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Low-severity fire as a mechanism of organic matter protection in global peatlands: Thermal alteration slows decomposition

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Abstract

Worldwide, regularly recurring wildfires shape many peatland ecosystems to the extent that fire-adapted species often dominate plant communities, suggesting that wildfire is an integral part of peatland ecology rather than an anomaly. The most destructive blazes are smoldering fires that are usually initiated in periods of drought and can combust entire peatland carbon stores. However, peatland wildfires more typically occur as low-severity surface burns that arise in the dormant season when vegetation is desiccated, and soil moisture is high. In such low-severity fires, surface layers experience flash heating, but there is little loss of underlying peat to combustion. This study examines the potential importance of such processes in several peatlands that span a gradient from hemiboreal to tropical ecozones and experience a wide range of fire return intervals. We show that low-severity fires can increase the pool of stable soil carbon by thermally altering the chemistry of soil organic matter (SOM), thereby reducing rates of microbial respiration. Using X-ray photoelectron spectroscopy and Fourier transform infrared, we demonstrate that low-severity fires significantly increase the degree of carbon condensation and aromatization of SOM functional groups, particularly on the surface of peat aggregates. Laboratory incubations show lower CO_2 emissions from peat subjected to low-severity fire and predict lower cumulative CO_2 emissions from burned peat after 1–3 years. Also, low-severity fires reduce the temperature sensitivity (Q_{10}) of peat, indicating that these fires can inhibit microbial access to SOM. The increased stability of thermally altered SOM may allow a greater proportion of organic matter to survive vertical migration into saturated and anaerobic zones of peatlands where environmental conditions physiochemically protect carbon stores from decomposition for thousands of years. Thus, across latitudes, low-severity fire is an overlooked factor influencing carbon cycling in peatlands, which is relevant to global carbon budgets as climate change alters fire regimes worldwide.

KEYWORDS

fire, low-severity, peatlands, physical protection, Q_{10}, respiration, soil organic matter, temperature sensitivity

1 | INTRODUCTION

Peatlands contain one of the Earth's largest terrestrial carbon stores holding approximately 560 gigatonnes (GT) of carbon, which is comparable to stores of 560 GT in terrestrial vegetation, 597 GT in the atmosphere, and 900 GT in the surface ocean layer (Stocker et al., 2013; Yu, 2012). The accretion of carbon in peatlands over the past 8,000–10,000 years has occurred due to a positive net ecosystem balance between carbon fixation by plants, and oxidative losses of carbon, most notably to respiration and fire. Recent literature has demonstrated that peat fires account for up to 15% of annual global greenhouse gas emissions (Rein, 2015). During 1997, megafires in Indonesia caused carbon emissions equivalent to between 13% and 40% of the global annual carbon emissions from fossil fuel consumption (Page et al., 2002). Such remarkable statistics highlight the importance of peatland fire to the global carbon budget. However, in typical years, these devastating peat-consuming fires are relatively rare, with the majority of blazes consuming aboveground plant biomass while leaving the long-term carbon stores in the underlying moist peat layer largely intact (Boby, Schuur, Mack, Verbyla, & Johnstone, 2010; Conard et al., 2002; Kuhry, 1994; Magnan, Lavoie, & Payette, 2012; Zoltai, Morrissey, Livingston, & Groot, 1998). In the recent past, lower-severity burns were characteristic of many Canadian wet boreal forests (Walker et al., 2019). Currently, boreal peatlands are experiencing increasingly severe fire regimes as temperature, and precipitation patterns change (Page & Hooijer, 2016; Rogers, Balch, Goetz, Lehmann, & Turetsky, 2020; Turetsky et al., 2014). Nevertheless, wildfires in Eurasian boreal forests are typically less severe than their North American counterparts due to less flammable aboveground fuels and a lower likelihood of summertime fires (Chen & Loboda, 2018; Ivanova, Conard, Kukavskaya, & McRae, 2011; Krylov et al., 2014; Rogers, Soja, Goulden, & Randerson, 2015). Our analyses of satellite burn-severity data show that low-severity fires dominate wetlands in the United States (see Figures S1 and S2).

Catastrophic belowground fires are still arguably atypical in undrained peatlands. They are most likely to occur during severe drought and/or in artificially drained areas where drier surface layers make peat vulnerable to the propagation of smoldering fires (Benscoter et al., 2011; Gorham, 1991; Joosten, 2010; Turetsky et al., 2014; Wilkinson, Moore, Flannigan, Wotton, & Waddington, 2018). If high-severity, peat-consuming fires were typical of peatlands with recurrent fire regimes, one might expect uniformly negative relationships between fire frequency and carbon accretion rates (Kuhry, 1994). However, several studies have shown nonexistent or even weak positive relationships between fire frequency and long-term carbon accumulation rates across ombrotrophic peatlands in northeastern North America (Charman et al., 2015; Magnan et al., 2012; van Bellen, Garneau, Ali, & Bergeron, 2012). Similarly, undrained Indonesian peatlands had unexpectedly frequent fires with a mean return interval of 133 years, yet large fires were rare, and typical surface fires had no negative influence on long-term carbon accumulation rates (Biagioni et al., 2015; Hapsari et al., 2017). The more typical long-term pattern of peatland fires shows blaze initiation before late-spring when the soil moisture content is high and dormant aboveground vegetation is desiccated (de Groot et al., 2013; Frost, 1998; Turetsky, Amiro, Bosch, & Bhatti, 2004). Thus, peatland fires often heat, but do not ignite, underlying saturated peat (Christensen, 1981; Kasischke, Christensen, & Stocks, 1995; Turetsky et al., 2004; Zoltai et al., 1998).

The severity of peat fires can vary widely across boreal landscapes. Hotspots of peat combustion can account for a large proportion of soil carbon emissions during fires, occurring in hydrologically disconnected areas such as the margins of peatlands, while the interiors of expansive peatland-dominated plains typically experience less severe fires (Hokanson et al., 2016; Lukenbach, Devito, Kettridge, Petrone, & Waddington, 2015; Wilkinson, Moore, & Waddington, 2019). While there is often substantial combustion of aboveground biomass in low-severity fires, only a minor portion of surficial peat layers are consumed (Soja et al., 2004; Zoltai et al., 1998). Instead, surface soil organic matter (SOM) is subject to rapid heating that can extend a few centimeters below the soil surface. This thermal alteration can physiochemically alter SOM to create a more stable and slower-cycling pool of soil carbon (Conard et al., 2002; DeBano, Neary, & Ffolliott, 1998; Gonzalez-Perez, Gonzalez-Vila, Almendros, & Knicker, 2004; Knicker, 2007; Randerson, Chen, van der Werf, Rogers, & Morton, 2012; Turetsky et al., 2004; Wade, Ewel, & Hofstetter, 1980; Zoltai et al., 1998).

Relatively, few studies have examined modifications of the chemistry of organic carbon in the soils underlying these low-severity surface fires, especially where no smoldering combustion of peat occurs. Existing studies, many examining a range of fire severity categories, identify several possible mechanisms of thermal alteration that could modify SOM chemistry in low-severity fires. These include hydrolysis, dehydration, decarboxylation, polymerization, aromatization, and Maillard reactions. These mechanisms are also responsible for the processes of coalification and hydrochar formation (Funke & Ziegler, 2010; Gonzalez-Perez et al., 2004; Knicker, 2011; Santín & Doerr, 2016). Additionally, if soil temperatures remain below 300°C, the volatilization and deposition of hydrophobic materials as films can occur on soil aggregate surfaces, this can produce both increased soil water repellency and aggregate stability (DeBano, 2000; DeBano, Mann, & Hamilton, 1970; Santín & Doerr, 2016). Lower temperature fires can selectively remove labile carbon compounds and concentrate stable carbon fractions (Alexis et al., 2010; Gonzalez-Perez et al., 2004; Hodgkins et al., 2018; Leifeld et al., 2018).

