum* cover and vegetation treatment (in PEATcosm) and WT level or Rainfall treatment, and (c) a model with only additive terms. Only the best model, determined using Bayesian Information Criteria, is presented in the results. All analyses were conducted using “R” statistical software version 3.6 “Planting of a Tree” (R Core Team, 2019). Linear mixed effects modeling was done using the “nlme” package in “R” (Pinheiro et al., 2019). Model fits were evaluated using the Bayesian Information Criterion (BIC), marginal R^2 (which describes the variance explained by fixed effects) and conditional R^2 (which describes variance explained by the full model) (Nakagawa & Schielzeth, 2013) using the anova.lme and rsquared.glmm functions in “R” (V3.0.1).

3. Results

3.1. Spectral Indices Related to Treatments

In PEATcosm, both CI and NDVI decreased in response to the removal of ericaceous shrubs (Figures 2a and 2b, Table 3), but not sedges. While the ANOVA on WT treatment levels (Figures 2a and 2b) does not indicate a reduction in CI or NDVI in PEATcosm in response to WT treatment, linear mixed effects modeling does indicate a small but highly significant reduction in CI and NDVI with deeper WT (Table 3). In Sphagnocosm, CI and NDVI were lower with lower WT, and this effect was greater in mesocosms originating from hollows than those from hummocks (Figures 2i, 2j, 2m, and 2n, Table 4). In Sphagnocosm, ANOVA indicated that under lowered WT, CI and NDVI were higher in hummocks than in hollows, but this does not show up as a significant interaction with WT level in the best linear mixed effect model (Table S1, Table 3). In Sphagnocosm, CI increased with increasing *Sphagnum* cover, but this was not the case in PEATcosm (Table 3, Table 4).

In PEATcosm, both WI and FWBI decreased in response to lowered WT (Figures 2c, 2d, 2g, and 2h, Table 3), while WI increased with increasing *Sphagnum* cover and decreased in response to the removal of both sedges and ericaceous shrubs according to linear mixed effects modeling (Table 3), but not ANOVA (Figure 2c). In general, because linear mixed effects modeling is accounting for repeated sampling on the same bins, as well

