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RESEARCH ARTICLE

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More than one way to kill a spruce forest: The role of fire and climate in the late-glacial termination of spruce woodlands across the southern Great Lakes

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Abstract

1. In the southern Great Lakes Region, North America, between 19,000 and 8,000 years ago, temperatures rose by 2.5–6.5°C and spruce *Picea* forests/woodlands were replaced by mixed-deciduous or pine *Pinus* forests. The demise of *Picea* forests/woodlands during the last deglaciation offers a model system for studying how changing climate and disturbance regimes interact to trigger declines of dominant species and vegetation-type conversions.
2. The role of rising temperatures in driving the regional demise of *Picea* forests/woodlands is widely accepted, but the role of fire is poorly understood. We studied the effect of changing fire activity on *Picea* declines and rates of vegetation composition change using fossil pollen and macroscopic charcoal from five high-resolution lake sediment records.
3. The decline of *Picea* forests/woodlands followed two distinct patterns. At two sites (Stotzel-Leis and Silver Lake), fire activity reached maximum levels during the declines and both charcoal accumulation rates and fire frequency were significantly and positively associated with vegetation composition change rates. At these sites, *Picea* declined to low levels by 14 kyr BP and was largely replaced by deciduous hardwood taxa like ash *Fraxinus*, hop-hornbeam/hornbeam *Ostrya/Carpinus* and elm *Ulmus*. However, this ecosystem transition was reversible, as *Picea* re-established at lower abundances during the Younger Dryas.
4. At the other three sites, there was no statistical relationship between charcoal accumulation and vegetation composition change rates, though fire frequency was a

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significant predictor of rates of vegetation change at Appleman Lake and Triangle Lake Bog. At these sites, *Picea* declined gradually over several thousand years, was replaced by deciduous hardwoods and high levels of *Pinus* and did not re-establish during the Younger Dryas.

5. *Synthesis*. Fire does not appear to have been necessary for the climate-driven loss of *Picea* woodlands during the last deglaciation, but increased fire frequency accelerated the decline of *Picea* in some areas by clearing the way for thermophilous deciduous hardwood taxa. Hence, warming and intensified fire regimes likely interacted in the past to cause abrupt losses of coniferous forests and could again in the coming decades.

KEYWORDS

abrupt change, boreal forests, climate change, disturbance, fire history, palaeoecology, pleistocene, regime shifts

1 | INTRODUCTION

Anthropogenic global warming is creating novel disturbance regimes, and the combination of warming and novel disturbance is altering the structure and function of boreal forest and taiga ecosystems in North America and Eurasia, with the potential to cause vegetation-type conversions (Girardin et al., 2009; Johnstone et al., 2016; Keeley et al., 2019; Noce et al., 2019; Turner, 2010). In North American boreal forests, temperatures are expected to rise by 4–11°C over this century (IPCC, 2014), causing fires to increase in size, severity, and frequency (Balshi et al., 2009; Cattau et al., 2020; Flannigan et al., 2000, 2005; Kasischke & Turetsky, 2006). The combination of warming and intensified fire regimes in boreal ecosystems can trigger abrupt transitions to new vegetation states, as boreal species are replaced by species that are well-suited to new climatic conditions (Chapin et al., 2004; Johnstone, et al., 2010; Weber & Flannigan, 1997). These transitions have already been documented in parts of the boreal forest, where dominant tree species have shifted from conifers like spruce *Picea* to broadleaf deciduous trees like aspen*Populus* and birch *Betula* (Beck et al., 2011; Johnstone & Chapin, 2006; Johnstone et al., 2010; Wang et al., 2020). These changes in boreal forest structure and composition cascade to effects on carbon sequestration, geomorphic processes, habitat availability and other ecosystem functions (Lininger & Wohl, 2019; Miquelajauregui et al., 2019; Turner et al., 2019; Whitman et al., 2017).

A similar ecosystem transition occurred across much of mid-latitude eastern North America during the end of the last ice age, offering the opportunity to study how rising temperatures and changes in fire activity interact to produce ecosystem transitions and regulate the pace of ecological change. Between 19,000 and 8,000 years ago, global surface temperatures rose by 3–5°C (Clark et al., 2012; Shakun & Carlson, 2010), including periods of abrupt warming that were similar in rate and magnitude to the rates of warming projected for this century (Williams & Burke, 2019). In eastern North America and elsewhere, major vegetation transitions occurred in response, as range boundaries of taxa shifted individualistically and usually northward, at both leading and trailing edges (Ordonez & Williams, 2013; Prentice et al., 1991). The role of fire in these ecosystem transitions is unclear, although in western North America, deglacial warming has been linked to increased biomass burning and fire activity (Marlon et al., 2009; Power et al., 2008).

In the Great Lakes Region of the United States, temperatures warmed by roughly 6.5°C during the late-glacial period, insolation became highly seasonal, and temperatures may have become highly seasonal as well (Fastovich et al., 2020; Kutzbach & Guetter, 1986; Williams & Jackson, 2007). *Picea*-dominated boreal forests and woodlands, which covered the landscape as the Laurentide Ice Sheet retreated, declined and were replaced by deciduous hardwoods, primarily ash *Fraxinus*, hop-hornbeam/hornbeam *Ostrya/Carpinus*, and elm *Ulmus*, as well as pine *Pinus*(Overpeck et al., 1992; Prentice et al., 1991; Webb, 1988; Williams et al., 2001, 2004). Some of these plant assemblages lack any equivalent vegetation type in North America today, so they have been described as 'no-analog' vegetation (Jackson & Williams, 2004; Overpeck et al., 1992; Williams & Jackson, 2007; Williams et al., 2001). Lake sediments analysed for branched glycerol dialkyl glycerol tetraethers (brGDGTs), a temperature proxy, indicate that the formation of mixed deciduous forests followed initial warming of several degrees during the late-glacial period, suggesting that temperature was a major driver of this transition (Fastovich et al., 2020; Watson et al., 2018). Changes in moisture availability likely also played a role, though the hydroclimate of the late-glacial period is poorly understood. Some pollen and sub-fossil wood isotope records suggest wet late-glacial conditions in the Midwest (Gonzales & Grimm, 2009; Voelker et al., 2015), while aeolian records indicate enhanced dune activity and dry conditions in the Midwest during the Younger Dryas (Campbell et al., 2011; Wang et al., 2012). Another factor that could have contributed to deglacial vegetation changes is loss of megafauna. The late-glacial decline of megafaunal populations released deciduous hardwoods

from herbivory pressure and may have facilitated the formation of no-analog communities (Gill et al., 2009, 2012). Individual sites have documented an increase in fire activity prior to or during the rise of deciduous hardwoods and formation of no-analog plant associations (Gill et al., 2009, 2012; Williams et al., 2015). However, no study has systematically assessed how rising temperatures and fire activity interacted to regulate the pace of and drive late-glacial losses of *Picea* forests/woodlands across multiple sites.

In this study, we analysed high-resolution vegetation and fire records from five sites across the southern Great Lakes Region to examine the impact of climate and fire activity on the late-glacial decline of *Picea* forests/woodlands. This study combines new macroscopic charcoal and fossil pollen records from Triangle Lake Bog, Ohio, with new charcoal and pre-existing pollen records from Stotzel-Leis, Ohio (Watson et al., 2018) and Bonnett Lake, Ohio (Fastovich et al., 2020), and pre-existing charcoal and pollen records from Appleman Lake, Indiana (Gill et al., 2009) and Silver Lake, Ohio (Gill et al., 2012). We aimed to address the following questions: (a) was intensified fire activity a necessary agent of change for the decline of *Picea* woodlands across the southern Great Lakes Region and (b) did fire accelerate the transition from *Picea* woodlands to mixed deciduous forests? A better understanding of the combined effect of warming and enhanced fire activity on late-glacial boreal systems will help inform how modern boreal coniferous forests are likely to respond to temperature and fire regime change in the coming decades.

1.1 | Study area

The southern Great Lakes Region of the United States has a mid-continental climate characterized by large seasonal differences in temperature. Summers are hot and humid with an average temperature of 22°C, and winters are cold and snowy with an average temperature of −3°C (Midwestern Regional Climate Center, 1981–2010 observations). The mean annual precipitation is 1,000 mm and precipitation is distributed relatively evenly throughout the year, though it is slightly higher in the spring and summer (Midwestern Regional Climate Center, 1981–2010 observations). The study area is close to Great Lakes Michigan and Erie, which has moderate seasonal temperature changes and increase moisture content in the air (Andresen et al., 2012). At the time of Euro-American settlement, the study area was covered by temperate broadleaf deciduous forests and savannas, with major species including American beech *Fagus grandifolia*, oak species *Quercus*, hickory species *Carya*, *Fraxinus* and *Ulmus* (Paciorek et al., 2017). These forests have been heavily modified by agricultural and other land use, with only small patches of mostly secondary forest remaining (Heilman et al., 2002).

Sedimentary bedrock types, mainly shales, siltstones and sandstones, dominate the regional geology (Indiana Geological Survey, 1990; Ohio Geological Survey, 2006). Surface topography has been shaped by glacial action during the Pleistocene glaciations, as cycles of glacial advance and retreat left till deposits and landforms including moraines, kettle lakes and kames (Glover et al., 2011). From west to east, the study area spans a range of topography, from the low-relief sandy glacial outwash of the Indiana Lake Plain to the rolling hills and moraines of the western Ohio Till Plain to the moderate relief and steep river valleys of the eastern Ohio Glaciated Allegheny Plateau (Indiana Geological Survey, 2001; Ohio Geological Survey, 1998).

