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Historical fire regimes of North American hemiboreal peatlands

Colleen M. Sutheimer [a,*], Jed Meunier [b], Sara C. Hotchkiss [c], Eric Rebitzke [d], Volker C. Radeloff [a]

[a] SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706, USA
[b] Wisconsin Department of Natural Resources, Division of Forestry, 2801 Progress Road, Madison, WI 53716, USA
[c] Botany Department, University of Wisconsin, 430 Lincoln Drive, Madison, WI 53706, USA
[d] USDA Forest Service, Hiawatha and Ottawa National Forests, 820 Rains Drive, Gladstone, MI 49837, USA

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ABSTRACT

Peatlands contain one-third to one-half of global soil carbon, and disturbances, specifically fire, directly influence these carbon stocks. Despite this, historical variability of peatland fire regimes is largely unknown. This gap in knowledge partly stems from reconstructions of peatland fire regimes with methods limited to evaluating infrequent, severe fire events and not capturing frequent, low-severity events. Furthermore, variability in fire regimes is likely higher in heterogenous landscapes like the hemiboreal subzone, the transition between boreal and temperate biomes, where peatlands are embedded in landscapes including forests with high proportions of fire-dependent species, such as red pine (*Pinus resinosa*), that are well adapted to frequent low-severity fires. Here, we sought to evaluate the role of low- and moderate-severity fires within hemiboreal peatlands in central North America to better understand historical variability in fire regimes. We reconstructed historical fire regimes using fine-scale (temporal and spatial) dendrochronology methods to estimate frequency of low- and moderate-severity fires, identify synchronous fire events among forested uplands within and surrounding individual peatlands as well as among sites, and assess fire-climate relationships. We collected 220 cross-sections or partial-tree sections within three poor fen peatlands across the Great Lakes Region. Using standard dendrochronological techniques, we crossdated 129 samples, assigning dates to 414 fire scars (128 unique fire years) comprising a 500-year tree-ring record (1520–2019). Prior to the mid-1900s, fire events were frequent and widespread within peatlands we evaluated, with mean fire return intervals (MFRI) ranging from 7 to 31 years. Fire events were also synchronous among forested uplands within and surrounding peatlands. Fires predominantly occurred in the dormant and latewood (growing season) positions and during regionally dry conditions corresponding to mild and moderate drought (Palmer Drought Severity Index ≥ -2.99) but interestingly not during regionally severe drought (Palmer Drought Severity Index ≤ -3.00). While large-scale, high-severity fires are important to the ecology of peatlands and to changing climate-fire interactions, our results suggest that widespread low- to moderate-severity fires were historically frequent in hemiboreal peatlands and likely central to their development and maintenance. Evaluating whether peatlands will continue to be carbon sinks or become carbon sources due to climate change requires an understanding of the inherent variability in fire regimes, especially in hemiboreal systems.

1. Introduction

Peatlands are waterlogged organically enriched wetlands that cover 3% of Earth's land area and provide a high proportion of global ecosystem services (Rydin et al. 2013), including climate regulation through carbon sequestration and storage (32–46% of global soil carbon; Bonn and British Ecological Society 2016, Page and Hooijer 2016). However, large pools of carbon sequestered in peatlands are vulnerable to changes in climate, primarily through altered fire regimes including larger, more severe fires that consume peat soils (Kasischke and Turetsky 2006, Grosse et al., 2011). Area burned in the North American boreal zone, which contains a high proportion of peatlands, is projected to increase up to 500% by the end of the 21st century due to climate change (Flannigan et al. 2009, Héon et al. 2014). Understanding the effects of current and future fire dynamics related to climate change requires knowledge of historical disturbance regimes (Bergeron et al. 2004a). Fire regime characteristics (e.g., frequency, extent, severity), for example, vary in conjunction with climate, topography, vegetative

structure, and species composition, contributing to highly complex and regionally variable disturbance regimes (Wein et al. 1983, Zoltai et al. 1998).

Fire regimes differ widely within the global boreal zone despite similar physiography, climate, and "fire weather" conditions (e.g., humidity, temperature, winds; Rogers et al. 2015). North American boreal fire regimes are characterized by infrequent (100 to 1000 year intervals), high-severity, stand-replacing fires (Wein et al. 1983, de Groot et al. 2013) which often eradicate legacies (e.g., wood) of past fires (Rolstad et al. 2017). By contrast, Eurasian boreal fire regimes are characterized primarily by relatively frequent (10–50 years) low-severity surface fires (Wooster 2004, de Groot et al. 2013, Drobyshev et al. 2014). Forest composition and the fire ecology of individual species contribute to the disparate fire regimes among high-latitude boreal forests across the globe (de Groot et al. 2013). Greater proportions of fire-dependent coniferous species (e.g., *Pinus* spp. and *Larix spp.*) are associated with frequent low-severity surface fires in lower boreal latitudes, whereas greater proportions of fire-resilient coniferous species (e. g., *Abies spp.* and *Picea spp.*) support less frequent high-severity crown fires in higher boreal latitudes (de Groot et al. 2013, Rogers et al. 2015). Fire-vegetation feedbacks greatly affect all boreal fire regimes, with overstory composition and fuel availability exerting a strong influence on fire severity in addition to fire weather (Walker et al. 2020).

Fine-scale variation and heterogeneity in forest composition is also characteristic of the North American hemiboreal subzone, the transition between boreal and temperate zones (Fig. 1; Brandt 2009). Much like Eurasian boreal forests, the hemiboreal subzone has high proportions of fire-dependent species (e.g., *Pinus resinosa*; Heinselman 1973, Wein et al. 1983, Drobyshev et al. 2008). Fire regimes in hemiboreal forests may be fundamentally different from those of high-latitude boreal ecosystems in North America (Bergeron et al. 2004a, Brandt 2009). Despite vegetative similarities to Eurasian boreal systems, where fires have been reconstructed based on tree rings (Drobyshev et al. 2014) that allow detection of decadal return intervals and low-severity surface fires (Swetnam et al. 1999), North American hemiboreal peatland fire regimes have been characterized by long fire return intervals (100s–1000s years) more typical of high-latitude North American boreal peatlands (Zoltai et al. 1998). Due to a paucity of data related to fire regimes in general and in peatlands especially, fire regimes across hemiboreal North America are often assumed to be similar to those of high-latitude boreal North America (Heinselman 1963, 1973, Bergeron et al. 2004b) regardless of vegetative characteristics.

