

Linear disturbances shift boreal peatland plant communities toward earlier peak greenness

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Abstract

Vast areas of boreal peatlands are impacted by linear disturbances known as seismic lines. Tree removal and ground disturbance alter vegetation communities and are expected to change ecosystem functioning. We investigate seismic line disturbances on peatland plant community composition and phenological patterns using readily available digital photography at a bog and a fen in Alberta, Canada. Our objectives were to: 1) compare the understory vegetation on seismic lines with those in adjacent undisturbed peatlands using two phenological metrics (green and red chromatic coordinates); 2) evaluate if vegetation greenness is directly related to vegetation community composition, and 3) determine whether plot-scale greenness predicts plant productivity. We found that disturbed peatlands have an earlier seasonal peak (maximum greenness) compared to undisturbed areas, and vegetation communities had a stronger relationship to greenness and gross primary production (GPP) at disturbed sites relative to undisturbed sites. This change in understory vegetation results in greater CO₂ uptake in disturbed sites. We demonstrate an easy-to-use application of digital photography that successfully quantifies phenological changes in boreal peatland vegetation. This non-destructive method for understanding vegetation phenology eliminated the need for fixed infrastructure and allowed us to sample more plots and study sites while allowing for repeated measures in the future. As boreal landscapes continue to be disturbed by linear disturbances, understanding the magnitude and mechanisms of vegetation and phenology changes is the first step toward predicting carbon cycling changes across broad spatial scales.

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Key Points:

- Linear disturbances cause a shift in vegetation communities and changes in green leaf phenology and greenness metrics.
- Readily available smartphone photography successfully captured the phenological characteristics of these vegetation types.
- The change in vegetation causes greater CO₂ uptake in the disturbed sites and greenness metrics were good predictors of these CO₂ changes.

Abstract

Vast areas of boreal peatlands are impacted by linear disturbances known as seismic lines. Tree removal and ground disturbance alter vegetation communities and are expected to change ecosystem functioning. We investigate seismic line disturbances on peatland plant community composition and phenological patterns using readily available digital photography at a bog and a fen in Alberta, Canada. Our objectives were to: 1) compare the understory vegetation on seismic lines with those in adjacent undisturbed peatlands using two phenological metrics (green and red chromatic coordinates); 2) evaluate if vegetation greenness is directly related to vegetation community composition, and 3) determine whether plot-scale greenness predicts plant productivity. We found that disturbed peatlands have an earlier seasonal peak (maximum greenness) compared to undisturbed areas, and vegetation communities had a stronger relationship to greenness and gross primary production (GPP) at disturbed sites relative to undisturbed sites. This change in understory vegetation results in greater CO₂ uptake in disturbed sites. We demonstrate an easy-to-use application of digital photography that successfully quantifies phenological changes in boreal peatland vegetation. This non-destructive method for understanding vegetation phenology eliminated the need for fixed infrastructure and allowed us to sample more plots and study sites while allowing for repeated measures in the future. As boreal landscapes continue to be disturbed by linear disturbances, understanding the magnitude and mechanisms of vegetation and phenology changes is the first step toward predicting carbon cycling changes across broad spatial scales.

Plain Language Summary

Industrial activities for oil and gas mining across boreal North America can result in a vast network of linear disturbances called seismic lines. These are narrow clearings cut across peatlands and forests, resulting in the removal of trees and compaction to the soil, leading to changes in how these ecosystems function. One such impact is on how the ground-layer vegetation communities green up over the course of the growing season and how this impacts how productive they are. In this study we investigated the greenness patterns of vegetation communities at two different peatland types impacted by seismic lines. To do this, we collect photographs using smartphones, alongside vegetation surveys and carbon exchange measurements. We found that these disturbances significantly impact the greenness of these communities, with disturbed sites becoming more productive faster. Using smartphones to collect photographs provided a quick and easy method to collect greenness data without the need for expensive equipment or fixed infrastructure. As boreal peatlands continue to be under threat from increased disturbances, this study provides a first step in understanding how their greenness and productivity may change in the future.

1. Introduction

Peatlands cover 25 – 30 % of the boreal zone and are important component of both regional and global carbon cycle dynamics (Wieder et al., 2006). However, industrial activities for resource extraction in these areas have led to an extensive network of linear disturbances known as seismic lines. In fact, there are an estimated 345,000 km (disturbing an area of ~1900 km²) of seismic lines crossing peatlands in the province of Alberta, Canada alone (Strack et al., 2019). These linear clearings can be between 1.5 and 10 m wide, creating a dense grid across the

landscape and are cleared using a combination of tree removal and soil disturbance/compaction altering hydrological conditions (Braverman & Quinton, 2016), vegetation communities (Echiverri et al., 2020) and ecosystem functions such as carbon exchange (Dabros et al., 2018; Davidson et al., 2020).

Given the geographic extent and impact of seismic lines, there is a push to restore them in order to return habitat quality and ecosystem function (Filicetti et al., 2019). Current restoration methods, however, are based on forestry practices developed for upland, drier ecosystems and may not translate to wetlands (Davidson et al., 2020). Restoration of seismic lines often involves a technique called mounding, used to bring back localised microtopography necessary for tree regeneration (Pyper et al., 2014). Yet, this method may be detrimental to the existing vegetation communities in peatlands, especially given that, although there is a shift in vegetation community on seismic lines, the species present are still peat forming and therefore important to the overall carbon balance (Echiverri et al., 2020). Furthermore, the disturbance caused by these mounding techniques has been shown to potentially increase decomposition and carbon loss from soils (Davidson et al., 2020). A greater understanding of peatland vegetation communities present post-disturbance is imperative for improving restoration best practices. Given the extent of the disturbed area, it would also be beneficial to develop techniques that capture plot-scale vegetation change and carbon dynamics that do not rely on fixed infrastructure.

Phenology is used to describe the development of plant properties related to temporal variation in life history events (e.g., flowering time, bud break, leaf senescence) (White et al., 1997). The phenology of leaf traits (e.g., greenness, timing of leaf-out and senescence) are important drivers of terrestrial carbon cycling (Hufkens et al., 2012). High quality measurements of green leaf phenology (hereafter referred to as phenology) are integral in understanding the effects of environmental change on ecosystem function and biosphere-atmosphere interactions (Hufkens et al., 2012). In peatlands, vegetation phenology is linked to abiotic drivers such as temperature, water, and nutrient availability (Bubier et al., 2006), is often the first to respond to environmental change (Richardson et al., 2018; Malhotra et al., 2020) and has downstream influences on ecosystem function such as increased ecosystem carbon losses (Hanson et al., 2020). A multitude of non-destructive vegetation assessments (Lavorel & Garnier 2002; Goud et al., 2017; Girard et al., 2020) and site-scale phenology-function investigations (Wilson et al., 2008; Goud et al., 2017) exist. However, evaluation of seismic line disturbance effects on peatlands requires a combination of non-destructive vegetation measurements and phenology-function link investigations that can be rapidly implemented across multiple sites and that can be revisited over multiple years.