The individual study sites are kettle lakes and depressions that vary in size and soil texture and drainage properties (Figure 1, USDA Web Soil Survey, accessed July 2019, available online). Appleman Lake, on the Lake Plain of Indiana, is a 21-ha kettle lake with very poorly drained peaty soils on the east side and well-drained fine sandy loams west of the lake. On the western Ohio Till Plain, Stotzel-Leis is a 1.1-ha wetland centred in a kettle depression, surrounded by a combination of somewhat poorly drained and well-drained silt loams. Silver Lake, also located on the Till Plain, is a 17-ha kettle lake with a very poorly drained silty clay loam unit on the north and west sides and well-drained silt loams surrounding the rest of the lake. On the eastern Ohio Glaciated Allegheny Plateau, Bonnett Lake is a



FIGURE 1 Location of kettle lake study sites in the southern Great Lakes Region, with the inset showing this region in the context of the contiguous U.S. The fossil pollen and macroscopic charcoal records for Triangle Lake Bog are presented for the first time in this study, as are the macroscopic charcoal records for Stotzel-Leis and Bonnett Lake, while the other fossil pollen and macroscopic charcoal records have been previously reported (Fastovich et al., 2020; Gill et al., 2009, 2012; Watson et al., 2018). Silver Lake and Bonnett Lake were also analysed for brGDGTs (Fastovich et al., 2020; Watson et al., 2018)

41-ha kettle lake that is directly surrounded by very poorly drained peaty soils and silty clay loams, with well-drained silt loams surrounding these units. Also on the Allegheny Plateau, Triangle Lake Bog is a 0.5-ha kettle hole bog within a 5.5-ha wetland that has mostly very poorly drained peaty soils and poorly drained silt loams. Peat moss *Sphagnum* has filled this lake from the edges inward, developing into a floating vegetation mat that covers most of the lake surface. The floating mat includes other species such as swamp loosestrife *Decodon verticillatus*, leatherleaf *Chamaedaphne calyculata*, highbush blueberry *Vaccinium corymbosum* and steeplebush *Spiraea tomentosa*. Today, Triangle Lake Bog and the surrounding vegetation are protected by the Ohio Department of Natural Resources (ODNR) as part of a 61-ha state nature preserve.

2 | MATERIALS AND METHODS

2.1 | Overview

This regional-scale study of vegetation–fire interactions integrates new and recently published records from five sites in the Indiana and Ohio region: Appleman Lake, Stotzel-Leis, Silver Lake, Bonnett Lake and Triangle Lake Bog. The lake sediment core from Triangle Lake Bog is a new record that was radiocarbon dated and analysed for fossil pollen and charcoal. The charcoal records for Triangle Lake Bog, Stotzel-Leis and Bonnett Lake are presented here for the first time, while those for Appleman and Silver Lakes have been previously published (Gill et al., 2009, 2012). The pollen records for all sites except Triangle Lake Bog have been previously published (Fastovich et al., 2020; Gill et al., 2009, 2012; Watson et al., 2018). Two sites, Silver and Bonnett Lakes, also have brGDGT temperature records (Fastovich et al., 2020; Watson et al., 2018). Age–depth models, pollen per cent abundances, charcoal accumulation rates and temperature reconstructions reported for these sites are the same as previously published, unless otherwise noted.

2.2 | Triangle Lake Bog coring and chronology

Two overlapping sediment cores were collected from the deepest portion of Triangle Lake Bog (41.119204°N, 81.262746°W) in August 2015. A Bolivian adapter was used to capture the sediment–water interface and a modified Livingstone piston corer was used for all following drives. Core A yielded 1,366 cm of sediment and Core B, in which drive intervals were offset downwards by 15 cm from Core A, yielded 1,350 cm of sediment. Core segments were measured and described in the field, then wrapped in plastic wrap and stored in split PVC tubes.

All cores were transferred to the National Lacustrine Core Facility (LacCore) at the University of Minnesota, where they were split longitudinally into halves, imaged and scanned for magnetic susceptibility and bulk density. Images were used to visually cross-correlate shared stratigraphic horizons in the two overlapping cores and create a composite core using the Corelyzer program (Table S1; Ito et al., 2018). All depths reported are for the composite core, which extends from 0 to 1,323.5 cm relative to core top.

The Triangle Lake Bog chronology was based on AMS radiocarbon dating of terrestrial plant macrofossils and pollen extracts (Table 1). Macrofossils were selected for initial dating, but a scarcity of upland plant macrofossils (likely due to taphonomic filtering by the bog and the floating vegetation mat that surrounds the lake) led us to extract fossil pollen from three depths for further dating, using procedures by Krause and Whitlock (2013). All samples were submitted to the University of California, Irvine's KECK Carbon Cycle AMS Laboratory or the National Ocean Science AMS facility at the Woods Hole Oceanographic Institution. Radiocarbon dates were calibrated to years before present (CE 1950) using IntCal13 (Reimer et al., 2013). Age models were developed using the RBACON package for Bayesian age modelling in R (Blaauw & Christen, 2011). The package divides a single core into many vertical sections and uses Markov chain Monte Carlo (MCMC) iterations to estimate

TABLE 1 List of all macrofossil and pollen samples, their ^{14}C ages and their calibrated ages used to build the age–depth model for Triangle Lake Bog

Laboratory ID	Core depth (cm)	^{14}C age and 1 − σ error	Calibrated median age (year BP)	95% Calibrated credible interval age range (year BP)	Dated material
NOSAMS-180328	215.5	4,015 ± 15	4,480	4,430–4,520	Wood fragment
NOSAMS-180329	672.5	9,275 ± 20	10,460	10,420–10,540	Wood fragment
NOSAMS-156610	814.5	10,200 ± 270	11,880	11,110–12,600	Terrestrial plant tissue
KCCAMS-205212	900	10,750 ± 25	12,700	12,680–12,710	Pollen
KCCAMS-205215	963.5	12,370 ± 30	14,340	14,210–14,600	Terrestrial plant tissue
KCCAMS-205211[a]	1,000[a]	16,505 ± 40[a]	19,930[a]	19,820–20,010[a]	Pollen[a]
NOSAMS-156611	1,085.5	12,600 ± 470	14,860	13,600–16,240	Conifer needle
KCCAMS-205210[a]	1,160[a]	20,395 ± 50[a]	24,470[a]	24,370–24,570[a]	Pollen[a]
NOSAMS-180330	1,260.5	14,310 ± 30	17,450	17,380–17,520	Wood fragment
NOSAMS-180331	1,301.5	14,220 ± 30	17,330	17,220–17,420	Wood fragment

[a]Outlier dates that lie outside the 95% confidence bounds of the Bacon age model.

the accumulation rate for each section and build the age–depth model. A new age model was run for Appleman Lake using RBACON and the site's original chronological controls, since the previously published age model was based on linear regression (Gill et al., 2009).

2.3 | Pollen and charcoal: Laboratory analyses and source areas

For all cores, subsamples of 1 cm^3 were taken at intervals of 4, 8 or 16 cm for pollen analysis. Samples were processed following standard protocols by Faegri et al. (1989). Prior to chemical processing, 1 ml of pollen spike suspension solution, which had a reported concentration of 5.0×10^4 polystyrene spheres/ml, was added to samples to determine pollen concentrations and accumulation rates (Davis et al., 1973). However, tests at LacCore revealed that a biofilm was growing on the batch of spike solution used for Stotzel-Leis, Bonnett Lake and Triangle Lake Bog, causing microspheres to adhere together (Heck, J., pers. comm., November 2018). Thus, the true concentration of the spike solution varied substantially among samples, making it impossible to calculate pollen accumulation rates for these three sites. Pollen accumulation rates are used as an alternate way to show changes in pollen abundances, as they are not subject to artefacts caused by the sum-to-one constraints for pollen percentages (but they are more sensitive than pollen percentages to variations in sedimentation rate and uncertainties in age–depth models; Davis, 1963; Davis et al., 1984). In the Supporting Information, we show pollen accumulation rates for Appleman and Silver Lakes to verify apparent changes observed in pollen percentage data (Figures S4 and S5). After processing, pollen grains were counted and identified at 40–100× magnification using a Zeiss compound light microscope and reference materials, including McAndrews et al. (1973), Kapp et al. (2000) and images from the Global Pollen Project (Martin et al., 2017). At least 300 pollen grains were identified per sample. All pollen counts are reported as a percentage of the total upland pollen sum.

For the Stotzel-Leis, Bonnett Lake and Triangle Lake Bog cores, subsamples of 1 cm^3 were taken at contiguous 1 cm intervals for charcoal analysis. Samples were processed following a modified version of protocols by Whitlock and Larsen (2001). Samples were first treated with 6% H_2O_2 then dried in a drying oven for 24 hr. Samples were then screened through a 125 μm sieve for Stotzel-Leis and Bonnett Lake and a 250-μm sieve for Triangle Lake Bog, rinsed with 6% H_2O_2 into plastic Petri dishes, and dried in the drying oven until all liquid was evaporated. Charcoal samples were counted on a gridded platform using a LW Scientific stereomicroscope and, for Triangle Lake Bog, identified as one of the nine morphotypes, which reflect fuel types (Jensen et al., 2007). Dark, porous, spongy, branched and bordered pit charcoal come from woody fuels, and cellular and fibrous charcoal come from herbaceous fuels. Charcoal identification was based on images from previous charcoal classification studies in the Great Lakes Region (Jensen et al., 2007; Tweiten et al., 2009).