Fire regimes in North American hemiboreal peatlands have generally been reconstructed via paleoecological analyses of sediments and charcoal (Booth and Jackson 2003, Booth et al. 2004) or settlement surveyor data (Whitney 1986, Cleland et al. 2004, Schulte and Mladenoff 2005). These methods are best suited for understanding high-severity fires that burn across large regions of continuous fuels as is typical for high-latitude North American boreal peatlands (Cyr et al. 2007, Kelly et al. 2013). Dendrochronology approaches can reconstruct frequent low-severity surface fires that are largely missed in sediment charcoal records and settlement surveyor data (Higuera et al. 2011, Remy et al. 2018). Given the higher proportion of fire-dependent species in hemiboreal peatlands, including *Pinus resinosa*, which is fire resistant
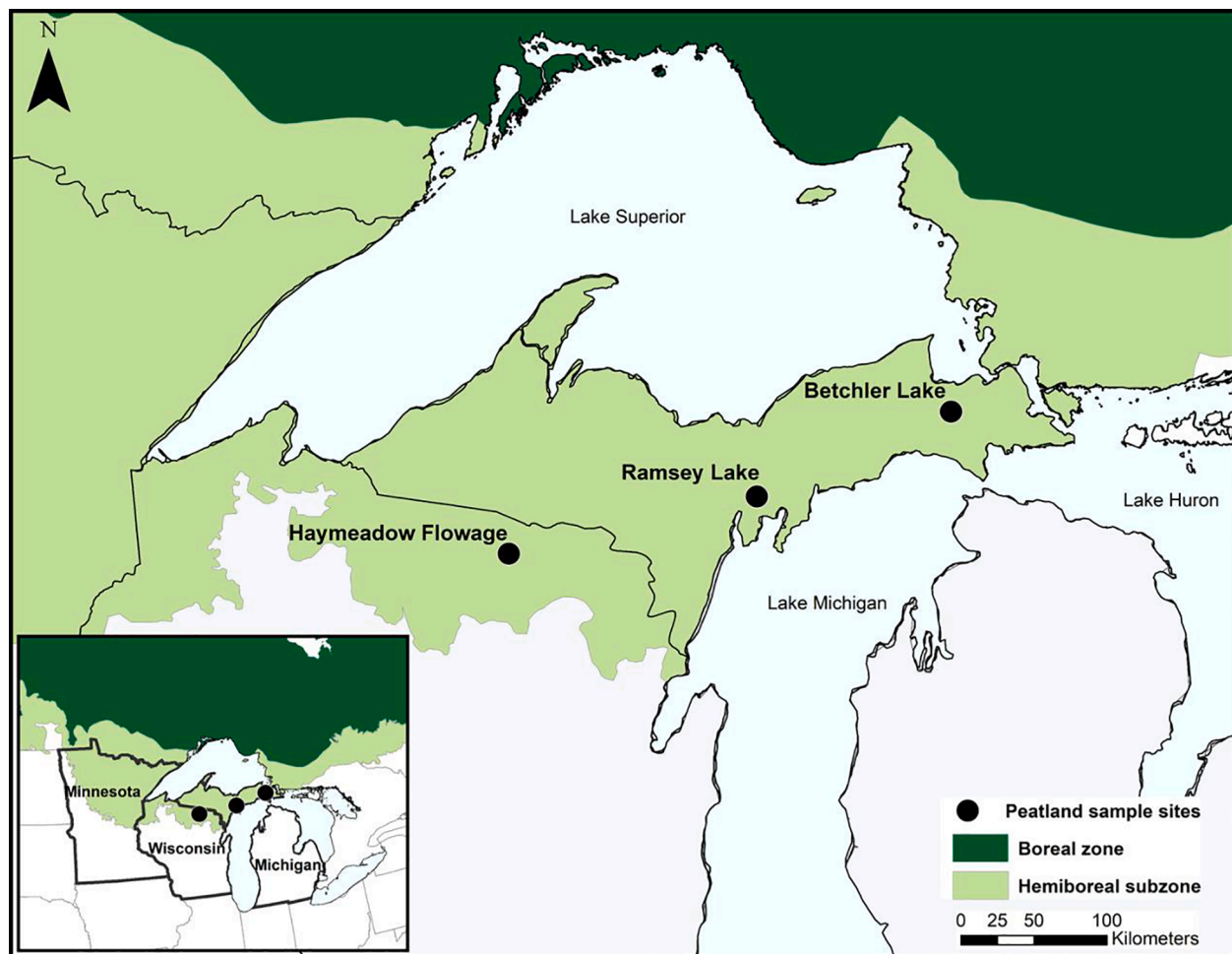
Fig. 1. Locations of peatland sample sites across the upper Great Lakes Region in North America with the true boreal and hemiboreal subzones (see Brandt 2009) differentiated. The inset shows the states of the upper Great Lakes Region: Minnesota, Wisconsin, and Michigan.

and typically survives and records surface fires, there is an opportunity to reconstruct fire regimes in hemiboreal peatlands using fire-scarred trees to address the paucity of data generally and specifically for low-severity fires (Flannigan and Bergeron 1998, Drobyshev et al. 2008). Detecting and quantifying variability in fire regimes that include frequent low-severity fire and infrequent, high-severity fire is prerequisite to identifying ecological consequences of altered fire regimes (McLauchlan et al. 2020) and understanding impacts of altered fire dynamics in hemiboreal peatlands.

Our goal was to reconstruct historical fire regimes of hemiboreal peatlands in the Great Lakes Region prior to European settlement to evaluate (1) low- to moderate-severity fire frequencies for fire events; (2) synchrony of widespread fire events among forested uplands within and surrounding peatlands; and (3) climate-fire relationships.