Red-Blue-Green (RGB) photography is one such non-destructive method that may be useful in understanding plant phenological characteristics. Land-surface phenology studies typically use remote sensing products, which inform large-scale phenological patterns. However given the highly heterogeneous nature of peatland ecosystems, RGB photography using hand-held cameras enables plot-scale studies that may provide valuable information that is lost at larger scales (Linkosalmi et al., 2016) and could also allow for a greater understanding of ecosystem carbon flux dynamics with very little interaction with the vegetation itself. RGB photographs can be used to calculate greenness indices such as the green chromatic coordinate (*Gcc*), which indicates vegetation greenness or 'health' across a number of ecosystem types (Sonnentag et al., 2012). Phenological characteristics can also be used to distinguish between different plant communities (e.g., Wu et al., 2021). Although greenness at one point in time

might not be a useful metric, the phenological pattern will vary between species and/or functional groups. RGB photographs can also be used to calculate other indices such as the red chromatic coordinate (*Rcc*). *Rcc* has been successfully used to monitor vegetation senescence (Liu et al., 2020) and investigate plant stress after water table drawdown (Peichl et al., 2015). The difference in reflectance in the red spectrum could also allow for separation among common peatland plant functional groups, namely vascular versus non-vascular plants, that have different impacts on ecosystem function (e.g., rates of nutrient cycling, carbon storage; Zeh et al., 2020).

The creation of seismic line disturbances is expected to influence peatland plant communities, phenological characteristics and carbon exchange, however studies on this are lacking. Strack et al. (2018) found a significant increase in graminoid cover linked to a shift in hydrological conditions on a winter road (a similar, fully vegetated, linear disturbance type) crossing a boreal peatland. This shift towards a more productive vegetation community resulted in disturbed plots acting as a greater CO₂ sink but larger methane (CH₄) source compared to adjacent peatland. Linked to this shift in vegetation community, is the reduced likelihood for tree sapling regeneration due to them being outcompeted by more productive understory vegetation such as sedges (Filicetti & Nielsen, 2020). Changes in plant species composition are likely to influence phenological characteristics, with cleared areas following disturbance potentially greening up faster due to an increase in solar radiation.

Phenological modelling of areas disturbed due to seismic lines is potentially a useful tool for both disturbance evaluation on peatland carbon exchange and future variations under a changing climate. Therefore, the objectives of this study were to: 1) evaluate differences in vegetation communities found on seismic lines and those in the adjacent undisturbed forested area using two phenological metrics, 2) evaluate if differences in greenness are related to vegetation composition and 3) determine whether plot-scale greenness is a strong predictor of CO₂ uptake (gross primary production; GPP). We hypothesized that plots on seismic lines would green up earlier and be overall greener than those in undisturbed areas, resulting in greater CO₂ uptake during the summer period.

2. Materials and Methods

2.1 Study sites and Experimental Design

We sampled two boreal peatland sites in northern Alberta, Canada (Figure 1A-C) between May and August 2019. Carmon Creek (hereafter referred to as bog; Figure 1D) is a treed bog approximately 40 km northeast of Peace River, Alberta (56°21'44" N, 116°47'45" W). The seismic lines at Carmon Creek were created approximately 5-15 years ago and are approximately 3 m wide. The second site IPAD (hereafter referred to as fen; Figure 1E) is a treed poor fen located approximately 40 km northeast of Peace River (56°23'51.22" N, 116°53'27.60" W). The seismic lines here were created approximately 20 years ago and are approximately 7 m wide. Disturbed locations (on the seismic lines) at both sites are without tree cover following disturbance. The 30 year (1981-2010) mean annual air temperature and annual total precipitation are + 1.6 ° C and 386.3 mm respectively (mean May-August air temperature and total precipitation are + 13.8 ° C and 213 mm; Environment Canada, 2019).

