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Key Points:
- Peatland soil organic matter stability can be evaluated through the relative abundances of carbohydrate and aromatic content in peat
- Peat at higher latitudes and elevations has larger carbohydrate and smaller aromatic content relative lower latitudes and elevations
- Our results foreshadow a transition of organic matter from higher latitude peatlands to a more recalcitrant form in response to warming

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

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Latitude, Elevation, and Mean Annual Temperature Predict Peat Organic Matter Chemistry at a Global Scale

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Abstract Peatlands contain a significant fraction of global soil carbon, but how these reservoirs will respond to the changing climate is still relatively unknown. A global picture of the variations in peat organic matter chemistry will aid our ability to gauge peatland soil response to climate. The goal of this research is to test the hypotheses that (a) peat carbohydrate content, an indicator of soil organic matter reactivity, will increase with latitude and decrease with mean annual temperatures, (b) while peat aromatic content, an indicator of recalcitrance, will vary inversely, and (c) elevation will have a similar effect to latitude. We used Fourier Transform Infrared Spectroscopy to examine variations in the organic matter functional groups of 1034 peat samples collected from 10 to 20, 30–40, and 60–70 cm depths at 165 individual sites across a latitudinal gradient of 79°N–65°S and from elevations of 0–4,773 m. Carbohydrate contents of high latitude peat were significantly greater than peat originating near the equator, while aromatic content showed the opposite trend. For peat from similar latitudes but different elevations, the carbohydrate content was greater and aromatic content was lower at higher elevations. Higher carbohydrate content at higher latitudes indicates a greater potential for mineralization, whereas the chemical composition of low latitude peat is consistent with their apparent relative stability in the face of warmer temperatures. The combination of low carbohydrates and high aromatics at warmer locations near the equator suggests the mineralization of high latitude peat until reaching recalcitrance under a new temperature regime.

Plain Language Summary Peatlands are a large global soil carbon reservoir, containing a quantity of carbon that is equivalent to about half or more of the carbon dioxide in the atmosphere. What will be their fate on a warming planet? Across a latitudinal gradient from 79°N to 65°S, we measured the fraction of the peat made up of carbohydrates, which are easily decomposed, and of aromatics, which are less easily decomposed. We found that peat from high latitudes and high elevations had greater carbohydrate content, while aromatic content showed the opposite trend. Larger carbohydrate content in organic matter indicates greater decomposability, while greater aromatic content indicates lower decomposability. We suggest that this latitude/elevation difference that we observed predicts how high-latitude and high-elevation peats may change under warmer conditions. Our work indicates that while a large portion of the carbohydrate fraction in these peats could be lost upon warming, releasing greenhouse gases, a residual fraction will survive and become more aromatic-rich, making the remainder more resistant to rapid decomposition.

1. Introduction

Northern (boreal and subarctic) peatlands are estimated to contain 500 ± 100 Gt of carbon (C), which accounts for a substantial fraction of global soil C, while only occupying about 3% of the terrestrial global surface (Gorham, 1991; Yu et al., 2010; Loisel et al., 2014, 2017), although a recent controversial estimate of peatland carbon is considerably greater (Nichols & Peteet, 2019). Tropical peatlands have only recently been included in the global soil carbon pool estimate, and even though northern peatlands contribute much more to this reservoir (estimates range from 455 to 621 Pg C; Gorham, 1991; Yu et al., 2010), peatlands closer to the equator add an estimated 65–105 Pg C (Dargie et al., 2017; Page et al., 2011; Yu et al., 2010).

Carbon accumulation measurements in peatland soils usually consist of defining the areal extent, depth, and carbon content of the peat, but the organic matter carbon quality should also be considered to accurately evaluate peatland soil carbon stability and potential carbon emissions in the face of climate change or other perturbations. Carbon accumulation and emission estimates could be improved by taking into account the chemical composition of the peat, which is one of the primary controls of degradability because of different activation energies of chemical bonds (Baldock et al., 1997; Hemingway et al., 2019; Keiluweit et al., 2016; LaRowe & Van Cappellen, 2011; Leifeld et al., 2012). One simple way to estimate organic matter carbon quality is to measure both carbohydrate

(O-alkyl carbon) content, which affects decomposition potential, and aromatic content, which affects recalcitrance (Baldock et al., 1997; Keiluweit et al., 2016).

1.1. FTIR Organic Matter Functional Groups

Peat can be classified by the major components of organic matter functional groups, which have different biological and chemical availabilities with respect to mechanisms of decomposition and transformation (Normand, 2017; Tfaily et al., 2014). Fourier Transform Infrared Spectroscopy (FTIR) is an excellent tool to classify these groups based on the infrared absorption due to the vibrational properties of the atomic bonds. The major structural assignments of peaks from FTIR spectra (wavenumbers 4000–650 cm^{-1} of the mid-IR range) are carbohydrates, aromatics, acids, and aliphatics. While the peak heights alone are not directly quantitative, after area normalization and baseline correction, comparing peak heights between samples is useful for determining the relative abundance of major structural groups (Hodgkins et al., 2018). In particular, the relative abundances of carbohydrates and aromatics are very well suited for evaluating levels of humification or decomposition. Carbohydrates (O-alkyl-C) are primarily found in peat-forming plants as cellulose, and are the most bio-labile constituent of peat (Hemingway et al., 2019; LaRowe & Van Cappellen, 2011; Tfaily et al., 2014). O-alkyl-C abundances have been shown to be the best proxy for decomposition potential compared to other factors such as soil pH, depth (age), and element ratios such as C/N, O/C, and H/C (Baldock et al., 1997; Leifeld et al., 2012). Aromatic compounds, including phenolics and some undissociated organic acids originating from plants like *Sphagnum*, are known to inhibit the decomposition of organic matter (Ballance et al., 2012; Bengtsson et al., 2018; Hájek et al., 2011; Hodgkins et al., 2014) and are much more refractory than carbohydrates. Lignin, a complex amorphous aromatic compound found in vascular peat-forming plants, has been identified as relatively stable in anaerobic peatland environments (Hodgkins et al., 2016; Kalbitz et al., 2003; Kirk & Farrell, 1987). Degradation of O-alkyl-C compounds by microbes can lead to residual enrichment of more recalcitrant components in peat (Tfaily et al., 2014). Peat decomposition is somewhat different from the decomposition of organic matter in mineral soils in that preservation through interaction with mineral grains (Hemingway et al., 2019) is not a factor in these mineral depleted soils.

1.2. Evidence for a Global Gradient

Our previous research has evaluated peat stability over a global latitudinal gradient based on FTIR spectra but with a much smaller set of samples (Hodgkins et al., 2018). Carbohydrate and aromatic content of peat from seven different locations spanning the latitudes 4°N-68°N were determined based upon calibration curves between the FTIR spectra peak heights and a set of reference samples that had been subjected to wet chemistry measurements of the same organic matter functional groups to determine % cellulose + hemicellulose (carbohydrates) and % Klason lignin (aromatics). Hodgkins et al. (2018) conducted FTIR analyses on both peat cores and fresh plant materials from the locations and found that the estimated % carbohydrates increased from lower latitudes to higher latitudes, decreased with depth, while the estimated % aromatics showed the opposite trend. It was also inferred from the fresh plant material spectra that their initial carbohydrate and aromatic content could contribute to the variations in relative abundance of carbohydrates and aromatics in peat between latitudes.