2. Methods

2.1. Study area

The Great Lakes Region contains ca. 6 million ha of peatlands and represents the center of the hemiboreal subzone in North America (Fig. 1; Boelter and Verry 1977). Climate in the region is continental and modulated by the Great Lakes, with warm humid summers, cold winters, and annual precipitation dependent on proximity to the Great Lakes (Albert 1995). The most expansive peatlands in the Great Lakes Region occur in glacial outwash plains dominated by sandy soils, but smaller peatlands are intermixed with forested uplands at the margins of outwash plains, kettle depressions, end moraines, and stabilized dunes (Heinselman 1963, 1965, Albert 1995). Near to the Great Lakes, forested dune fields typically protrude from peatlands (Silbernagel et al. 1997). Peatlands and uplands often intermix in the Great Lakes Region, resulting in high vegetative heterogeneity and species diversity (Silbernagel et al. 1997, Grondin et al. 2014).

We sampled forested uplands within and surrounding three hemiboreal peatlands in the Chequamegon-Nicolet and Hiawatha National Forests from northeastern Wisconsin to the eastern end of the upper peninsula of Michigan (Fig. 1) spanning ca. 320 km. The area sampled in each peatland ranged from 210 to 1200 ha (Table 1). We selected forested uplands within and surrounding peatlands and with minimal post-European settlement era land-use (1920s to present; Dickmann and Cleland, 2005) where intact remnant wood with fire scars remained. Forested uplands surrounding peatlands were contiguous mixed-pine forests adjacent to the peatlands and generally extended into peatland margins. Forested uplands within peatlands included conifer-dominated islands (uplands with topographic relief and surrounded by peatland) and ridges (long, narrow uplands within peatlands; Fig. 2). At Haymeadow Flowage we sampled two adjacent uplands and six islands (Fig. 2a), at Ramsey Lake we sampled six ridges (Fig. 2b), and at Betchler Lake we sampled three adjacent uplands, one ridge, and 12 islands (Fig. 2c).

All sites were poor fens intermixed with dry to dry-mesic forested uplands. Poor fens are weakly minerotrophic, acidic peatlands with shallow peat (1–3 m), continuous saturation of soils from a stable water table, and often transition sedge- and rush-dominated northern fens and sphagnum dominated bogs (Cohen et al. 2015). Fine-leaved sedges (*Carex* spp.*)* and low shrubs including leatherleaf (*Chamaedaphne calyculata)*, bog Labrador tea (*Ledum groenlandicum*), bog birch (*Betula pumila*), and other *Ericaceae* were prevalent in the peatland vegetation of our sites (Minnesota Department of Natural Resources 2003). Sphagnum (*Sphagnum* spp.) was also abundant with variable development of hummock formation. Overstory trees of forested portions of peatlands included scattered tamarack (*Larix laricina*) and black spruce (*Picea mariana*). Forested uplands within and surrounding peatlands were predominantly red pine (*Pinus resinosa*) with occasional white pine (*P. strobus*), jack pine (*P. banksiana*), and *Populus* spp. Understories were sparse, dominated by bracken fern (*Pteridium aquilinum*) and wintergreen (*Gaultheria procumbens*).

2.2. Data collection and analysis

We collected fire-scarred samples (cross sections from remnant tree stumps or partial sections from living trees and snags) from multiple forested uplands within and surrounding peatlands to capture landscape-scale fires that burned across peatlands. We used targeted sampling in order to reconstruct fire history with relatively small sample sizes (Van Horne and Fulé 2006). Decomposition of remnant wood limited the availability of intact samples, especially on islands within peatlands where fire scars were evident but often unsampleable. We collected cross sections with chainsaws from remnant red pine – and occasionally white or jack pine – stumps, i.e., trees that were harvested during the Great Lakes Region cutover period (ca. 1850–1920). We selected only stumps that contained at least one fire scar and >50 growth rings. We nondestructively sampled select living trees, standing snags, and fallen snags with evidence of fire scars by removing partial sections (Arno and Sneck 1977).

We dried and surfaced all samples with increasingly finer-grit sand paper to reveal cellular structure of annual rings, and digitally scanned each sample to measure widths of annual rings (Speer 2010). In the laboratory, we used a dissecting microscope to crossdate tree samples using standard dendrochronological techniques, assigned exact calendar dates to all fire scars, and determined season of fire when possible (Grissino Mayer and Swetnam 2000, Speer 2010) based on fire-scar position. We followed the convention of assigning ring-boundary scars (dormant season position) to the subsequent year containing the early-wood immediately following fire scars (Muzika et al. 2015, Johnson and Kipfmueller 2016, Meunier et al. 2019b) and assessed the sensitivity of our major conclusions to this convention by repeating analyses with ring-boundary scars assigned to the previous year (Supplementary Material). We correlated ring width patterns to master chronologies for the region (Wendland and Swain Henselman 2002, Stambaugh and Guyette 2013, Stambaugh et al. 2013) using Cybis CDendro version 9.3.1 to assist with crossdating (Larsson 2018). We independently verified crossdating with two individual researchers. We compiled and analyzed fire scar data using Fire History Analysis and Exploration System (FHAES version 2.0.2) and the burnr package in R version 4.0.2 (Brewer et al. 2015, Malevich et al. 2018).

Table 1
Mean fire return intervals (MFRI) among hemiboreal peatlands of the upper Great Lakes Region.

