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A high-resolution paleolimnological study of climate and human impacts on Lac Noir, Québec, over the past 1000 yr

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Abstract

Diatom assemblages in lake sediments of Lac Noir, southwestern Québec, were studied at a resolution of 10 yr to determine principal drivers of primary producers for the past ~1000 yr. Generalized additive modeling revealed strong links between broadscale climate intervals of the late Holocene, forest composition, and diatom flora. During the Medieval Warm Period (~AD 1200) and onset of the Little Ice Age (~AD 1450), increases in *Tabellaria flocculosa* str. IIIp at the expense of *Discostella stelligera* reflected low lake productivity. At AD 1630, an abrupt shift to cooler temperatures and dry conditions triggered a decline in hemlock (*Tsuga*), replaced by disturbance and cool-adapted taxa. Greater nutrient availability and soil erosion in the catchment led to a corresponding and rapid increase in diatoms with higher optima for nitrogen, such as *Asterionella formosa* and *Fragilaria crotonensis*. After AD 1870, an increase in pollen of taxa associated with disturbances signaled the arrival of Euro-Canadians, and associated nutrient inputs to the lake triggered increases in S*tephanodiscus minutulus* and *Achnanthidium minutissimum*. Overall results of the study indicate that climate played an important underlying role in lake-ecosystem dynamics; however, disturbances affecting forest composition had more direct influences on the diatom communities of Lac Noir.

Keywords: Diatom; Varve; Holocene; Paleolimnology; Medieval Warm Period; Little Ice Age; Generalized additive models (GAMs); European settlement

INTRODUCTION

In southern Québec and Ontario, global climate models project a rise in annual mean temperature of 1–5°C by the end of the twenty-first century (Boulanger et al., 2017). This will undoubtedly trigger significant changes in lake health and productivity in the region (Barker et al., 2005), as climate plays a major role in freshwater ecosystem dynamics (Bradshaw et al., 2005). In small, temperate lakes, for example, greater primary production in response to warmer temperatures could ultimately lead to lake anoxia, with indirect impacts on higher trophic levels (Dove-Thompson et al., 2011). Variations in precipitation, including periods of sustained droughts, could also alter lake hydrologic cycles, increasing their vulnerability to deteriorating water quality and eutrophication (Barker et al., 2005).

Changes in forest vegetation and catchment soils associated with climatic variability and human disturbances also exhibit strong influences on lake water chemistry and aquatic biota (Carignan and Steedman, 2000). The close coupling of watershed processes and lake ecosystems is documented in paleolimnological studies; for example, Beck et al. (2016) noted a shift to a more nutrient-rich catchment surrounding Wishart Lake, southern Ontario, following the mid-Holocene decline of hemlock (*Tsuga canadensis*), which ultimately led to the eutrophication of the lake. Studies from southern Ontario and Québec describe significant responses of aquatic communities to human-induced disturbances following European settlement (Ekdahl et al., 2007: Neil and Gajewski, 2017). Climate change, as well as sustained and potentially increased impacts of anthropogenic activities in the future, will likely present challenges for predicting how lake ecosystems will respond and recover to environmental changes (Johnstone et al., 2016).

Paleorecords and historical data document responses of vegetation and aquatic taxa to major climatic variations of the late Holocene (e.g., Gajewski, 1988; Williams et al., 2002), such as the Medieval Warm Period (MWP; ~AD 800–1200) and the Little Ice Age (LIA; ~AD 1450–1850). However, local forcings or disturbances (e.g., fire, anthropogenic

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activity) often mask these broad climatic signals in the data as they alter the rate and timing of ecological change among sites (Paine et al., 1998; Williams et al., 2011). This was demonstrated in a study that compared the vegetation histories from two proximate lakes, Lac Noir and Lac Brûlé, in southern Québec (Lafontaine-Boyer and Gajewski, 2014). A decline in hemlock pollen at Lac Noir was attributed to cooling temperatures during the LIA, but a similar decrease occurred centuries earlier at Lac Brûlé in response to a local fire in the catchment area (Lafontaine-Boyer and Gajewski, 2014). To distinguish the effects of climate and nonclimatic processes on watershed-lake interactions, replication of multiproxy studies within a limited spatial area is thus necessary.