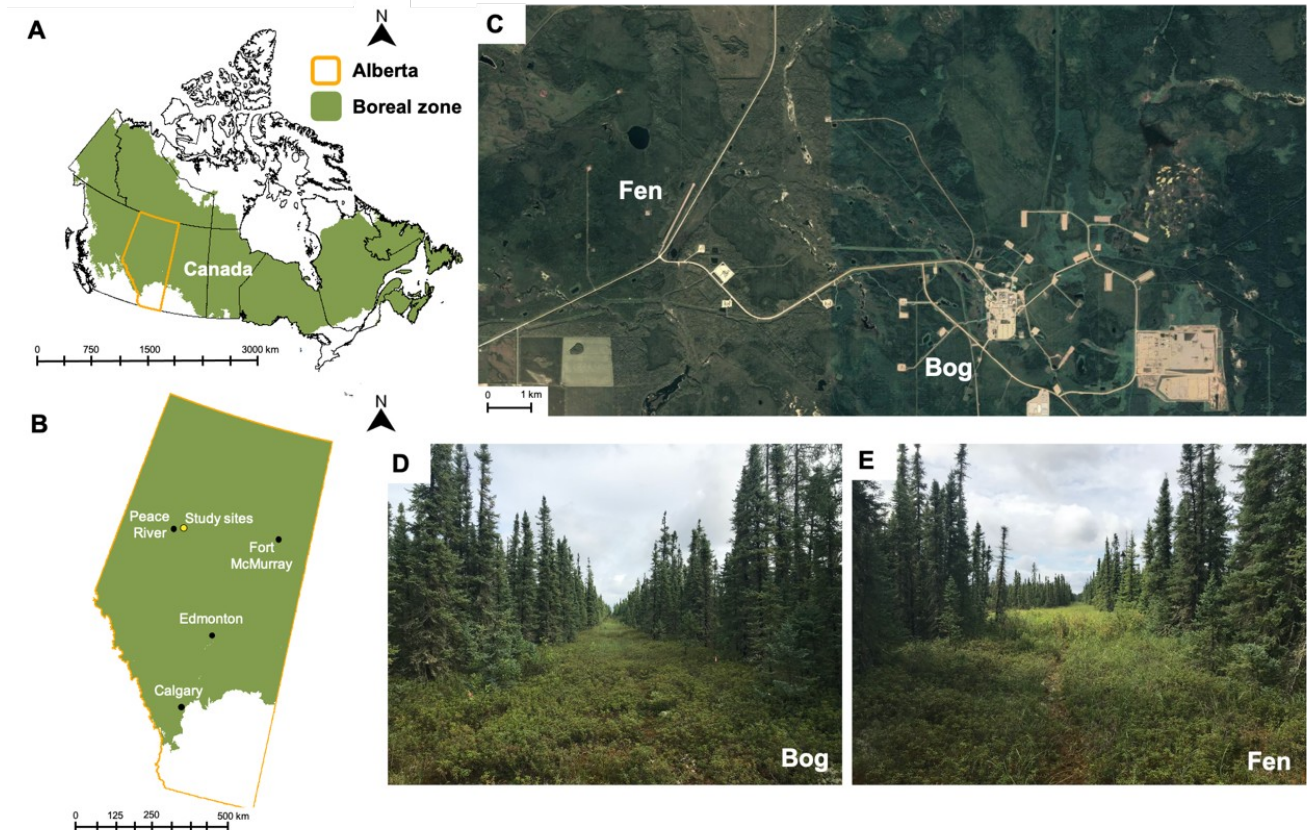


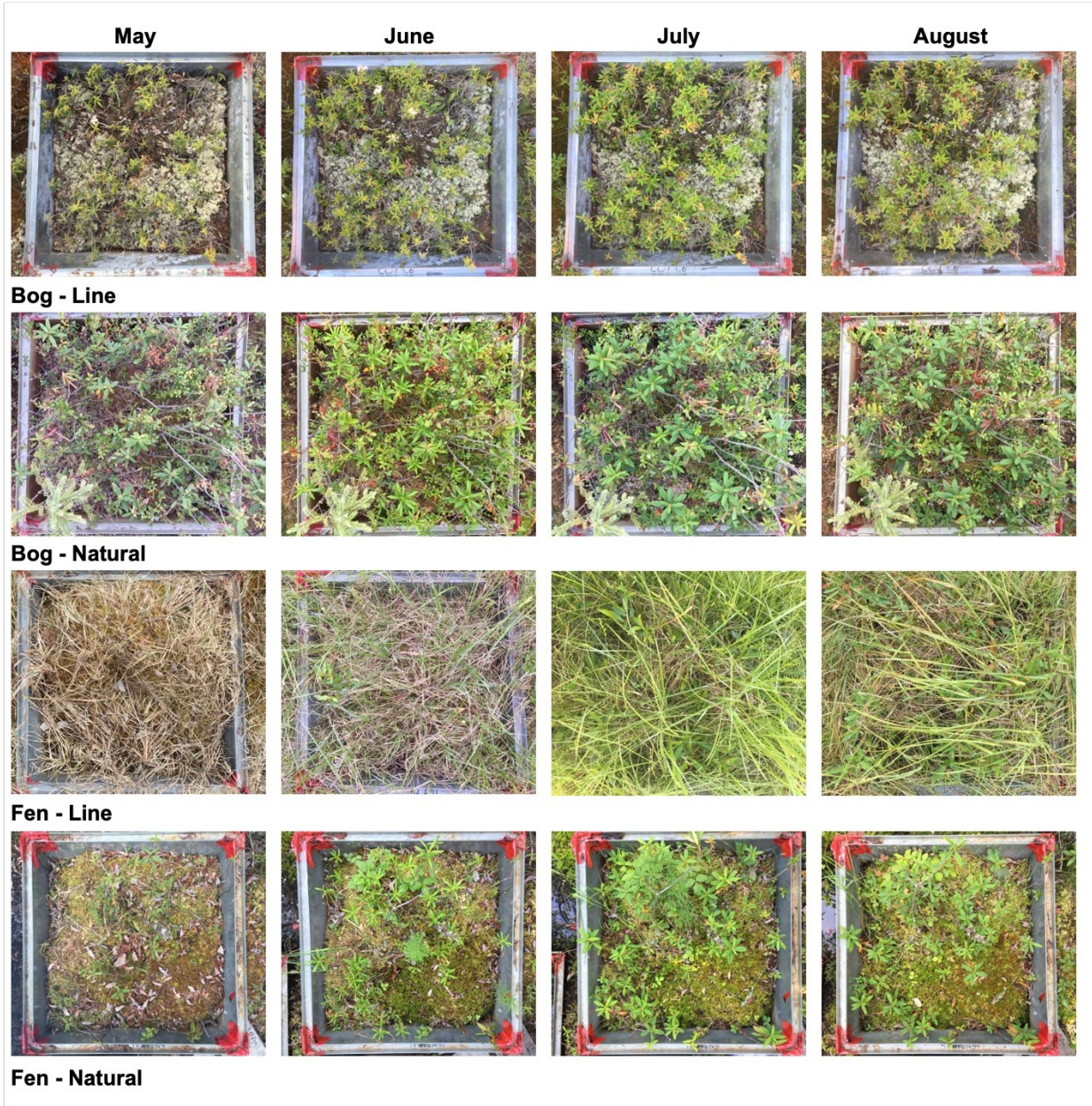
Figure 1. a) The location of the boreal zone (NRCan North American boreal zone layer; Brandt, 2009) and Alberta within Canada. b) The location of the study sites within Alberta, c) The location of the two study areas (bog: 56°21'44" N, 116°47'45" W and fen: 56°23'51.22" N, 116°53'27.60" W) (base map: Google Earth: TerraMetrics (Accessed February 9th, 2021) and photographs of the seismic line cutting across the d) bog and E) fen study sites.

In May 2018, 36 square plots (60 x 60 cm) were established for image, vegetation, and gas flux measurements. Grooved aluminum collars were permanently installed to allow for repeated measurements in the same location, located adjacent to boardwalks to minimize disturbance to the peat and vegetation. Plots were established at three positions on a seismic line in the dominant vegetation community present, and three in the adjacent undisturbed area at two lines at the fen site (12 plots) and four lines at the bog site (24 plots).