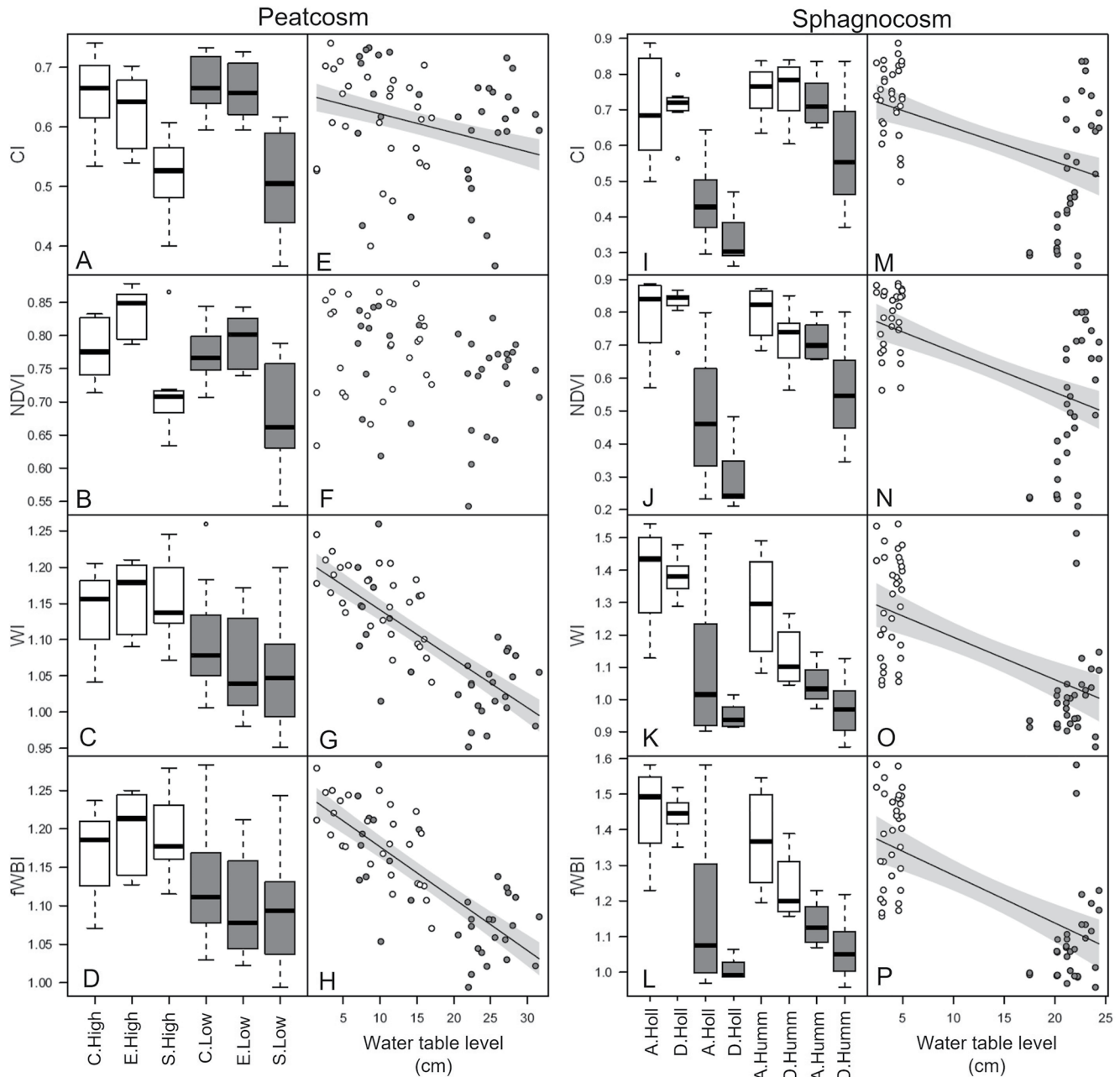


Figure 2. (a–d) (PEATcosm) and (i–l) (Sphagnocosm) boxplot of spectral indices by vegetation (C = Control, E = Ericaceous shrubs, S = Sedges; holl = hollow, humm = hummock) and water table (WT) treatment (white = high WT, gray = low WT), and rainfall treatment (A = average, D = drought) in Sphagnocosm. Open shapes indicate high WT and gray shapes indicate low WT. Letters above boxes represent significant differences based on analysis of variance. (e–h) and (m–p) scatterplots of spectral indices by measured water table levels. Where a linear fit is shown indicates a significant partial effect based on linear mixed effects model.

as the effects of other continuous factors, we base our discussion primarily on the results of this analysis, but retain the ANOVA statistics in the boxplots because these statistics most precisely reflect the comparisons made in those figures. In Sphagnocosm, both WI and FWBI decreased in response to lowered WT (Figures 2k, 2l, 2o, and 2p, Table 4), and lower in the hummock treatment under reduced rainfall (Figure 2, marginal effect of drought treatment on WI in Table 4), while Sphagnum cover was associated with higher WI (Table 4). Because CI and NDVI, as well as WI and FWBI were highly correlated ($R^2 = 0.81$ and 0.98 , respectively), we focus our analysis on CI and WI.

Table 3

Linear Mixed Effects Model Coefficients and *p*-Values for Best Model of Spectral Indices Chlorophyll Index and Wetness Index in PEATcosm, Along With Model Fit Statistics

	Chlorophyll index		Wetness index	
	β	<i>p</i> -Value	β	<i>p</i> -Value
Sphagnum cover	−0.06	0.50	0.17	0.027
Ericaceae treat	−0.01	0.66	−0.05	0.026
Sedge treat	−0.15	<0.0001	−0.07	0.003
WT	−0.003	<0.0001	−0.007	<0.0001
T_{air}	0.004	<0.0001	0.001	0.06
BIC	−184		−201	
Marginal R^2	0.73		0.74	
Conditional R^2	0.91		0.88	

Note. Bold numbers indicate *p*-values < 0.05.

3.2. CH₄ Efflux and Net Ecosystem Exchange of CO₂ (NEE) Related to Treatments

In PEATcosm, CH₄ efflux was reduced by lowered WT levels, and increased with increasing air temperature (Figures 3a and 3c, Table 6), with only marginal or no effect of other factors. In Sphagnocosm, CH₄ efflux was reduced by both lowered WT and drought, and was substantially higher in hollows than in hummocks, while there was no effect of *Sphagnum* cover (Figures 3e and 3g, Table 6).

In PEATcosm, NEE increased (i.e., either ecosystem respiration increased, gross primary production decreased, or some combination of both) with lower live *Sphagnum* cover (Table 5) and in response to the removal of Ericaceous shrubs (Figure 3b, Table 5), and was higher at lower WT levels (Figure 3d, Table 5), but not overall in response to the WT treatment (Figure 3b). In Sphagnocosm, NEE increased with lower live *Sphagnum* cover, and higher WT level (Figures 3f and 3h, Table 6), and the increase in NEE under lower WT was greater in hollows than in hummocks, while there was a marginal increase in NEE in hummocks compared to hollows under drought (Figure 3f, Table 6).

3.3. CH₄ Efflux and Net Ecosystem Exchange of CO₂ (NEE) Related to Spectral Indices

In PEATcosm, CH₄ efflux increased with increasing CI, WI and FWBI, but not NDVI (Figures 4a–4d, Table 7). In Sphagnocosm, log-transformed CH₄ efflux increased with increasing WI, and FWBI, but CI and NDVI were not significant predictors (Figures 4i–4l; Table 7). In PEATcosm, NEE declined (i.e., either gross primary production increased, ecosystem respiration decreased, or both) with increasing CI and NDVI, but not WI and FWBI (Figures 4e–4f; Table 7). In Sphagnocosm, NEE similarly declined with increasing CI, NDVI, and while a trend was visually apparent with WI and FWBI, linear mixed effects modeling indicates it was not significant (Figures 4m–4p; Table 7), possibly the correlation of CI and WI ($R^2 = 0.62$).