The purpose of this study is (1) to analyze aquatic primary producers (diatoms) in Lac Noir in relation to environmental changes and nutrient fluxes and (2) to understand their responses within the context of regional paleorecords of the late Holocene in southern Québec and Ontario. Diatoms are indicators of lake response to external forcings, as they are abundant, respond rapidly to physical/chemical changes in the water column, and are typically preserved in lake sediments (Stoermer and Smol, 2001). Generalized additive models (GAMs) are used here to hierarchize the influences of external forcings on diatom assemblages and to separate ecological responses linked to regional climate variability and/or site-specific factors. Results of the diatom analysis are compared with a previous study of Lac Noir, in which climate and vegetation changes of the past 1000 yr were identified through a high-resolution pollen analysis of the lake sediments (Paquette and Gajewski, 2013). The overall results are compared with those from the nearby Lac Brûlé (Neil and Gajewski, 2017).

METHODS

Study site

The study area is located in southwestern Québec, 60 km northeast of Ottawa (Fig. 1). Lac Noir (45°46′32.89″N, 75°08′05.65″W; 176 m) is the main site for which data are presented here; it is a small lake (25 ha) and has continuously laminated sediments, with a maximum depth of ~16 m (Paquette and Gajewski, 2013). In 2013, the pH of the lake was 7.7 near the surface, and the conductivity was 20.0 µS/cm. Based on low concentrations of total phosphorus (TP; 9 µg/L), total nitrogen (TN; 260 µg/L), and chlorophyll-α (0.59 µg/L) at this time, the lake was characterized as ultra-oligotrophic (Cooper et al., 2016).

Lac Noir is underlain by Precambrian Shield and is situated within a transition zone between the boreal (to the north) and deciduous (to the south) forest. The mixed forest surrounding the lake is dominated by red and white pine (*Pinus resinosa*, *Pinus strobus*), white and black spruce (*Picea glauca*, *Picea mariana*), eastern Hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), various species of maple (*Acer saccharum*, *Acer pensylvanicum*, *Acer*

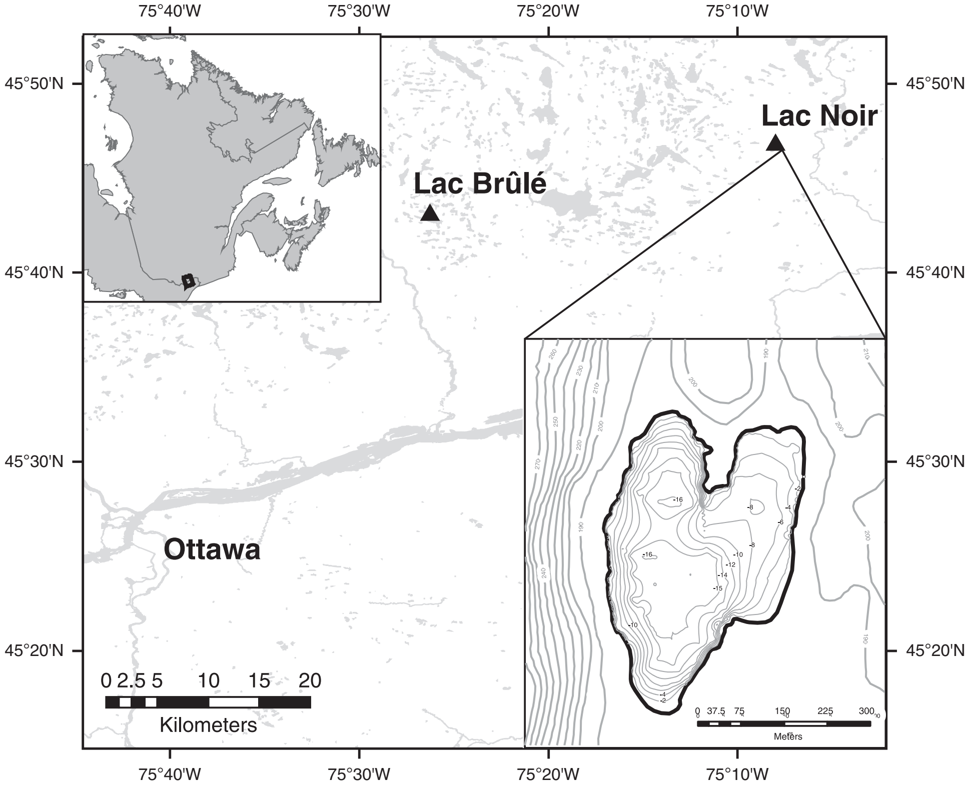

Figure 1. Map of the location and bathymetry of Lac Noir, southwestern Québec.