The size fraction(s) of charcoal counted varied among sites. At Appleman and Silver Lakes, the fraction of charcoal >125 μm and the fraction of charcoal >250 μm were both counted. At Stotzel-Leis and Bonnett Lake, all charcoal >125 μm was counted, but the 250 μm fraction was not separately sieved or counted. At Triangle Lake Bog, only charcoal >250 μm was sieved and counted. To maximize intersite comparability, we analysed all records except Triangle Lake Bog at the >125 size fraction, aggregating the two size fractions for Appleman and Silver Lakes. In the Supporting Information, we show and assess Appleman and Silver Lake charcoal accumulation rates calculated with just charcoal >250 μm and with all charcoal >125 μm to confirm that trends align among the size factions (Figure S2).

While pollen and charcoal methods were consistent across sites, the lakes vary in area, which affects the source area of pollen and charcoal deposited in the lakes. Airborne pollen source area generally increases with lake area, though source area varies among taxa based on grain size and fall speed (Jackson, 1994; Jacobson & Bradshaw, 1981). Macroscopic charcoal particles are not transported far from the source fire before they are deposited in lakes via slopewash or airborne fall-out (Whitlock & Larsen, 2001). Thus, the pollen records represent larger source areas than the charcoal records, with source radii on the order of several hundred kilometres (Dawson et al., 2016; Trachsel et al., 2020) for Appleman, Silver and Bonnett Lakes (17–41 ha lake area) and tens of kilometres for Stotzel-Leis and Triangle Lake Bog (0.5–1.1 ha). Macroscopic charcoal is used to calculate fire frequency, which is interpreted to represent local fire history (within 1–3 km of each lake), and background charcoal, which typically integrates over a broader domain (>10 km) (Higuera et al., 2010).

2.4 | Numerical analyses

For each individual pollen record, vegetation zones were identified using stratigraphically constrained cluster analysis (CONISS) by the incremental sum-of-squares method in the RIOJA R package (Juggins, 2017). For each record, all non-aquatic pollen types that reached at least 1% were used for analysis. We then used Bayesian change point analysis to identify significant increases and decreases in the *Picea* pollen abundance time series using the *bcp* algorithm in R (Erdman & Emerson, 2007). We considered change points to be 'significant' when they had a posterior probability of at least 0.9, as visual inspection of the *bcp* results indicated that clearly defined changes in *Picea* abundance occurred when posterior probability was 0.9 or above. The *bcp* analysis does not explicitly differentiate among sources of uncertainty, for example, pollen count uncertainty, but it blends all of these sources when assessing significance of reported change points. Lastly, we estimated the rate of vegetation composition change for each record by taking the squared chord distance (SCD) between each

consecutive pair of pollen samples and dividing by the number of years between those pollen samples.

In all records, charcoal counts were converted to charcoal accumulation rates (CHAR) by multiplying charcoal concentrations (pieces/cm^3) by local sediment accumulation rates (cm/year). CHAR was interpolated to the median temporal resolution of each record, then decomposed into peak and background series using CharAnalysis (Version 1.1, see Table 2 for parameters; Higuera et al., 2009). Even though the charcoal records for Appleman and Silver Lakes have been previously published, these records were rerun in CharAnalysis to ensure consistent parameterizations for all sites. The background series was estimated using a robust Lowess smoother with a 700-year moving window, then was subtracted from the raw CHAR series to produce the peak charcoal series. Peaks were identified using a locally fitted Gaussian mixture model, then screened to see if they had a <5% chance of coming from a Poisson distribution of charcoal counts over the previous 75 years. If so, they were marked as 'significant' and interpreted to represent one or several closely adjacent within-watershed fire events (Higuera et al., 2010). Fire frequency was calculated from significant peaks with a 1,000-year moving window.

We first visualized the pollen and charcoal data by aligning the *Picea* pollen abundance time series and its change points with the CharAnalysis output to assess whether significant change points in *Picea* corresponded with periods of high or low charcoal accumulation rates and fire frequency. We then quantified the relationship between vegetation composition change and fire activity by running generalized additive models (GAMs) using the MGCV package in R (Wood, 2011). GAMs were first run to test rates of vegetation composition change as a function of charcoal accumulation rates, with charcoal accumulation rates designated as the smoothing parameter. Models were then run to test rates of vegetation composition change as a function of fire frequency, with fire frequency designated as the smoothing parameter. To account for temporal autocorrelation in the pollen and charcoal data, time-scaled residuals were added to the models as an error term (Carstensen et al., 2013). We fit separate GAMs for the *Picea*-dominated and other major vegetation zones established by CONISS, because we expected fire–vegetation relationships to vary among vegetation types. For Zone C, which had 10 observations or less at all sites except Triangle Lake Bog, GAMs were run without a smoothing parameter, which makes them generalized linear models (GLMs). Models for each zone were evaluated based on the significance of the smoothing parameter, the adjusted r^2 value, and the total deviance explained by the model (Tables S6 and S7).

For Silver and Bonnett Lakes, the two sites with brGDGT temperature records (Fastovich et al., 2020; Watson et al., 2018), we used the *approx* function in R to estimate temperature at times corresponding to pollen samples. The rate of temperature change was calculated by taking the temperature difference between each consecutive pair of pollen samples and dividing by the number of years between those pollen samples. We then took the absolute value of temperature change rates, as we assumed higher rates of vegetation composition change to be associated with high rates of temperature change regardless of direction. We ran GLMs to test the relationship between vegetation composition change and temperature change for each of the major vegetation zones in a similar procedure as the methods described above.

TABLE 2 The parameters used for running CharAnalysis on each site's charcoal record. The average SNI calculated by CharAnalysis is reported as a metric of how well each record is suited for peak identification analysis, with a SNI > 3 indicating sufficient separation between charcoal peaks and noise (Kelly et al., 2011)

	Parameter	Appleman Lake	Stotzel-Leis	Silver Lake	Bonnett Lake	Triangle Lake Bog
Pretreatment	Years interpolated	23 years	9 years	15 years	20 years	11 years
	Log transform	None	None	None	None	None
Smoothing	Method	Robust Lowess smoother	Robust Lowess smoother	Robust Lowess smoother	Robust Lowess smoother	Robust Lowess smoother
	Background smoothing window	700 years	700 years	700 years	700 years	700 years
Peak analysis	Peak identification	Residuals	Residuals	Residuals	Residuals	Residuals
	Threshold type	Locally defined	Locally defined	Locally defined	Locally defined	Locally defined
	Threshold method	Gaussian mixture model	Gaussian mixture model	Gaussian mixture model	Gaussian mixture model	Gaussian mixture model
Peak analysis results	Threshold (percentile of noise distribution)	0.99	0.99	0.99	0.99	0.99
	Fire frequency smoothing window	1,000 years	1,000 years	1,000 years	1,000 years	1,000 years
Post-analysis	Average signal-to-noise index (SNI)	4.07	5.28	5.6	3.67	5.73

3 | RESULTS

3.1 | Chronology and resolution

Ten radiocarbon dates were used to develop the age–depth model for Triangle Lake Bog (Figure 2). Two basal dates indicate that sediment began accumulating between 17.45 and 17.33 kyr BP, and eight additional dates constrain the age–depth relationship until 4.48 kyr BP, the age of the uppermost radiocarbon sample. All radiocarbon dates carry uncertainties of ±15–50 radiocarbon years except for two dates at 814.5 cm and 1,085.5 cm, which carry uncertainties of ±270 and ±470 radiocarbon years, respectively, due to low sample mass. Dated pollen had high analytical precision, but two of the three pollen dates were rejected as outliers because they were dated older than stratigraphically lower macrofossils. These inaccuracies may have resulted from resistant organic matter that was not fully removed during pollen processing. Pollen sampling temporal resolution ranged from 180 years, when samples were taken at 16 cm intervals, to 45 years, when samples were taken at 4 cm intervals. The temporal resolution for the contiguous 1-cm charcoal samples ranged from 8 to 25 years, with a median sample resolution of 11 years.

3.2 | Pollen-based vegetation history

CONISS analysis identified four distinct vegetation zones at Triangle Lake Bog and the other southern Great Lakes sites, with a consistent zonation across sites (Figure 3; Figure S3). Zone A, which extended from record onset until 15.8–14 kyr BP, was dominated by *Picea* (>65%). This interval contained small amounts of *Pinus* (<15%) and some cold-tolerant deciduous taxa, including alder *Alnus*, willow *Salix* and *Betula*. During this zone, upland herbs, primarily ragweed *Ambrosia*, mugwort *Artemisia*, sedges (Cyperaceae) and grasses (Poaceae), made up the understorey. The proportion of upland herbs varied across sites, reaching ~25% at Triangle Lake Bog but only ~10% at Bonnett Lake. The Zone A pollen assemblages indicate that *Picea* woodlands—open *Picea* forests with a tundra-like understorey—covered the southern Great Lakes Region early in the late-glacial period.

Zone B (from 15.8–14 kyr BP to 13.3–11.6 kyr BP) was marked by a decline in *Picea* pollen across all sites. However, the magnitude of this decline varied among sites. For example, at Silver Lake, *Picea* declined from ~70% to 30%, while at Triangle Lake Bog, *Picea* declined from ~50% to 30%. At all sites, *Picea* was replaced by deciduous hardwood taxa, including *Fraxinus*, *Ostrya/Carpinus* and *Ulmus*. The relative abundance of these hardwood taxa also varied among sites, as these taxa exceeded 45% at Stotzel-Leis but only reached ~25% at Appleman Lake. This combination of taxa suggests that the region was covered by mixed deciduous forests/woodlands, composed of waning populations of *Picea* and new populations of deciduous hardwood trees.