2.2 Image collection and processing

Between 10 and 12 photographs were collected for each plot at each site between 12th May and 22nd August 2019 (Figure 2) using a smartphone (iPhone 6, Apple, USA). All 420 photographs were captured under clear-sky or as near to clear-sky conditions as possible and between 10:00 and 13:00. A marker was placed on the boardwalk at each plot to ensure placement of the smartphone was approximately 1 m above the top of the ground layer canopy and in the same position each time. The image acquisition mode was set to auto white balance and autofocus. Photographs were stored in the joint photographic expert group (JPEG) format at a resolution of 1334 x 750 dpi. Any photos with standing water were removed from the analysis.

168 (five photos across two collars in total) to avoid backscatter skewing the calculated greenness
 169 values.



170

171 **Figure 2.** Example photographs of plots at each peatland type and location (where line indicates that the plot was on
 172 a seismic line and natural was the undisturbed plot) for each month of study indicating both the difference in
 173 vegetation community and visual change in ‘greenness’ over the growing season

174 We used the R package ‘Phenopix’ version 2.3.1 (Filippa et al., 2016) to calculate the
 175 green chromatic coordinate; G_{cc} ;

176

$$G_{cc} = \frac{G_{DN}}{R_{DN} + iG_{DN} + iB_{DN}} \quad (1)$$

Where R_{DN} , G_{DN} and B_{DN} are the average red, green and blue digital numbers. Gcc was chosen as it is generally more effective than other indices in minimizing the effects of scene illumination (Sonnentag et al., 2012), which is particularly useful when using hand-held equipment.

We also calculated the red chromatic coordinate; Rcc ;

$$Rcc = \frac{R_{DN}}{R_{DN} + G_{DN} + B_{DN}} \quad (2)$$

We used the *DrawROI* function to delineate the Region-Of-Interest (ROI) for each plot within the boundaries of the flux collar. We then used the *ExtractVIs* function to calculate the chromatic coordinate indices on a per-pixel basis (Toomey et al. 2015).

2.3 Modelling seasonal greenness

To compare the seasonal trajectory of Gcc in a standardized way across our plots, while accounting for missing measurements, we fit a Gaussian model to our Gcc values by day of year (DOY) following Malhotra et al. (2015). We used the following model:

$$Gcc = a \times e^{-0.5 \left[\frac{DOY - b}{c} \right]^2} \quad (3)$$

Where a , b and c are parameters describing the seasonal trajectory of Gcc : the peak value of Gcc (a), the critical point i.e., DOY at peak Gcc (b) and the growth rate of the curve (c). These parameters allows us to compare the peak, timing of peak and progression of phenology across our plots. We generated this Gaussian model each for our 36 plots (Figure S1/S2) and analyzed the three model parameters across bog/fen and line/natural site types. The majority of our Gaussian model fit R^2 values were above 0.8 (22 plots), some between 0.7 and 0.8 (9 plots), between 0.7 and 0.5 (3 plots) and below 0.5 (2 plots).

2.4 Plant species composition

Plant species composition within each plot was surveyed in July 2018. Percentage cover of all vascular and non-vascular plant species were visually estimated and recorded as 0.1 (present), 1 (occasional, few individuals) or 3 (occasional, more individuals), and then rounded up to the nearest 5%. All individuals were identified to species level, with species nomenclature following the USDA online plants database (<http://plants.usda.gov>).

2.5 Gross primary production (GPP)

Carbon dioxide (CO_2) exchange was determined using the closed dynamic chamber method (Alm et al. 2007). A clear acrylic chamber ($60 \times 60 \times 30$ cm) was placed on a stainless-steel collar (60×60 cm). A groove in the collar was filled with water to create a seal when the chamber was placed. A battery-operated fan circulated the headspace air throughout the measurement period and the chamber was removed from the collar between each measurement to equilibrate back to ambient CO_2 concentration and temperature. The concentration of CO_2 (ppm) was determined inside the chamber at 15 second intervals for a maximum of 2.5 minutes

using a portable infrared gas analyser (EGM-4, PP systems, Massachusetts, USA). The linear change in CO₂ concentration over time was used to calculate net ecosystem exchange (NEE; g CO₂ m² d⁻¹). Ecosystem respiration (ER; g CO₂ m² d⁻¹) was determined by darkening the chamber with an opaque cloth shroud. Gross primary production (GPP; g CO₂ m² d⁻¹) was calculated as the difference between NEE and ER. We express GPP as positive, indicating CO₂ uptake.

2.6 Statistical analysis

All analyses were performed in R3.5.3 (R Core Team 2019). We used two-way analysis of variance (ANOVA) to look at the difference in *Gcc* and *Rcc* between on and off-line positions across both sites. We performed correspondence analysis (CA) using the ‘cca’ function in the ‘vegan’ R package (Oksanen et al., 2019) to assess variation in plant species composition among sites. CA maximizes between-group variance, assumes unimodal species responses along environmental gradients, and is suitable for data matrices that contain many zero values (Legendre & Legendre, 2012). We applied a Hellinger transformation on the percent cover data matrix prior to CA analysis because of its ability to reduce asymmetry while being insensitive to double zeroes. Linear regression was used to look at the relationship between maximum *Gcc* and *Rcc* and the output of the correspondence analysis. An analysis of covariance (ANCOVA) was used to look at the relationship between *Gcc* and GPP between plots on the seismic lines and in the natural, undisturbed areas at both sites. Finally, a multiple regression model was used to look at the relationship between both *Gcc* and *Rcc* on GPP at both peatland types and locations. All statistics were performed on measured *Gcc* and not modelled *Gcc*. The modeled parameters were primarily reported for a descriptive comparison of the seasonal peak timing (Table 1).

3. Results

3.1 Plot level phenology metrics

At the bog site, the plots on the seismic line were consistently greener over the course of the growing season in comparison to the plots off-line in the adjacent natural area (Figure 3a). By the end of August, both the disturbed and natural sites saw a dip in *Gcc*, likely linked to the beginning of the senescence period. Unfortunately, due to logistical limitations, we were unable to obtain photographs for the autumn period. At the fen site, the natural plots were greener in the spring, but the on-line plots quickly caught up and by the end of the growing season both areas had similar greenness levels (Figure 3a). Overall, greenness was significantly lower at the bog compared to the fen (ANOVA; $F_{1,403} = 19.8$, $p < 0.001$). Yet, no significant difference in greenness was found between on and off-line across both sites (ANOVA; $F_{1,403} = 0.2$, $p = 0.7$). In comparison to the bog site, both locations at the fen site saw less of a decrease in *Gcc* at the end of the growing season, likely due to the composition of the vegetation community present.