rubrum, *Acer negundo*), and green and speckled alder (*Alnus crispa*, *Alnus rugosa*). The closest long-term weather station to Lac Noir (Notre-Dame de la Paix) records mean daily temperatures ranging from −11.9°C in January to 19.1°C in July (Environment Canada, 2017). Total annual precipitation in the region is 985 mm, approximately 30% of which falls as rain in the summer months (June, July, August [JJA]) (Environment Canada, 2017). Human activity in the catchment area surrounding Lac Noir is restricted; there are currently two small summer cabins on the shore. A few small towns and agricultural fields are located ~1 to 2 km east of the lake, but immediately to the west the landscape is relatively steep and appears undisturbed.

Sampling and chronology

In 2010, three continuously laminated sediment cores were collected from Lac Noir. Paquette and Gajewski (2013) identified the laminations as annual varves (confirmed by ^{210}Pb and ^{14}C dating), and cross-correlated the varved sequences from each of these cores to establish a chronology for the site. The majority of the core (6.6–91 cm) was sectioned into 10 yr intervals based on the varve chronology; however, disturbances in the uppermost 6.5 cm prevented varves from being reliably counted in this section. Instead, results from ^{210}Pb dating were used to assign ages to samples corresponding with this upper section of the core (for details, see Paquette and Gajewski, 2013). To enable direct comparisons of diatoms with the previously published high-resolution pollen record from Lac Noir, subsamples in this study were taken from the same sections of the core used by Paquette and Gajewski (2013) in their analyses.

In their study, Paquette and Gajewski (2013) estimated European settlement at ~AD 1810 based on a rise in *Ambrosia* pollen in Lac Noir. Historical records indicate that European colonization of the region began in the early nineteenth century, but human activities affecting the environment (e.g., logging, agriculture) only increased in the second half of the century (Smith, 1967). In 2014, a palynological study of a nearby lake with varved sediments, Lac Brûlé, recorded an increase in *Ambrosia* pollen at AD 1860 (Lafontaine-Boyer and Gajewski, 2014). Following Lafontaine-Boyer and Gajewski (2014), we revised the Lac Noir chronology in this study to place the *Ambrosia* rise at AD 1860. The varves from the Lac Brûlé core were undisturbed in the upper section and thus likely more accurate, and an increase in *Ambrosia* at AD 1860 seems to fit more reasonably with the historical record of the region.

Laboratory analysis

From the same sections of the Lac Noir sediment core used for the palynological study, subsamples averaging ~0.02 g of dry sediment were extracted into 20 mL glass vials in AD 2017 for diatom analysis. Hydrogen peroxide (30%) was added to each vial and left to digest in a water bath at 80°C for 3–4 hours (Battarbee et al., 2001). To enable estimations of diatom influx rates, a known volume of microsphere solution (concentration of 5.0×10^6 spheres/mL) was added to each subsample. A small amount of diatom slurry was diluted with deionized water before being pipetted onto a cleaned coverslip. The coverslips were left to air dry in a dry hood, after which they were permanently mounted onto microscope slides with Naphrax. Diatoms were identified with a Nikon 90i microscope at 1000× magnification under oil emersion, using Patrick and Reimer (1975, 1966), Siver et al. (2005), and Antoniades et al. (2008) as taxonomic references. For each sample, a minimum of 500 diatom valves were counted; these counts were translated into both relative abundance data and influx rates for each diatom species. Chrysophyte scales were enumerated on each slide, and a chrysophyte scale to diatom valve index (CS/DV) was calculated following Karmakar et al. (2015).

Numerical analysis

Using the "vegan" package in the statistical program R3.2.5 (R Development Core Team, 2013), diatom assemblages consisting of the most abundant taxa (>3% relative abundance in at least one sample) were summarized with principal components analysis (PCA). Prior to the PCA, species relative abundance data were Hellinger transformed (Legendre and Gallagher, 2001). Significant PCA axes were identified using a scree plot of the axis eigenvalues, and the diatom percentage diagram was divided into biostratigraphic zones based solely on changes in the scores of the PCA. For each of the 110 samples from Lac Noir, additional data from Paquette and Gajewski (2013) were available for analysis, including pollen percentages (summarized with a separate PCA), pollen influx, organic matter (loss-on-ignition [LOI] 550%) and carbonate (LOI 950%) content, charcoal influx, and reconstructed JJA temperature and precipitation, derived from the pollen data using the modern analogue technique.