Fire can also alter the soil microbial community, yielding reductions in microbial biomass, and substantially changing community composition (Dooley & Treseder, 2012; Egidi et al., 2016; Gonzalez-Perez et al., 2004; Knicker, 2007; Pietikäinen, Hiukka, & Fritze, 2000), often through an increased dominance of bacteria and *Ascomycota* fungi (Holden, Rogers, Treseder, & Randerson, 2016), and by affecting microbial enzyme activity (Holden, Gutierrez, & Treseder, 2013; Ludwig et al., 2018). Indeed, the steam-heat associated with rapidly spreading aboveground fires atop moist soil is particularly effective at killing soil microbes, with lethal temperatures

for a given organism often being half of those observed in dry soil (Choromanska & DeLuca, 2002; Klopatek & Klopatek, 1987; Wells et al., 1979). Such sub-combustive heating may influence the kinetics of microbial decomposition of SOM. The thermal alteration of SOM by fire changes the temperature sensitivity (Q_{10}) of microbial respiration in peatlands, which has important implications for the response of peatland carbon cycles to climate change (Chen et al., 2018; Davidson & Janssens, 2006; Holden et al., 2016; O'Donnell et al., 2009). Newer literature has proposed that the decomposability of SOM can be limited by physiochemical barriers, such as adsorption to soil minerals and occlusion within aggregates, making SOM inaccessible to enzymes and microbes. This physical protection results in an 'apparent' temperature sensitivity that can differ substantially from predictions based solely on the chemical quality of SOM (Conant et al., 2011; Davidson & Janssens, 2006; Dungait, Hopkins, Gregory, & Whitmore, 2012; Moinet et al., 2018).

The deposition of hydrophobic substances on soil surfaces during a fire is thought to potentially protect SOM from microbial access and increase carbon sequestration in soil (Davidson, Janssens, & Luo, 2006; DeBano, 2000; DeBano et al., 1970; Piccolo, Spaccini, Drosos, Vinci, & Cozzolino, 2018; Spaccini, Piccolo, Conte, Haberhauer, & Gerzabek, 2002). Low-severity fire has the potential to affect decomposition kinetics by altering carbon quality and by protecting/occluding organic matter within surface films of hydrophobic and/or polyaromatic compounds (Davidson & Janssens, 2006; Davidson et al., 2006; DeBano et al., 1970; Gonzalez-Perez et al., 2004; Kang, Li, Fan, & Chang, 2012; Knicker, 2007; Santín & Doerr, 2016; Spaccini et al., 2002). However, the physical protection of SOM through these mechanisms has been largely ignored in peat soils because the process is thought to occur at temperatures below 300°C, lower than those seen in high-severity fires.

The effects of wildfire on carbon cycling have been widely studied in both boreal and tropical peatlands (Ingram, Moore, Wilkinson, Petrone, & Waddington, 2019; Page & Hooijer, 2016; Turetsky et al., 2014; Wieder et al., 2009; Wilkinson, Moore, et al., 2019). However, there is a tendency of fire studies to target severe-fire areas where peat is known to have burned (Turetsky et al., 2004). Thus, sparse literature exists on the thermal alteration of moist SOM during fires having relatively low-temperature regimes. In this study, we examine mechanisms whereby low-severity fire can affect long-term carbon budgets in peatlands. Our objectives are to (a) characterize the effects of low-severity fires on the chemical characteristics of SOM, (b) quantify whether the resulting alterations of peat chemistry affects heterotrophic respiration, (c) evaluate whether changes in the apparent temperature sensitivity of peat subjected to such fires can better be explained by changes in carbon quality or physical protection, and (d) assess how low-severity fire alters the long-term stability of peat. We examine these processes in multiple peatlands spanning a north to south latitudinal gradient across several ecozones and a range of fire regimes. We hypothesize that, despite the relatively low belowground temperatures associated with low-severity fire, substantial thermal alteration of peat will increase the pool of stable soil carbon by altering the chemical and physical properties of SOM. The resulting reductions in the long-term rates of microbial respiration and alterations of the temperature sensitivity of decomposition have substantial implications for long-term carbon sequestration and storage in peatlands across the globe.

2 | METHODS

2.1 | Study sites

We identified four peatlands located along a latitudinal gradient from hemiboreal to tropical peatlands located in North and South America in order to study the effects of low-intensity fire on a range of peatland types. Our study sites are located in peatlands from MN (Marcell Experimental Forest, 47.5°N), to NC (Pocosin Lakes National Wildlife Refuge, 35.7°N), to FL (Loxahatchee National Wildlife Refuge, 26.5°N) to the vast peat deposits of the Amazon Basin in Peru (Los Amigos Biological Station, 12.5°S). The four study peatlands differ significantly in the circumstances of their formation and dominant vegetation. The SPRUCE bog site (Marcell Experimental Forest, USFS) in Minnesota (MN) is acidic (pH 4.0), dominated by *Sphagnum* mosses, and contains 3–5 m of peat. Pocosins comprise the largest extent of acidic evergreen shrub bog on the Atlantic coastal plain with over 2 million ha in NC alone (Richardson, 2012). The Everglades area, known as the Loxahatchee, is a low pH bog system, which is a historically oligotrophic wetland dominated by *Cladium* and Evergreen shrubs (Richardson, 2008). The PERU site is an acid peatland located on a terrace adjacent to the Madre de Dios River (Winton, Flanagan, & Richardson, 2017) and is dominated by Maurita Palm (*Mauritia flexuosa*; Figure 1; Table 1).

2.2 | Soil sampling

Soils were sampled using a 7.5 cm box corer that was used to collect six replicated cores. We selected the 0–5 cm layer for our incubation studies based on field measurements of maximum depth of heating recorded during our monitoring of prescribed burns occurring over moist peat (see further discussion below). Our samples were minimally processed to avoid the disturbance of soil structure, by removing large fragments (>2 mm) and live roots, and then sifting through a No. 4 sieve. We divided processed SOM into unburned and burned subsamples for use in simulated fires. Further subsamples of burned and unburned materials were collected for chemical analysis with a moist subsample stored at 4°C and a subsample dried at 60°C.

To characterize the temperature and duration of low-severity fire in peatlands, we monitored soil temperatures at the surface of litter during a prescribed fire in the Pocosins Lake National Wildlife Refuge during March 2015; the initial average soil moisture content was 370% by mass. The prescribed fire displayed a rapid consumption of aboveground biomass by fire, and soil surface temperatures reached a peak temperature of 450°C within 3 min and then dropping below 60°C within 10 min after the fire front passed.