We also compared plot-scale modelled parameters of *Gcc* seasonal trajectory (Equation 3) across bog/fen and line/natural sites (Figure 3c, Table 1). At both the bog and fen, the line plots had an earlier seasonal peak (maximum greenness) compared to natural areas. At the bog, on average, the seasonal peak of *Gcc* was 7 days earlier on the line than in natural areas. At the fen, the seasonal peak of *Gcc* was 19 days earlier than that in natural areas (Table 1).

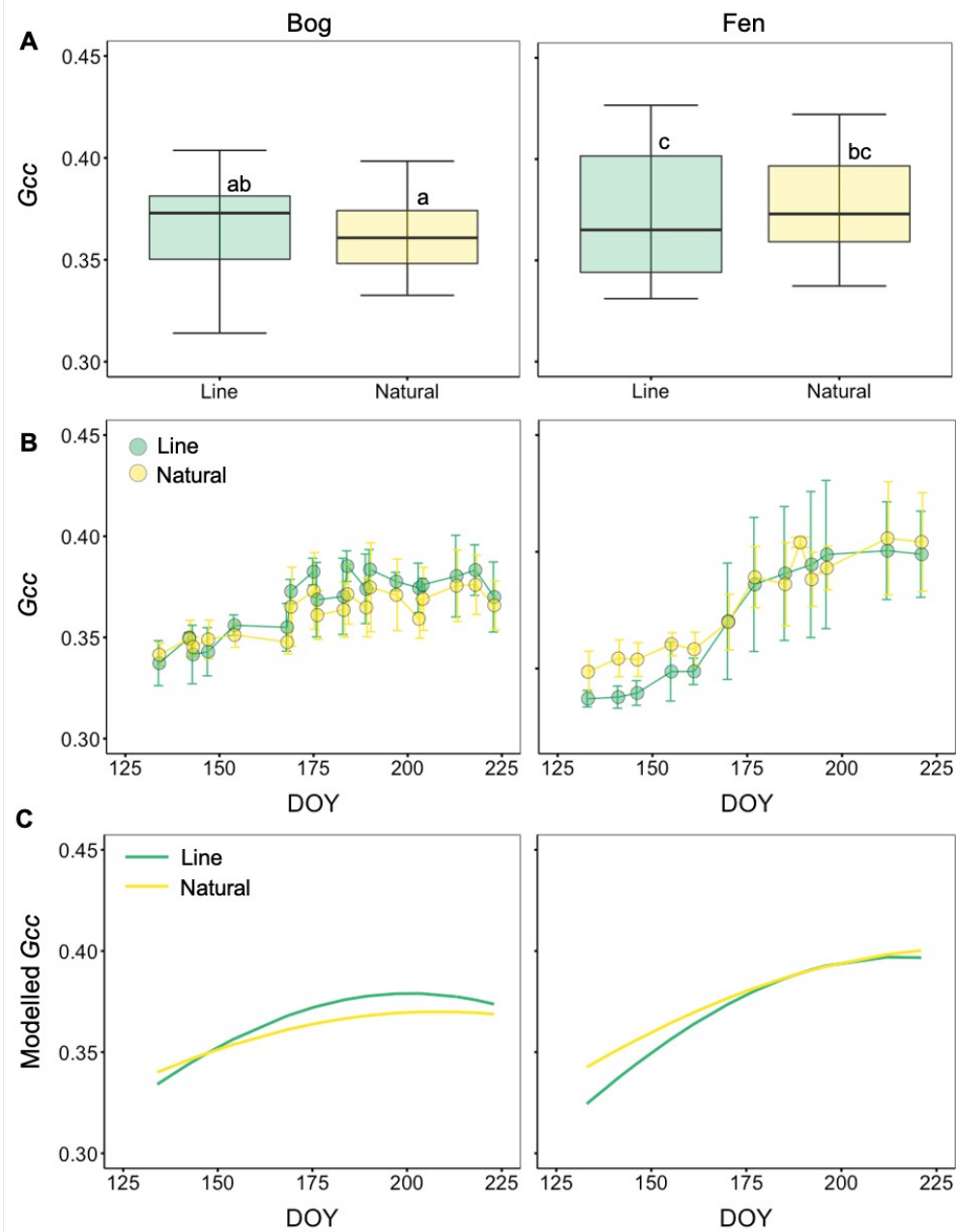


Figure 3. a) box plots of G_{cc} (Bog $n = 126$, Fen $n = 78$). Two-way ANOVA followed by a Tukey HSD ($p < 0.05$). Groups sharing letters are not significantly different, b) Time series of mean (\pm standard deviation) green chromatic coordinate (G_{cc}) over the growing season at the bog and fen sites and c) Modelled G_{cc} and associated parameters (Table 1) suggesting that line sites have an earlier seasonal peak than natural sites.

Table 1: Summary of model parameters describing seasonal trajectories of Gcc across line and natural bog and fen sites. Peak value is the peak Gcc or maximum greenness over the growing season. Critical point is the DOY at peak Gcc value. Growth rate of the Gcc curve against DOY reflects length of greenness season (larger values have wider curves i.e., longer growing seasons).

	Bog				Fen			
	Line		Natural		Line		Natural	
	Estimate	Std Error	Estimate	Std Error	Estimate	Std Error	Estimate	Std Error
Peak Value	0.38	0.01	0.37	0.00	0.40	0.01	0.40	0.01
Critical Point	201	2.99	208	7.25	215	8.48	234	24.06
Growth Rate	132.80	9.19	180.40	23.52	129.40	15.13	179.54	39.68

261

262 A difference in *Rcc* was also found at both the bog and fen sites between the line and the
 263 natural sites, although the effect of disturbance was different between the peatland types. At the
 264 bog site, the plots on the line had significantly higher *Rcc* than the nearby adjacent natural area
 265 (Figure 4a and c, ANOVA; $F_{1,403} = 82.0$, $p < 0.001$). This was the opposite to the fen site, where
 266 the natural site had significantly higher *Rcc* than the plots on the line. Furthermore, at both the
 267 disturbed and natural fen sites, the *Rcc* remained stable throughout much of the growing season
 268 apart from one time point at the disturbed site (~ day 180) and increasing towards the end of the
 269 summer, indicating the beginning of the senescence period.