Zone C (from 13.3–11.6 kyr BP to 12–10.5 kyr BP) was marked at all sites by an increase in *Pinus* and a decline in deciduous hardwood taxa except for *Ulmus*, which increased or remained stable throughout the zone. At some sites, *Picea* recovered—the 'second spruce peak' in the Ohio region often associated with the return to colder conditions during the Younger Dryas (Shane & Anderson, 1993)—while at others, *Picea* did not. At Stotzel-Leis and Silver Lake, *Pinus* reached 15%–30% at the same time as the second *Picea* peak. At Appleman Lake, Bonnett Lake and Triangle Lake Bog, *Pinus* became highly abundant, reaching 60%–80%. These sites showed no evidence of the second *Picea* peak, instead, *Picea* continued to decline throughout Zone C at these sites. These pollen assemblages represent the development of closed coniferous forests, with forests containing a mix of *Pinus* and *Picea* at some sites and almost entirely *Pinus* at other sites. In the records where *Pinus* species were differentiated, jack pine *Pinus banksiana* made up the majority of *Pinus* through most of Zone C, with white pine *Pinus strobus*

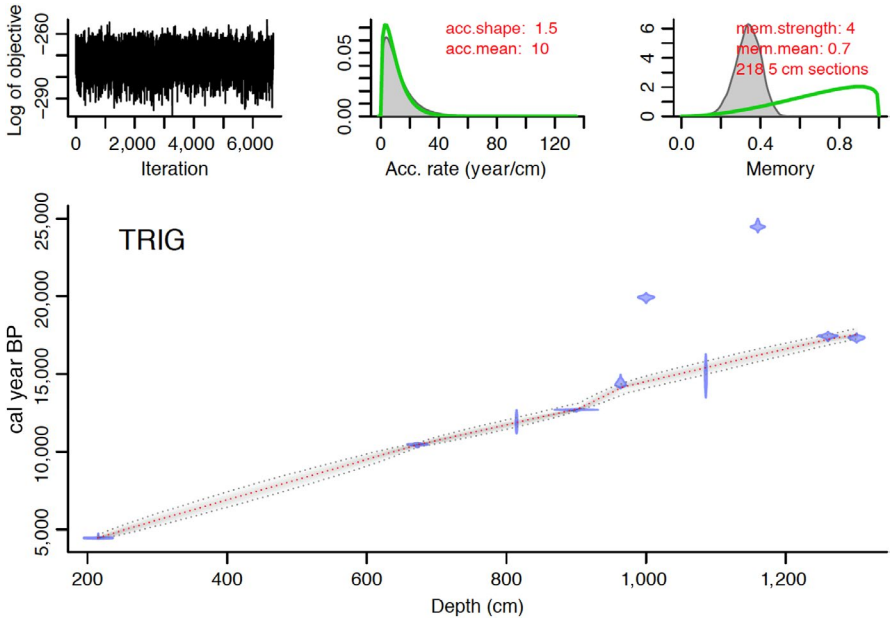


FIGURE 2 The Triangle Lake Bog age–depth model from the RBACON package (Blaauw & Christen, 2011), based on ^{14}C-calibrated dates. The inset panels show: on the left, the convergence of the model over iterations; in the middle, the prior (green) and posterior (grey) distributions for inverse sediment accumulation rate; and on the right, the prior (green) and posterior (grey) distributions for memory. The main panel shows the median predicted age (dashed red line) and the 95% credible interval (grey shading) for each depth, along with the calibrated age probability distributions (blue) for each ^{14}C sample

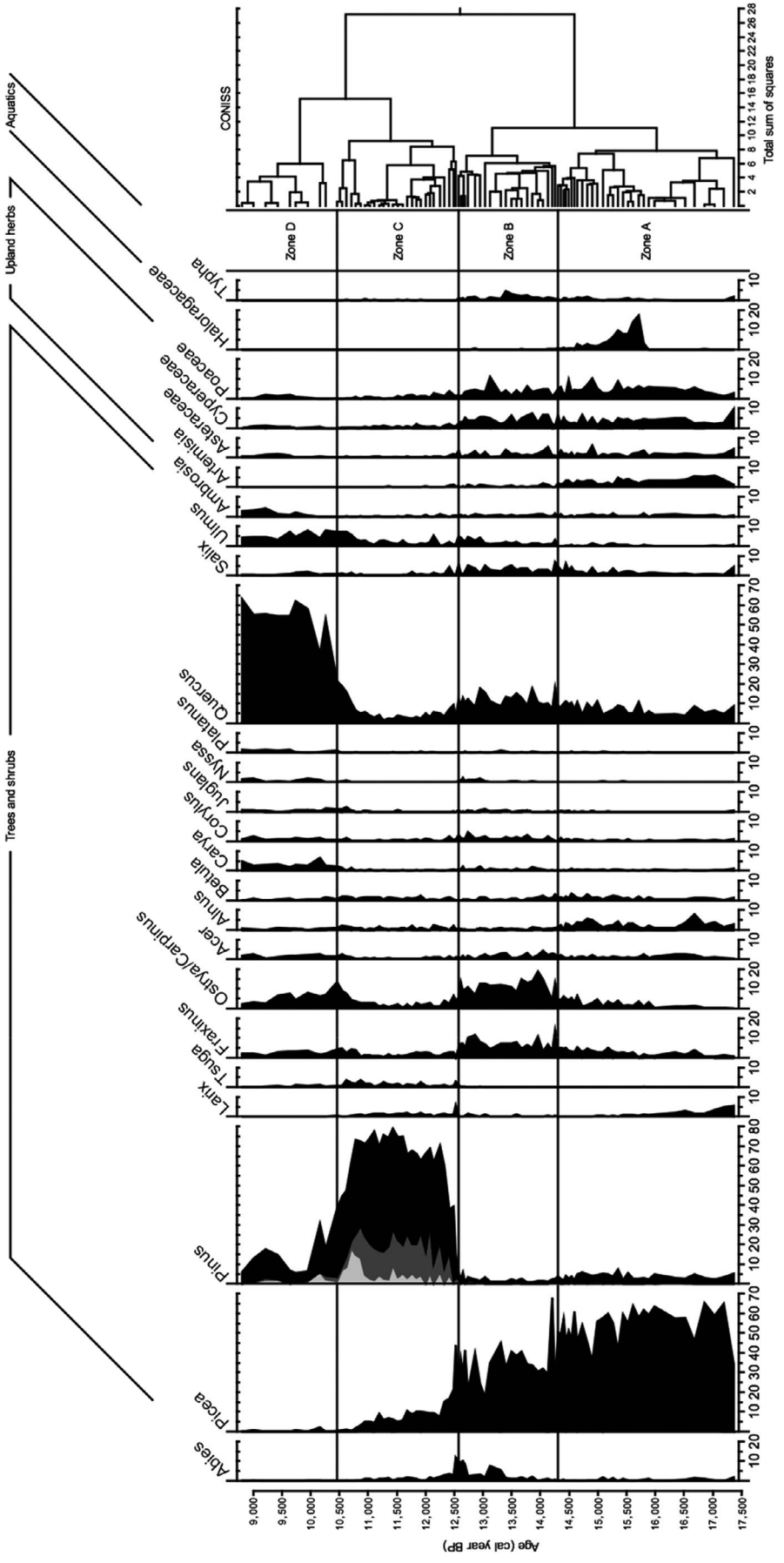


FIGURE 3 Pollen percentages of major taxa (mean abundance >1%) at Triangle Lake Bog. Pollen types are summed to the genus or family level except for *Pinus*, which is shown at the subgenus level (light grey = *Pinus strobus*, medium grey = *Pinus banksiana/resinosa*, black = undifferentiated). CONISS vegetation zones are shown at right of diagram

becoming equally or more abundant than *Pinus banksiana* at the end of the zone (Figure 3).

Zone D (from 12–10.5 kyr BP to the end of the records at 8.8–7.8 kyr BP) started with a sharp decline in *Pinus* and the rise of temperate deciduous forests at all sites. In this zone, *Quercus* became highly abundant on the landscape, reaching ~40% at Stotzel-Leis and >60% at the other sites. *Carya* increased to 5%–15% and *Ulmus* remained at 5%–15%. Upland herbs, namely *Ambrosia*, other members of the Aster family (Asteraceae), and Poaceae, rose in abundance towards the end of Zone D. Although the records in this study were not analysed for the past 8 kyr BP, the records from Spicer Lake, Indiana and Crystal Lake, Illinois, show that temperate deciduous forests and *Quercus* savannas persisted in the southern Great Lakes Region through the Holocene (Gonzales & Grimm, 2009; Wang, 2013).