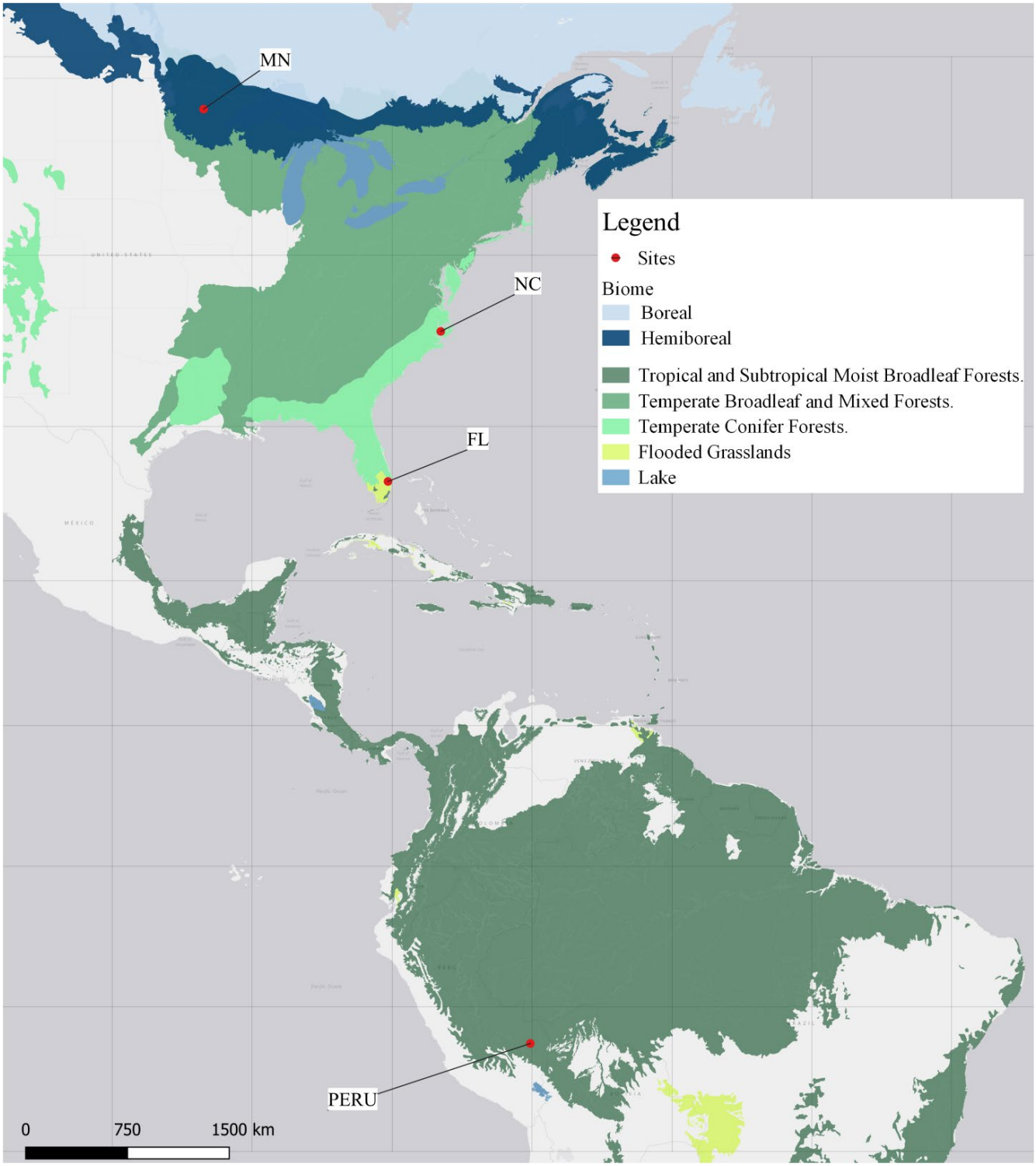

FIGURE 1 Locations of study sites across gradients of latitude and biomes. (MN) Marcell Experimental Forest, Minnesota, USA; (NC) Pocosin NWR (North Carolina, USA); (FL) Loxahatchee, NWR (Florida, USA); (PERU) Los Amigos Biological Station (Madre de Dios, Peru). (Brandt, 2009; Olson & Dinerstein, 2002)

We replicated these temperature conditions during simulated burns using moist soils (350% moisture content by mass) in a muffle furnace initially heated to 750°C while tracking the surface and interior temperatures of our samples using insulated k-type thermocouples. Samples were heated until they reached target temperatures of 450 and 101°C at the surface and center, respectively, which occurred in 6–8 min. After the burned material cooled to room temperature, it was reinoculated with a slurry of unburned peat (1:20 ratio) to prevent sterilization of the burned material. Changes in soil moisture during simulated fires were tracked by weighing samples before and

TABLE 1 Geographic and ecological features of peatland field sites located in Minnesota (MN), North Carolina (NC), Florida (FL), and Peru (PERU)

Site	Zone	Latitude	Dominant cover type	Soil order	Fire return interval (years)
MN	Hemiboreal	47.51	Mosses (*Sphagnum* sp.)	Histosol	80–200[a]
NC	Temperate	35.69	Ericaceous shrubs (*Lyonia*, *Ilex* sp.)	Histosol	4–25[b]
FL	Sub-Tropical	26.52	Sedge (*Cladium jamaicense*)	Histosol	7–25[b]
PERU	Tropical	−12.56	Palm (*Mauritia flexiosa*)	Histosol	850[c]

[a]Turetsky and St. Louis (2006).
[b]Frost (1995).
[c]Thonicke, Venevsky, Sitch, and Cramer (2001).

after simulated burns, and burned soils were rehydrated to match the in-situ moisture of unburned soils using Millipore deionized water. Losses of SOM were tracked by calculating and comparing the dry mass of the soil before and after simulated fires. Soils were placed in 500 ml jars which were then located in dark, temperature, and humidity-controlled chambers to prevent drying—at temperatures of 5, 15, and 25°C—with each jar containing approximate 5 g of soil as a dry mass equivalent. Each treatment (4 sites × 2 fire × 3 temperature treatment) had four replicates for a total of 96 jars. The jars were covered with airtight lids fitted with rubber septa to allow headspace sampling. Before sampling, jars were flushed with analytical air and overfilled by 15 ml of air to create positive pressure inside the incubation jar. Samples of headspace were withdrawn and at times 0, 60, 120, and 180 min and transferred into scintillation vials that were flushed with ultra-high-purity N2 (3×) before evacuation and analyzed the same day for CO_2 concentration using a Varian 450-GC gas chromatograph. Microbial respiration was expressed as μg CO_2-C g^{-1} dry soil day^{-1}. An exponential equation was used to measure the relationship between incubation temperature and microbial respiration, where MR_T indicates microbial respiration at temperature *T* and *a* and *b* are model parameters.

$$MR_T = a \times \exp^{b \times T}. \quad (1)$$

Parameter *b* was then used to calculate temperature sensitivity (Q_{10}) using the following equation (Meyer, Welp, & Amelung, 2018):

$$Q_{10} = \exp^{10 \times b}. \quad (2)$$

2.3 | Fourier transform infrared spectroscopy

We used diamond-attenuated total reflectance Fourier transform infrared spectroscopy (FTIR) for molecular analysis of the functional groups present in a finely ground and homogenized powder. Thus, FTIR characterized the dominant functional groups distributed throughout the samples rather than characterizing the surface of aggregates (see Section 2.4 below). Analysis of samples was performed using a Nicolet 6700 FT-IR spectrometer fitted with a KBr beam splitter and diamond crystal Diamond with ZnSe lens. We loaded samples in direct contact with the crystal surface and then applied downward pressure to create good contact between the ATR crystal and the sample. Spectra were acquired by averaging 64 scans over the range of 4,000–550 cm^{-1}. We corrected the spectra for the baseline and ATR shifts with the instrument software (OMNIC, Thermo-Fisher Scientific Inc.). We assigned absorption peaks indicative of SOM functional groups as follows: (a) unsaturated aliphatic chains to peaks at ~2,920 and ~2,850 cm^{-1}, (b) aromatic skeletal C=C or CO of amide groups to ~1,510 cm^{-1}, (c) peaks at ~1,630 cm^{-1} to aromatic C=C and symmetric COO− groups, and (d) peaks at ~1,030 cm^{-1} to cellulose or carbohydrates (Biester, Knorr, Schellekens, Basler, & Hermanns, 2014; Cocozza, D'Orazio, Miano, & Shotyk, 2003; Niemeyer, Chen, & Bollag, 1992). Variations in sample chemistry between site locations and treatments, caused slight shifts in the wavelengths of peaks associated with functional groups of interest; thus the exact locations peaks were in individually determined for each sample and normalized to corrected peak heights using methods described in Hodgkins et al. (2018). The ratio of normalized peak intensities at 1,630/1,030 cm^{-1} (representing the contribution of aromatics and lignin, that is, Humification index) and the ratio 1,510/1,030 cm^{-1} (representing the contribution of lignin and phenolics, i.e., Decomposition index) were calculated to examine the contribution of refractory compounds versus labile carbohydrates (Artz et al., 2008; Biester et al., 2014; Moore, Knorr, Thompson, Roy, & Bubier, 2019; Tfaily et al., 2014) as indicators of changes in the stability of SOM that result from thermal alteration by fire.