GAMs were generated using the "mcgv" package in R (Wood, 2008, 2011) to assess the degree to which individual external forcings influenced the Lac Noir diatom community. The response variable in each GAM was one of three significant diatom principal components (PCs) axes. Predictor variables included pollen PC axes, pollen influx, LOI 550%, LOI 950%, CS/DV, and microcharcoal influx; these were interpreted as indicators of general climatic conditions, productivity of terrestrial vegetation, disturbances in the catchment (e.g., erosion, fire), and lake trophic status. Parameterization of the GAMs included a restricted maximum likelihood (REML) smoothness selection, a shrinkage method by double penalty approach on each of the smoothing terms (Marra and Wood, 2011), and thin plate splines as the type of basis dimension.

RESULTS

Diatom biostratigraphy and environmental data

A total of 130 diatom species were identified from the sediment samples, 15 of which occurred with >3% relative abundance in at least one sample (Fig. 2); only these more

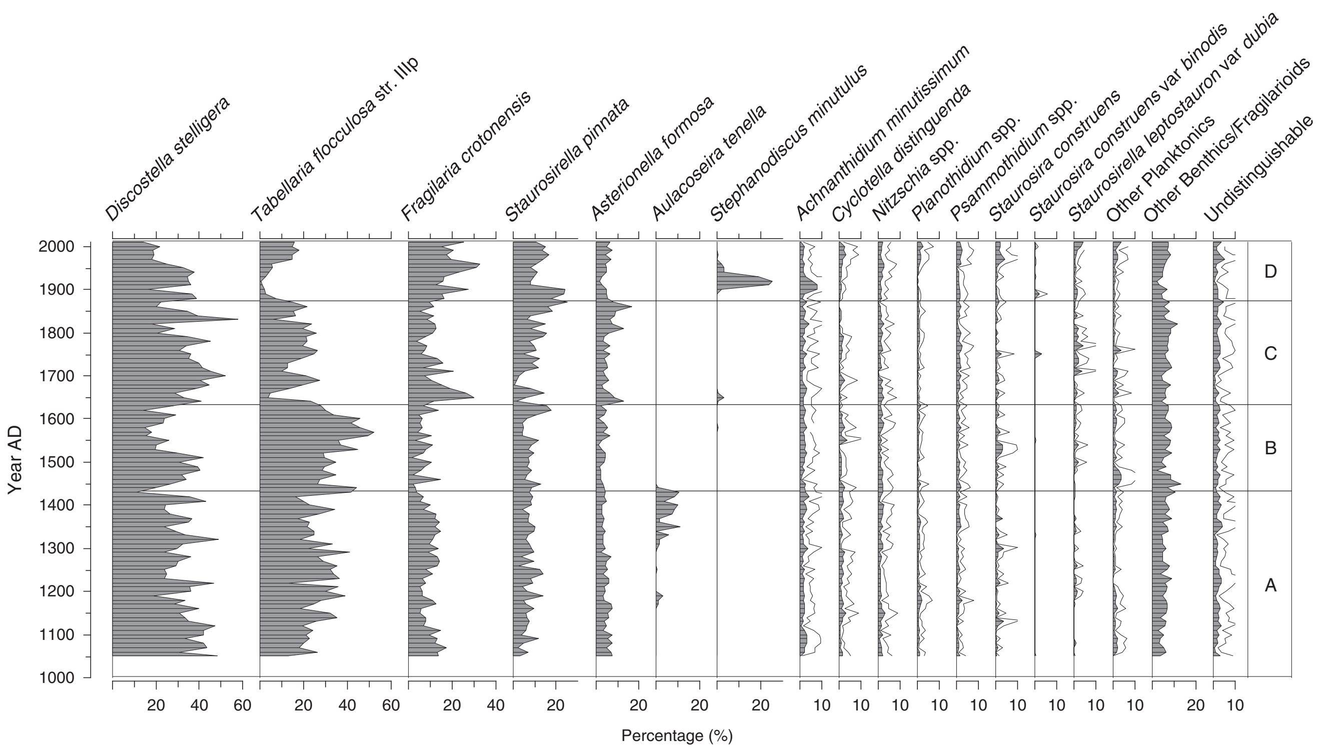

Figure 2. Lac Noir diatom stratigraphy, expressed as percentages of total diatom abundance. Taxa with ≥3% relative abundance in at least one sample are shown, and a 3 × exaggeration (unfilled gray line) is applied to taxa representing a smaller portion of the total diatom sum.