Site	Area sampled (ha)	Crossdated samples	No. fire years	All fires MFRI (yr)	10% MFRI (yr)	25% MFRI (yr)	Landscape MFRI (yr)	Time span (yrs)
Haymeadow Flowage	210	26	25	8	10	18	7	1785–1944
Ramsey Lake	930	41	40	13	18	24	27	1637–1932
Betchler Lake	1220	62	77	10	15	31	21	1548–1955

Notes: Number of fire years corresponds to all years with fire events regardless of number of samples scarred. Mean fire return intervals (MFRI) were estimated only for fire events on at least two samples. Successive filtering (e.g., fire years occurred on ≥10% of fire-scarred samples and fire years occurred on ≥25% of fire-scarred samples) identifies more widespread fire events. Landscape mean fire return intervals were estimated for fire years recorded on more than two forested uplands within and surrounding peatlands. Time span corresponds to span between first and last fire year.
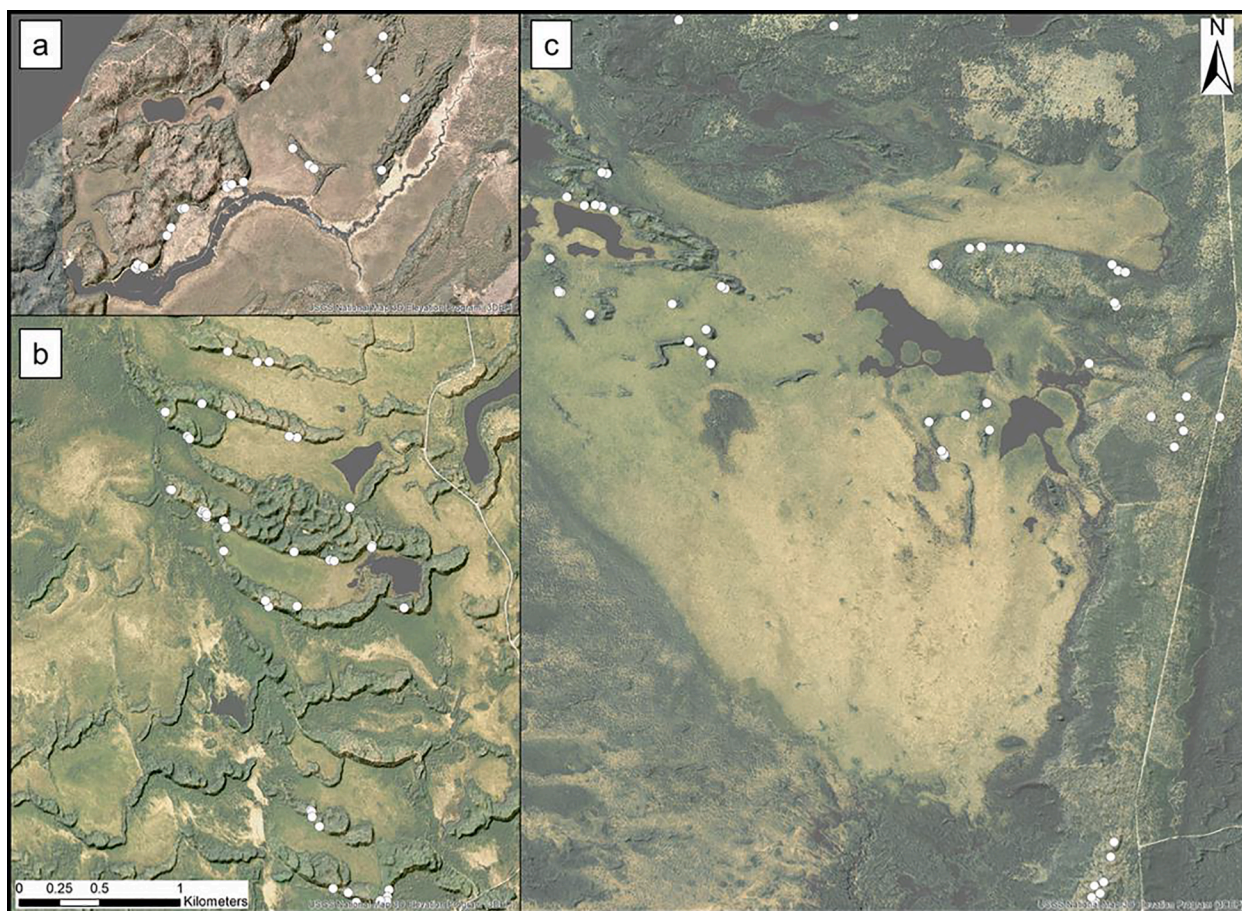
Fig. 2. Fire-scarred tree samples on forested uplands within and surrounding peatlands for (a) Haymeadow Flowage, (b) Ramsey Lake, and (c) Betchler Lake. Leaf-off aerial imagery has been overlaid with the USGS 3D Elevation Program Bare Earth Dynamic Elevation Model to distinguish vegetational and topographical differences used to delineate forested uplands within and surrounding peatlands.

We analyzed fire frequency by estimating mean fire return intervals and filtering to identify synchronous, and more widespread, fire years. Level of filtering provides evidence of more widespread fires by selecting only fire events that are recorded by multiple samples at a study site (e. g., 10% or 25% of all samples; Farris et al. 2010, 2013, Meunier and Shea 2020). Spatially distributed fire-scarred tree samples record fires relative to area burned, with larger percentage of fire-scarred trees positively correlated with total area burned (Farris et al. 2010, Swetnam and Baisan 2003). We estimated mean fire return intervals at each site for fire years recorded on at least two samples for (1) all fire years with at least two samples recording; (2) fire years in which ≥10% of samples were scarred, (3) fire years in which ≥25% of samples were scarred; and (4) landscape fire years that were recorded on more than two forested uplands within and surrounding the peatlands. We assumed that synchronous fire events on multiple forested uplands (within and surrounding peatland sites) were indicative of widespread fires that burned across peatland landscapes. We omitted single-fire scar years to avoid including single-lightning scarred trees that may have been scarred but where fire did not spread. Using two or more fire-scarred samples avoided such events while still retaining small but ecologically significant fires.