2.4 | X-ray photoelectron spectroscopy

X-ray photoelectron spectroscopy (XPS) is an analytic technique that is suited for characterizing films or coatings produced by thermal alteration of SOM by thin films within a maximum depth of 10 nm (Cheng, Lehmann, Thies, Burton, & Engelhard, 2006). Also, XPS can analyze the composition of carbon functional groups without the structural alterations potentially associated with physical or chemical extraction without the need for any chemical or physical extraction (Gerin, Genet, Herbillon, & Delvaux, 2003). We used XPS to characterize the carbon functional groups on the surface of the burned and unburned soil

aggregates. Samples containing intact aggregate surfaces were prepared for XPS analysis by drying drops of peat-water slurry at 60°C (Huang et al., 2017). XPS analyses were performed using a Kratos Analytical Axis Ultra with high-resolution scans performed using a mono Al X-ray source with an emission current of 10 mA and an anode voltage of 15.0 kV. High-resolution C1 spectra were collected with the use of a neutralizer and analyzer pass width of a 23.1 eV and a 0.1 eV step centered at 288.45 eV. Peak fitting and calculation of the peak areas of the carbon-containing functional groups were evaluated using the CasaXPS software (Walton, Wincott, Fairley, & Carrick, 2010). The Shirley background and a least-squares routine were used for peak fitting. Peaks corresponding to aliphatic (C–C and C–H) and aromatic C were identified at 284.7 eV. A shift in C1s binding energy of 1.7 eV was assigned as peaks for C–OR groups (ether or hydroxyl), a shift of 3.0 eV for carbonyl (C=O), and a shift of 4.5 eV for (COOR) carboxy functional groups (Cheng et al., 2006). We used these data to calculate a Carbon Condensation Index as the ratio of aromatic carbon abundance to the summed abundance of oxygen-containing groups:

$$\mathrm{CCI} = \frac{C_1}{C_2 + C_3 + C_4}, \quad (3)$$

where C_1 is the aromatic carbon abundance, C_2 ether/hydroxyl (–COR), C_3 carbonyl groups (–C=O), and C_4 carboxy (–COOR) abundance. The CCI is the simple inverse of an index described by Nguyen et al. (2009).

2.5 | Characterization of carbon functional groups

Because many of the changes of the chemistry in low-severity fires likely occur due to change on the surface of aggregates such as deposition of volatilized hydrophobic substances (DeBano, 2000; Gonzalez-Perez et al., 2004; Knicker, 2007; Mataix-Solera, Cerdā, Arcenegui, Jordán, & Zavala, 2011) and polymerization of aromatic compounds (Kang et al., 2012), we used several techniques to characterize the surface chemistry of peat. These included scanning electron microscope (SEM), XPS, and FTIR spectroscopy to assess changes in functional groups at the aggregate surface and observe films deposited by fire on soil surfaces. FTIR analysis of ground peat was used to characterize bulk soil (Biester et al., 2014), while XPS analysis was used to characterize the surface chemistry soil aggregates (Cheng et al., 2006).

2.6 | Statistical and spatial analysis

We used the R statistical package (R Core Team, 2019) to perform all statistical analyses. After applying the Shapiro–Wilk test to assure data met assumptions of normality, we utilized one-way ANOVA procedure to evaluate the statistical significance of changes in SOM characteristics resulting from fire treatment effects including elemental composition, XPS indices of carbon condensation (CCI), FTIR indices of decomposition and humification, and the CO_2 emissions Q_{10} of SOM respiration. ArcMap™ (ESRI, 2019) was used to tabulate remotely sensed burn severity data by wetland landcover.

3 | RESULTS

3.1 | Spatial analysis

Our tabulation of remotely sensed fire severity data for wetlands of the states of Minnesota, North Carolina, and Florida shows that 90% of the acreage was classified as low-severity or less (Figure S1). Similarly, our analysis of wildfires in Alaskan boreal wetlands (Figure S2) were also dominated by low-severity categories (63.5%). These results are similar to those of Sorbel and Allen (2005) for wildfires occurring within National Parks located in Alaska.

3.2 | Scanning electron microscope

Laboratory simulations of low-severity burns resulted in obvious charring on the surface of peat material used in our incubation studies. To examine the physical structure of this char material deposited on the peat surface, we utilized SEM to observe the morphology of altered organic matter surfaces. Figure 2a shows the leaf stoma from unburned surface material obtained from our Pocosin site (NC), which is dominated by Ericaceous shrubs. In Figure 2b, a film of char

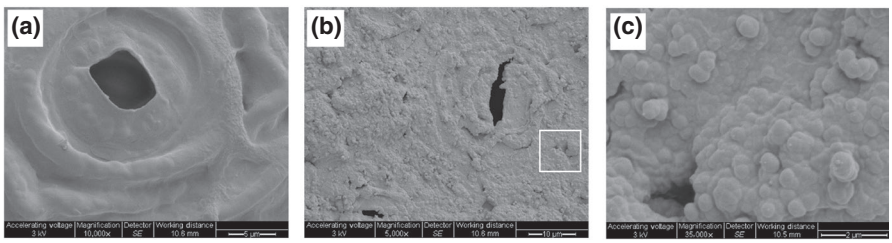

FIGURE 2 Results of scanning electron microscopy (SEM) showing alteration of surface litter during a low-severity fire prescribed fire. (a) Material prior to fire showing a well-defined leaf stomata, (b) occlusion of leaf surface by pyrogenic material, and (c) higher magnification image of the area in the box in (b) showing spherical structures similar to those seen on the surface of hydrochar

produced in our simulated fire occludes a similar stoma. In Figure 2c, we magnify a small region of charred material to reveal a morphology that is visually similar to hydrochars produced from wood lignins produced under moist conditions at relatively similar temperatures (225°C) and produced by decomposing lignin to phenols through hydrolysis followed by deposition of aromatic polymer films on SOM surfaces. These materials are known to have a longer residence time in soils than unburnt precursors.

3.3 | X-ray photoelectron spectroscopy

We used XPS to characterize how fire alters carbon functional groups on the surface of peat aggregates, which can differ significantly from the characteristics of SOM in the center of soil aggregates after rapid heating that might not heat aggregates uniformly or may deposit volatilized material as soil cool after fires abate.

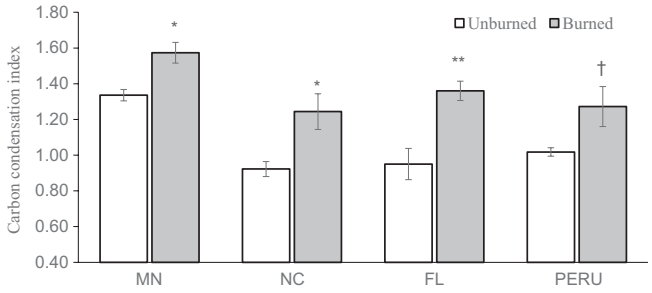

FIGURE 3 The ratio of condensed to oxygen-bonded carbon groups, that is, Carbon Condensation Index, on the surface of soil aggregates as quantified by X-ray photoelectron spectroscopy. The bars and error bars represent mean ± *SE*, $n = 3$. Symbols denoting burned and unburned treatments are significantly different at a given site (one-way ANOVA, $n = 3$, $df = 1$, $^{\dagger}p < .1$, $^{*}p < .05$, $^{**}p < 0.1$). One-way ANOVA *p* values MN (.023), NC (.046), FL (.005), and PERU (.089)

High-resolution spectra from each treatment were deconvolved to quantify the abundance of different carbon forms on the surfaces of soil aggregates (Figure S3). Figure S4 summarizes the changes in the relative abundance of aromatic and oxidized carbon forms on the aggregate surfaces of our burned and unburned samples. In all treatments, thermal alteration results in an increase in aromatic carbon, while oxygen-containing ether/hydroxyl (–COR) and carbonyl groups (–C=O) decrease substantially. We see a significant increase in carbon condensation at all of our sites due to thermal alteration from our experimental fires (Figure 3), which is consistent with the increasing stability of organic carbon seen during the processes of humification and coalification.

3.4 | Fourier Transform Infrared Spectroscopy

We used FTIR on finely ground SOM to characterize functional groups distributed throughout our sample. Stacked FTIR spectra presented illustrate differences in the molecular structure of burned and unburned peat across our sites (Figure 4). The spectra display several absorption bands that are used to characterize the relative abundance of functional groups that are relevant to explaining comparative rates of microbial respiration and assessing the state of humifaction of organic matter (Figure S5). The surface samples from our sites in Peru and Minnesota show relatively high absorption at the O-alkyl-C peak (~1,030 cm^{-1}), indicating a relative abundance of carbohydrates compared to sites in Florida and North Carolina. Peat from sites in MN and NC showed prominent peaks associated with carboxylic acid (~1,720 cm^{-1}) not observed in samples from our subtropical and tropical sites.