4. Discussion

With mounting evidence that drier conditions associated with climate change may reduce carbon (C) storage in *Sphagnum* peatlands (L. I. Harris et al., 2020, although see Gallego-Sala et al., 2018), it is increasingly

important that we develop tools to remotely assess peatland surface moisture and its effect on gaseous C fluxes. In this study, we evaluated the use of four hyperspectral indices to detect drought and vegetation effects on CH₄ and CO₂ exchange in *Sphagnum*-dominated Northern peatlands, which is an important step toward improving our ability to understand and predict terrestrial feedbacks to climate change (Lees et al., 2020). Our primary hypothesis that drought and vegetation effects on CH₄ and CO₂ exchange would be detectable via spectral indices of vegetation greenness and water content was broadly supported (Figure 5), with some caveats described below. Indeed, we found that linear mixed effects models containing only two indices (CI and WI) exhibit equally good fit to net ecosystem exchange of CO₂ as models containing data on vascular plant and *Sphagnum* cover, WT level, rainfall treatments and air temperature ($R^2 = 0.41$ vs. 0.45 for PEATcosm, and 0.65 vs. 0.63 for Sphagnocosm). The models of CH₄ efflux with only two indices are comparable to (although somewhat underperform) the “all factors” models ($R^2 = 0.57$ vs. 0.61 for PEATcosm, and 0.32 vs. 0.56 for Sphagnocosm). These findings build on previous studies demonstrating that the spectral indices we used are effective at detecting peatland vegetation water content (A. Harris, 2008; A. Harris et al., 2005; Peñuelas et al., 1993) and WT alterations (Lees et al., 2020; Meingast et al., 2014); that these spectral indices also relate to CO₂ uptake in *Sphagnum* (Lees et al., 2019, 2020;

Table 4

Linear Mixed Effects Model Coefficients and *p*-Values for Best Model of Spectral Indices Chlorophyll Index and Wetness Index in Sphagnocosm, Along With Model Fit Statistics

	Chlorophyll index		Wetness index	
	β	<i>p</i> -Value	β	<i>p</i> -Value
Hummock	−0.097	0.17	−0.12	0.013
Sphagnum cover	0.51	0.002	0.44	0.031
WT	−0.016	<0.0001	−0.013	<0.0001
Drought	−0.003	0.96	−0.086	0.067
T_{air}	0.002	0.35	0.007	0.012
Hummock × WT	0.014	0.001	—	—
Hummock × drought	0.08	0.24	—	—
BIC	−121		−100	
Marginal R^2	0.74		0.63	
Conditional R^2	0.96		0.95	

Note. Bold numbers indicate *p*-values < 0.05.

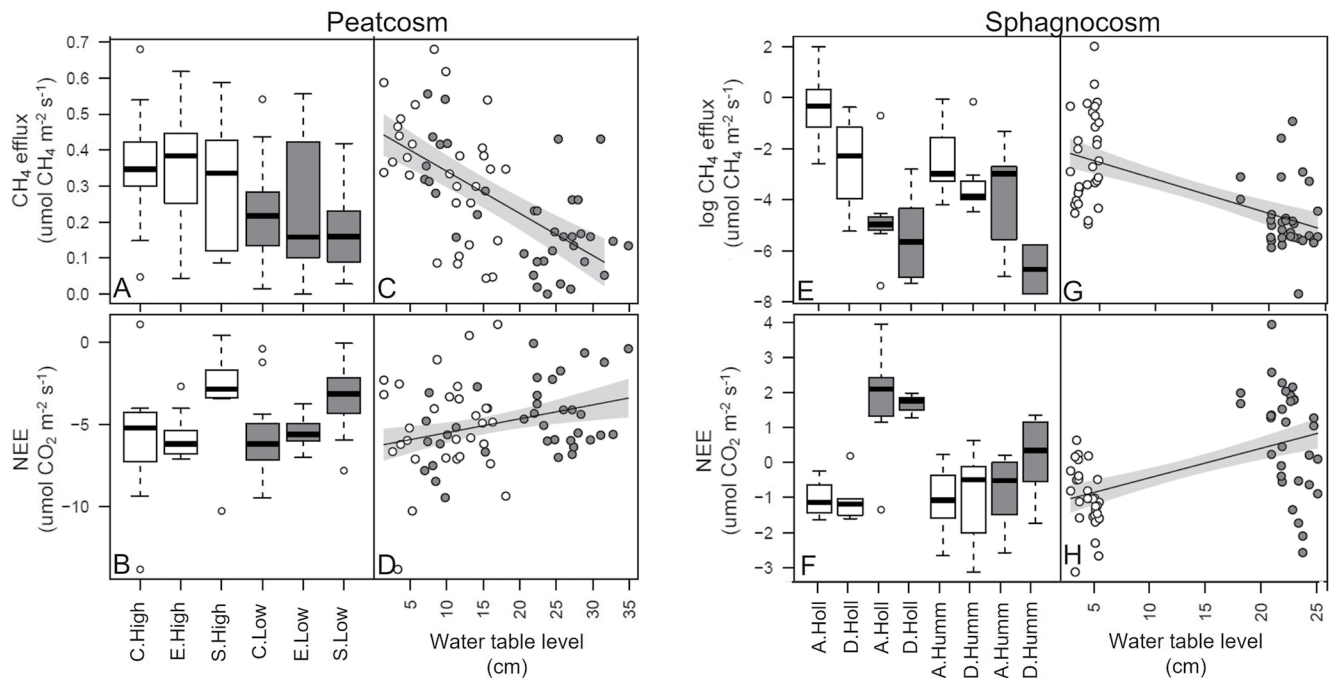


Figure 3. (a and b) (PEATcosm) and (e and f) (Sphagnocosm) boxplot of gas fluxes by vegetation (C = control, E = ericaceous shrubs, S = sedges; holl = hollow, humm = hummock) and water table (WT) treatment (white = high WT, gray = low WT), and rainfall treatment (A = average, D = drought) in Sphagnocosm. Letters above boxes represent significant differences based on analysis of variance. (c and d) and (g and h) scatterplots of gas fluxes by measured WT levels. Where a linear fit is shown indicates a significant fit based on linear regression. Open shapes indicate high WT and gray shapes indicate low WT.