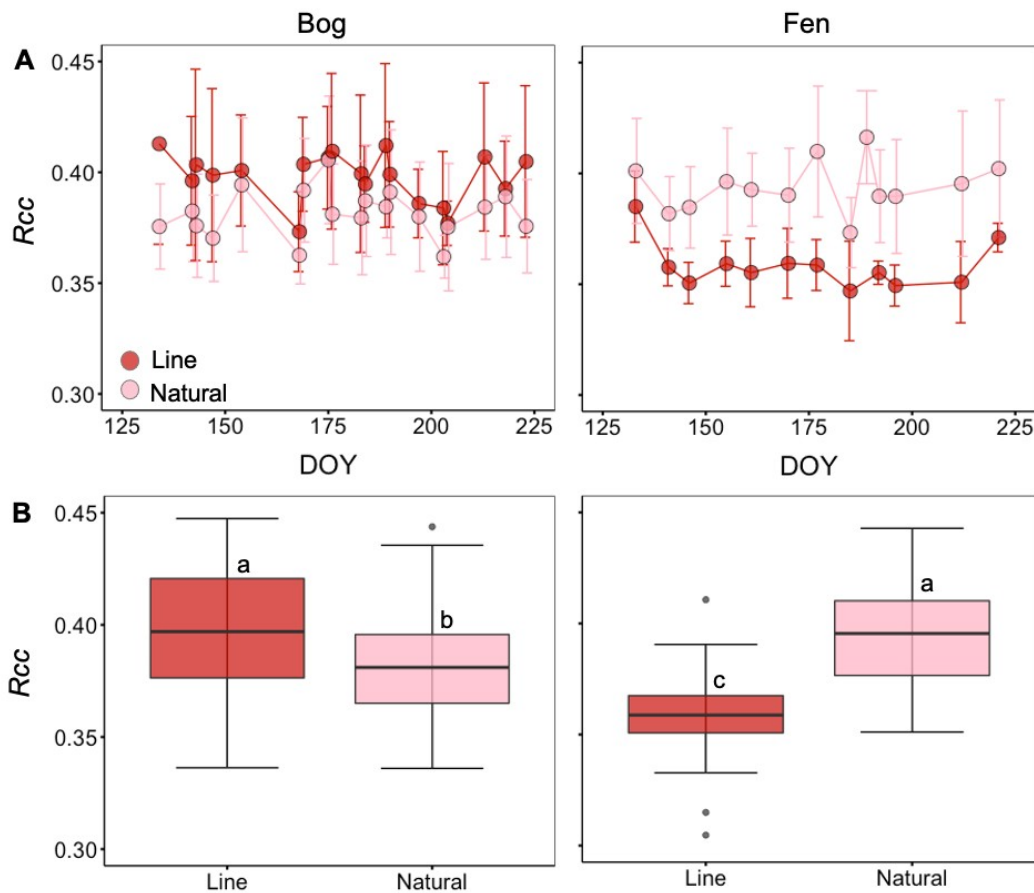


Figure 4. a) Time series of mean (\pm standard deviation) red chromatic coordinate (R_{cc}) over the growing season at the bog and the fen sites and b) box plots of R_{cc} (Bog $n = 126$, Fen $n = 78$). Two-way ANOVA followed by a Tukey HSD ($p < 0.05$). Groups sharing letters are not significantly different.

3.2 Plant species composition

Sites were primarily distributed along two CA axes that both distinguished between the bog and fen and between natural and disturbed (line) sites (Figure 5a). The first CA axis (27%) distinguished between bog and fen plant communities, and was primarily associated with variation in *Carex aquatilis* Wahlenb., *Cladina rangiferina* (L.) Nyl., and *Salix planifolia* Pursh, with additional contributions from *Sphagnum fuscum* (Schimp.) Klinggr., *Vaccinium oxycoccos* L., and *Vaccinium vitis-idaea* L. The second CA axis (21%) distinguished between natural and line sites across both bog and fen, and was primarily associated with variation in *Pleurozium schreberi* (Brid.) Mitt., *Andromeda polifolia* L., *Chamaedaphne calyculata* (L.) Moench, and *Picea mariana* (Mill.) Britton, Sterns & Poggenb., with additional contributions from *Polytrichum strictum* (Brid.), *Rubus chamaemorus* L., and *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng. *Maianthemum trifolium* (L.) Sloboda, *Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd, and *Vaccinium cespitosum* Michx. Contributed equally to both CA axes (Table 2). Maximum G_{cc} positively correlated with the first CA axis ($R^2 = 0.23$, $p = 0.002$; Figure 5b), corresponding to changes in species composition between natural and disturbed (line)

sites across bogs and fens (Figure 5b). Maximum *Rcc* was not significantly correlated with the first CA axis ($R^2 = 0.1$, $p = 0.06$; Figure S3).

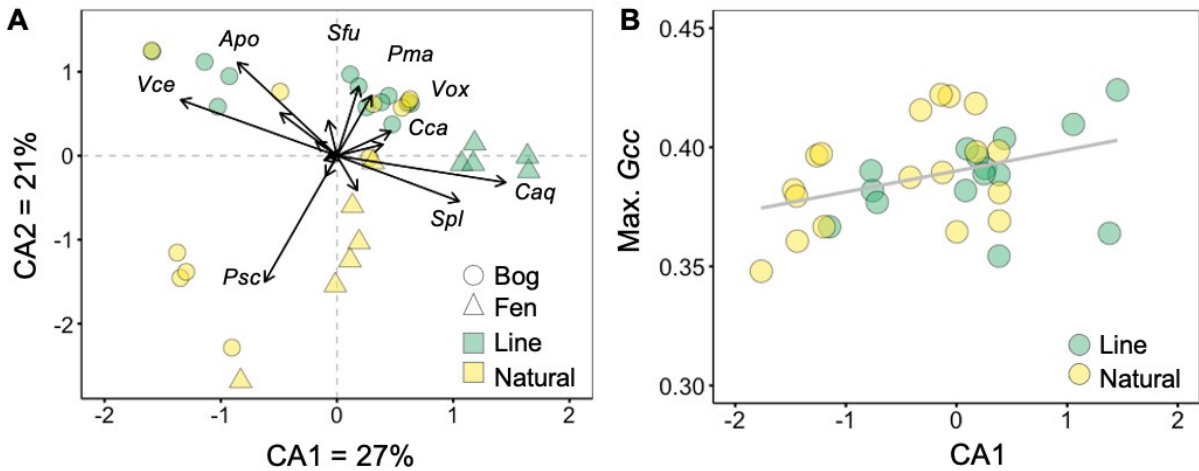


Figure 5. A) Correspondence analysis (CA) plot showing the distribution of natural and disturbed peatland sites in relation to 16 plant species, and B) the relationship between maximum greenness (*Gcc*) and the first CA axis ($R^2 = 0.23$, $p = 0.002$). Species names and abbreviations are found in Table 2.