3.3 | Spruce declines, rates of vegetation composition change and fire activity

Across the southern Great Lakes sites, the *bcp* analysis and pollen diagrams indicate that *Picea* did not decline at a constant rate, but rather as a series of rapid drops interspersed with periods of relative stasis or slow decline. The late-glacial trajectories of *Picea* pollen at the sites can be grouped into two different patterns (Figure 4). The first, seen at Stotzel-Leis and Silver Lake, is a 'decline-and-return' pattern, in which *Picea* declined through a series of abrupt transitions, then returned to moderate abundance (~30%) during Zone C, with a final decline after this zone. The second pattern, seen at Appleman Lake, Bonnett Lake and Triangle Lake Bog, is a 'stair-step' pattern with no recovery. At these sites, *Picea* experienced a stepped decline from high (50%–70%) to mid-level (30%–50%) abundance by

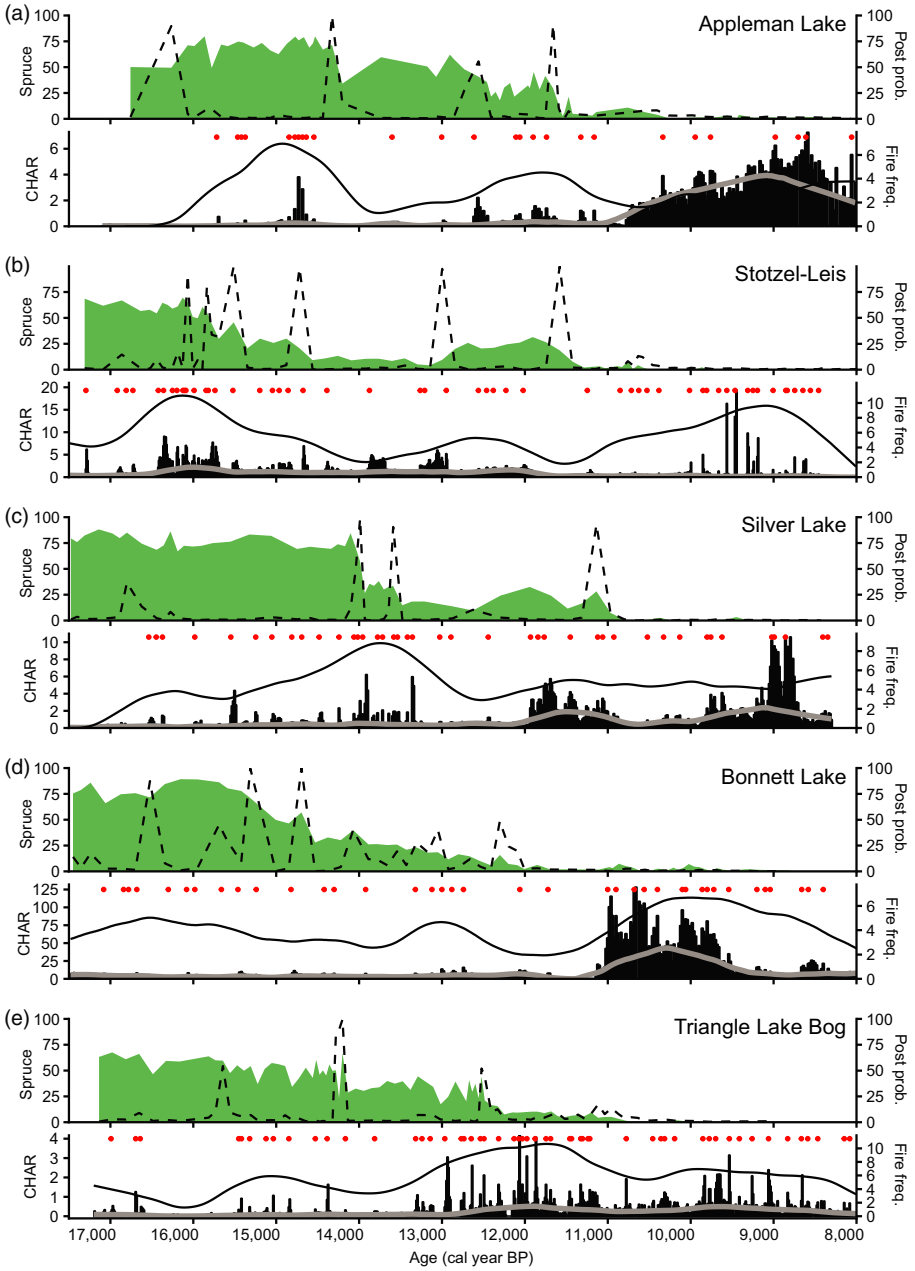


FIGURE 4 *Picea pollen* percentages and CharAnalysis output for the five sites: (a) Appleman Lake, (b) Stotzel-Leis, (c) Silver Lake, (d) Bonnett Lake and (e) Triangle Lake Bog. In each paired panel set, the upper panel shows *Picea* pollen per cent abundance (green) and probability of a change point in *Picea* abundance based on Bayesian change point analysis (black dashed line). The lower panel shows: charcoal accumulation rate (pieces cm^{-2} $year^{-1}$, black bars), background charcoal smoothed with a 700-year window (pieces cm^{-2} $year^{-1}$, grey curve), significant charcoal peaks (red dots, interpreted as fire events) and fire frequency smoothed over 1,000 years (fires/1,000 years, black curve). The vertical axes for charcoal accumulation rate and fire frequency differ by site to reflect varying levels of fire activity across the sites. See also Figure S8 for time series of vegetation rate of change

14 kyr BP, then remained at moderate abundance for several thousand years, before experiencing another step decline to low abundance (<20%) at the start of Zone C.

The two patterns of *Picea* decline were associated with different levels of fire activity. At Stotzel-Leis and Silver Lake, the sites showing the decline-and-return pattern, abrupt declines in *Picea* coincided with periods of enhanced fire activity (Figure 4). Both charcoal accumulation rates (Figure 6, Stotzel-Leis: adj. $r^2 = 0.56$, $p < 0.001$, Silver Lake: adj. $r^2 = 0.61$, $p < 0.001$) and fire frequencies (Figure 7, Stotzel-Leis: adj. $r^2 = 0.76$, $p < 0.001$, Silver Lake: adj. $r^2 = 0.64$, $p < 0.001$) were highly significant predictors of vegetation composition change rates during the *Picea* declines. At these sites, *Picea* was mostly replaced by deciduous hardwoods, though *Picea* returned with low levels of *Pinus* (<30%) during Zone C (Figure 5).

At Stotzel-Leis, *bcp* identified a series of abrupt declines in *Picea* pollen around 16 kyr BP, which coincided with intensified fire activity marked by increases in charcoal accumulation and the highest fire frequency (11 fires/1,000 years) of the record (Figure 4b). As *Picea* dropped to low abundance, deciduous hardwoods expanded to 50% and fire frequency decreased to 2 fires/1,000 years (Figures 4b and 5b). Fire frequency remained low until Zone C, after *Picea* re-established, when it reached a secondary peak of 5 fires/1,000 years (Figures 4b and 5b). At Silver Lake, *bcp* identified an abrupt decline in *Picea* pollen at 13.9 kyr BP, which coincided with high charcoal accumulation rates (6.2 pieces cm^{-2} $year^{-1}$) and the highest fire frequency (9 fires/1,000 years) of the record (Figure 4c). As *Picea* declined, deciduous hardwoods increased to ~35% and upland herbs also increased, reaching ~15% (Figure 5c). Charcoal accumulation and fire frequency declined thereafter, though fire frequency began to rise again, stabilizing at 5 fires/1,000 years, after *Picea* re-appeared on the landscape in Zone C (Figures 4c and 5c).

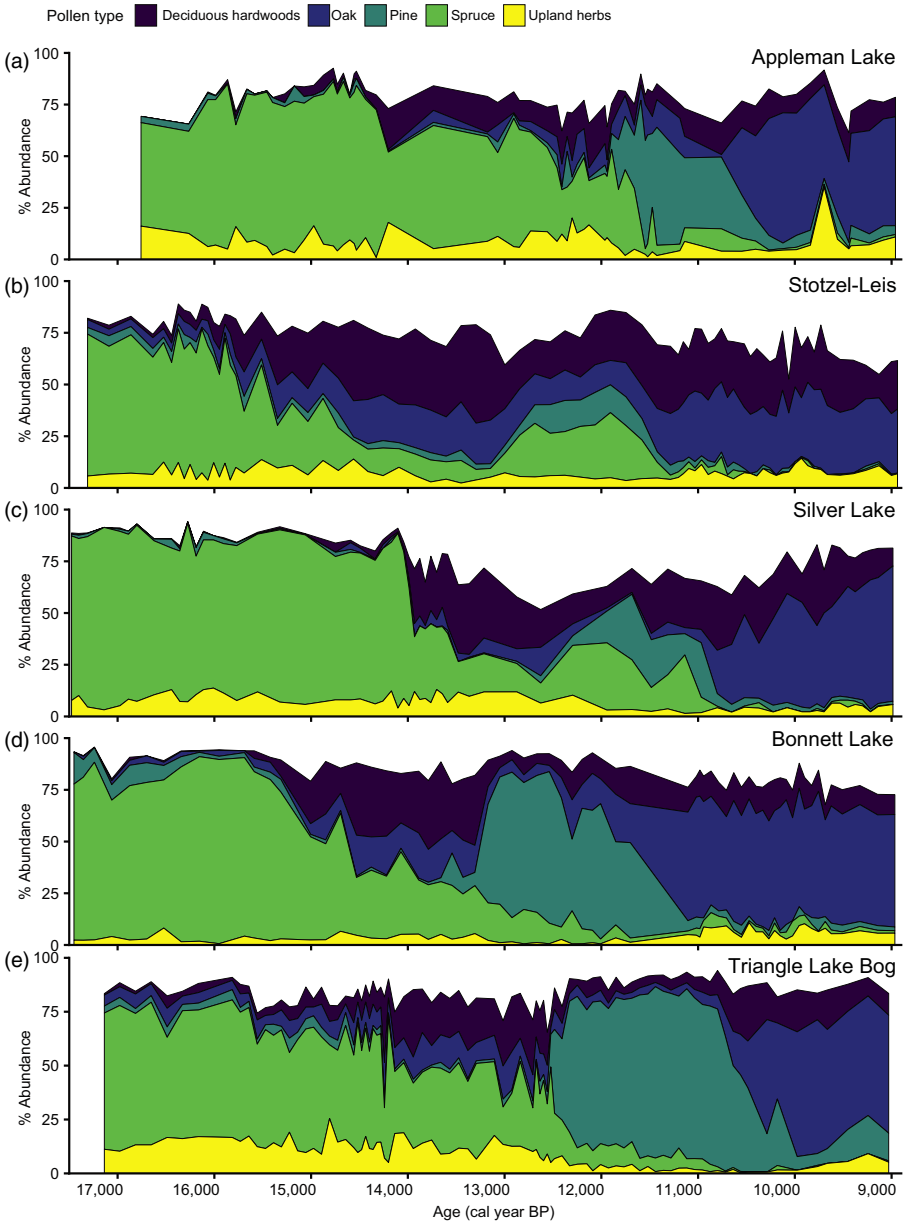


FIGURE 5 Stacked histograms of pollen percentages for selected taxa at the five study sites: (a) Appleman Lake, (b) Stotzel-Leis, (c) Silver Lake, (d) Bonnett Lake and (e) Triangle Lake Bog. The pollen types displayed are *Picea*, *Pinus*, *Quercus*, summed deciduous hardwood taxa (*Fraxinus*, *Ostrya/Carpinus*, *Ulmus*) and summed upland herb taxa (Asteraceae, Cyperaceae, Poaceae). At Stotzel-Leis and Silver Lake, *Picea* was replaced by mixed deciduous forests, while at Appleman Lake, Bonnett Lake and Triangle Lake Bog, *Picea* persisted until the period of high *Pinus* abundance