Van Gaalen et al., 2007); and that WT and precipitation alterations strongly affect *Sphagnum*-peatland CO₂ (Letendre et al., 2008; Robroek et al., 2009; Titus & Wagner, 1984) and CH₄ exchange (Ballantyne et al., 2014; Chanton et al., 1995). Our study takes the important step of systematically linking hyperspectral responses to altered WT and precipitation with trace gas production in peatland ecosystems. To our knowledge, this is one of the first studies linking these spectral indices to CH₄ effluxes in peatlands. We suggest that our findings may support development of methods for assessing the effects of altered hydrology on gaseous C fluxes at regional scales in northern peatlands.

Table 5
Linear Mixed Effects Model Coefficients and *p*-Values for Best Model of CH₄ Efflux and Net Ecosystem Exchange by All Factors in PEATcosm, Along With Model Fit Statistics

	CH ₄ efflux		NEE	
	β	<i>p</i> -Value	β	<i>p</i> -Value
<i>Sphagnum</i> cover	−0.06	0.83	−0.21	0.028
<i>Ericaceae</i> treat	−0.06	0.39	0.04	0.054
Sedge treat	−0.1	0.099	0.06	0.009
WT	−0.02	0.0005	0.005	0.002
T _{air}	0.01	<0.0001	−0.001	0.06
<i>Sphagnum</i> × WT			0.003	0.39
BIC	−91		−91	
Marginal R ²	0.61		0.61	
Conditional R ²	0.84		0.84	

Note. Bold numbers indicate *p*-values < 0.05.

4.1. CH₄ Emissions in Response to Altered WT, Precipitation, and Vegetation

While there is increasing interest in remote detection of methane effluxes in northern wetlands (Engram et al., 2020), and in upscaling these estimated fluxes to improve models to link to global circulation models (Baird et al., 2013; Peltola et al., 2019), we are not aware of previous work linking CH₄ emissions from peatlands to the spectral indices evaluated in this study. Methane effluxes in peatlands exhibit high sensitivity to alterations of WT dynamics, as a result of the balance of two processes – methanogenesis occurring in anoxic zones, and methane oxidation occurring in oxic zones (Ballantyne et al., 2014; Blodau et al., 2004; J. L. Bubier et al., 1995; Chanton et al., 1995; Lai, 2009; Moore & Knowles, 1989; Moore et al., 1998). As such, we hypothesized that the WI spectral index reflecting WT level and surface moisture would be a good predictor of CH₄ effluxes. Indeed, we found that in both experiments, CH₄ efflux was significantly correlated with WI and FWBI with *r*² ranging from 0.32 to 0.40, and that inclusion of both CI and WI into a linear mixed model of CH₄ efflux improved model R² of 0.32–0.57. Declines in CH₄ emissions with lower

Table 6
Linear Mixed Effects Model Coefficients and p-Values for Best Model of CH₄ Efflux and Net Ecosystem Exchange by All Factors in Sphagnocosm, Along With Model Fit Statistics

	CH ₄ efflux		NEE	
	β	p-Value	β	p-Value
Hummock	−0.79	0.043	−0.51	0.75
Sphagnum cover	−0.56	0.72	−3.48	0.009
WT	−0.12	<0.0001	0.15	<0.0001
Drought	−1.31	0.001	−0.48	0.24
T _{air}	0.07	0.14	0.065	0.08
Hummock × WT	−	−	−0.13	0.0002
Hummock × Drought	−	−	1.13	0.054
BIC	235		235	
Marginal R ²	0.56		0.56	
Conditional R ²	0.67		0.67	

Note. Bold numbers indicate p-values < 0.05.

WT and reduced rainfall were mirrored by reductions in the WI in response to those treatments, although this response was only marginal for rainfall in Sphagnocosm.

In this study, we demonstrate that the spectrally observed water content of *Sphagnum* mosses is a good proxy for CH₄ exchange, although in natural conditions the value as a proxy would most likely be contingent on a suite of other drivers (Couwenberg et al., 2011; Lai, 2009). Nevertheless, we expect that this method can be extended, with further research and method development, to many northern peatland ecosystems, because the relation of WT and surface water content to CH₄ emissions has well understood process-based foundations. That is, CH₄ emissions are determined by the balance of CH₄ production in water-saturated layers and CH₄ consumption generally occurring in drier conditions in the surface layers. Our spectral measurements of water content directly measure the water content of *Sphagnum* mosses in the upper few centimeters (Meingast et al., 2014), which corresponds to the layer at which *Sphagnum*-associated methanotrophs consume a large fraction of methane produced from deeper layers under moderately dry, aerobic conditions (Kip et al., 2010). Additionally, because *Sphagnum* water content during the growing season is primarily driven by capillary transport from the WT, surface spectral water content is a reasonable proxy for WT level (Meingast et al., 2014), and higher WT corresponds both to a greater