At all sites, we see a broad band of absorption around 2,900 cm^{-1}, associated with aliphatic compounds that are intensified and further differentiated into more distinct peaks at 2,920 and 2,850 cm^{-1}, a transformation of aliphatic moieties and accumulation of refractory aliphatic compounds as a result of thermal alteration.

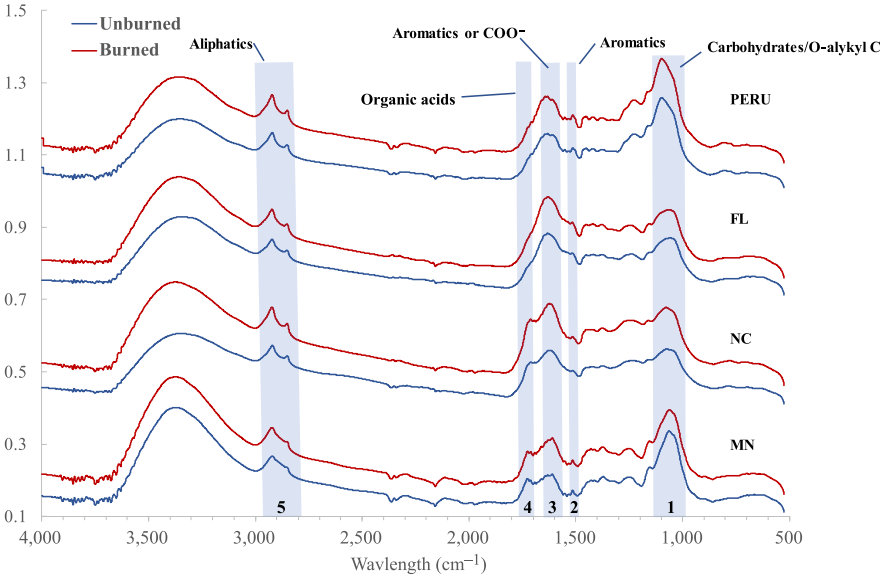

FIGURE 4 Average of $n = 3$ Fourier transform infrared spectra from subsamples of burned and unburned peat from four study sites. Band number 1 represents carbohydrates/cellulose/O-alkyl-C; band number 2 represents aromatic carbon; band 3 represents aromatic C or carboxylate; band 4 represents organic acids; and band 5 represents aliphatic compounds. Spectra are stacked, and differences along the *y*-axis are showing relative differences in absorbance

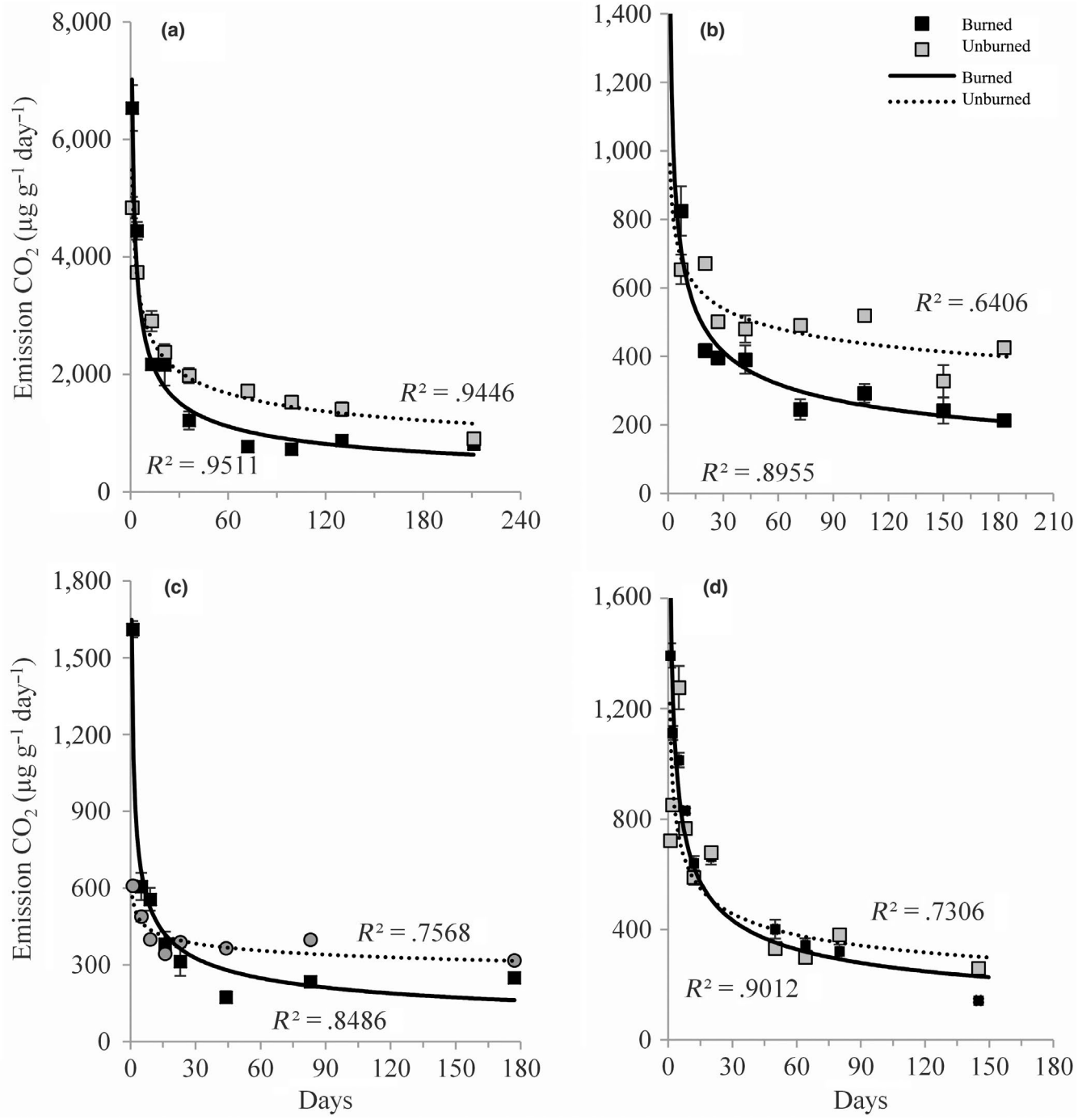

FIGURE 5 Emission of CO_2 per gram of soil during laboratory incubations (moist, aerobic conditions at 25°C) of burned and unburned moist peat from the following sites: (a) Minnesota, (b) North Carolina, (c) Florida, and (d) Peru. Emissions are per gram of dry soil

Thermal alteration caused an increase in the prominence of a peak associated with vibrations of aromatic skeletal C (~1,510 cm^{-1}), and a peak ascribed both to aromatic C=C and COO– groups (~1,630 cm^{-1}). Simulated fires reduced the intensity of peaks assigned to carbohydrates (~1,030 cm^{-1}) consistent with selective removal of more labile carbohydrates and increased peak intensity at bands associated with aromatic compounds (~1,510 cm^{-1} to ~1,630 cm^{-1}). Indices of humification and decomposition suggest that rapid thermal alternation of peat is associated with a weak trend of more abundant refractory compounds, that are associated with increased stability, in the bulk chemistry of burned SOM (Figure S5).