We evaluated climate-fire relationships by superimposing fire years on a regional drought reconstruction and with superposed epoch analyses in the burnr package in R version 4.0.2 to compare regional interannual drought with the aggregated fire years from successive filtering (Grissino Mayer and Swetnam 2000, Cook et al. 2007). We averaged summer (June–August) Palmer Drought Severity Index (PDSI) for six PDSI grid points (206, 207, 215, 216, 224, 225) across Wisconsin and Michigan to reconstruct regional drought patterns during the period 1650–1950 when there was the most temporal overlap among tree-ring records (Cook et al. 2007, Falk et al. 2011). We analyzed climate-fire relationships for successive levels of filtering to identify more widespread fire events. We plotted fire years on averaged PDSI time series from 1650 to 1950 to evaluate climate-fire conditions (Palmer 1965). We also used superposed epoch analysis to compare climate conditions (averaged PDSI) in fire event years, and conditions prior to and following fire years, to randomly selected years from 1650 to 1950. We used 1000 non-parametric simulations for bootstrapped confidence intervals to assess statistical significance (p-$value$ < 0.05) of departure from mean annual PDSI for fire years, as well as for two years prior to and after fire years (Grissino Mayer and Swetnam 2000, Malevich et al. 2018).

3. Results

We collected 220 fire-scarred tree samples in three hemiboreal peatlands across the upper Great Lakes Region from 2018 to 2019. We crossdated 129 samples (60% of all samples) spanning 1520 to 2019 and determined exact calendar year for 414 fire scars (128 unique fire years) ranging from 1548 to 1955 (Fig. 3). The number of samples we collected within sites directly correlated to the size of peatlands, with more sampling in larger sites (Table 1). Temporal extent of tree-ring records varied across the three sites with the shortest at Haymeadow Flowage (first year 1697) and the longest at Betchler Lake (first year 1520).

Prior to 1955 fires were historically frequent across peatland sites, with within-site mean fire return intervals from 7 to 31 years depending
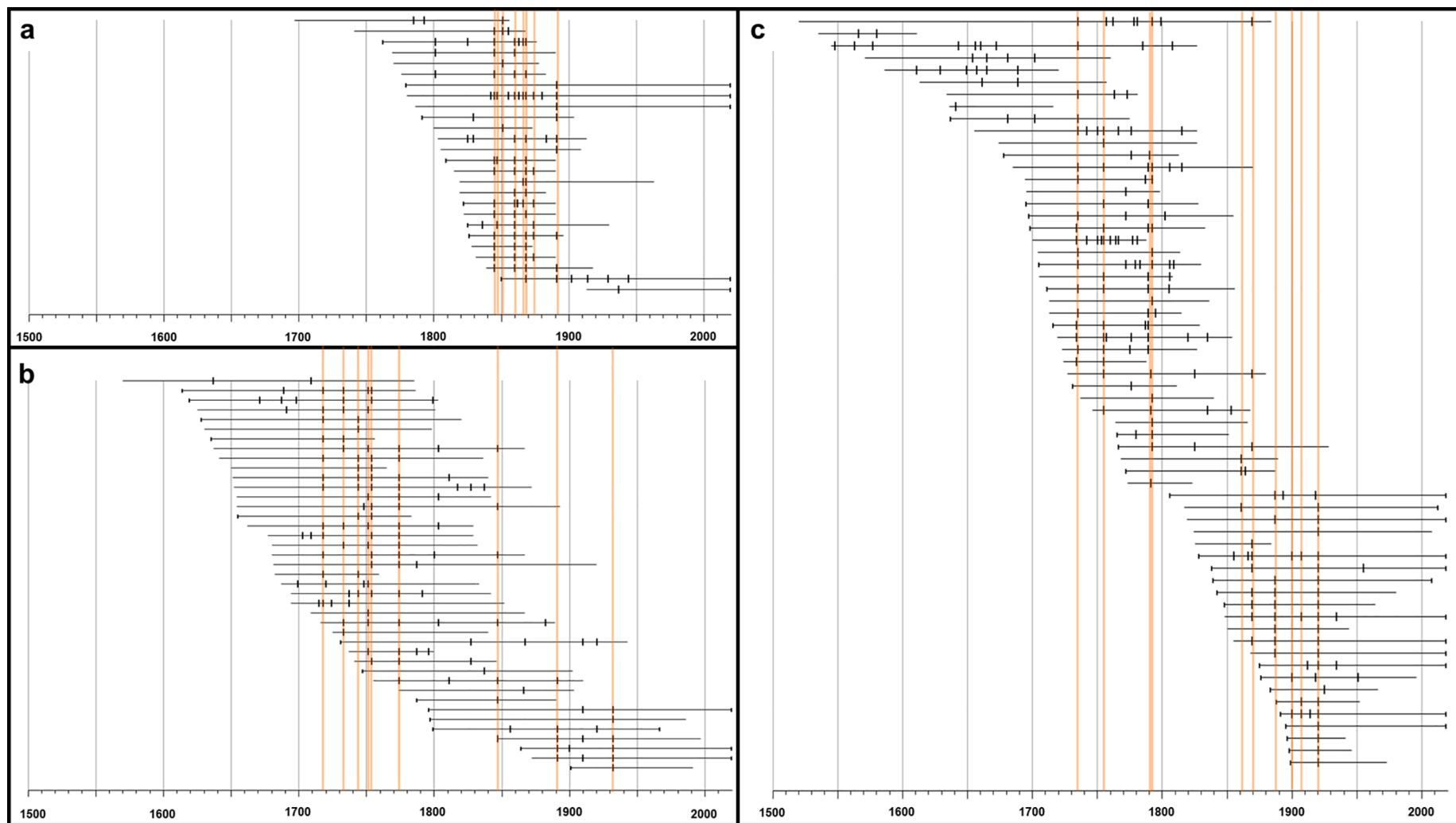
Fig. 3. Fire histories for three hemiboreal peatlands across the upper Great Lakes Region arranged by site. (a) Haymeadow Flowage, (b) Ramsey Lake, and (c) Betchler Lake. Each horizontal line is a sample (remnant stump, standing snag, fallen snag, or living tree), longer black vertical lines are recorded fire events, and shorter black lines are pith/bark years. Orange vertical lines highlight years where fire events were recorded on more than two forested uplands within and surrounding peatlands representing widespread fire years.

on site and level of filtering (Table 1). Mean fire return intervals increased with successive filtering levels as we selected for more widespread events. Filtering by synchronous fire years on forested uplands, which we expected to yield the longest mean fire intervals, produced results comparable to 10% and 25% filtering levels (7–27 vs. 10–31 years, Table 1).