zone of methanogenesis, as well as a reduced region of methanotrophy and overall higher CH₄ effluxes. We note however, that this method does not preclude the misidentification of high WT during periods where the *Sphagnum* surface is wet from a recent rainfall, yet the WT is low due to longer term drought or other factors, and as such, some caution must be taken when inferring CH₄ effluxes based on single point in time measurements without considering the timeline of recent weather and hydrologic changes. We highly recommend subsequent research examine the occurrence of these possible conditions and their potential effect on estimates of CH₄ exchange, and explore the use of repeated spectral measurements combined with weather data to better predict WT dynamics and impacts on fluxes. Periods of frequent oscillations between saturated, anoxic conditions and drier, oxic conditions may be particularly important for CH₄ emissions, which may not be accurately captured using mean spectral water content (Wilmoth et al., 2021). Additionally, it must be noted that previous research has found small differences in CH₄ emissions between light and dark chamber measurements in hummock microforms (Luan & Wu, 2014) which may alter the analysis presented here.

Surprisingly, the relationship between WT level, WI and CH₄ emissions were stronger for PEATcosm than for Sphagnocosm, despite (or perhaps because of) a more complex vegetation community in the former. In addition, higher CI was associated with increased CH₄ emission in PEATcosm but not Sphagnocosm. These results may reflect the role of vascular plants and in particular sedges in transporting CH₄ from saturated layers (Noyce et al., 2014), but we did not see a clear indication that sedge removal strongly influenced CH₄ efflux in this data set. An analysis of the full multi-year data set from PEATcosm reveals that sedge removal did have an effect on CH₄ efflux, but that is beyond the scope of this paper (Lilleskov, *personal communication*). Nonetheless, it is important to note that vascular plant transport is often the dominant emission pathway (Knoblauch et al., 2015) because CH₄ diffusing through aerobic peat layers can be oxidized by methanotrophic bacteria, whereas CH₄ transported via plant transport bypasses oxidation. Further, vascular plant traits such as aerenchyma and leaf area have been shown to be useful predictors of CH₄ fluxes in northern peatlands (Goud et al., 2017). Thus, the weaker relationship of CH₄ emissions to WI in Sphagnocosm, and the interaction with CI in PEATcosm may reflect aerenchymatous vascular plant transport of CH₄ from deeper anoxic layers. In Sphagnocosm the hollows exhibited higher CH₄ efflux than did the hummocks, which was only partially reflected by the indirect effect of *Sphagnum* landform on WI, suggesting species or topographic position-specific effects on the underlying processes, which is consistent with previous research (Juottonen, 2020; Kip et al., 2012; Lai, 2009). This result is in line with the idea that microtopography controls the moisture regime and methanotroph/methanogen communities of *Sphagnum* and thus methane oxidation in northern peatlands (Basiliko et al., 2004). The importance of vegetation and