3.5 | Soil respiration

We incubated burned and unburned peat at three temperatures (5, 15, and 25°C) for 5 months and measured CO_2 emissions and

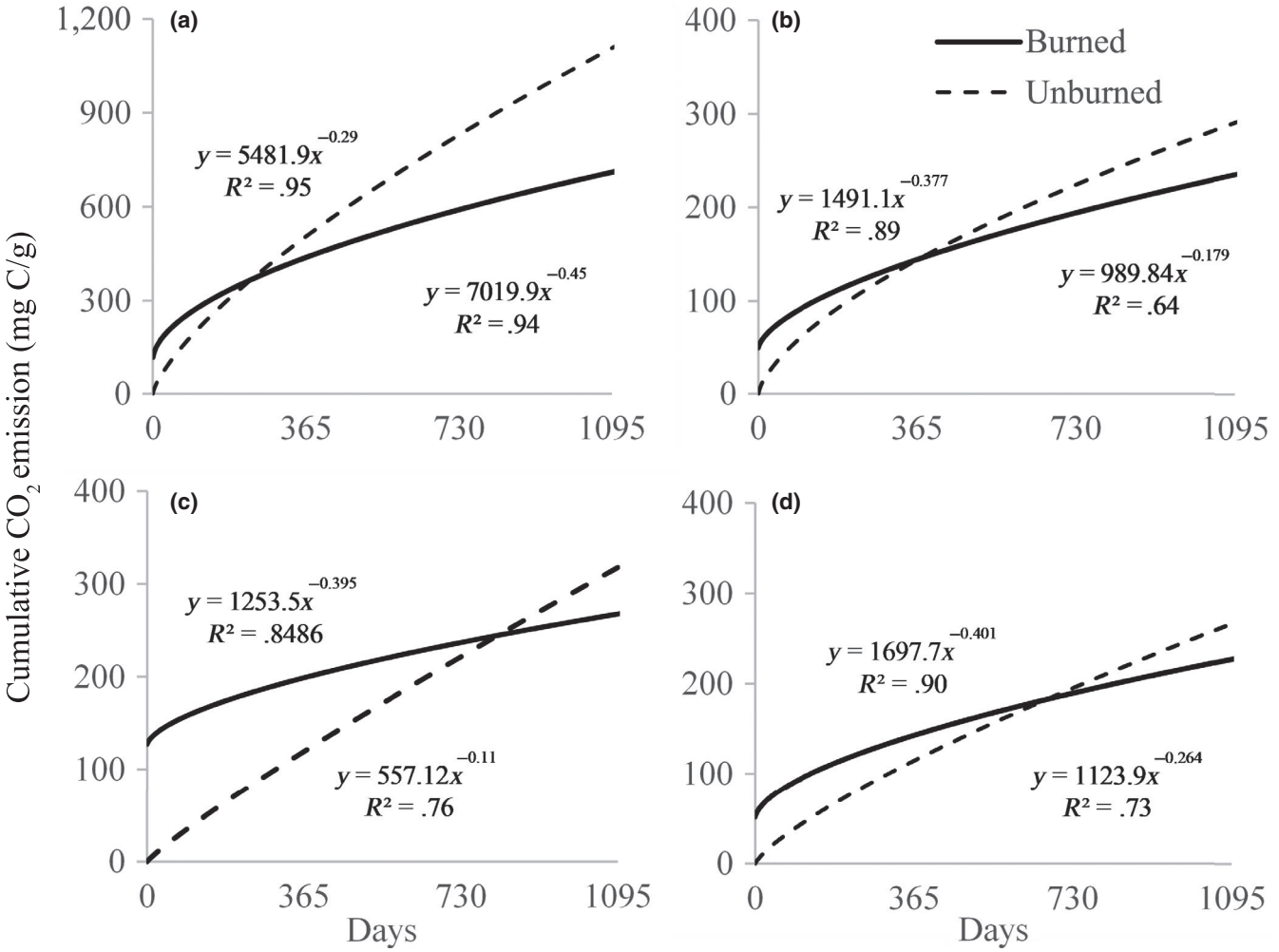

FIGURE 6 Three-year plots of fitted power regression equations for cumulative CO_2 emission per gram of soil due to microbial respiration and thermal oxidation during experimental burns. The *y*-intercept of the burned curve represents initial soil organic matter losses to simulated fire. Curves are fitted to the microbial respiration data presented in Figure 7. A crossover-point where cumulative emission from the burned treatment is lower than the unburned treatment occurs after ~1 to 3 years. (a) Minnesota, (b) North Carolina, (c) Florida, and (d) Peru

calculated the associated temperature sensitivity. Figure 5 shows the results of 25°C incubations of burned and unburned peat from all four sites. In all incubations, burned peat showed a brief initial period of higher emissions than unburned peat. However, in less than 15 days, emissions from burned peat dropped below those of unburned peat and stayed lower for the duration of the incubation period. Fitted power regression equations of CO_2 versus incubation time (Figure 6) were used to model cumulative CO_2 emissions over 3 years. After accounting for measured losses of SOM to combustion in the burned treatments, cumulative carbon losses to fire and respiration were lower after 1–2 years due to lower rates of microbial respiration from burned treatments at all sites.

Emission data from three incubation temperatures were used to calculate temperature sensitivity coefficients (Q_{10}) for each measurement day. Mean Q_{10} coefficients for each treatment are presented in Figure 7. A linear regression between the surface aromaticity of peat aggregates assessed using XPS (CCI) and temperature sensitivity Q_{10} is shown in Figure 8, which shows a highly significant negative correlation between CCI and Q_{10}.

3.6 | Bulk soil characterization

The analysis of soil from our sites showed few clear latitudinal trends related to elemental composition (Table 2; Figure S6). We observed a general trend in increased nitrogen content of tropical and subtropical peat (PERU and FL) compared to peat from temperate (NC) and hemiboreal (MN) biome. Peat from sites with frequent fires (NC and FL) showed lower O/C ratios than peat from sites with relatively infrequent fires (MN and PERU), indicating lower carbohydrate and carboxylic contents of organic matter. MN showed higher H/C ratios than the other sites, which may be a reflection of the very high polysaccharide content of *Sphagnum* sp. derived peat. Peat samples originating from sites with regimes of frequent fires show a greater degree of dehydration (Figure S6). However, our simulated

low-severity fires only resulted in minor changes to the elemental chemistry of bulk soils between burned and unburned treatments at a given site (Table 2; Figure S6). We did see an interesting trend concerning C/N ratios, which show a consistent positive association with latitude but are increased only slightly by low-severity fire.

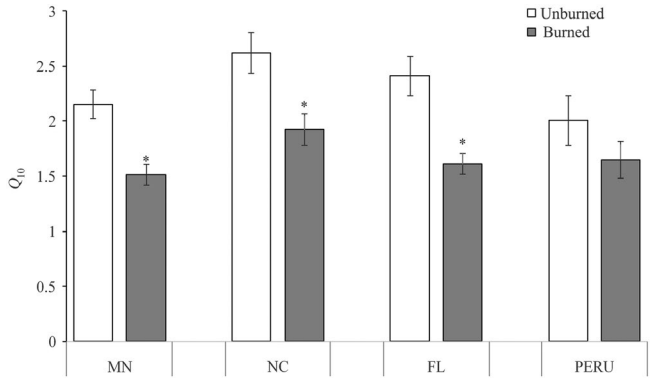

FIGURE 7 Temperature coefficient (Q_{10}) of burned and unburned peat from aerobic incubations at three temperatures (5, 15, and 25°C). Bars show mean ± *SE*. One-way ANOVA, $n = 8$, $df = 1$, p values MN (.023), NC (.012), FL (.011), and PERU (.22). *$p < .05$

4 | DISCUSSION

Our results support the hypothesis that low-severity fire can create a pool of slower-cycling carbon in peatlands located in many different ecozones. Our fire treatments caused significant condensation of carbon in SOM, especially on the surface of soil aggregates (Figure 3), without causing substantial losses of soil carbon, and unlike high-severity fires, causing little impact to the elemental chemistry of our bulk soils (Table 2).