1.3. Botanical Composition of Peat

One key factor affecting peat chemistry is the chemical characteristics of the organic matter inputs (Zeh et al., 2020). Peatlands vary in vegetation composition, and the dominant factors affecting plant community composition include latitude, mean annual temperature (MAT), elevation, and hydrology, especially groundwater versus rainwater inputs. The resulting plant community variation affects the type of organic inputs and the degradation of organic matter (Wang et al., 2021). At higher northern latitudes where most peatlands are located, peat is often composed of non-woody litter. Graminoids typically dominate litter inputs at minerotrophic (groundwater-fed) peatlands, characterized by higher pH. Conversely, *Sphagnum* moss litter dominates in the more acidic ombrotrophic (rain-fed) and oligotrophic (nutrient-poor) northern peatlands (bogs and poor fens; Thomas & Pearce, 2004). Some *Sphagnum* peatlands are also present at lower latitudes, typically at higher elevations (Grover & Baldock, 2012; Urbina & Benavides, 2015). Graminoid litter inputs tend to be relatively labile, decomposing rapidly if exposed to oxygen (Scheffer et al., 2001; Verhoeven & Toth, 1995; Vitt et al., 2009). In contrast, *Sphagnum* mosses are more resistant to decomposition, and so are considered keystone species in

northern acidic peatland ecosystems (Van Breemen, 1995; Walker et al., 2017). *Sphagnum* mosses have unique physical and chemical properties that help preserve organic matter including microbiocidal pectins (Ballance et al., 2012), high cation exchange capacity (Bengtsson et al., 2018; Painter, 1991; Thomas & Pearce, 2004), and some lignin-like phenolics (Bengtsson et al., 2018).

At lower latitudes and elevations, peat swamp forests are the dominant peatland types (Gumbricht et al., 2017; Page et al., 2011). These are dominated by angiosperm trees and palms, and hence the dominant inputs to these peatlands are woody or palm litter with a relatively high lignin content (Dargie et al., 2017; Gandois et al., 2013; Könönen et al., 2016; Lahteenoja and Page, 2011; Lahteenoja et al., 2009). However, our measurements of *Shorea albida*, a tree dominant in tropical Southeast Asia, were roughly 40% carbohydrate and 30% aromatic as determined with FTIR (Hodgkins et al., 2018). Wood is relatively high in cellulose (Hodgkins et al., 2018). At higher northern latitudes, peat forming environments can, in some cases, be dominated by conifer species such as northern white cedar (*Thuja occidentalis*) at higher pH, or Pinaceae (e.g., *Larix, Picea*, and *Pinus*) at lower pH. Other rarer peatland types include cushion peatlands dominated by a diversity of herbaceous monocot and dicot cushion-forming species common in the Andes and Patagonia (Broder et al., 2012; Cooper et al., 2010; Mathijessen et al., 2019), restiad peatlands dominated by Restionaceae (Poales) in Australia and New Zealand (Clarkson et al., 2017), and graminoid peatlands like the Florida Everglades.

1.4. Peat Organic Matter Decomposition

In oxic soils, the depolymerization of organic matter is largely dependent on aerobic decomposition processes with oxygen as the terminal electron acceptor; whereas under oxygen-depleted conditions, oxidative enzyme activity is suppressed, anaerobic decomposers are dominant, and alternative electron acceptors are utilized along with hydrolytic enzymes (Keiluweit et al., 2016). Although hydrolytic enzymes can function under anoxic conditions, lower temperatures can reduce rates of enzyme activity, apparently by constraining enzymatic decomposition of polymers like cellulose (Conant et al., 2011). When organic matter decomposition is controlled by anaerobic decomposers, aromatics are selectively preserved (Baldock et al., 1997). Using solid-state ^{13}C Nuclear Magnetic Resonance spectroscopy, Baldect et al. (1997) showed many examples where the accumulation of aromatic carbon structures with decomposition was closely associated with a decrease in O-alkyl-C structures. They suggested that since an increase in aromatic content in humified peat coincided with carbohydrate loss, the relative abundances could serve as a sensitive index of decomposition. Biester et al. (2014) compared a number of decomposition proxies and found that the changes observed were mainly attributed to decomposition and to a lesser extent due to change in vegetation. They found preferential decomposition of phenols and polysaccharides and enrichment of aromatics with decomposition. Keiluweit et al. (2016) also showed that soil organic matter decomposition is constrained by the lability and recalcitrance of the carbon moieties present. Depolymerization of organic matter is limited by hydrolysis-resistant compounds such as lignin-like aromatics, whereas O-alkyl-C structures like carbohydrates are readily degradable by hydrolysis and fermentation (Keiluweit et al., 2016). Thus, humification of organic matter–and consequent decrease in O-alkyl-C and increase in aromatic-C–acts as a negative feedback to further decomposition, as the remaining organic matter has a lower content of labile O-alkyl structures and a higher content of recalcitrant aromatics. Low intensity fires can also affect organic matter degradation rates (Flanagan et al., 2020).

In addition to direct temperature effects on peat diagenesis, some latitudinal differences in peat chemistry could derive from the relative differences in the chemistry of peat litter inputs. Whatever its origin, there is likely a larger store of cellulose and other homopolymers that is preserved in colder high-latitude and high-elevation peat that would be susceptible to increased enzymatic depolymerization under a warmer climate (Hodgkins et al., 2018). With climate-change mediated temperature increase, which is relatively greater at high latitudes (Dorrepaal et al., 2009; Gallego-Sala et al., 2018; Meehl et al., 2007; Tingley & Huybers, 2013), a portion of the soil organic carbon that was formerly stable may become more accessible to microbial decomposition, via direct effect of rising temperature, indirect effects of water tables (Bäckstrand et al., 2010; Fenner & Freeman, 2011), or due to vegetation changes (McPartland et al., 2020; Norby et al., 2019). However, the timescale of this process is not known (Laine et al., 2019).

1.5. Study Objectives

This study aimed to characterize the chemical composition of peat as defined by FTIR spectroscopy of organic matter functional groups. A total of 1335 peat samples were measured using FTIR. After omitting samples that had
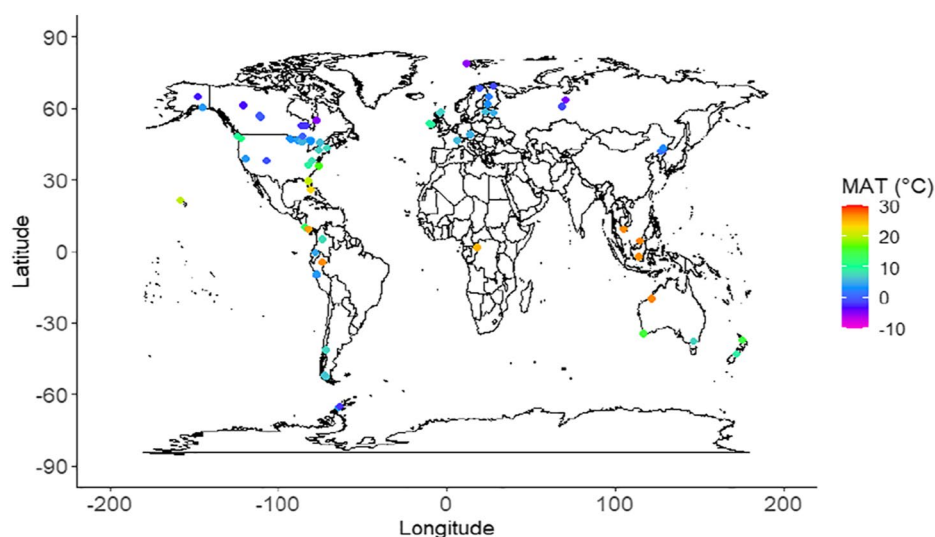
Figure 1. Peatland sampling locations measured in this study and the corresponding mean annual temperatures (°C). Peat cores were collected across a global latitudinal gradient of 79°N–65°S.

a high enough mineral content to create interference with the carbohydrate peak as described in the methods (Broder et al., 2012; Zimmermann et al., 2007), a total of 1034 samples across a latitudinal gradient of approximately 79°N–65°S were included in the final analysis (Table S1 in Supporting Information S1). All peat samples used in this study were collected from unmodified locations, which have not been directly subjected to experimental treatments or extensive impacts from human activities. The objective of this study was to test the following hypotheses: (a) carbohydrate content will increase along a latitudinal gradient from the equator toward the poles (35–8,765 km from the equator was sampled); (b) aromatic content will decrease along this gradient; and (c) elevation will have a similar effect to latitude, with higher carbohydrates and lower aromatics at high elevations relative to low elevations at similar latitudes (0–4,773 m was sampled). The relationships of carbohydrates and aromatics with latitude and elevation will primarily be due to strong changes in MAT along latitude and elevation gradients. These patterns are predicted to hold even after controlling for botanical origin of the peat because latitude and elevation are closely related to MAT, and they are primarily driven by decomposition (Hodgkins et al., 2018). This large database of samples not only expands upon the previously observed global latitudinal trends in peat chemistry (Hodgkins et al., 2018) with a much larger number of samples, it introduces elevation as another significant influence on peat organic matter carbon quality and provides a global-scale explanation of the observed patterns.