Fire scars for which we could assign intra-annual ring position (53.7%) primarily occurred in the dormant and latewood positions (Table 2). Fire scars recorded at Haymeadow Flowage ($n = 91$) and Betchler Lake ($n = 190$) for which ring position was assigned were primarily within dormant ring positions, indicating these fire scars formed either after onset of dormancy (i.e., late fall) or prior to new wood formation (i.e., early spring) of the next year. Fire scars at Ramsey Lake ($n = 132$), for which ring position was assigned were predominantly in the latewood position (i.e., late growing season). Generally, fire seasonality was mixed, with fire events occurring in dormant, earlywood, and latewood positions. Sensitivity analyses (Supplementary Material) confirmed major conclusions were the same regardless of the year dormant fire scars (143 out of 413 total fire scars) were assigned to.

Fire years were synchronous among forested uplands within and surrounding all peatlands (Fig. 3 a-c), indicating fires likely burned across the peatland complexes. This pattern was independent of filtering method. Twenty percent of all fire years were synchronous among forested uplands within and surrounding peatlands and two of these synchronous fire years (1847 and 1891) occurred among multiple sites (Ramsey Lake and Haymeadow Flowage). We found five synchronous fire years in more than two sites (1787, 1825, 1847, 1891, and 1920) for fire years that scarred a minimum of two samples. At Haymeadow Flowage 48% of fire years were detected on only one sample (Fig. 3a), while 53% and 61% of fire years were detected on only one sample at Ramsey and Betchler Lakes respectively (Fig. 3b, Fig. 3c).

More than a quarter of fire years detected occurred during moderate regional drought and less than five percent of all fire events occurred during severe regional drought (Table 3; Palmer 1965). Widespread fire years with ≥25% of samples scarred and fires recorded across multiple peatlands occurred during regional mild and moderate droughts (Fig. 4; Palmer 1965). Only two fire years (1665 and 1910) occurred during regionally severe drought and no fire years occurred during extreme drought (Fig. 4; Palmer 1965). Fire years among all of the three peatland sites were associated with significantly (*p-value* < 0.05*) dry conditions across all filters (Fig. 4). The year preceding fire years was also associated with significantly (*p-value* < 0.05) dry conditions except for the smallest fire years where at least two samples were scarred (Fig. 4).

4. Discussion

Peatlands in the hemiboreal zone differ from those in most of the North American boreal zone (Heinselman 1963, 1973, Schulte and

Table 2

Percentages of fire scars identified to dormant, earlywood, and latewood positions within tree rings and fire scars where ring position was not determined among hemiboreal peatlands of the upper Great Lakes Region.

Site	Unknown fire scars	Dormant fire scars	Earlywood fire scars	Latewood fire scars
Haymeadow Flowage	42.9%	50.5%	6.6%	0.0%
Ramsey Lake	46.2%	12.9%	3.8%	37.1%
Betchler Lake	47.9%	42.1%	0.5%	9.5%

Notes: Percentages were determined out of total number of fire scars at each site: Haymeadow Flowage (n = 91), Ramsey Lake (n = 132), and Betchler Lake (n = 190). Dormant corresponds to fire scars occurring between the latewood and earlywood ring margins and is assigned to the following earlywood year. Earlywood corresponds to fire scars occurring at any position (early, middle, or late) in the earlywood portion of the tree ring. Latewood corresponds to fire scars occurring at latewood positions in the tree ring.

Table 3

Percentages of fire years in corresponding drought conditions (Palmer 1965) among hemiboreal peatlands of the upper Great Lakes Region.

Drought condition	All fire years	10% scarred fire years	25% scarred fire years	Landscape fire years
Wetter, near normal, incipient drought	66.7%	66.7%	63.7%	64.0%
Mild and moderate drought	29.8%	28.2%	31.8%	36.0%
Severe drought	3.5%	5.1%	4.5%	0.0%

Notes: All fire years are years with fire events on at least two samples. Filtering (e.g., fire year occurred on ≥10% of fire-scarred samples and fire year occurred on ≥25% of fire-scarred samples) at the landscape scale identifies more widespread fire events. Landscape fire years are fire events recorded on > two forested uplands within and surrounding peatlands. Drought conditions are designations from Palmer 1965 with wetter, near normal, and incipient drought corresponding to PDSI ≥ −0.49, mild and moderate drought corresponding to −2.99 ≤ PDSI ≤ −0.50, and severe drought PDSI ≤ −3.00.

Mladenoff 2005). Historical fire regimes in hemiboreal peatlands have largely been reconstructed using methods designed to capture infrequent high-severity fires (Whitney 1986, Cleland et al. 2004) that are typical for the North American boreal zone and burn thousands of hectares (Wein et al. 1983, Zoltai et al. 1998, Kasischke and Turetsky 2006). Our methods reconstructed fire regimes at finer spatial and temporal scales and we detected frequent low-severity fire events, which have been largely overlooked in North American peatland fire ecology (Cleland et al. 2004, Booth et al. 2004, Dickmann and Cleland, 2005). Our results indicate that low-severity fire events were frequent (7–31 year mean fire return intervals; Table 1), widespread (Fig. 3), and an important component of hemiboreal peatland fire regimes. We sampled long-lived, fire-adapted and rot-resistant *Pinus resinosa* on forested uplands within and surrounding several peatland complexes to reconstruct low- to moderate-severity fire events using fine scale (annual to intra-annual resolution) dendrochronology. Moreover, we found that fire years did not occur during severe annual drought across the region but rather most often occurred during regional moderate drought conditions (Fig. 4).