X-ray spectroscopy analysis of surface chemistry showed that thermal alteration by low-severity fire significantly increased the index of carbon condensation (CCI), which is consistent with production and/or selective concentration of aromatic functional groups, or the deposition of polyaromatic and/or aliphatic C–H polymers on the surface of soil aggregates (Figures 3 and 4; Figure S5a). These results are consistent with processes observed during the formation of polyaromatic films during hydrochar formation (Figure 2; Kang et al., 2012) and with the presence of hydrophobic functional groups on the surface of soil aggregates (Woche et al., 2017; Xu, Zhou, & Qiu, 2017). Such hydrophobic coatings are commonly created during low-severity fires (DeBano et al., 1970) and have low water solubility

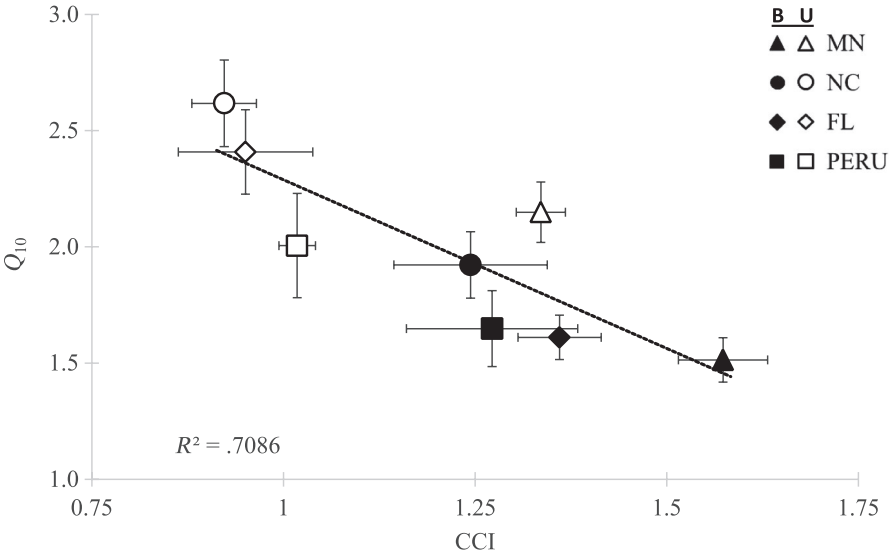

FIGURE 8 The relationship between the degree of carbon condensation (CCI) at the surface of soil aggregates and the temperature sensitivity coefficient (Q_{10}) for each treatment. Black symbols represent the burned (B) treatment for a given site, while hollow white symbols represent unburned (U) treatment. Symbols show the mean ± *SE* of a given parameter. At any given site, burned and unburned treatment pairs are significantly different for both CCI and Q_{10}. See Figures 3 and 7. Legend symbols filled = burned (B) and hollow = unburned (U)

TABLE 2 Elemental analysis of burned and unburned peat samples from study sites, O/C and H/C proportions are calculated using atomic ratios

Site	Treatment	%C	%N	%H	%O	O/C	H/C	C/N
MN	Unburned	46.6	0.8	5.9	45.6	0.734	1.529	67.958
MN	Burned	46.9	0.8	5.9	45.4	0.727	1.510	68.396
NC	Unburned	49.5	1.4	5.0	43.0	0.652	1.224	41.250
NC	Burned	49.9	1.4	5.0	43.5	0.654	1.213	41.583
FL	Unburned	47.6	3.0	5.5	42.9	0.675*	1.379*	18.511
FL	Burned	48.2	3.0	5.4	42.4	0.659	1.338	18.744
PERU	Unburned	42.6	2.5	5.1	48.7	0.857*	1.435*	19.880
PERU	Burned	43.0	2.5	4.9	48.6	0.848	1.372	20.017

Abbreviations: FL, Florida; MN, Minnesota; NC, North Carolina; PERU, Peru.

Symbols denoting burned and unburned treatments are significantly different at a given site (one-way ANOVA, $n = 3$, df = 1, *$p < .05$)

(Gonzalez-Perez et al., 2004; Knicker, 2007), giving these coatings the potential for long-term persistence in soil affected by fires. Another recent study also found that relatively low-temperature fire caused the rapid formation of hydrophobic coatings on the surface of peat soils with minimal structural changes to bulk SOC (Wu, Zhang, Slater, Waddington, & de Lannoy, 2020). Our XPS results also point to the increased abundance of aromatic compounds on the surface of aggregates, a pattern similar to charcoal and biochar, which has been shown to produce positive or negative priming of microbial respiration depending on feedstock and temperature of production. Wood biochar produced at high temperature generally showed a long-term negative priming effect, suggesting that char addition to soil might reduce heterotrophic respiration and encourage a shift to microbial communities dominated by slow-growing taxa (Aaltonen et al., 2019; Chen et al., 2018; Cheng, Lehmann, & Engelhard, 2008; Maestrini, Nannipieri, & Abiven, 2015; Nguyen et al., 2009; Singh, Fang, Cowie, & Thomsen, 2014).

Our FTIR results for bulk soil (Figure 4; Figure S5) show weak, that is, non-significant patterns of humification and decomposition that are consistent with selective loss of carbohydrates during our experimental fires (Artz et al., 2008; Biester et al., 2014; Cocozza et al., 2003; Hodgkins et al., 2018). These changes occurred in a matter of minutes resulting in the transformation of soil carbon into a composition that is relatively resistant to decomposition (Leifeld, Steffens, & Galego-Sala, 2012; Moore & Basiliko, 2006; Rollins, Cohen, & Durig, 1993). We see much stronger evidence of significantly altered carbon chemistry on the surface of soil aggregates as shown by our XPS results (Figure 3; Figures S3 and S4), suggesting thermal alteration of SOM occurred primarily on aggregate surfaces, where soil pore-space likely allowed higher temperatures during fires and provided pathways for deposition of volatile compounds as soils cooled. The contrasts between burned and unburned peat from this study show a pattern of labile compound losses and aromatic compound concentration that mirrors a spatial pattern of humification observed in peatlands along a gradient from low to high latitude (Hodgkins et al., 2018).

The thermal alteration of SOM by low-severity fire is associated with reduced rates of heterotrophic respiration that persist for many months (Figure 5), and leads to lower cumulative carbon losses after 1–3 years, even after accounting for carbon losses to fire (Figure 6). Similar decreases in microbial biomass, respiration, and enzyme activity were reported in studies of peatlands and boreal forests after experiencing severe fires (Dooley & Treseder, 2012; Holden et al., 2016; Ludwig et al., 2018; O'Donnell et al., 2009; Pressler, Moore, & Cotrufo, 2019; Tas et al., 2014), with long-term alterations of community composition (Dooley & Treseder, 2012; Holden et al., 2016; Pressler et al., 2019; Tas et al., 2014). Wildfire reduces fungal taxa abundance and phenol-oxidase activity in peatlands (Waldrop & Harden, 2008), which has been associated with reduced rates of heterotrophic respiration (Freeman, Ostle, Fenner, & Kang, 2004; Waldrop & Harden, 2008; Wang, Richardson, & Ho, 2015).

Our data show both long-term reductions in heterotrophic respiration (Figures 5 and 6) and reductions in Q_{10} (Figure 7), findings that are consistent with the physical protection of SOM by low-severity fire. Thermal alteration of peat consistently reduced rates of microbial respiration and reduced the temperature sensitivity (Q_{10}) of decomposition in the burned treatments in all of our laboratory incubations (Figures 7 and 8). The strong negative relationship between Q_{10} and CCI (Figure 8) suggests that the thermal alteration of peat surface chemistry restricted microbial access to organic matter, resulting in lower apparent temperature sensitivity, as posited by Davidson and Janssens (2006).

We compared typical areal rates of SOC loss to combustion during peat fires to our model estimates of cumulative reductions of heterotrophic respiration. Our experimental burns resulted in losses to combustion ranging from between 5% and 12% of initial SOC mass, which corresponds to an areal loss of between 5.9 and 14.1 kg C/m^2, assuming the typical total soil carbon store of 118 kg C/m^2 in boreal peatlands (Yu, 2012). Benscoter and Wieder (2003) found that wildfires in boreal peatlands caused losses of SOC that typically ranged between 1.7 and 2.3 kg C/m^2. The SOC losses in our experimental fires (5%–12%) correspond to between 0.2 and 2.7 kg C/m^2 of young soil carbon accreted within a representative fire return interval (Table S1). To better contextualize the ability of peatlands at our study sites to recover SOC losses represented by our laboratory fire simulations, we estimated the time required for reduced in CO_2 emissions from thermally altered peat to offset combustion of recently accumulated SOC, that is, the SOC accumulated since the previous fire, assuming a typical fire return interval and rate of carbon accretion. We found that reduced heterotrophic respiration can offset SOC losses to fire within the fire return interval at all of our sites except Florida (FL), where typical fire losses consume most of the carbon accreted during the inter-fire period (Figure S7; Table S1). Similarly, Wieder et al. (2009) showed that bogs in Alberta, Canada, with a fire return interval of 123 years, resumed acting as a net carbon sink within 13 years and remained long-term carbon sinks if the fire return interval remained longer than 61 years.