2. Methods

2.1. Peat Sampling

We assessed the chemical composition of organic matter in 1034 peat samples representing 165 unmodified locations spread across all continents from tropical to high latitude peatlands (Figure 1; Table S1 in Supporting Information S1). The samples were a subset of those from a larger study (The global peatland microbiome project, Lamit and Lilleskov et al., personal communication 2021) aimed at characterizing microbial communities and biogeochemistry in the Earth's peatlands. At each location, we collected one or more cores (most frequently three cores) using a variety of sampling methods, and material from the 10–20 cm, 30–40 cm, and 60–70 cm depth increments below the peat surface was saved for processing (in some cases only the shallower depths were collected). All samples represent 10 cm depth increments. However, the diameter of the cores varied from ∼5 cm diameter Russian peat corers to approximately 10 cm diameter box corers. From each depth increment, a representative ∼50 g of fresh peat was saved for processing. Although variation in core size could lead to some extraneous variation being added to the response variables we measured, we do not believe that variation at this small sampling scale would confound the overall interpretation of the peat chemistry.

Samples were frozen, chilled or freeze-dried and rapidly shipped to the USDA Forest Service, Northern Research Station, Houghton, MI, USA for further processing. We recorded the latitude, longitude, and elevation of
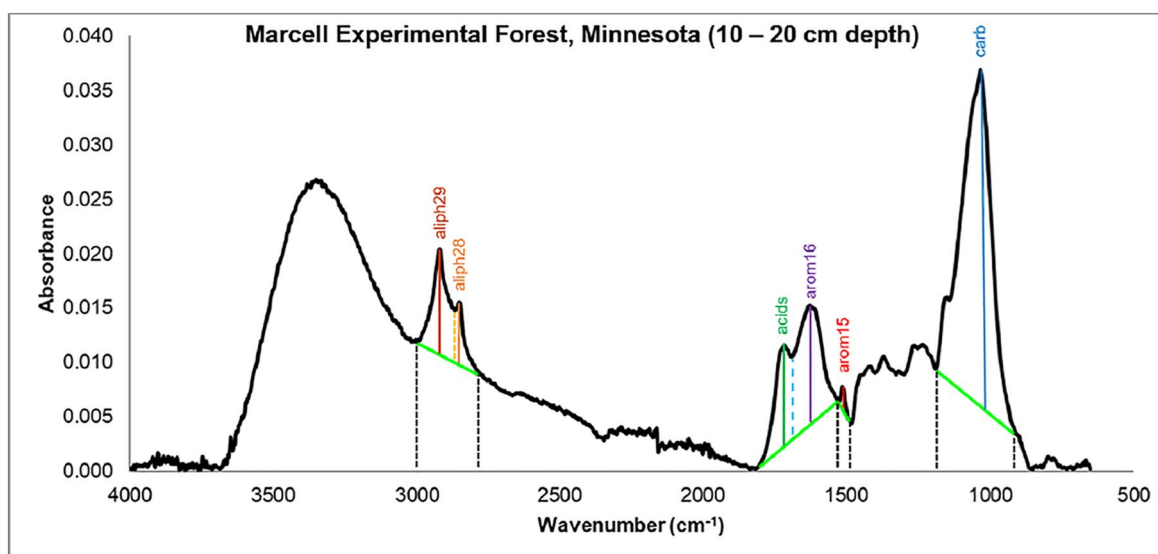
Figure 2. Example of peak finding using the *R* script with a Fourier Transform Infrared Spectroscopy spectrum of a Minnesota bog/poor fen 10–20 cm depth sample. The organic matter functional groups are shown with baseline correction of each peak and normalization to the integrated area of the spectrum.

coring locations, and scored the von Post humification index (Ekono, 1981; von Post, 1922), an ordinal index of decomposition degree (see Rydin & Jeglum, 2013), on moist peat from each depth increment. The von Post index ranges from 1 to 10, with 1 being the least decomposed and 10 being the most decomposed, and is based on characteristics such as the integrity of plant material in the peat, and the viscosity and color of what passes through the fingers when the peat is squeezed.

2.2. FTIR Analysis

Subsamples of each depth increment were freeze-dried or oven-dried (55°C), then ground to a fine powder with a SPEX SamplePrep 5100 Mixer/Mill ball grinder. A PerkinElmer Spectrum 100 FTIR spectrometer fitted with a CsI beam splitter and a deuterated triglycine sulfate detector was used to collect % transmittance spectra between wavenumbers 4,000–650 cm^{-1}. The spectra were obtained by averaging four scans at a resolution of 4 cm^{-1} after placing samples directly on an attenuated total reflectance (ATR) crystal and applying force so that the samples were held against the crystal. The Universal ATR accessory with a single-reflectance system was made from a zinc selenide/diamond composite. After both ATR-correction and baseline-correction by the instrument software, all spectra were converted from transmittance to absorbance. The standard deviations of carbohydrate and aromatic carbon values were within 5% of the mean values when 4 replicate aliquots were run and scanned four times. That is, if a sample was found to be 30% carbohydrate, the analytical error on 4 aliquots that were each scanned 4 times was 1.5%.

2.3. Peak Finding

A custom *R* script was used to determine the exact location of peaks in pre-defined regions of the FTIR spectra (https://github.com/shodgkins/FTIRbaselines; R Core Team, 2018). Peak regions were located individually for every sample (Figure 2) because variations in peat chemistry slightly shifted the baseline endpoints of the peaks. The minimum absorbance values within the expected region of the peak were used to define the baseline. Several important organic matter functional groups are known to fall between wavenumbers 4,000–650 cm^{-1} and can be categorized by an absorbance peak maximum.

Carbohydrates appear as a peak with absorbance maximum at approximately 1,030 cm^{-1}, aromatics at 1,510 cm^{-1}, and 1,630 cm^{-1} (added together for this study), acids at 1,720 cm^{-1}, and aliphatics at 2,850 cm^{-1} and 2,920 cm^{-1}. After finding the endpoints of the peak, absorbance values were then baseline-corrected by subtracting everything below the baseline, and the exact peak locations and peak heights were then determined by locating the maximum baseline-corrected absorbance value between the baseline endpoints. The *R* script calculates both peak height and area, and additionally normalizes the absorbance values by dividing them by the total integrated area of the spectrum.

To avoid interference from silicates, which produce a large peak that interferes with the carbohydrate peak ($\sim$1,030 cm^{-1}), samples that contained clay (determined based on the presence of a peak at 780 cm^{-1} combined with a large peak at $\sim$1,030 cm^{-1}) were excluded from analysis (Table S1 in Supporting Information S1). For the 780 cm^{-1} peak, area-normalized absorbance greater than 0.00005 was used as the cutoff as the sample likely contained silicate minerals. After the peak heights were baseline-corrected, normalized, and checked for mineral interference, they were then converted into estimated % cellulose + hemicellulose (carbohydrates) and estimated % Klason lignin (aromatics; by weight) using the linear calibration equations generated in Hodgkins et al. (2018). More info about the specifics of these equations can be found in Hodgkins et al. (2018).

$$\text{Carbohydrate calibration: } y = 49204x - 1.7606,$$

where y = estimated % carbohydrates and x = carbohydrate peak height ($\sim$1,030 cm^{-1}). Standard error of y estimate: $\pm 9\%$.

$$\text{Aromatic calibration: } y = 42332x + 7.3476,$$

where x = combined aromatic peak heights ($\sim$1,510 cm^{-1} and $\sim$1,630 cm^{-1}). Standard error of y estimate: $\pm 5\%$.