Mean fire return intervals in our study sites (7–31 years; Table 1) were comparable to Eurasian boreal systems where more frequent and less severe fire is a key ecological process (de Groot et al. 2013, Drobyshev et al. 2014). Hemiboreal peatland fire regimes have been characterized by mean fire intervals of 100–200 years (Bergeron et al. 2004b, Whitney 1986, Cleland et al. 2004), which is considerably longer than the intervals we found, and this difference is likely a result of different methodologies. Our results suggest that it is time to reassess the role of fire in hemiboreal peatlands and include both high- and low-severity fire when describing fire regimes of these systems. The exclusion of low-severity fire in hemiboreal peatlands since the mid-1900s (Fig. 3) could have unintended ecological consequences including losing fire-adapted species and changing fuels that carry fire which could contribute to reduced fire resistance of hemiboreal peatlands under a changing climate.

We analyzed synchrony of fire events within and among sites to estimate landscape (across uplands within and surrounding peatlands) and regional (among sites) scale fires and identify widespread fire years. Fires are spatially heterogeneous, and while fire scars cannot capture the spatial complexity or continuity of burning, fire-scar synchrony accurately represents area burned (Farris et al. 2010, 2013). Synchronous scarring results from widespread fires burning within and among sites (Farris et al. 2010) and is a useful way to understand fire events at multiple spatial scales (Morgan et al. 2001, Meunier and Shea 2020). Fire was synchronous and widespread (Fig. 3) within peatlands we studied including years like 1891 - a regionally significant fire year recorded by other studies across the region (Drobyshev et al. 2008,
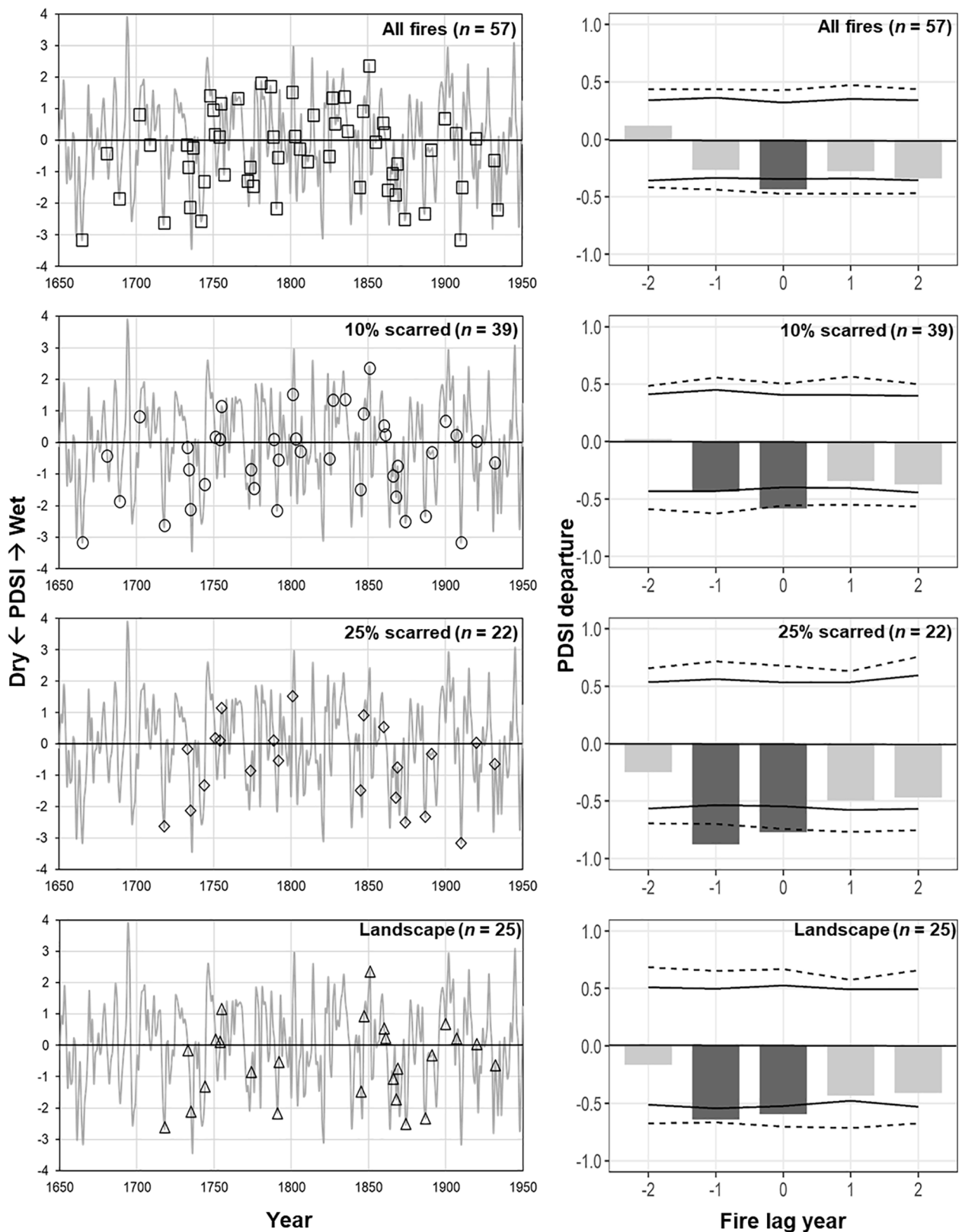
Fig. 4. Plotted average summer Palmer Drought Severity Index (PDSI; Cook et al. 2007) with fire years superimposed on the PDSI time series and superposed epoch analyses of departure from average PDSI across the upper Great Lakes Region during fire years. Fire years included years detected among the three hemiboreal peatland sites for all fire events recorded on at least two samples, fire events recorded ≥10% of samples, ≥25% samples, and fire events that occurred on more than two forested uplands within and surrounding peatlands at each site (Landscape). Positive PDSI indicate wet conditions and negative indicate dry conditions. Dark grey bars indicate a significant departure (*p-value* < 0.05) from average summer PDSI. Solid horizontal lines correspond to 95% confidence interval and dashed lines are 99% confidence interval.