Table 2: Eigenvector loadings for the first two correspondence analysis (CA) axes, describing the strength of associations between the distribution of 16 peatland plant species among natural bog and fen sites, and those disturbed by linear seismic lines.

Species	Abbreviation	CA1	CA2
<i>Andromeda polifolia</i>	Apo	-0.85719	1.11217
<i>Carex aquatilis</i>	Caq	1.45048	-0.31865
<i>Chamaedaphne calyculata</i>	Cca	0.18607	0.82738
<i>Cladina rangiferina</i>	Cra	-1.34465	0.6652
<i>Cladonia chlorophaea</i>	Cch	-0.0742	0.41958
<i>Maianthemum trifolium</i>	Mtr	-0.07206	-0.0185
<i>Picea mariana</i>	Pma	0.29672	0.71567
<i>Pleurozium schreberi</i>	Psc	-0.62162	-1.50083
<i>Polytrichum strictum</i>	Pst	0.1731	-0.41218
<i>Rhododendron groenlandicum</i>	Rgr	-0.18219	0.16921
<i>Rubus chamaemorus</i>	Rch	-0.09649	-0.24086
<i>Salix planifolia</i>	Spl	1.05086	-0.5413
<i>Sphagnum fuscum</i>	Sfu	0.46354	0.2926
<i>Vaccinium cespitosum</i>	Vce	-0.48988	0.50987
<i>Vaccinium oxycoccus</i>	Vox	0.39465	0.13528
<i>Vaccinium vitis-idaea</i>	Vvi	-0.11018	-0.05213

3.3 *Gcc* as a predictor of GPP

As hypothesized, we found that *Gcc* was a good predictor of GPP and this relationship differed between natural and disturbed sites. At both the bog and fen, there was a significant interaction between *Gcc* and location (natural vs. line) on GPP (bog; ANCOVA, $F_{1,185} = 8.01$, $p = 0.005$ and fen; ANCOVA, $F_{1,116} = 5.2$, $p = 0.02$) (Figure 6). This arose due to GPP increasing more quickly as *Gcc* increased on lines in natural plots. Overall, there was a significant effect of *Gcc* (ANCOVA, $F_{1,185} = 76.7$, $p < 0.001$) and location (natural vs. line) (ANCOVA, $F_{1,185} = 53.2$, $p < 0.001$) on GPP at the bog site. This model explained 45% of the variability in GPP. Similarly, at the fen site, there was a significant effect of *Gcc* (ANCOVA, $F_{1,116} = 45.4$, $p < 0.001$) and location (ANCOVA, $F_{1,116} = 74.9$, $p < 0.001$). This model explained 48% of the variability in GPP. Since the rate of change in GPP in response to *Gcc* varied between natural and disturbed sites, we explored whether including *Rcc* in models with *Gcc* (but without disturbance category) could improve GPP prediction. A multiple regression model predicting GPP using both *Gcc* and *Rcc* explained 44% ($F_{4,184} = 38.39$, $p < 0.001$) and 46% ($F_{4,115} = 26.42$, $p < 0.001$) of the variability at the bog and fen, respectively.

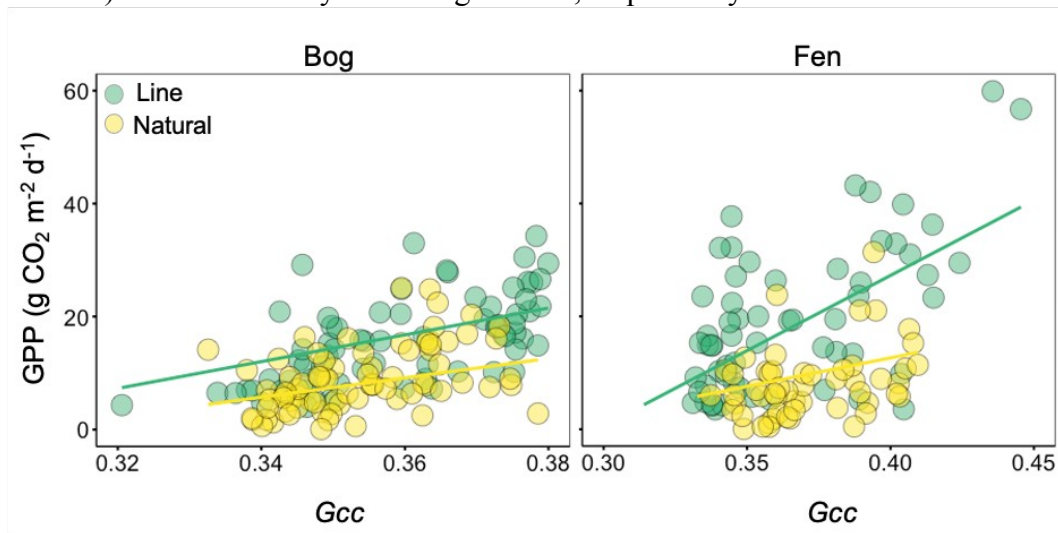


Figure 6. Understory gross primary production (GPP; g CO₂ m² d⁻¹) as a function of greenness (green chromatic coordinate; *Gcc*) at both the bog and fen.

4. Discussion

Our goal was to investigate if linear disturbances from seismic lines impact boreal peatland plant communities and their green leaf phenology, and ultimately the ecosystem carbon function. Our RGB image-based methodology successfully described the seasonal trajectory of plot-level phenology metrics (*Gcc* and *Rcc*) across two different peatland types; thus highlighting a non-destructive and relatively low-cost and low-effort field method for evaluating phenological changes in disturbed peatlands. Our results suggest that seismic lines lead to peatland disturbances wherein a shift in plant species composition alters the phenological trajectory and plot-scale *Gcc* and *Rcc*. Finally, given that our phenological metrics were a strong predictor of CO₂ uptake in our plots, in the future, they could be developed as carbon cycle proxies for rapid disturbance assessments of larger peatland areas.