At Appleman Lake, Bonnett Lake and Triangle Lake Bog, the sites showing the stair-step pattern, decline in *Picea* and included several abrupt events, but the relationships between *Picea* declines and fire activity were less clear (Figure 4). At these sites, charcoal accumulation rates were not significant predictors of vegetation composition change rates during the transition from *Picea* to mixed forests (Figure 6). Fire frequencies were significant predictors of vegetation composition change rates at Appleman Lake and Triangle Lake Bog (Figure 7, Appleman Lake: adj. $r^2 = 0.26$, $p = 0.01$, Triangle Lake Bog: adj. $r^2 = 0.42$, $p = 0.03$), however, fire frequencies explained much less model deviance at these sites (33% and 47%, respectively) than at Stotzel-Leis (78%) and Silver Lake (68%). As *Picea* declined at Appleman Lake, Bonnett Lake and Triangle Lake Bog, the increase in deciduous hardwoods was modest and the *Pinus* increase was larger (Figure 5).

At Appleman and Silver Lakes, the >250 μm charcoal record and the >125 μm charcoal record showed similar trends in charcoal accumulation rates (Figure S2). Hence, analysis of just the >250 μm fraction at Triangle Lake Bog likely did not substantially affect overall trends in charcoal accumulation at this site. However, the use of a larger size fraction likely produced a more localized record of fire activity that was sensitive to high-intensity fire events and/or events closer to the lake's edge (Ohlson & Tryterud, 2000; Ward & Hardy, 1991).

3.4 | Rates of vegetation composition change and temperature change

At Silver and Bonnett Lakes, vegetation composition change rates were significantly and positively associated with temperature change rates across all vegetation zones, although these relationships had low explanatory power. At Silver Lake, the linear relationship explained 5% of the variance in vegetation composition change rates (Figure 8, $r^2 = 0.05$, $p = 0.05$) and at Bonnett Lake, the linear relationship explained 7% of the variance in vegetation

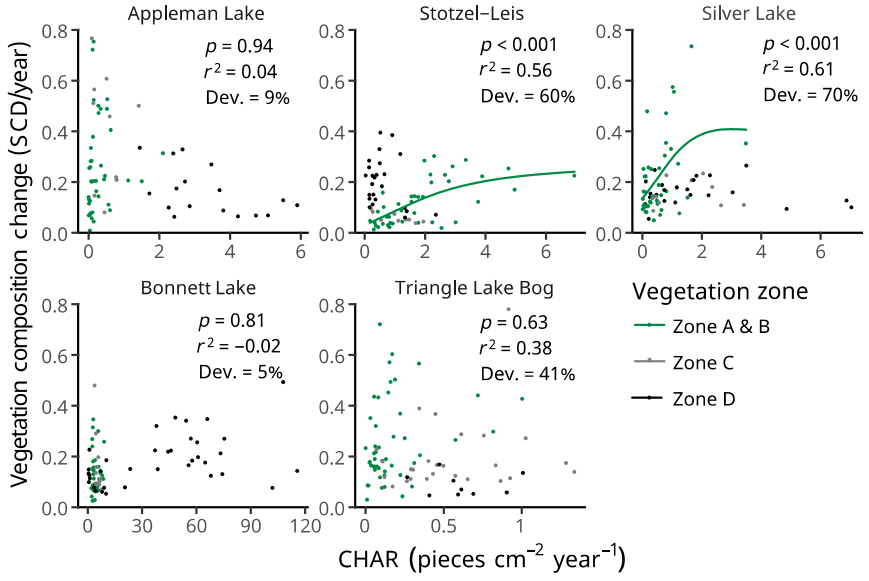


FIGURE 6 General additive models (GAMs) showing vegetation composition change rates as a function of charcoal accumulation rates, where charcoal accumulation is the designated smoothing parameter, at the five study sites. The models were run separately for the major vegetation zones, with Zones A and B combined to cover the state transition from *Picea* to mixed deciduous forests. The smoothing parameter *p*-value, adjusted r^2 value and percentage of deviance explained by the model are shown for Zones A and B at each site. Highly significant relationships between vegetation composition change rates and charcoal accumulation rates were found for Zones A and B at Stotzel-Leis ($p < 0.001$) and Silver Lake ($p < 0.001$)

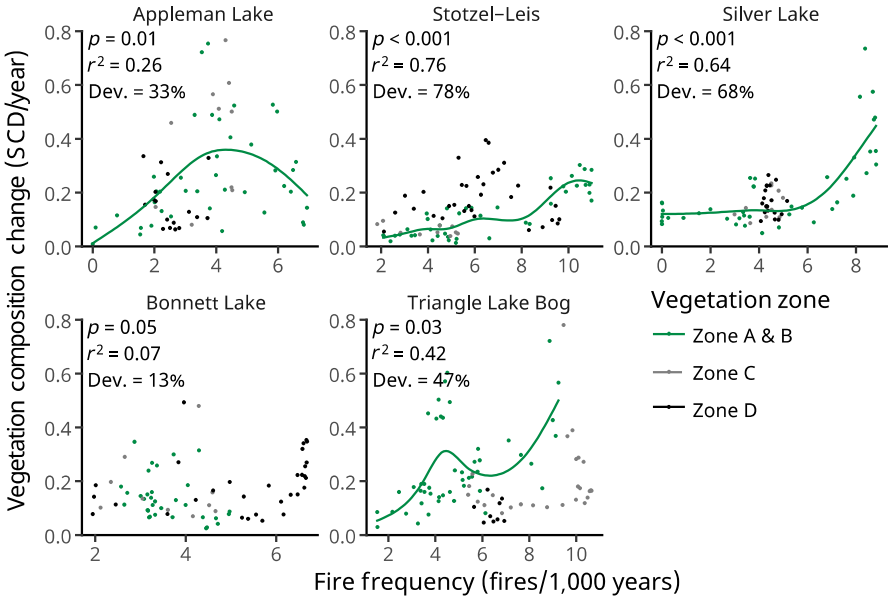


FIGURE 7 GAMs showing vegetation composition change rates as a function of fire frequency, where fire frequency is the designated smoothing parameter, at the five study sites. Figure format follows that of Figure 6. Significant relationships between vegetation composition change rates and fire frequency were found for Zones A and B at Appleman Lake ($p = 0.01$), Stotzel-Leis ($p < 0.001$), Silver Lake ($p < 0.001$) and Triangle Lake Bog ($p = 0.03$)