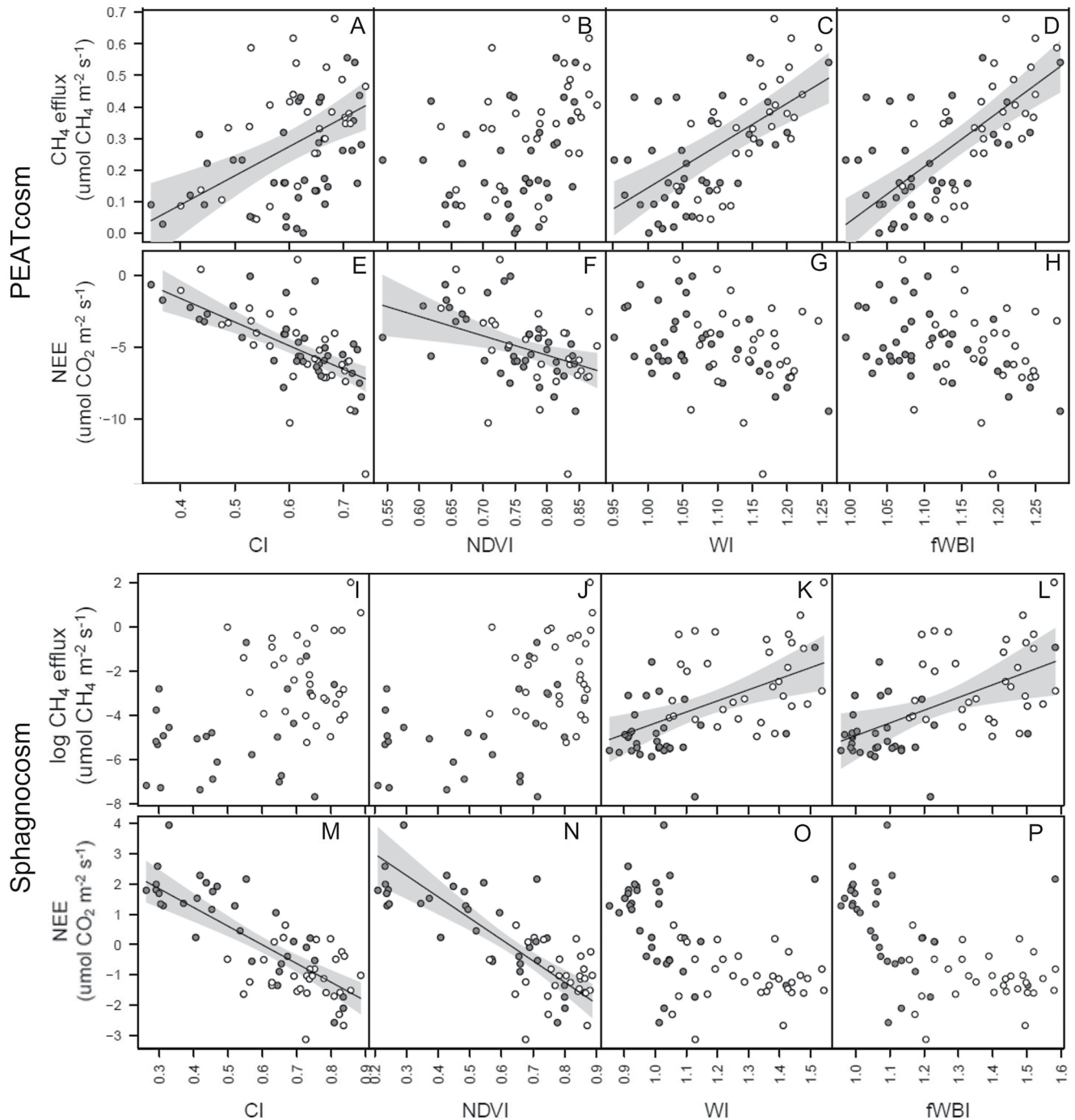


Figure 4. Scatterplots of CH₄ efflux (a–d) (PEATcosm) and (i–l) (Sphagnocosm) and net ecosystem exchange (e–h) (PEATcosm) and (m–p) (Sphagnocosm) and by spectral indices. Open shapes indicate high water table (WT) and gray shapes indicate low WT. Where partial regression lines from linear mixed effects models are shown the fit is significant.

topographic controls on CH₄ exchange emphasizes that, while WT may govern CH₄ fluxes in the short term, ecosystem succession in response to drying, including vegetation change and alteration of hummock-hollow topography (Kolari et al., 2021; Robitaille et al., 2021) could have more significant effects on long-term CH₄ exchange and spectral indices of wetness alone would not be sufficient to evaluate changes in CH₄ exchange over longer time periods.

Table 7

Linear Mixed Effects Model Coefficients and p -Values for Best Model of Net Ecosystem Exchange and CH_4 Efflux by Chlorophyll Index and Wetness Index, Along With Model Fit Statistics

	PEATcosm				Sphagnocosm			
	NEE		CH_4 efflux		NEE		log CH_4 efflux	
	β	p -Value	β	p -Value	β	p -Value	β	p -Value
CI	−16.5	<0.0001	0.96	0.0002	−6.2	<0.0001	0.48	0.76
WI	−4.5	0.2	1.34	<0.0001	−0.5	0.49	4.6	0.002
BIC	263		−77		188		237	
Marginal R^2	0.45		0.57		0.63		0.32	
Conditional R^2	0.45		0.88		0.7		0.66	

Note. Bold numbers indicate p -values < 0.05.

4.2. Net Ecosystem Exchange of CO_2

In both experiments NEE increased (i.e., less net CO_2 uptake by the ecosystem, more to the atmosphere) in response to lower WT level, reflecting a combination of reduced photosynthesis as the *Sphagnum* layer dried, and increased respiration from decomposition of deeper peat as it was exposed to oxygen, consistent with previous work in this area (Blodau et al., 2004; J. Bubier et al., 2003; Helfter et al., 2015; Moore et al., 1998; Sulman et al., 2010). NEE also increased with the removal of sedges and shrubs, or lower live *Sphagnum* cover, consistent with the straightforward expectation that reduced vegetation biomass would reduce CO_2 uptake. This suite of effects of altered WT, precipitation, and vegetation community on NEE were reflected in the relationship between NEE and the two spectral indices of vegetation function, CI and NDVI. In particular, CI was strongly negatively correlated with NEE, and this correlation was consistent with the vegetation, WT, and precipitation treatment effects (Figure 5). For instance, in PEATcosm, NEE increased with the removal of sedges and increasing WT level, while CI decreased in response to those treatments. Similarly, in Sphagnocosm, NEE increased with