2.4. Additional Variables

Four additional types of variables were derived to utilize in subsequent analyses. First, the package leaderCluster (Arnold, 2014) implemented in *R* 3.6.3 (R core team, 2020) was used to group peat samples into 1 and 50 km radius spatial clusters. Second, distance from the equator was calculated from latitude values using the geosphere package (Hijmans, 2019). Third, MAT was obtained from the 2.5 min WorldClim (version 2.1) data set (Fick & Hijmans, 2017) using latitude and longitude coordinates for each sample, using the packages sp. (Pebesma & Bivand, 2005) and raster (Hijmans, 2020). Because WorldClim does not include Antarctic climate records, MAT for the Antarctic sites were obtained from long-term records of the closest weather stations (Palmer Station: https://doi.org/10.1016/j.quascirev.2017.10.033; Vernadsky Station: http://www.nerc-bas.ac.uk/icd/gjma/faraday.temps.html). Fourth, we created binary vegetation variables to represent three key components of the peat forming vegetation associated with coring locations, which were coded as 0 when below a given % cover threshold, or 1 when equal or above the threshold. These included total ground cover of *Sphagnum* (threshold = 50% cover), total overstory tree canopy cover (threshold = 50% cover), and total Cyperaceae cover (threshold = 35% cover). In most cases, these variables were obtained from percent cover data collected from 1 m^2 quadrats centered over each core location, although in some cases they were estimated from photos of the core locations. We reasoned that at levels above these thresholds each of the vegetation types would be more likely to be important contributors to the botanical composition of the peat, at least in the upper peat profile, however preliminary analyses with the cover thresholds adjusted up or downwards yielded equivalent interpretations of statistical results. The threshold for Cyperaceae cover was set lower than the other variables because the diffuse nature of their aboveground portions led Cyperaceae species to be less dense than the other variables even at locations where they comprised the vast majority of the plant community and were the known primary peat forming vegetation.

2.5. Statistical Analysis

A suite of linear mixed models were run using *R* 3.6.3 to identify key predictors of carbohydrates, aromatics, and the von Post index. All mixed models were run with the package lmerTest (Kuznetsova et al., 2017), with F-tests obtained using the Kenward-Roger approximation, and the package partR2 (Stoffel et al., 2020) was used to obtain R^2 values. The first set of models used the full data set to examine the relationship of carbohydrates, aromatics and, von Post index with distance from the equator. Each model included distance from the equator as a continuous independent variable, and the categorical fixed effect of depth in the peat profile (10–20, 30–40, and 60–70 cm). Terms for individual peat core, 1 km radius spatial clusters and 50 km radius spatial clusters were also included in these models as a series of explicitly nested random intercept effects to account for potential non-independence of samples collected from the same core or nearby locations. We used distance from the equator instead of latitude in models to allow for direct comparisons among regression coefficients. Second, we fit models for carbohydrates, aromatics and the von Post index using subsets of the data from a single individual depth at a time; these models included distance from the equator and the 1 and 50 km radius spatial clusters

as random effects. Third, to incorporate the potential effect of elevation, we fit models with the full data set containing distance from the equator, depth, elevation, and the random effects of core plus 1 and 50 km radius spatial clusters. Fourth, additional models were run with the full data sets using MAT (instead of distance from the equator and elevation) as a continuous independent variable, the categorical fixed effect of depth in the peat profile (10–20, 30–40, and 60–70 cm), and the random effects of peat core, 1 km radius spatial clusters and 50 km radius spatial clusters. Models with MAT did not include distance from the equator and elevation because these variables strongly covaried with MAT (Distance from the equator: partial $r = -0.93$, $P < 0.0001$; elevation: partial $r = -0.76$, $P < 0.0001$) and their inclusion could lead to issues with collinearity.

To account for the influence of vegetation on estimated carbohydrates, estimated aromatics, and the von Post index, we reran the three models described above that included the full data set. These updated models included a model with distance from the equator, another with distance from the equator and elevation, and a third with MAT, as the independent variables of interest. Each of these models also included the three binary vegetation covariates (i.e., ≥50% *Sphagnum* cover, ≥50% tree canopy cover, ≥35% Cyperaceae cover), as well as the fixed effect of depth in the peat profile and the random effects of peat core, 1 km radius spatial clusters and 50 km radius spatial clusters. Data points from cores that did not have at least one of the three vegetation covariates above the given threshold were excluded from these models because they could have been dominated by a variety of unique non-target peat forming vegetation types (Table S3 in Supporting Information S1).

Lastly, we investigated the relationship of carbohydrates and aromatics with the von Post index. These linear mixed models contained the von Post index as a continuous independent variable, as well as the random effects of peat core, 1 km radius spatial clusters and 50 km radius spatial clusters.

3. Results

There were strong latitudinal and depth gradients in peat organic matter chemistry. The estimated % carbohydrates in peat found through FTIR analysis increased with greater distances from the equator, while the estimated % aromatics decreased (Table 1; Figure 3), therefore confirming our first two hypotheses. Estimate carbohydrate content also strongly decreased with increasing depth in the peat profile, whereas estimated aromatic content increased (Table 1; Figures 3a and 3b). While the larger slopes associated with depth highlighted the sharp average change in carbohydrates and aromatics over the ~0.5 m depth gradient, semi-partial R^2 values indicated that the more gradual chemical changes associated with increasing distance from the equator explained a greater proportion of the variance (particularly for carbohydrates; Table 1). Importantly, models fit individually within each depth showed very similar results as the full model containing samples from all depths (Table S2 in Supporting Information S1). The importance of the latitudinal gradient is highlighted in the FTIR spectra of peat samples from depth 10–20 cm from both the Northern and Southern Hemisphere (Figure 4), where it is clear that the carbohydrate peak height (~1,030 cm^{-1}) was much larger in peat from higher latitudes relative to peat from lower latitudes, and the aromatic peaks (1,510 cm^{-1} and 1,630 cm^{-1}) showed the opposite trend. Carbohydrate content increased with elevation while aromatic content decreased, confirming our third hypothesis. When elevation was added as another variable in the models with distance from the equator and sampling depth, elevation explained less of the variance in carbohydrates and aromatics than did distance from the equator but more than depth (Table 1). However, the slopes for the elevation effect were larger in magnitude than those of distance from the equator because the changes in carbohydrates and aromatics occurred over a much shorter distance (Table 1). Incorporating elevation into the models with distance from the equator and depth increased the total amount of variance explained by the main effects in the models by ~50% (carbohydrates) to 100% (aromatics) of the variance explained in models lacking elevation (Table 1). Adding elevation into the models also strengthened the relationship (semi-partial R^2 and slopes) between distance from the equator and the FTIR variables (Table 1). The patterns seen with the full data set were also evident within individual sampling depths (Table S2 in Supporting Information S1). When the peat samples were divided into groups of sampling locations below and above 1,500 m elevation (Figures 3c and 3d), the carbohydrate and aromatic content of peat from higher elevations more closely matched that of peat from higher latitudes even when the peat was from lower latitudes (Figure 5).