abundant species are shown. Three of the taxa dominated the fossil assemblages and when combined accounted for 45% to 80% of the total diatom sum: *Discostella stelligera* (Cleve et Grunow) Houk et Klee, 2004; *Tabellaria flocculosa* str. IIIp (Roth) Kützing, 1844; and *Fragilaria crotonensis* Kitton, 1869 (Fig. 2). More detailed changes in the Lac Noir diatom record (Fig. 2) and environmental variables (Fig. 3) throughout the late Holocene are described in this section in relation to four major biostratigraphic zones. Note that these zones were defined based solely on changes in the diatom assemblages, as summarized by a PCA (Fig. 4; discussed subsequently).

Zone A (AD 1050–1430)

In zone A, the relative abundance of *D. stelligera* declined steadily. *T. flocculosa* str. IIIp represented on average 30% of the total diatom sum, and *F. crotonensis* percentages fluctuated gradually, reaching a minimum for the record at the boundary between zones A and B (<5%). In AD 1150, *Aulacoseira tenella* (Nygaard) Simonsen, 1979 first appeared in the record, increasing at AD 1300 (Fig. 2). Diatom influx was relatively low and did not significantly change in zone A (Fig. 3). There was a slight decrease in CS/DV just before AD 1200, which coincided with a brief peak in charcoal influx (two consecutive samples), and a small decline in pollen influx occurred at AD ~1250 (Fig. 3).

Zone B (AD 1440–1630)

At the beginning of zone B, *A. tenella* abruptly disappeared and remained absent from the rest of the record. The relative abundance of *T. flocculosa* str. IIIp increased up to a maximum of 52% in AD 1570, before declining rather abruptly (Fig. 2). Total diatom, pollen, and charcoal influx rates and CS/DV were stable throughout zone B (Fig. 3).

Zone C (AD 1640–1870)

In zone C, *D. stelligera* began to increase, reached a peak in relative abundance at AD ~1700, and then declined to ~20% of the total diatom sum at the end of the zone. The percentage of *T. flocculosa* str. IIIp was initially low (<5%), when *Asterionella formosa* Hassal, 1850; *F. crotonensis*; and *Staurosira pinnata* (Ehrenberg) D.M. Williams et Round, 1988 were more abundant. Despite this initially low relative abundance, *T. flocculosa* str. IIIp quickly stabilized at ~25% of the total diatom sum in the rest of the zone. *S. pinnata* grew in abundance more gradually, reaching a peak of 25% only at the end of zone C (Fig. 2). At the beginning of the zone, CS/DV and pollen influx declined abruptly and remained relatively low, whereas aquatic pollen rapidly increased (Fig. 3). Total diatom influx showed a single peak at AD 1690, most likely caused by a low microsphere count for that sample, which created a false signal in the data. At the beginning of the zone, there was also an abrupt decrease in JJA precipitation to values below the long-term average for the record, which persisted throughout the zone.

Zone D (AD 1880–2010)

The relative abundance of *F. crotonensis* began to increase in zone D, at the same time that *T. flocculosa* str. IIIp and *A. formosa* declined. At AD 1900, *Stephanodiscus minutulus* (Kützing) Cleve et Möller, 1882 appeared abruptly in the