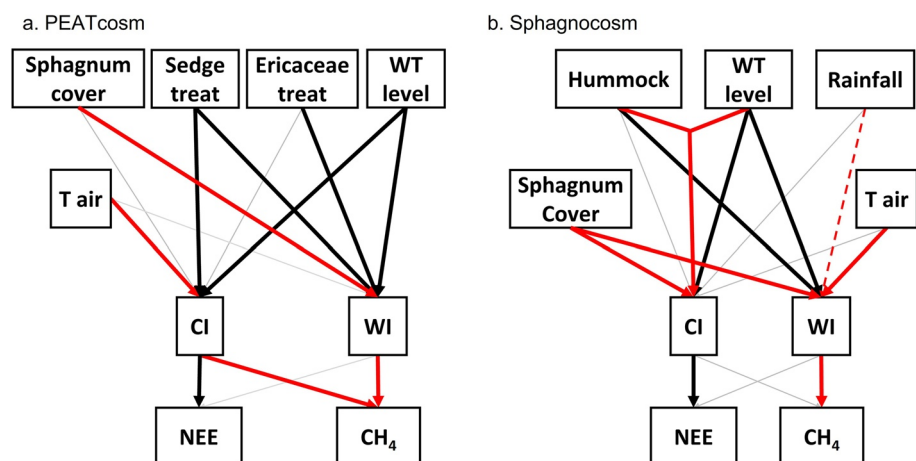


Figure 5. Summary of direct linear effects of vegetation and altered water table (WT) and rainfall on chlorophyll and wetness indices, and those indices on CH_4 and net ecosystem exchange in panel (a) PEATcosm and (b) Sphagnocosm based on linear mixed effects model coefficients from Tables 3–7. Red arrows ($\rightarrow$) represent a positive effect, black arrows ($\rightarrow$) represent a negative effect, dashed arrow ($\rightarrow$) represent marginally significant effect ($0.05 < p < 0.1$) and light gray arrows ($\rightarrow$) represent a non-significant effect that was included in the model. In panel (a) “Sphagnum cover” is the total cover of all *Sphagnum* species, “Sedge treat” and “Ericaceae treat” are the sedge-only and ericaceous shrub-only treatments in PEATcosm. “Hummock” is the hummock landform in Sphagnocosm. “WT level” is the measured WT level with lower WT being a larger number. “T air” represents air temperature measured during the gas flux measurement with the flux chamber. “Rainfall” is the rainfall treatment in Sphagnocosm.

reduced live *Sphagnum* cover and increasing WT level, and increased more in hollow mosses subjected to lower WT, consistent with previous observations of the capacity of hummock mosses to tolerate drier conditions than hollow mosses (Mazziotta et al., 2019; Rydin & McDonald, 1985), while CI showed the opposite response to each of those drivers. Thus, CI represented an effective single index for integrating vegetation, WT, and precipitation effects on NEE in our *Sphagnum* dominated mesocosms.

Previous work has demonstrated significant correlation between peatland *Sphagnum* CO₂ uptake and both CI and NDVI. A. Harris (2008) demonstrated that photosynthesis increased significantly with NDVI, while Letendre et al. (2008) showed that CI was a stronger predictor of net CO₂ uptake than NDVI in a *Sphagnum* dominated peatland, consistent with our results. Similarly, Lees et al. (2020) found that a modified CI was better than NDVI in predicting gross primary productivity in *Sphagnum* peatlands, and suggest that it was the best index to use when the vegetation composition is unknown. This work confirms prior observations and builds on prior studies by adding a broader range of carefully controlled WT table conditions, rainfall exclusion, and vegetation treatments. It is worth noting that these results cannot be directly extrapolated to peatlands which undergo significant afforestation after drainage, where lowered water tables have in some cases been observed to result in increased C uptake as forest growth more than compensated for peat C loss (Minkinen et al., 1999; Talbot et al., 2010), and where *Sphagnum* mosses may be less readily observed (or replaced by feather mosses) under the tree canopy.

4.3. Spectral Indices Reflect Altered WT, Precipitation, and Vegetation Community

Our work builds on previous findings to help advance our understanding of spectral indices of peatland hydrology. For example, Meingast et al. (2014) (note that we use a subset of the same data from PEATcosm) demonstrated that FWBI and WI were highly correlated to WT position and peat volumetric water contents in PEATcosm and in a paired field study. Based on this finding, we expected to find a strong correlation between FWBI, WI and WT and rainfall treatments in Sphagnocosm, and while that was true for WT level (Figure 2, Table 4), we found that reducing the rainfall volume by 50% resulted in only a marginal ($p = 0.067$) reduction of WI in Sphagnocosm, even considering that half of our measurements were within 3 hr of rainfall addition. In Sphagnocosm, we found that WI increased with living *Sphagnum* percent cover, and was higher in hummocks than in hollows. In both cases, it is likely that the higher WI reflects increased capillary transport by live mosses, and *S. fuscum* in particular, which has small capitula and densely-packed stems to promote capillary transport and retention of rainwater compared to *S. fallax* and other hollow species (Clymo & Hayward, 1982; Mazziotta et al., 2019; Yazaki et al., 2006). It is worth noting that in Sphagnocosm we did find nearly twice as steep of a relationship between WT level and WI compared to PEATcosm ($\beta = 0.013$ vs. 0.007), which likely reflects attenuation of the signal strength by the presence of vascular vegetation in PEATcosm. This has clear implications for extending these relationships to larger scales in natural peatlands—i.e., WI-based predictions of peat moisture or WT level might need an estimate of vascular plant cover as an additional factor in the model. In an intact peatland, Lees et al. (2020) found no relationship between wetness indices and WT level, although in that case the absence of a water signal was attributed to the wet and invariant water content over the duration of the study, and strong relationships were found between spectral indices and water content in a growth chamber component of that study. In natural peatlands in our own study system FWBI and WI were highly correlated with WT level (Meingast et al., 2014), as were FWBI and a moisture stress index in a peatland in Wales (A. Harris, 2008).