Mean annual temperature was a very strong predictor of carbohydrate and aromatic content. When MAT was used in place of distance from the equator and elevation in models, its explanatory power was similar to distance from the equator and elevation combined (Table 1; Figures 3e and 3f). For example, MAT and depth together

Table 1

Linear Mixed Model Results of Carbohydrate, Aromatic and von Post Responses to Distance From the Equator (Dist), Sampling Depth, Elevation (El), Mean Annual Temperature (MAT)[a,b,c,d,e]

Models	Distance from the equator F (df) P R^2 B	Depth F (df) P R^2 B	Elevation F (df) P R^2 B	Mean annual temperature F (df) P R^2 B	Full model R^2 (marginal/ conditional)
Carbohydrates					
Dist + Depth	24.7 (1, 62.7) **<0.001**, 0.15, 0.0023	195.7 (2, 647.9) **<0.001**, 0.08, −3.9/-7.8			0.22/0.84
Dist + El + Depth	56.6 (1, 53.8) **<0.001**, 0.28, 0.0033	195.5 (2, 648.7) **<0.001**, 0.07, −3.9/-7.8	23.9 (1, 57.5) **<0.001**, 0.14, 4.6		0.36/0.85
MAT + Depth		196.4 (2, 649.2) **<0.001**, 0.07, −3.9/-7.8		66.8 (1, 53.3) **<0.001**, 0.33, −0.76	0.39/0.85
Aromatics					
Dist + Depth	13.2 (1, 65.3) **<0.001**, 0.09, −0.00040	78.3 (2, 670.3) **<0.001**, 0.06, 0.82/1.5			0.14/0.70
Dist + El + Depth	40.5 (1, 59.3) **<0.001**, 0.22, −0.00065	78.2 (2, 671.8) **<0.001**, 0.05, 0.81/1.5	28.5 (1, 63.7) **<0.001**, 0.16, −1.2		0.29/0.70
MAT + Depth		78.5 (2, 671.2) **<0.001**, 0.05, 0.82/1.5		27.0 (1, 60.2) **<0.001**, 0.18, 0.13	0.23/0.71
von Post index					
Dist + Depth	11.8 (1, 63.5) **0.001**, 0.08, −0.00026	213.2 (2, 658.0) **<0.001**, 0.13, 0.93/1.6			0.19/0.74
Dist + El + Depth	13.4 (1, 60.1) **0.001**, 0.10, −0.00032	212.8 (2, 657.9) **<0.001**, 0.12, 0.92/1.6	1.6 (1, 64.5) 0.206, 0.02, −0.23		0.21/0.75
MAT + Depth		212.8 (2, 658.2) **<0.001**, 0.12, 0.92/1.6		13.6 (1, 59.0) **<0.001**, 0.10, 0.07	0.22/0.75

[a]All models also include three nested random effects terms that group samples by core, 1 km radius spatial clusters and 50 km radius spatial clusters. No null hypothesis test was applied to these factors. Bolded numbers indicate *p* values. [b]R^2 for individual main effects (fixed factors and numerical independent variables) represent semi-partial R^2 values. For full model R^2, marginal values are the proportion of variance explained by main effects, while conditional values represent the variance explained by main plus random effects. [c]B = non-standardized regression coefficients. Two coefficients are reported for depth: the slope from the 10–20 to 30–40 cm depth, and then 10–20 to the 60–70 cm depth. Units for distance from the equator (Dist) and elevation (El) are kilometers. Units for mean annual temperature (MAT) are degrees Celsius. [d]For the carbohydrate and aromatic models in this table: Samples = 1,034, Core = 423; Clusters 1 km radius = 116; Clusters 50 km radius = 67. [e]For the von Post model in this table: Samples = 417, Core = 117, Clusters 1 km radius = 114; Clusters 50 km radius, = 65. This is because a few samples did not have von Post scores performed on them.

explained nearly four-tenths of the total variance in carbohydrates, while distance from the equator, elevation, and depth together explained slightly less (Table 1). The large contribution of MAT as a predictor for peat carbohydrate and aromatic content in the models, combined with its strong correlation with distance from the equator and elevation, suggest that the influence of distance from the equator and elevation on the relative abundances of carbohydrates and aromatics is primarily due to MAT.

In models that included the dominant peat forming surface vegetation as covariates, much more variation in carbohydrates, aromatics, and von Post was attributable to distance from the equator, elevation, MAT and/or depth than could be attributed to any of the vegetation covariates (Table S3 in Supporting Information S1). However, carbohydrates did show a distinct increase when *Sphagnum* was ≥50%, and a distinct decline when overstory canopy cover was ≥50% (Table S3 in Supporting Information S1), while the Cyperaceae covariate was not significant. In contrast, aromatics, and von Post did not show clear relationships with any of the vegetation covariates (Table S3 in Supporting Information S1). These results suggest that the relationships of carbohydrates, aromatics, and von Post with distance from the equator, elevation, and MAT are in part decoupled from shifts in surface peat forming vegetation.

Values of the von Post index shifted with distance from the equator, elevation, MAT, and depth (Table 1), and also covaried with the FTIR variables. The main effects in the models containing distance from the equator, elevation, depth and/or MAT all explained ∼ one-fifth of the variance in the von Post index (Table 1), with the von Post
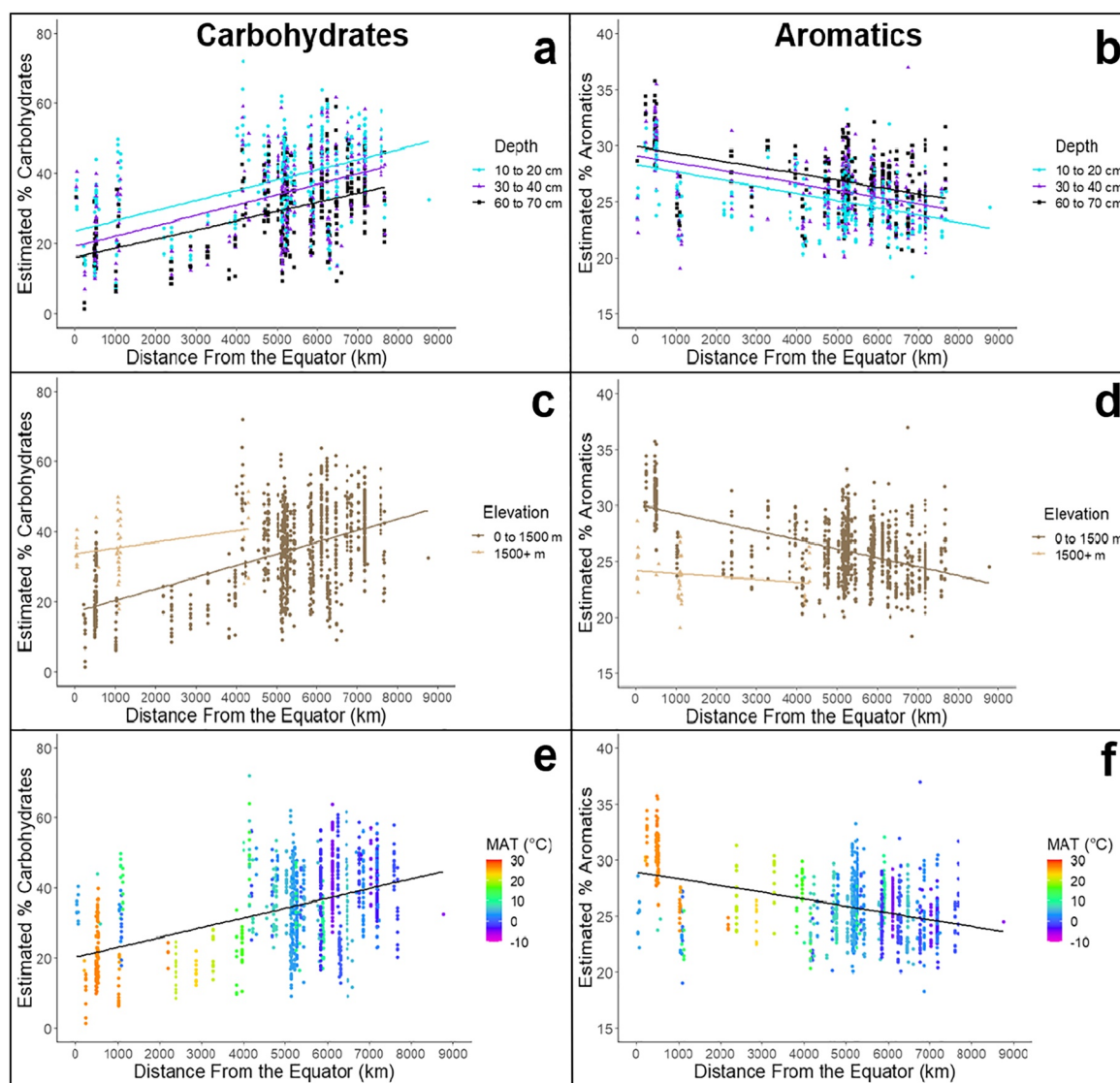
Figure 3. Estimated % carbohydrates (±9%) and aromatics (±5%) for all 1034 peat samples with corresponding distance from the equator (km north or south). Peat samples are divided by depth categories 10–20 cm, 30–40 cm, and 60–70 cm for (a) carbohydrate content and (b) aromatic content, by elevation categories 0–1,500 m and 1500 + m for (c) carbohydrate content and (d) aromatic content, and by mean annual temperature (°C) for (e) carbohydrate content and (f) aromatic content. Statistical analysis presented in Table 1 and Table S2 in Supporting Information S1.