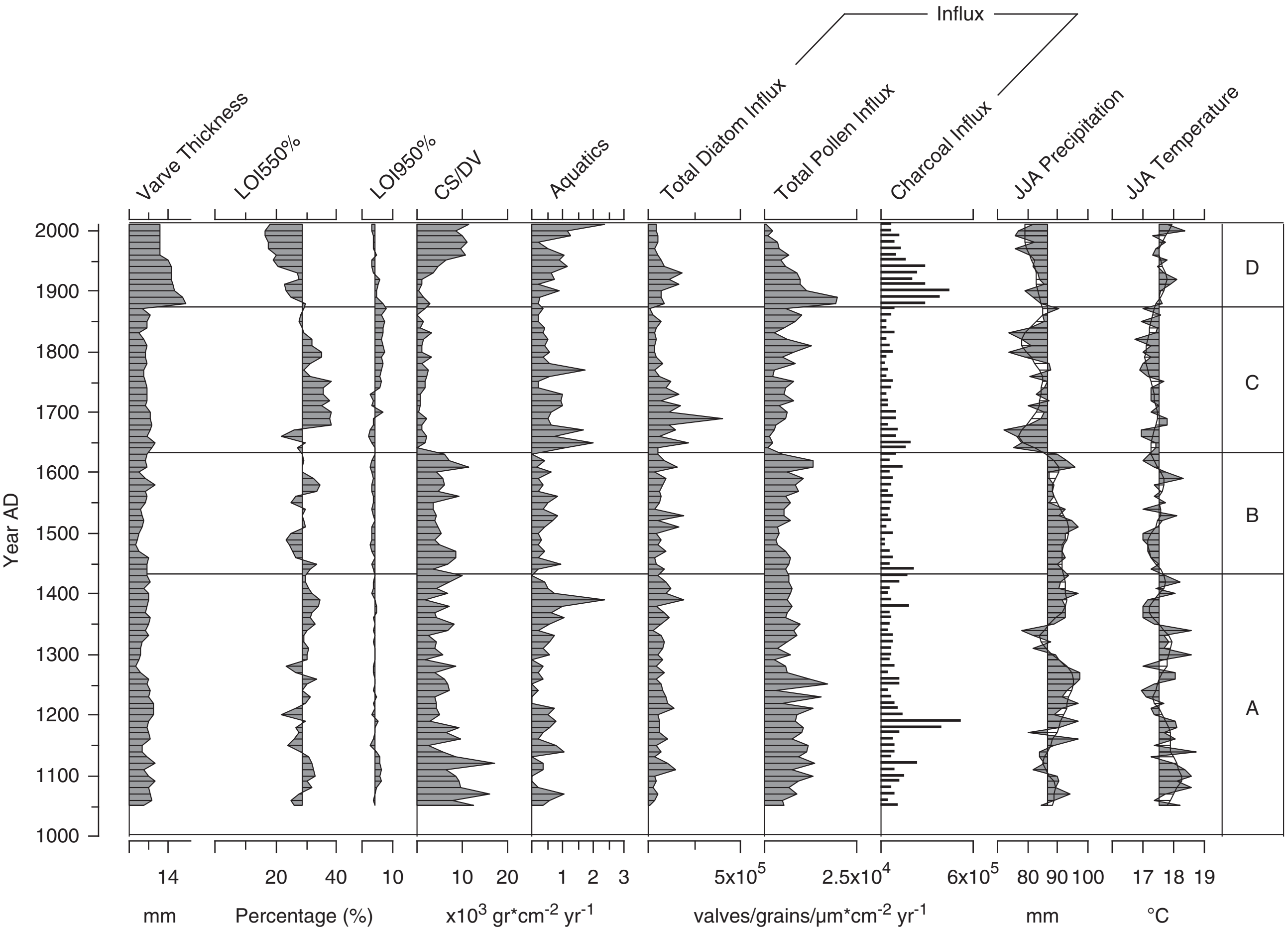

Figure 3. A paleoenvironmental summary for Lac Noir, southwestern Québec. Data obtained from Paquette and Gajewski (2013) include varve thickness, organic/carbonate content, aquatic pollen percentage, pollen and charcoal influx, and paleoclimate reconstructions (derived from the pollen record using the modern analogue technique). LOI, loss-on-ignition; CS/DV, chrysophyte scale to diatom valve index; JJA, June, July, August.

record, reaching a brief peak at AD 1920 before declining. At the same time, *Achnanthidium minutissimum* (Kützing) Czarnecki, 1994 showed a small increase in relative abundance. After AD 1940, *D. stelligera* declined by 20%, whereas some of the more rare taxa increased slightly (*Cyclotella distinguenda* Hustedt in Gams, 1928; *Staurosira construens* Ehrenberg, 1843; *Planothidium* spp.; and *Psammothidium* spp.) (Fig. 2). Total diatom, pollen, and charcoal influx increased at the beginning of zone D and subsequently decreased at the end of the zone. Aquatic pollen and CS/DV only increased after AD 1930 but kept rising throughout the zone.