4.1 Linear disturbance effects on plant phenology, species composition, and carbon exchange

Our results highlight a distinct shift in phenology and species composition between natural sites and seismic lines, with an earlier peak in greenness and overall increases in greenness and productivity in seismic line plots. Specifically, the greenness peak of line plots were 1-3 weeks earlier than in natural areas (Figure 3, Table 1). Variation in greenness was related to changes in plant species composition (Figure 5). At both peatland types, a clear shift in vegetation communities was found on plots located on the seismic line compared to the nearby adjacent undisturbed areas. At the bog site, there was a ground layer of feather moss (*P. schreberi*) and lichen (*C. rangiferina*) in the natural plots and these were replaced by a continuous ground layer of *S. fuscum* on the lines (Figure 5a). Vegetation changes were even more apparent in the fen, with a large shift towards sedge and willow dominance with decreases in moss abundance. The larger *Gcc* values found in the line plots at both sites is likely due to reductions in lichen cover, which has naturally low greenness and photosynthetic rates (Harris et al. 2018). Similarly, the earlier peak in *Gcc* in line plots is likely caused by both an increase in herbaceous perennials that display a strong leaf-out in the spring (e.g., *C. aquatilis*, *R. chamaemorus*) in combination with the loss of mosses (e.g., *P. schreberi*) that stay green late into the autumn (Figure S4). The *Rcc* values measured show an inverse relationship to *Gcc*, especially at the fen site (Figure 4). This is likely due to both the higher red pigmentation of the moss species found in the natural sites compared to the greener species found on the line and senescing leaves towards the end of the summer (Moore et al., 2017).

The creation of seismic lines involves tree removal, flattening of localised microtopography, and peat compaction, resulting in wetter conditions (Lovitt et al., 2018). These environmental disturbances are likely to have caused the observed shifts in understory vegetation, allowing for more moisture-loving species to establish and dominate, such as *C. aquatilis* at the fen and *S. fuscum* at the bog. Linked to this shift in vegetation communities is the reduced likelihood for tree sapling regeneration due to potential competition with more productive understory vegetation such as sedges (Filicetti & Nielsen, 2020). Disturbances across peatlands often result in vegetation shifts following, for example, drainage (Strack et al., 2006), fire (Noble et al., 2019), permafrost thaw (Camill et al., 2001) and flooding/re-wetting (Goud et al., 2018; Tuittila et al., 2000). Increased greenness and primary productivity in the line plots at the fen was likely due to a switch from moss to sedge-dominated communities. Sedges are highly productive, often displaying larger rates of growth and carbon exchange relative to lichen, mosses and shrubs (Goud et al. 2017; Harris et al., 2018). Given that a dominance of sedges allows for more CO₂ uptake (Leppälä et al., 2008), this may explain the tighter and steeper relationship between greenness and GPP on seismic lines, particularly at the fen (Figure 6). Although there are relatively few studies on carbon exchange following linear disturbances, Strack et al. (2018) also found a significant increase in graminoid cover on a winter road crossing a boreal peatland. Similar to our results, this linear disturbance impacted hydrology and carbon dynamics, with disturbed plots having greater CO₂ uptake compared to the adjacent peatland. The removal of the tree canopy also reduces overall tree biomass and associated net primary production, further influencing carbon stocks in these systems. In the long term, it is possible that understory productivity could increase enough to compensate for this loss, indicative of a potential tradeoff between overstory and understory carbon uptake following disturbance (Strack et al., 2018). However, the shift towards a more sedge-dominated system at the fen site in this study could not only lead to more carbon uptake but could also lead to higher respiration rates and larger CH₄ emissions through increased rates of plant-mediated transport

(Strack et al., 2018). Given that Strack et al. (2019) calculated that there are approximately 790 km² of seismic lines crossing fens in Alberta alone, potentially leading to a substantial increase in CH₄ emissions, this has widespread implications for the carbon balance and net radiative forcing of these systems.

4.2 Applications of phenological measurements for peatland monitoring and management

Monitoring phenology is a useful metric for understanding disturbance-induced vegetation shifts and function and could provide a useful way of identifying restoration progress and future priority areas. In this study, using a smartphone to collect imagery eliminated the need for fixed infrastructure, allowing us to sample more small-scale (understory) plots and study sites relative to other commonly used phenological methods such as remote sensing and measurements of plant anatomical traits and biomass. Although digital photograph collection provides a lower temporal resolution than we would get from a fixed or remote sensing platform, it provides an accessible low-cost method with many advantages (Weil et al. 2017). Hand held digital photography allowed us to focus on the understory peatland vegetation communities, rather than having to use a landscape-scale image which would likely mask any ground-layer changes in vegetation community and phenology. Field-based spectral reflectance discrimination of peatland and tundra vegetation communities have been successfully undertaken in various studies (Bubier et al., 1997; Davidson et al., 2016). Similar methodologies could be applied using phenological data. The significant differences in the chromatic coordinates, in particular the *Rcc*, between disturbed and natural plots indicate its usefulness as a tool for monitoring differences in species composition following disturbance at larger spatial scales without needing to go further and use more expensive near infra-red based sensors (Weil et al., 2017). This could prove especially useful in terms of peatland restoration and when trying to understand poor tree recovery on seismic lines through competition with other peatland plant species such as *Sphagnum* or sedge species. Furthermore, our ability to link the easy-to-measure *Gcc* and *Rcc* with GPP also shows promise as a way to monitor and map shifts in peatland carbon exchange in response to linear disturbances and recovery over time. This would be valuable to regional to national accounting of greenhouse gas emissions. Finally, the greenness measured at the plot scale using these photographs could be upscaled using remote sensing products (e.g. high resolution, high frequency satellite imagery such as Planet (PlanetLabs, San Francisco, USA) that incorporate the overstory canopy in order to investigate temporal changes in vegetation productivity across much larger spatial scales and help improve management and restoration post-disturbance.

5. Conclusion

Peatlands across the boreal zone in Canada and their vast carbon stocks are vulnerable to climate and land-use change. Vegetation communities and their phenological trajectory are often the first ecosystem components to respond to environmental change and may influence peatland net carbon balance. Here, we demonstrate a low-cost and readily available method to assess phenological change in peatlands. We observe strong phenological changes in peatlands disturbed by seismic lines and find that these changes are driven by vegetation community shifts, and ultimately, influence ecosystem carbon uptake. We provide an easy-to-use method that could help improve the understanding of vegetation community, phenology and carbon exchange

post-disturbance across a variety of different ecosystems with high spatial resolution without the need for fixed infrastructure and expensive sensors. Since boreal landscapes will continue to be threatened by a variety of disturbances, improving our understanding of the magnitude and mechanisms of vegetation and phenology changes post-disturbance is the first step toward predicting changes to the carbon cycle of these ecosystems across broad spatial scales.

CRediT author statement

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Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability statement

Data available via the Dryad Digital Repository:
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