In this study, we found that vegetation indices CI and NDVI were sensitive to WT and vegetation treatments, and to some degree the interaction of the two, consistent with previous work (A. Harris, 2008; A. Harris & Dash, 2011; Lees et al., 2019, 2020; Letendre et al., 2008; Meingast et al., 2014; Van Gaalen et al., 2007). Unsurprisingly, both the removal of Ericaceae, and lower live *Sphagnum* cover were associated with lower CI. Somewhat more interestingly, lower WT reduced CI, and this reduction was greater in the hollow treatment than in the hummock treatment – which corresponds to the easily visible bleaching that occurred in hollows in response to lower WT, and is a sign of environmental stress in *Sphagnum* (Ferguson & Lee, 1980; Harley et al., 1989; Marshall et al., 2019; van Breemen, 1995). The result aligns with well-known differences between hummock and hollow species, with hummock species being more resistant to drought (Rydin & McDonald, 1985). Overall, CI appeared to be sensitive to alterations of both water content and vegetation, and hence may not be well-suited to disentangling the effects of these factors, but rather could be a useful indicator of the joint effect of these factors on overall CO₂ uptake capacity.

4.4. Remote Sensing of Climate Change Impacts on Peatland Environments

As climate changes and high latitude wetlands experience a changing environment, it is imperative to understand how this important C reservoir and source of methane will respond. Our ability to represent these processes in C models is currently limited, with best estimates of contemporary methane emissions from wetlands varying drastically depending on what model or method is used (Fisher et al., 2014). As recently identified at the “Arctic-Boreal C-Flux Upscaling Workshop” hosted by Woodwell Climate Research Center (October 2020), one of the largest drivers of the uncertainty was a critical data gap in the accurate identification and mapping of the distribution and type of wetlands in high northern latitudes. Remote sensing linked to field data is the key to characterizing the distribution and extent of peatlands (e.g., Bourgeau-Chavez, Endres, Graham, et al., 2017; Merchant, 2021) and monitoring drivers of C-exchange and application of spectral indices by plant functional type and WT will allow us to understand the role of C in northern peatland systems. Quantifying and understanding the role of peatlands in global C-cycling may be facilitated by scaling the relationships between spectral indices and CH₄ and CO₂ exchange through satellite remote sensing. However, the assessments must be developed using characterizations of drivers of peatland C-exchange, first mapping plant functional types (Bioucas-Dias et al., 2012; Roberts et al., 1998; Rupp et al., 2019) and also monitoring WT position and inundation within those peatlands. Arroyo-Mora et al. (2018) demonstrated how the spectral indices evaluated in the present study can be used, in association with remotely sensed vegetation and hydrology, to estimate landscape scale CO₂ fluxes in ombrotrophic peatlands, and our work is a significant step toward building similar methods for CH₄ fluxes. Goetz et al. (2021) identified spatial estimation and prediction of CH₄ fluxes as a key remaining uncertainty in arctic and boreal regions, and highlighted the need for improvement and validation of terrestrial biosphere models. Using remotely sensed vegetation and wetness over this domain to make inferences about potential CH₄ fluxes may provide one useful tool for training or validating those models. For instance, segmenting the boreal landscape of interest by ecotype (i.e., rich fens, poor fens, bogs) using multi-temporal radar and satellite optical imagery (Bourgeau-Chavez, Endres, Powell, et al., 2017), and using SAR/multispectral data for evaluating WT using Sentinel-2 unmixing can provide the constraints within which the relationships found with spectrometry demonstrated in this paper can be applied to gain better estimates of CH₄ fluxes (Räsänen et al., 2021).

4.5. Conclusions and Suggestions for Future Research

In this paper we demonstrate that spectral indices of peatland water content and vegetation function have utility for evaluating effects of changes in water table, precipitation, and vegetation community on CH₄ and CO₂ exchange with the atmosphere. We demonstrate the potential utility of these methods within a narrow peatland class (northern ombrotrophic *Sphagnum*-peatlands) which, although widely distributed, represent only a fraction of global peatlands. Therefore, we further recommend future research evaluate the generalizability of these methods across multiple peatlands classes. For CO₂ exchange, our work broadly supports recent research (Lees et al., 2020; Letendre et al., 2008) evaluating hyperspectral detection of CO₂ efflux in peatlands, and adds some nuance to this work in the context of how drainage versus rainfall reduction alter spectral indices and CO₂ fluxes, as well as evaluating the effects of vegetation removal and different *Sphagnum* landforms. For CH₄ efflux, we demonstrate for the first time that spectral indices which have been previously shown to reflect water table level (WI and FWBI) are well-correlated with CH₄ efflux, and so could be used as a model parameter to improve remotely-sensed predictions of CH₄ efflux. Because emissions of CH₄ from naturally occurring wetlands are both the largest and most uncertain source of CH₄ to the atmosphere (Saunio et al., 2020), improved methods for estimating CH₄ efflux in northern peatlands represents an important step toward better quantification of their climate-change feedback potential, at a time when these feedbacks potentially represent a tipping point in the Earth's climate system.

Data Availability Statement

Data are available at <https://doi.org/10.5281/zenodo.6491340>.

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