Muzika et al. 2015, Meunier and Shea 2020). We found a high level of synchrony of fire events among forested uplands within and surrounding peatlands, suggesting that fires were burning across different ecosystems within the larger landscapes. Similarly, we found relatively minor effects of different filtering levels (e.g., 10% or 25 % scarred) also suggesting fires were widespread. However, we did not find a high degree of synchrony of fire years across the three different peatland complexes. This may be an artifact of our low sample depth, resulting in poor temporal overlap of chronologies among sites, and perhaps related to extensive distances among sites (Fig. 1), but it also highlights important variability in how climate, vegetation, and fire interact among different hemiboreal peatlands.

Determining seasonality is especially difficult in peatlands where successive summer droughts, which we detected in our SEA, could cause fires to burn continuously from fall into early spring (Scholten et al. 2021) corresponding to trees being scarred in either of two years or even in both years with latewood, dormant, and earlywood scar positions possibly resulting from the same fire event. Indeed, we observed a preponderance of back-to-back fire years at Betchler Lake including known large fire events (e.g., 1734/1735 and 1791/1792) which could be either fires burning across multiple seasons or multiple fire events, as fuel limitations are unlikely in this region compared to semi-arid regions. Similarly, there is little research in the Upper Great Lakes region on phenology of wood development hence no information on when latewood or earlywood formation begins and ends in red pine. However, our dating is consistent with other studies in this region including large fire years (Heinselman 1973, Drobyshev et al. 2008, Muzika et al. 2015, Guyette et al. 2016, Johnson and Kipfmueller 2016, Kipfmueller et al. 2017, Meunier et al. 2019a, Meunier et al. 2019b, Meunier and Shea 2020), and our major conclusions were the same regardless of whether dormant fire scars (143 of 413 total fire scars) were assigned to the previous or subsequent year (Supplemental Material).

Climatically driven fire regimes characterized by high-severity fire are typical of North American boreal ecosystems (Wein et al. 1983, Zoltai et al. 1998, Kasischke and Turetsky 2006) and they are also an important part of North American hemiboreal landscapes (Heinselman 1965, Whitney 1986). While climate effects are often broad in scale, localized influences of plant species and ecosystem processes can also have strong influences on fire regime characteristics (Scheller and Mladenoff 2005, Loudermilk et al. 2013, Walker et al. 2020). Disparity among drivers of fire dynamics at fine scales in the North American boreal forest has relevant implications for hemiboreal peatlands (Sedano and Randerson 2014) where species composition, intermixing of uplands and peatlands, and greater landscape heterogeneity likely shape fire regimes.

Somewhat counterintuitively fire events in our study sites occurred during moderate drought conditions but not severe drought (Fig. 4). While somewhat surprising for peatlands, large fire years in the Great Lakes Region more generally have also occurred during moderate, but not severe, droughts (Guyette et al. 2016, Meunier and Shea 2020). Local and seasonal conditions, not just annual to multi-year regional drought conditions, may be a determinant of fire frequency and fire severity in hemiboreal peatlands. This finding suggests that fire-vegetation-climate interactions in hemiboreal peatlands, specifically in relation to frequent widespread low-severity fire events, are strongly influenced by short-term seasonal drying, forest composition, and fire ecology of species, but not by severe regional droughts.

Localized and seasonal drying disproportionately affect peatland surface vegetation, contributing to heterogeneity in peatland surface fuels even while belowground peat soils retain water (Shetler et al. 2008, Benscoter et al. 2015). Patterning in peatland surface fuels increases protection of peat soils by supporting rapid lateral fire movement through dried surface fuels while preventing vertical ground fire spread, limiting prolonged smoldering in peat soils, and preventing consumption of deeper peats (Shetler et al. 2008, Benscoter and Vitt 2008, Benscoter et al. 2015). These patterns are especially evident in transitional hemiboreal peatlands like poor fens where peat remains inundated with water throughout the year while finer surface fuels like sedges atop the peat dry out, promoting fire spread laterally across peatlands while vertical movement into peat soils is inhibited. These self-organizing patterns in peatland surface vegetation maintain peatland ecosystems' function and are reinforced by low- to moderate-severity fire (Benscoter et al. 2015). Frequent low-severity fires maintain diversity in peatlands by maintaining diverse fire-adapted plant communities, and long fire-free intervals in peatlands could result in decreased ecosystem stability and greater vulnerability to future disturbances (Benscoter et al. 2015, Flanagan et al. 2020).

While the role of fire varies widely among peatlands around the globe (Zoltai et al. 1998), frequent and widespread low-severity fire events play an integral part in the maintenance of peatlands including reducing encroachment by woody and non-peatland vegetation. This was particularly evident in the hemiboreal peatlands we studied with high abundances of fire-adapted plant communities (red and jack pine forests) and evidence of frequent and widespread low-severity fire events historically (fire-scarred trees on forested upland islands within expansive peatlands). Species composition (high proportion of fire-adapted species like *Pinus resinosa*), peatland surface fuel patterning, and localized drying likely maintained historical fire regimes in hemiboreal peatlands. Local variability in fire frequencies is also influenced by natural and anthropogenic ignition sources and barriers to fire spread (Falk et al. 2011). Altered fire regimes in peatlands, related to both increasingly severe fires driven by climate change and suppression of frequent and widespread low-severity fire, may destabilize peatland ecosystems making them more vulnerable to climate change and future disturbances (Flanagan et al. 2020). Peatlands in the Great Lakes Region are among the most vulnerable ecosystems under future climate change (Dahl 2011, Angel et al. 2018) and understanding the role of fire in relation to resilience in hemiboreal peatlands over the last 500 years is a necessary first step to determine how they will be affected by, and contribute to, a warming world.

CRediT authorship contribution statement

Colleen M. Sutheimer: Conceptualization, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Jed Meunier:** Conceptualization, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Sara C. Hotchkiss:** Conceptualization, Writing - review & editing, Supervision. **Eric Rebitzke:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition. **Volker C. Radeloff:** Conceptualization, Writing - review & editing, Supervision.

Declaration of Competing Interest

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

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improved the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119561.

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