index decreasing with greater distance from the equator and elevation, and increasing with greater depth in the peat profile and MAT (Table 1, Table S2 in Supporting Information S1). The von Post index exhibited significant relationships with both FTIR variables (Figure 6), although von Post index was a stronger predictor of carbohydrates ($F_{1, 901.5} = 382.1$, $P < 0.001$, $B = -2.75$, marginal $R^2 = 0.21$) than aromatics ($F_{1, 1001.1} = 66.3$, $P < 0.001$, $B = 0.35$, marginal $R^2 = 0.07$). Importantly, higher von Post index values signify more decomposed peat, which is demonstrated by the strong increase in von Post index with depth (see also Figure S1 in Supporting Information S1); this relationship of von Post index with carbohydrates and aromatics confirms that these FTIR-derived chemical variables are also indicators of the degree of decomposition.

Comparisons of marginal to conditional full model R^2 values indicate that peat chemistry exhibited strong spatial effects (Table 1; Tables S2 and S3 in Supporting Information S1). In all analyses, the total proportion of variance explained by random effects (individual peat core, 1 km radius spatial clusters and 50 km radius spatial clusters considered together) was typically greater than that explained by fixed effects, often by far more than double. This indicates that carbohydrates, aromatics, and von Post values are on average more similar for samples collected near each other than samples from distant locations.
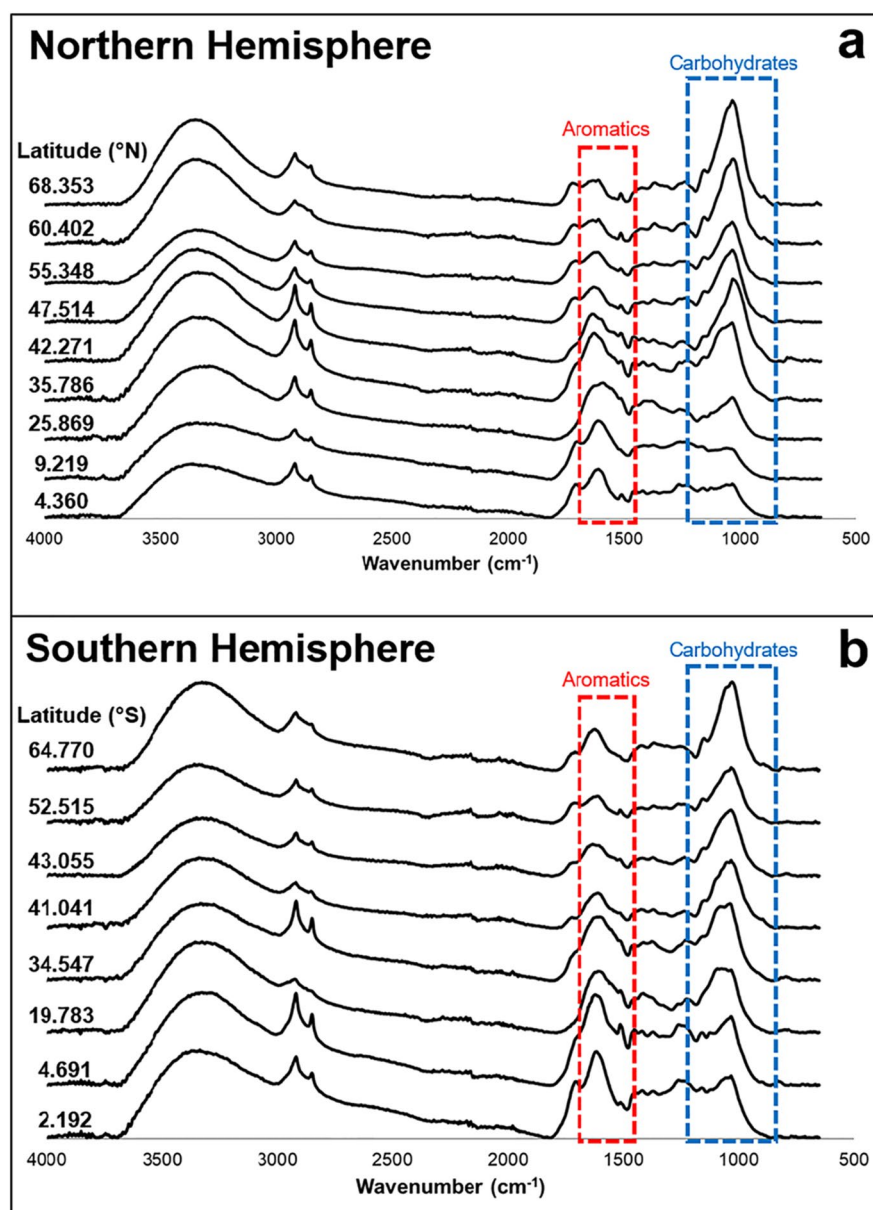
Figure 4. Fourier Transform Infrared Spectroscopy spectra of 10–20 cm depth peat samples. (a) Locations in the Northern Hemisphere from low to high latitudes: Mendaram, Brunei (4.360°N); Mekong delta, Vietnam (9.219°N); Everglades, Florida, USA (25.869°N); Alligator River, North Carolina, USA (35.786°N); Dong Tu, NE China (42.271°N); Marcell, Minnesota, USA (47.514°N); Kuujjuarapik, Quebec, Canada (55.348°N); Copper River Delta, Alaska, USA (60.402°N); Stordalen Mire, Sweden (68.353°N). (b) Locations in the Southern Hemisphere from low to high latitudes: Sabangau Forest, Indonesia (2.192°S); Peruvian Amazon, Peru (4.691°S); Saunders Spring, Mandora Marsh (Walyarta) Great Sandy Desert, NW Australia (19.783°S); Poorginup Swamp, SW Australia (34.547°S); Puerto Blest, Argentina (41.041°S); South Island, New Zealand (43.055°S); Seno Skyring Patagonia, Chile (52.515°S); and Litchfield Island, Antarctic Peninsula (64.770°S). Carbohydrate peak is at 1,030 cm^{-1}, and aromatic peaks are at 1,510 cm^{-1} and 1,630 cm^{-1}.