PCA

The PCA explained 41% of the variance in the diatom assemblages on the first three axes (Fig. 4; component 1, 17%; component 2, 14%; component 3, 10%). The first diatom PC axis represented changes in the abundance of *T. flocculosa* str. IIIp, *F. crotonensis*, and *S. minutulus* (Table 1). It had positive values in zones A and B (AD 1050–1630), negative values in zone C (AD 1640–1870), and larger negative values in zone D (AD 1880–2010) (Fig. 4). The second diatom PC axis had more high-frequency variability, but with two rather distinct shifts from negative to positive values; the first is the transition between zones B and C, and the second occurred in zone D at AD 1900. The second component was positively loaded on *D. stelligera* and negatively loaded on *S. pinnata* and *Psammothidium* spp. Finally, the third diatom PC axis had decreasing values at the transition between zones A and B, mostly negative values throughout zone C, and an abrupt increase to positive values in zone D at AD 1900. This axis was positively correlated with *A. tenella*, *A. minutissimum*, and *Nitzschia* spp.

As mentioned previously, the biostratigraphic zones were defined strictly by changes in the diatom PC axes. However, major changes in the Lac Noir pollen record, summarized in a separate PCA (Fig. 4, Table 2), occurred at the same key points in time. Likewise, a PCA including both species data (diatom and pollen PCs) and environmental variables from Lac Noir showed clear groupings of samples associated with each of the major biostratigraphic zones (Fig. 5).

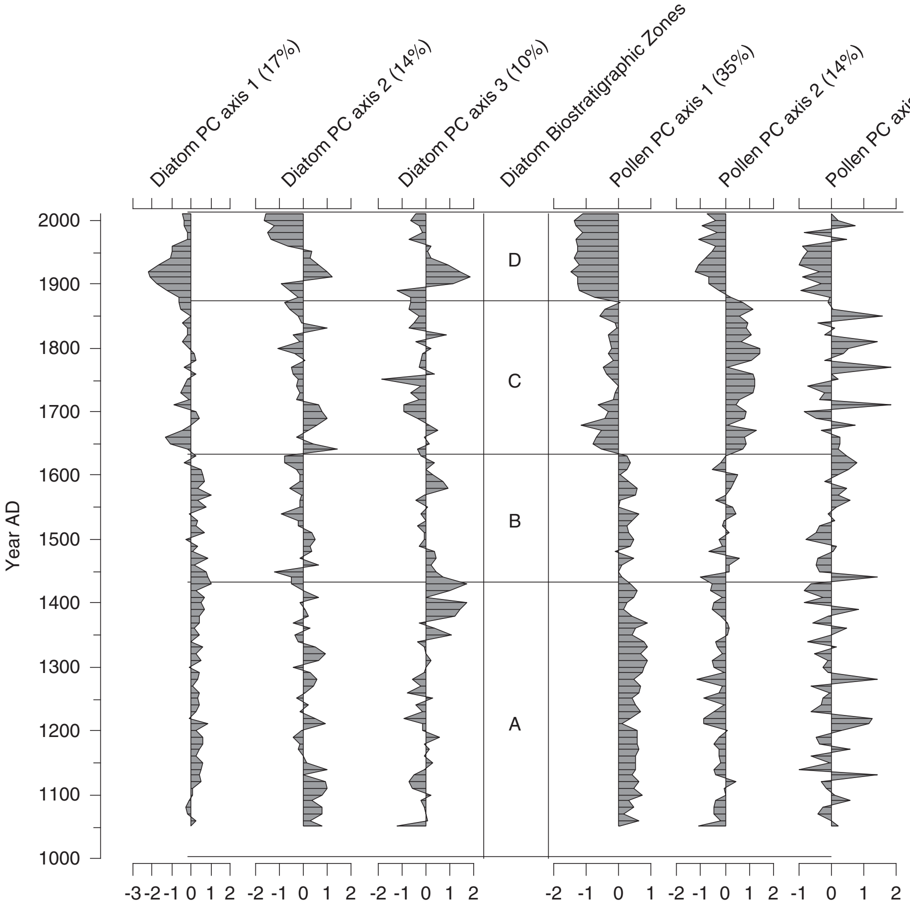

Figure 4. Diatom and pollen principal components (PCs) sample scores for Lac Noir (see Tables 1 and 2 for loadings); only significant principal components analysis (PCA) axes are shown. Explained variance of each axis is indicated as a percentage. The division of the diagram is based solely on changes in the diatom PCA. The pollen PCA axes were derived from the pollen record of Paquette and Gajewski (2013).