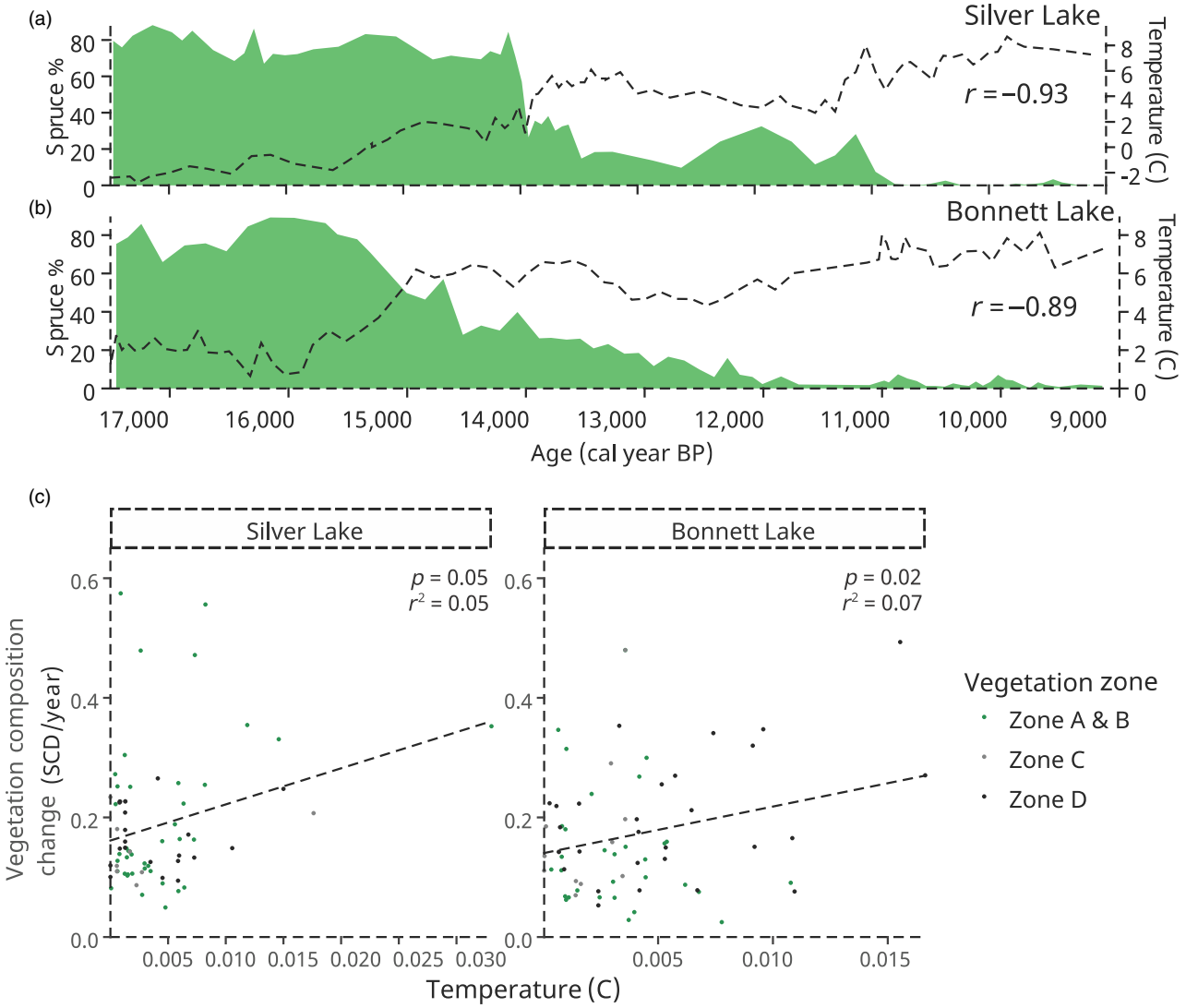


FIGURE 8 en percentages and brGDGT temperature reconstructions from the late-glacial period through the early-Holocene at (a) Silver Lake and (b) Bonnett Lake (Fastovich et al., 2020; Watson et al., 2018). *Picea* and temperature had a correlation coefficient of −0.93 at Silver Lake and −0.89 at Bonnett Lake. (c) General linear models (GLMs) showing vegetation composition change rates as a function of temperature change rates for all vegetation zones at Silver Lake and Bonnett Lake. Significant positive relationships were observed at Silver Lake ($p = 0.05$) and Bonnett Lake ($p = 0.02$), though temperature had low explanatory power

composition change rates (Figure 8, $r^2 = 0.07$, $p = 0.02$). Vegetation composition change rates were not significantly associated with temperature change rates in individual vegetation zones except for Zone D at Bonnett Lake, when temperature change rates explained 16% of the variance in vegetation composition change rates (Figure 8, $r^2 = 0.16$, $p = 0.02$). Hence, in these records, temperature variation had little explanatory power for within-type vegetation variations and some explanatory power for between-type vegetation variations. At Silver Lake, temperature and vegetation composition change rates reached their highest points of the records, 0.033°C/year and 0.74 SCD/year, respectively, at 14 kyr BP. At Bonnett Lake, vegetation composition change rates reached a maximum value of ~0.5 SCD/year at 13.3 kyr BP and 11 kyr BP, with the first maximum corresponding to a small peak in temperature change rates (0.004°C/year) and the second maximum corresponding to the highest temperature change rate of the record (0.02°C/year).

4 | DISCUSSION

4.1 | Climate and fire controls on spruce declines during the late-glacial period

The observations here are consistent with a hierarchy of controls on the loss of *Picea* populations and the widespread vegetation-type transitions that occurred across the southern Great Lakes Region during the late-glacial period. In this framework, climate change and temperature variations were the ultimate causes of *Picea* declines, with fire accelerating these transitions at some

sites. Other factors may have contributed as well, notably the progression from functional to final extinctions of the Pleistocene megafauna (Section 4.3).

During the late-glacial period, temperatures rose across the mid-latitudes, causing boreal species to decline in the southern Great Lakes and hardwoods to expand (Webb et al., 1993). While temperatures increased, seasonal differences in solar radiation became amplified, likely leading to warmer-than-present summer temperatures and colder-than-present winter temperatures (Kutzbach & Guetter, 1986). Warming climates with highly seasonal changes in insolation, and potentially, temperature may have favoured deciduous hardwood species like *Fraxinus*, *Ostrya/Carpinus* and *Ulmus* for several reasons (Williams & Jackson, 2007). First, these species can grow in a wide range of temperatures, making them able to withstand seasonal temperature variations. For example, black ash *Fraxinus nigra* has a winter temperature range of −22 to 0°C and a summer temperature range of 12 to 25°C and American hop-hornbeam *Ostrya virginiana* has a winter temperature range of −21 to 25°C and a summer temperature range of 15 to 30°C (Thompson et al., 1999). Second, taxa like *Ostrya/Carpinus* have a diffuse-porous wood structure, which allows them to grow rapidly during early spring warming but also withstand freezing temperatures. Diffuse-porous wood has small and numerous vessels, which begin conducting water and nutrients at the onset of spring warming in the 'first flush' period (Delcourt & Delcourt, 1994). The small size of the vessels also makes trees with this wood more resistant to embolism, or cavitation of xylem vessels, caused by freezing than trees with ring-porous wood, like *Quercus* (Sperry & Sullivan, 1992). Hence, as solar radiation, and likely temperatures, became highly seasonal, deciduous hardwood species replaced boreal species like *Picea*. A similar process is occurring today in boreal forest patches of the northern Great Lakes Region, where *F. nigra* and *O. virginiana* abundances are increasing in the understorey as a response to rising summer temperatures (Fisichelli et al., 2014). However, the loss of *Picea* was not an irreversible transition. During the Younger Dryas, when temperatures dropped by as much as 1.25°C in the Great Lakes Region (Fastovich et al., 2020), *Picea* re-established at Stotzel-Leis, Silver Lake, and elsewhere in Ohio (Shane & Anderson, 1993), demonstrating that major declines in species abundances can be reversed if climatic conditions become favourable once again.

The weak relationships between temperature and vegetation composition change rates at Silver and Bonnett Lakes, the two sites with brGDGT temperature records, have several possible explanations. One is uncertainty in the brGDGT proxy, which primarily results from the calibration dataset used to equate the relative abundance of brGDGTs to mean air temperatures. Microbes that produce brGDGTs in soil respond to locally heterogeneous temperatures where soil samples for the calibration dataset are taken, but these conditions likely differ from the meteorological air temperature observations that are used in the calibration dataset. In addition, while the calibration dataset is based on soil samples taken in a specific location, lake sediments receive brGDGTs from the surrounding watershed, resulting in spatial averaging of the brGDGTs present in a lake core (Fastovich et al., 2020). A second possible explanation for the weak temperature–vegetation relationships is that brGDGT calibrations are used to reconstruct mean annual temperature, while plant species distributions and abundances are more sensitive to seasonal temperature extremes (Woodward, 1987). A third possible explanation is lags between abrupt temperature and vegetation change on the order of several centuries in the southern Great Lakes Region (Fastovich et al., 2020). Even so, at both sites, peaks in vegetation composition change rates that marked the rise of deciduous hardwoods followed warming of ~4.5°C. The apparent timing of this warming varied among sites, with warming at Silver Lake following warming at Bonnett Lake by ~1,600 years (Figure 8). This apparent lag could result from age model uncertainty, as the late-glacial interval is sparsely dated at both sites. Regardless, warming and the rise of deciduous hardwoods developed nearly synchronously at both sites, suggesting that widespread vegetation-type transitions were strongly affected by temperature changes during the late-glacial period (Fastovich et al., 2020).

At Stotzel-Leis and Silver Lake, increased fire activity appears to have accelerated the transition from boreal to mixed deciduous vegetation, perhaps by fire clearing *Picea* from the landscape and allowing deciduous hardwood taxa to expand. Both sites showed high fire frequency associated with abrupt declines in *Picea*, with fire frequency reaching 11 fires/1,000 years at Stotzel-Leis and 9 fires/1,000 years at Silver Lake during periods of abrupt change (Figure 4). In addition, at both sites, indices of fire activity (charcoal accumulation rates, fire frequency) were highly significant predictors of vegetation composition change rates (Figures 6 and 7). The apparent correspondence between abrupt vegetation change and enhanced disturbance is particularly strong at Silver Lake, with *Picea* dropping from 70% to 30% within ~200 years, associated with a cluster of at least three fire events within 100 years. During this transition, the majority of charcoal at Silver Lake was dark charcoal, which comes from woody material, or bordered pit charcoal, which comes from conifer wood (Gill et al., 2012). The morphology of the charcoal, along with the large magnitudes of the charcoal peaks, suggests that the fire regime was characterized by crown fires that burned down *Picea* stands rather than surface fires, which would be indicated by high levels of grass charcoal (Jensen et al., 2007; Walsh et al., 2008). Variations in fire activity at Stotzel-Leis and Silver Lake may also have played a role in the return of *Picea* at these sites, as *Picea* re-established during periods of low fire frequency (<4 fires/1,000 years).

While boreal forests with black spruce *Picea mariana* are resilient to high-severity, stand-replacing fire regimes (Heinselman, 1981; Higuera et al., 2009; Kelly et al., 2013; Lynch et al., 2003), increasing fire frequency can cause state transitions in these forests because *Picea* stands need several decades to develop a sufficient seed supply for successful post-fire regeneration (Greene & Johnson, 1999). In boreal forests of northwestern Canada, mixed *Picea* and *Pinus* stands that were >75 years old when they burned re-established as conifer stands, but stands that were <25 years old when they

burned experienced low post-fire conifer recruitment and shifted to deciduous-dominated stands (Johnstone & Chapin, 2006). Another study in the boreal forests of Canada found that sites with shorter fire-free intervals had shallow organic layers and greater proportions of woody deciduous species, like *Populus* and *Salix*, than sites with longer fire-free intervals (Johnstone, 2006). There is evidence that the resilience of dry conifer forests has already decreased over the last several decades due to rising temperatures and fire activity (Stevens-Rumann et al., 2018), making larger, more severe fires driven by rising temperatures and dense fuel loads a top priority for forest management efforts across North America (Flannigan et al., 2009).