4. Discussion

We found that the estimated relative abundances of carbohydrates increased from the equator toward the poles, and the estimated relative abundances of aromatics decreased, supporting hypotheses 1 and 2. Higher elevation peat from lower latitude peatlands also had greater carbohydrate content and lower aromatic content than lower elevation peat from similar latitudes, supporting hypothesis 3. These differences in peat organic matter carbon quality may provide a sensitive proxy for decomposition potential, with higher relative abundances of
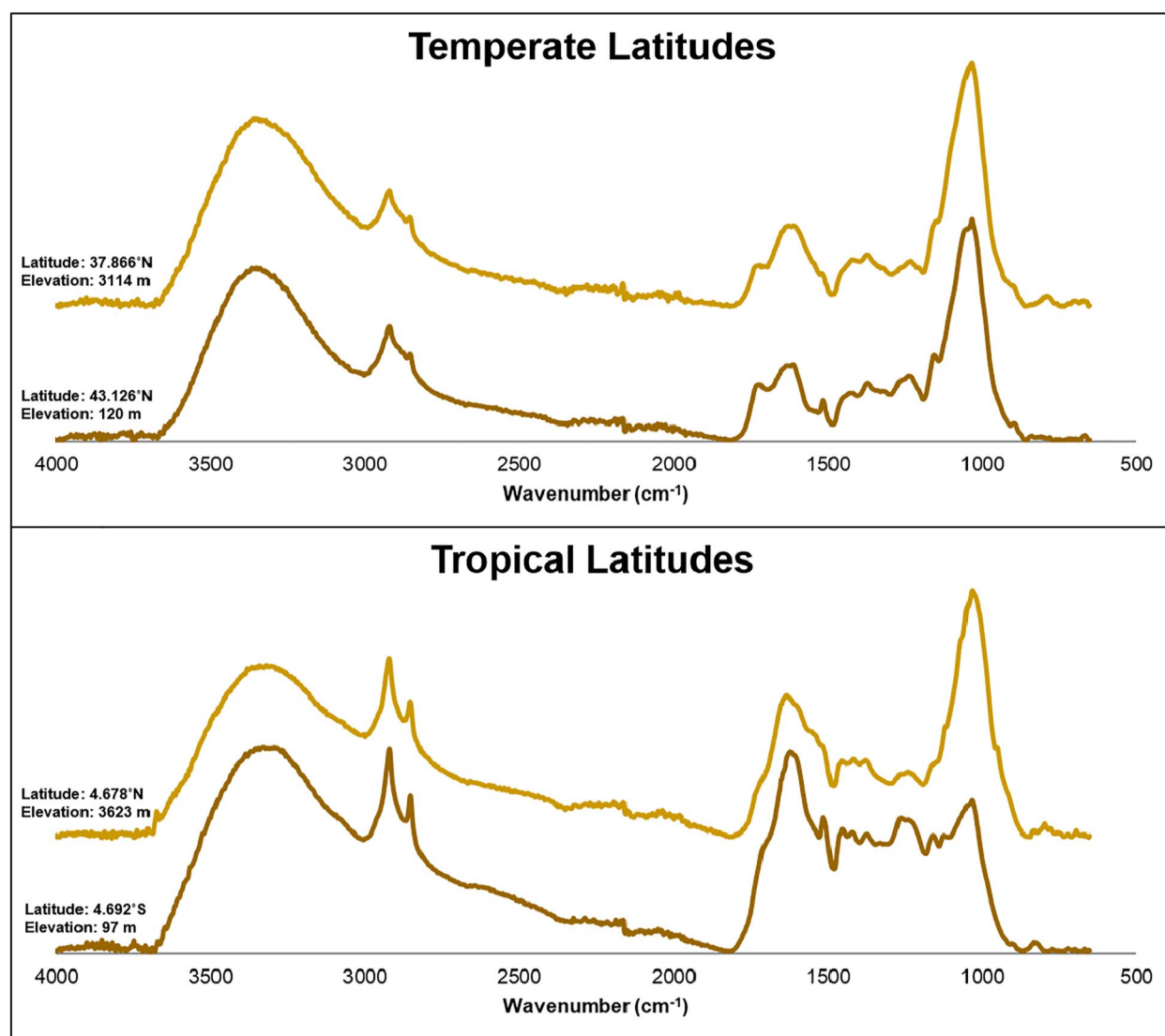
Figure 5. Fourier Transform Infrared Spectroscopy spectra of 10–20 cm depth peat samples from similar latitudes but different elevations. Temperate latitude samples are from Chattanooga Fen, Tennessee (37.866°N, 3,114 m elevation) and Sallie's Fen, New Hampshire (43.126°N, 120 m elevation). Tropical latitude samples are from Chingaza National Park, Colombia (4.678°N, 3,623 m elevation) and the Peruvian Amazon, Peru (4.692°S, 97 m elevation). Carbohydrate peak is at 1,030 cm⁻¹ and aromatic peaks are at 1,510 cm⁻¹ and 1,630 cm⁻¹.

carbohydrates indicating bio-lability and higher relative abundances of aromatics indicating more recalcitrance (Baldock et al., 1997; Grover & Baldock, 2010, 2012; Treat et al., 2014). Organic matter with more carbohydrates would also have a higher nominal oxidation state of carbon (Keiluweit et al., 2016; LaRowe & Van Cappellen, 2011) offering a theoretical basis for greater reactivity of carbohydrates under anaerobic conditions. Peat with lower carbohydrate content and higher aromatic content was generally classified as more highly decomposed on the von Post index of humification. The less decomposed peat from higher latitudes showed greater potential for mineralization owing to the larger relative abundance of carbohydrates to aromatics, a trait shared by peat originating from higher elevations.

Peat stability and decomposition rates are influenced by a combination of many factors, including water table depth, electron acceptor availability (Blodau, 2011; Heimann et al., 2009), and microbial community (Bragazza et al., 2016; Hodgkins et al., 2015; LaRowe & Van Cappellen, 2011; Norby et al., 2019), but also by the source vegetation and associated organic matter quality (Wang et al., 2021; Zeh et al., 2020). After accounting for dominant peat-forming surface vegetation in our analyses, latitude and elevation had by far the strongest relationships
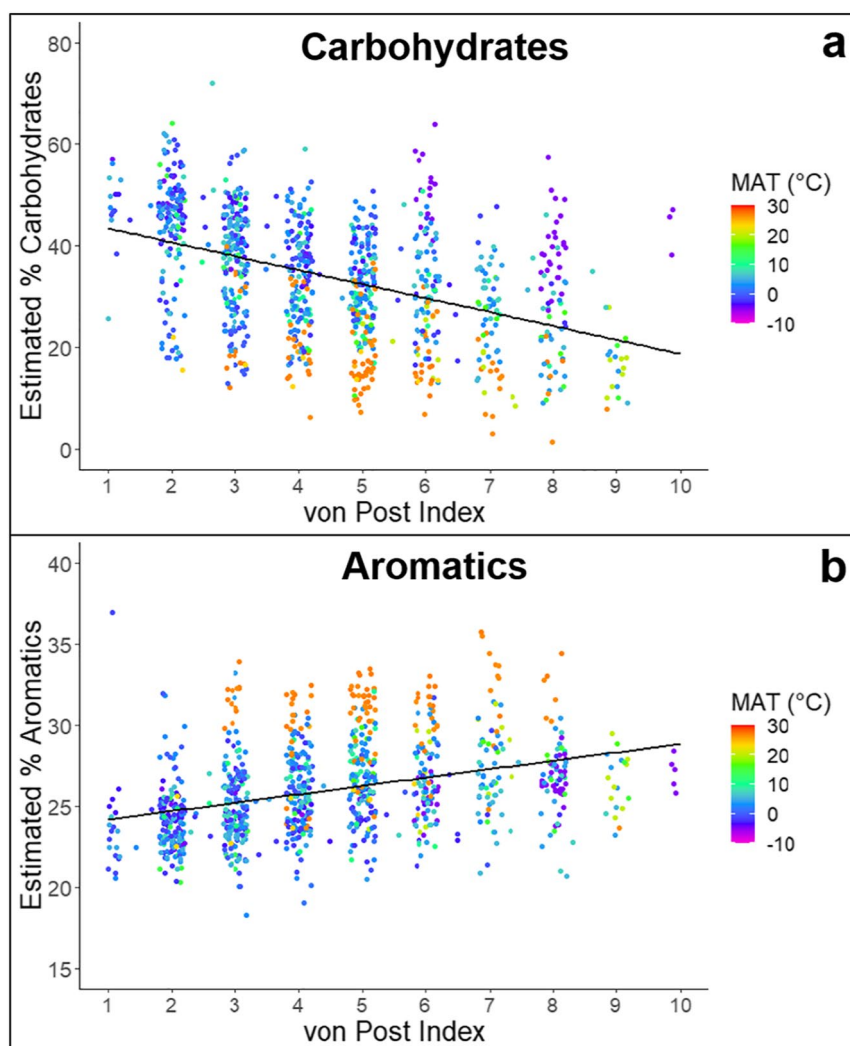
Figure 6. (a) Estimated % carbohydrates (±9%) and (b) aromatics (±5%) with corresponding von Post index values for all three (10–20, 30–40, and 60–70 cm) depths. The von Post index is a scale of humification, with 1 being the least decomposed and 10 being the most decomposed. Color scale is mean annual temperature (°C). Individual depth segments are plotted in Figure S1 in Supporting Information S1.