Our temperature sensitivity results are contrary to predictions based solely on the carbon quality-temperature (CQT) theory of decomposition (Aaltonen et al., 2019; Bosatta & Agren, 1999; Conant et al., 2011; Davidson & Janssens, 2006; Davidson et al., 2006). A growing body of literature recognizes a model of apparent temperature sensitivity that is determined by interactions between substrates, microbial communities, and abiotic variables (Bosatta & Agren, 1999; Conant et al., 2011; Dungait et al., 2012; Gentsch et al., 2018; Gillabel, Cebrian-Lopez, Six, & Merckx, 2010; Kleber et al., 2011; Moinet et al., 2018; Tang, Cheng, & Fang, 2017; Wagai et al., 2013; Zimmermann, Leifeld, Conen, Bird, & Meir, 2012). Thermal alteration of SOM by fire has been shown to alter the temperature sensitivity of microbial respiration in peatlands, which has important implications for the response of peatland carbon cycles to climate change (Chen et al., 2018; Davidson & Janssens, 2006; Holden et al., 2016; O'Donnell et al., 2009; Sawamoto, Hatano, Yajima, Takahashi, & Isaev, 2000).

Figure 8 shows the strong negative association between the carbon condensation of SOM (CCI) and the temperature sensitivity

of microbial respiration (Q_{10}), suggesting that the alteration of peat surface chemistry by fire can limit microbial access to SOM (Dungait et al., 2012; Moinet et al., 2018). Our observed relationship between CCI and Q_{10} is consistent with the proposed model of 'apparent' Q_{10} caused by physical protection of SOM (Davidson & Janssens, 2006; Davidson et al., 2006; Zimmermann et al., 2012), with several recent studies demonstrating evidence for attenuation of Q_{10} by physical protection of SOM (Gentsch et al., 2018; Gillabel et al., 2010; He, Du, Wang, Lu, & Zhang, 2016; Moinet et al., 2018). Spaccini et al. (2002) showed that hydrophobic humic substances could physically protect labile SOM from mineralization. Additions of char to soil have demonstrated simultaneous reductions of microbial respiration and Q_{10} (Chen et al., 2018; Pei et al., 2017; Wang, Chen, Wang, Zhang, & Zhang, 2019). Several studies have demonstrated reduced rates of microbial respiration in burned ecosystems that may persist for decades, and which may be typical of many boreal forests (Amiro, Ian MacPherson, Desjardins, Chen, & Liu, 2003; Conard & Solomon, 2008; Holden et al., 2016; Hu, Sun, Hu, Weise, & Guo, 2017; Kim & Tanaka, 2003; Sawamoto et al., 2000; van Bellen, Garneau, & Bergeron, 2010). These effects were particularly significant in surficial soils (Pressler et al., 2019).

Estimates of the turnover time for pyrogenic organic matter PyOM in soils is 86 years using a one-pool model and 870 years when modeled with a separate slow-cycling pool (Singh, Abiven, Torn, & Schmidt, 2012). Recent studies conclude that differences in litter quality are strongly predictive of the degree of decomposition of peat as it passes through a zone of oxygen exposure over a period spanning tens or hundreds of years before reaching anaerobic conditions where organic matter often resides for thousands of years (Philben et al., 2015; Philben, Kaiser, & Benner, 2014). Our results show that thermal alteration by low-severity fire can create a slower-cycling pool of SOM through the creation of hydrophobic or aromatic layers on the surface of SOM aggregates (Figures 5–8). Many models of peatland development and SOM accumulation imply that a slow-cycling cohort of SOM, due to thermal alteration of litter, would allow a substantially greater proportion of SOM to survive vertical migration into kinetic 'cold spots' of decomposition within the soil profile: These anoxic conditions and lower soil temperatures provide additional environmental constraints (protection) from decomposition that can allow organic matter to persist for millennia (Bauer, 2004; Davidson & Janssens, 2006; Frolking et al., 2001; Morris, Waddington, Benscoter, & Turetsky, 2011; Yu, 2006). Indeed, pyrogenic carbon accounted for an average of 13.5% of carbon stocks across 19 European peatlands and up to 50% of carbon stocks within degraded sites, suggesting PyOM makes up a substantial portion of SOC in many peatlands, and that the selective concentration of this slower-cycling carbon pool occurs during peatland degradation (Leifeld et al., 2012, 2018).

Several studies have shown a negative effect of fire on the reestablishment of *Sphagnum* species and on the long-term carbon accretion (Kuhry, 1994; Noble, Crowle, Glaves, Palmer, & Holden, 2019; Noble et al., 2018; Pitkänen, Turunen, & Tolonen, 1999). The effects of fire on *Sphagnum* establishment can also affect the water yield of peat surface layers, with fire creating more saturated conditions during periods with stable water table levels, but with greater vulnerability to water table drawdown drying during drought. Fire can also substantially increase surface temperatures and microbial respiration by reducing the albedo of the soil surface. However, low-severity fires can cause drying of surface soil layers and increased hydrophobicity that creates an insulating layer, can impede evaporation, and thus help maintain cool, saturated conditions (Kettridge, Thompson, & Waddington, 2012; Thompson, Benscoter, & Waddington, 2014; Wilkinson, Verkaik, Moore, & Waddington, 2019).

Often, a regime of low to intermediate fire frequency and intensity increases carbon storage in the soils of many ecosystem types (Cong, Gao, Han, Li, & Wang, 2020; Pingree, Homann, Morrissette, & Darbyshire, 2012; Richards, Cook, & Lynch, 2011; Wirth et al., 2002). This trend has implications for the preservation of stored carbon in peatlands facing increased drought frequency and duration associated with climate change predictions (Karl, Melillo, Peterson, & Hassol, 2009) and the resulting increase in the frequency of fire (Turetsky et al., 2014; Walker et al., 2019). In some ecosystems, low-severity fire has been shown to create a pool of slower-cycling carbon (Figure 6; Figure S7) that can mitigate future carbon losses (Cong et al., 2020; Efremova & Efremov, 2006; Leifeld et al., 2012, 2018; Ludwig et al., 2018). Moreover, alteration of microbial communities can reduce heterotrophic respiration, potentially resulting in a negative feedback mechanism to climate change (Holden et al., 2013, 2016). Conversely, long-term fire suppression can cause accumulations of aboveground fuel loads that increase the likelihood of initiating destructive smoldering peat fires in drained areas or during periods of severe drought resulting in catastrophic impacts on long-term carbon stores (Turetsky et al., 2011; Wilkinson et al., 2018).

Thus, some peatlands with fire-adapted plant communities have demonstrated long-term accumulation of stable carbon pools concomitantly with a regime of low-severity fire. This pattern is likely not globally applicable to all peatlands, especially with the present trends of increasing fire severity in many regions, but rather represents a process that has contributed to the development of stable carbon pools over the last few thousand years in peatlands affected by recurring low-severity fires.

5 | CONCLUSIONS

Our analysis of peat that was thermally altered by low-severity fire shows significant changes to the carbon functional groups on the surface of soil aggregates, with little actual loss of SOM. The thermal alteration of SOM caused substantial reductions in both CO_2 emissions and temperature sensitivity (Q_{10}) of microbial respiration. This pattern is best explained by changes in the accessibility of SOM to microbes and/or microbial enzymes. To our knowledge, the physical protection of SOM caused by low-severity fires in peatlands, with the associated attenuation of Q_{10}, has never been described in the scientific literature. The prevalence of fire-adapted plant communities, paired with the pervasiveness of PyOM in peatlands across the epoch of carbon accretion, suggests that periodic low-intensity fire

can support long-term carbon storage. Thermal modification of SOM by low-severity fires may enlarge the pool of stable carbon found in the aerobic layers of peatland soils, thus increasing the proportion of organic matter that survives decades-long vertical migration into regions of the peatland soil profile where anaerobic conditions and lower temperatures cause physiochemical stabilization of SOM, resulting in residence times of many millennia. A potential negative consequence of climate change, paired with widespread drainage of peatlands, is an increase in the proportion of surface blazes that ignite smoldering deep muck fires, due to decreased ambient moisture content at the soil surface. Accordingly, low-severity fire is a process of underestimated importance to global carbon cycles whose influence on carbon accretion may wane with climate-induced increases in peatland fire severity.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Duke University Research Data Repository (https://doi.org/10.7924/r4s46nm6p).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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