At Appleman Lake, Bonnett Lake and Triangle Lake Bog, however, the relationships between enhanced fire activity and the transition from *Picea* to deciduous hardwoods were less clear, with fire frequency having significance at some sites and charcoal accumulation rates having no significance (Figures 6 and 7). At Bonnett Lake and Triangle Lake Bog, fire frequency was relatively low through the period of high *Picea* abundance, never exceeding 6 fires/1,000 years, and closely spaced fire events did not align with step declines in *Picea* abundance. At Appleman Lake, fire frequency reached a peak at 14.9 kyr BP, but fire frequency was decreasing by the time the first step decline in *Picea* abundance occurred at 14.3 kyr BP. At these sites, the decline in *Picea* was more prolonged and gradual, albeit with some stair-step drops in abundance. It is likely that temperature change or another factor was the primary cause of the more gradual transition from *Picea* to mixed deciduous hardwood forests, with little mediation by variations in disturbance regime.

In the western United States, climate change and fire activity were important controls on abrupt vegetation change and regime shifts in closed coniferous forests over the last 11,000 years. In some cases, Holocene changes in temperature and insolation explained community turnover, while fire played an insignificant role. For example, in the subalpine forests of the Bear River Range, Idaho, a state transition from *Picea* and fir *Abies* to *Quercus* and upland herbs was driven by changes in summer temperatures (Lundeen & Brunelle, 2016). In other areas, Holocene climate change drove vegetation change, but fire events caused more abrupt transitions. For example, in a subalpine forest of northern Colorado, climate was the main driver of late-Holocene vegetation change, but fires triggered an abrupt state change from a closed subalpine forest to a modern ribbon forest (Calder & Shuman, 2017). In a coniferous forest of the Pacific Northwest, fire initiated several state changes, while climate velocity was high in the early-Holocene, but later in this period, state changes were unrelated to fire events (Crausbay et al., 2017). Likewise, in the Olympic mountains, fire was positively associated with rates of community change between 14.7 and 7 kyr BP, when climate variability was high, but fire was not associated with community change in the late-Holocene, when climate variability was low (Gavin et al., 2013). Hence, these western studies suggest that fire can accelerate climate-driven vegetation state changes, but these state changes can also occur without fire mediation.

4.2 | Soil and vegetation controls on intersite variability in climate–fire–vegetation interactions

The high intersite variability reported here is consistent with other studies that found sites in close proximity had contrasting fire histories due to local factors like soil type, topography, slope position and microclimate (Brunelle et al., 2005; Gavin et al., 2006; Heyerdahl et al., 2001; Lynch et al., 2014; Taylor & Skinner, 2003; Tweiten et al., 2015). The sites used in this study span a transect from Indiana to Ohio, so sites overlay different soil units with varying drainage properties (Figure 1, USDA Web Soil Survey, accessed July 2019, available online). Soil drainage properties can affect the flammability of a landscape, as sites with poorly drained soils tend to support moist fuels, which lower the probability of ignition, rate of fire spread, and the resulting fire frequency at these sites (Bonan & Shugart, 1989; Larsen, 1997). This might help explain why sites like Bonnett Lake, which is directly surrounded by very poorly drained soils, did not show a relationship between fire activity and vegetation composition change, while sites like Silver Lake, which is surrounded by mixed loams, showed an association between increased fire activity and high rates of vegetation composition change.

The importance of site-level factors in explaining different fire patterns among sites located in close proximity has been demonstrated on the sand plain of northwestern Wisconsin (Lynch et al., 2014; Tweiten et al., 2015). In this area, which is dominated by coarse well-drained soils but contains some finer loamy soils, sites with sandier, well-drained soils showed an increase in fire frequency during the Little Ice Age that was not seen at other sites. The well-drained sites also showed faster shifts in pollen assemblages during this interval, suggesting that increased fire activity triggered rapid shifts in vegetation composition (Tweiten et al., 2015). Other factors like fire breaks were also important in explaining different fire patterns, as sites with more fire breaks showed lower fire activity during late-Holocene climatic shifts than sites with only a few fire breaks. In this case, increased fire activity did not contribute to shifts in vegetation composition, but rather, it maintained community resiliency because of the positive feedbacks between fire and *Pinus banksiana* forests (Lynch et al., 2014).

Soil drainage has also been shown to affect fire activity in the modern boreal forests of Canada and Alaska. In northwest Canada, mixed *Picea* stands were more likely to burn at a young age, and thus experience higher fire frequency in areas with well-drained soils because these areas were more easily ignited compared to areas with poorly drained soils, which had longer fire-free intervals (Johnstone & Chapin, 2006). In interior Alaska, mixed *Picea* stands in well-drained areas with high severity burns were more likely to experience a shift in successional trajectory to one dominated by broadleaf deciduous trees, while stands in poorly drained areas were more likely to sustain a cycle of *Picea* self-replacement (Johnstone, et al., 2010). Spatially variable patterns of fire activity and vegetation composition change will continue to be seen in the coming decades; landscape simulation modelling has shown that well-drained *Picea*

stands are more likely to transition to alternative vegetation states across a range of fire frequencies than poorly drained *Picea* stands, which are likely to transition to alternative states only at high fire frequencies (Hart et al., 2019).

Changes in landscape vegetation and fuel characteristics can act as bottom-up controls on fire activity, which helps explain why sites subject to the same climatic drivers can experience different patterns of fire activity. For example, fire activity decreased across northern Europe during late-Holocene cooling, but this change was not synchronous across the region (Ohlson et al., 2011). Instead, individual records showed a close association between the rise of Norway spruce *Picea abies* and decreasing fire activity, suggesting that the effect of vegetation change exceeded the influence of the cooling trend. In the Brooks Range, Alaska, mid to late-Holocene cooling allowed white spruce *Picea glauca* and *P. mariana* forest to establish on the landscape, which led to increased fire frequency despite the cooling, because the expansion of *P. mariana* significantly increased landscape flammability (Higuera et al., 2009). In the Great Lakes Region, the association between fire regime and vegetation change is strongest at sites where *Picea* was replaced by deciduous hardwoods and weakest at sites with intervals of high *Pinus* abundance.

4.3 | Other factors

This study's emphasis on climate and fire does not rule out the influence of other drivers on the late-glacial transition from *Picea* to mixed deciduous hardwood forests, particularly the trophic effects associated with the Pleistocene megafauna extinction. The collapse of megafauna could have played a role in the establishment of deciduous forests by releasing hardwoods from herbivory pressure, allowing them to expand on the landscape (Gill et al., 2009, 2012). In addition, the extinction of large grazers and browsers could have allowed greater amounts of fuel to build up on the landscape, contributing to late-glacial increases in fire activity (Gill et al., 2009, 2012). The late-glacial collapse of megafaunal populations has been documented using coprophilous fungal spores in lake sediment cores from New York, Indiana and Ohio (Gill et al., 2009, 2012; Robinson et al., 2005), but the timing of these coprophilous spore declines precedes the final extinctions recorded by direct radiocarbon dating of bones (Feranec et al., 2011). A new analysis and synthesis of coprophilous spore records from sites across the north-central and southeastern United States is currently underway (Perrotti, A., unpubl. data, July 2020).

5 | CONCLUSIONS

These records suggest that the broad loss of *Picea* forests/woodlands across the southern Great Lakes during the last deglaciation was accelerated in some, but not all, places by intensified fire regimes. This regional heterogeneity may have been governed by site-level differences in soil texture and water holding capacity and local vegetation-fire feedbacks. Hence, while rising temperatures were likely the ultimate cause of this vegetation state transition, fire likely acted as an agent of abrupt ecological change by limiting post-fire conifer recruitment and clearing the way for deciduous hardwoods that were well-adapted to warmer climates with large seasonal differences in insolation. Evidence that warming and enhanced fire regimes interacted to cause abrupt losses of *Picea* at some sites parallels what is happening in boreal forests today, as novel climates and disturbance regimes are reducing coniferous forest resilience. Based on past fire and vegetation dynamics, we expect that intensified fire regimes will accelerate vegetation state changes this century. However, fire regimes will be influenced by local geophysical and vegetation conditions, causing the pace of ecological change to be spatially variable during the current anthropogenic warming.

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AUTHORS' CONTRIBUTIONS

A.M.J. and J.W.W. conceived and designed the study; J.B., K.H., K.B.L., C.R. and G.C.S. searched for macrofossils and led charcoal processing and counting for the Great Lakes cores; A.M.J., D.F., J.L.G. and B.I.W. led pollen processing and counting for the Great Lakes cores; D.F., B.I.W. and J.M.R. led the brGDGT temperature reconstructions for Silver Lake and Bonnett Lake; A.M.J., S.T.J., J.M.R. and J.W.W. analysed and interpreted the pollen and charcoal records; A.M.J. wrote the manuscript with editing by J.W.W. and input from co-authors. All co-authors gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All radiocarbon, pollen and charcoal data are publicly available in the Neotoma Paleoecology Database (http://www.neotomadb.org). Pollen Dataset IDs: 14957 (Appleman Lake), 40168 (Stotzel-Leis), 17717 (Silver Lake), 45816 (Bonnett Lake), 45695 (Triangle Lake Bog). Charcoal Dataset IDs: 45817 (Appleman Lake), 45818 (Stotzel-Leis), 45821 (Silver Lake), 45820 (Bonnett Lake), 45819 (Triangle Lake Bog).

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SUPPORTING INFORMATION

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

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