with carbohydrates and aromatics (Table S3 in Supporting Information S1). This is consistent with our hypothesis that the observed carbohydrate and aromatic patterns arose for the most part as a response to climate (Artz et al., 2008), and is not strongly driven by botanical composition at the global scale. However, we do recognize that there are limitations to our approach. Most importantly, surface vegetation does not necessarily reflect the botanical origin of the peat, especially for deeper depths in the profile that may have formed when the peatland was dominated by different plant species. An important next-step for the scientific community would be to utilize macrofossils to compare FTIR derived carbohydrate and aromatic values to the specific vegetation composition of the peat in each sample, but that is beyond the scope of the current study. Although not part of our explicit hypotheses, the analyses also show that a large portion of the variation in peat carbohydrates and aromatics can be attributed to random effects associated with core and spatial clusters. This strong spatial effect is to be expected because samples from nearby locations have very similar ecological characteristics, including climates, hydrology, and botany, that should similarly influence peat stability and decomposition. An important aim of this study was to decouple the global pattern from local spatial effects in order to pull out the global-scale gradient, and the fact that we found clear patterns in spite of the expected strong spatial effects adds to the robustness of the findings.

There is likely both a direct climatic effect, and an indirect effect of climate on peat organic matter chemistry as mediated by changes in the dominant peatland types and their associated plant functional groups. The combination of the inhibitory effects of aromatic compounds from plants such as *Sphagnum* and shrubs (Wang et al., 2015), and the higher recalcitrance of lignin-like compounds, make aromatics one of the most influential factors in peat stability. Aromatic compounds from *Sphagnum* and vegetation with similar chemical composition found at higher latitudes are significant for peat stability in northern peatlands because the plant tissue decomposition rates are much slower than that of other source vegetation (Könönen et al., 2016; Moore et al., 2007; Scanlon & Moore, 2000), but the higher initial aromatic content of source vegetation at lower latitudes shown in Hodgkins et al. (2018) could increase the recalcitrance of the soil organic matter even without inhibitory compounds from *Sphagnum* (Könönen et al., 2015, 2018). Our FTIR-derived aromatics have been calibrated against "Klason Lignins" (Hodgkins et al., 2018), a quite diverse operationally defined pool that includes not just structural lignin, but also other aromatics such as tannins, and other non-lignin-derived polyphenols (De la Cruz et al., 2016).

Our finding of lower carbohydrates in peat near the equator is important because O-alkyl-C compounds have a higher carbon oxidation state than aromatic compounds, causing faster rates of decomposition under anaerobic conditions in peat with larger carbohydrate abundances (LaRowe & Van Cappellen, 2011). Higher aromatic abundances accompanied by lower carbohydrate abundances produce a reduced oxidation state, suggesting that peatlands exhibiting these chemical qualities will decompose at slower rates even with warmer temperatures (Hodgkins et al., 2018; Worrall et al., 2017). In contrast, decomposition rates are more rapid for surface peat than deep peat due to a higher concentration of bio-labile organic matter (Charman et al., 2013; Normand, 2017). Hodgkins et al. (2018) also suggested that warmer temperatures at lower latitudes could be causing surface peat to transition to a more recalcitrant state faster than at higher latitudes.

It is worth noting that based on von Post, the variation from almost undecomposed to completely decomposed peat (1–9) resulted in a 50% decrease in carbohydrates (42%–22%), whereas it resulted in only a 12% increase (24%–27%) in aromatics (Figure 6). Hodgkins et al. (2018) observed a relatively greater decrease in carbohydrates with depth while the increase in aromatics was less. These observations suggest that during peat decomposition, carbohydrates are lost at a faster rate than overall C, whereas aromatics appear to degrade at a slower rate than overall C. Our finding of increased humification with depth, as reflected in von Post index values as well as carbohydrate and aromatic content, is consistent with broad understanding of peat diagenesis. For example, based on these values, Scanlon and Moore (2000) showed that the level of humification generally increased with depth, and Charman et al. (2013) found that decomposition rates were slower at depth in anoxic zones where recalcitrant organic matter accumulates. Colder temperatures and anaerobic conditions are essential to peat preservation, but increased recalcitrance of soil organic matter at depth and at lower latitudes suggests that chemical quality might have a greater impact on preservation than previously thought. Higher abundance of O-alkyl carbon increases rates of C mineralization in peat soils (Grover & Baldock, 2010, 2012; Normand, 2017), so whatever the cause, there is evidence that high latitude and high elevation soils are poised for higher reaction rates than equatorial peats.

O-Alkyl-C compounds have been preserved in higher latitude peatlands due to colder temperatures, but with warmer temperatures (as predicted particularly for these regions), carbohydrates would likely be the first constituent of peat to be lost through decomposition processes while the aromatics would be left behind. Carbohydrate abundances are low in deeper peat (Hodgkins et al., 2018; Tfaily et al., 2014), so it is likely that mainly surface peat will be affected while deeper peat would not decompose as much (Wilson et al., 2016; Worrall et al., 2018). Such effects were observed in long-term drained peatlands–once more available compounds (as measured by FTIR) were depleted following a few decades of drainage, the decomposition slowed due to residual high content of recalcitrant compounds (Urbanová et al., 2018). Of course, it may be argued that recalcitrant compounds are not residuals, but rather are the products of decomposition itself (Prescott, 2010). We think of humification (Lehmann & Kleber, 2015) as the loss of oxygenated compounds from the peat, which is coincident with the increase of alkyl and aromatic residuals or products.

If our conceptual model derived from this gradient analysis is correct, namely that high carbohydrate containing peat is more labile in the face of rising temperatures, then in high-latitude peatlands subject to warming we speculate that the following may occur: initial increases in decomposition of more labile carbohydrate-rich surface peat, with preferential removals of carbohydrates, leading to increases in peat aromatic:carbohydrate ratios, which will in turn slow decomposition and constrain the resultant positive climate feedback of greenhouse gas

emissions. Models that can capture this dynamic are more likely to accurately reflect the response of peatlands to climate change. However, further studies are necessary in order to better relate the expected chemical changes of stored peat to associated rates of greenhouse gas release in response to climate warming. It has been suggested that as the Earth transitioned from glacial times to an interglacial state during the Holocene, the soil organic reservoir transitioned from permafrost mineral soils to peat (Lindgren et al., 2018). It is our hope that our study has shed some light on what may occur as we now transition from the Holocene to the Anthropocene. We realize that a myriad of other factors in addition to temperature will affect peatland carbon storage including water table changes (Roulet et al., 1993), fires (Flanagan et al., 2020; Turetsky et al., 2015), and vegetation changes such as increasing shrubification and *Sphagnum* loss (Malhotra et al., 2020; McPartland et al., 2020; Norby et al., 2019). In addition, peat may be buried under mineral soils with changing climate and thus preserved for periods of time on the order of hundreds of thousands of years (Treat et al., 2019). Our study indicates that loss of carbohydrates or o-alkyl functionality plays a central role in long term carbon storage.

Data Availability Statement

The data used in this analysis are publicly available at the US Forest Service Research Data Archive (at the following DOI: https://doi.org/10.2737/RDS-2021-0045).

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