GAMs

In the first GAM, predictor variables explained 71% of the variance in the fitted diatom PC axis 1 scores. The largest contributor to the fitted values was pollen PC axis 1 (P value <0.001), which was interpreted as an indicator of both climate and watershed disturbances. In the time series representing the effects of this variable on the fitted diatom PC axis 1 scores (Fig. 6), two abrupt shifts toward negative values at ~AD 1630 and ~AD 1870 indicate rapid and synchronous changes in pollen and diatom assemblages. There were also shifts in the LOI 550% time series (toward positive values this time), though they lagged the transitions above by ~40–60 yr. Only one other variable, LOI 950%, was significant in this GAM, for a brief period between AD 1720 and 1870.

Approximately 51% of the variance in the fitted diatom PC axis 2 scores was explained in the second GAM. The scores were most strongly influenced by LOI 550% in this model, with significant contributions occurring after AD 1920 (Fig. 7). The time series representing the contributions of charcoal and pollen influx were rather similar (e.g., a simultaneous peak at AD 1890). Changes in the time series representing the effects of pollen PC axis 2 were more gradual and closely resembled the biostratigraphic zones (defined by the diatom PCA). This predictor variable was interpreted as an indicator of climate.

Finally, 43% of the variance in the fitted diatom PC axis 3 scores was explained in the third GAM. Several predictor variables contributed significantly to the fitted values, with the most influential being LOI 550% and pollen PC axis 1 (Fig. 8). Temporal trends in the contribution time series showed results similar to those from the GAMs described previously.

DISCUSSION

Zone A: culmination of the MWP (AD 1050–1430)

The varve-based chronology from Lac Noir indicated an age of AD 1050 for the bottom of the core, which in southern Québec corresponded to the latter part of the MWP (~AD 800–1200; Viau et al., 2006, 2012). A local pollen record from the lake showed higher abundances of deciduous taxa and *Tsuga* during this period, as well as relatively low abundances of northern taxa (e.g., *Picea*) or taxa indicative of disturbance (e.g., shrubs, herbs, *Pinus strobus*). This led to a pollen-based summer (JJA) temperature reconstruction that was 0.5–1.0°C warmer than the long-term average for the late

Table 1. Loadings and explained variance (eigenvalues) of a principal components analysis on diatom percentages from Lac Noir, southwestern Québec.

Taxon	Component 1	2	3
Discostella stelligera	−0.145	1.084	−0.545
Tabellaria flocculosa str. IIIp	1.330	−0.130	0.020
Fragilaria crotonensis	−1.082	−0.102	−0.109
Staurosirella pinnata	−0.524	−0.993	0.047
Asterionella formosa	−0.267	−0.093	−0.568
Aulacoseira tenella	0.549	−0.013	0.799
Stephanodiscus minutulus	−1.110	0.287	0.610
Achnanthidium minutissimum	−0.632	−0.123	0.797
Cyclotella distinguenda	0.567	−0.096	0.167
Nitzschia spp.	0.121	−0.161	0.754
Planothidium spp.	0.636	−0.652	−0.355
Psammothidium spp.	−0.315	−0.873	0.092
Staurosira construens	0.023	−0.606	−0.591
Staurosira construens var. *binodis*	−0.259	−0.219	−0.582
Staurosirella leptostauron var. *dubia*	−0.672	−0.823	−0.343
Other planktonics	0.066	−0.451	0.293
Other benthics/fragilarioids	0.465	−0.919	0.152
Eigenvalues	0.17	0.14	0.10

Table 2. Loadings and explained variance (eigenvalues) of a principal components analysis on pollen percentages from Lac Noir, southwestern Québec (Paquette and Gajewski, 2013).

Taxon	Component 1	2	3
Pinus diploxylon	−0.956	−0.097	0.836
Pinus haploxylon	−0.615	1.019	0.040
Picea	−0.689	0.521	0.425
Abies	−0.364	0.898	−0.211
Tsuga	1.283	−0.456	0.115
Acer	0.866	−0.783	−0.202
Betula	0.378	0.171	−0.370
Fagus	1.248	−0.580	−0.116
Other arboreal spp.	−0.276	0.202	−0.173
Alnus	−1.285	0.188	−0.250
Salix	−0.842	0.097	−0.270
Other shrub spp.	−0.612	−0.465	0.966
Asteraceae	−0.842	−0.317	−0.653
Ambrosia	−1.153	−0.489	−0.479
Poaceae	−1.214	−0.576	−0.348
Plantaginaceae	−0.796	−0.613	−0.412
Rumex type	−0.929	−0.733	0.177
Other nonarboreal spp.	−0.748	−0.699	0.452
Eigenvalues	0.35	0.14	0.08

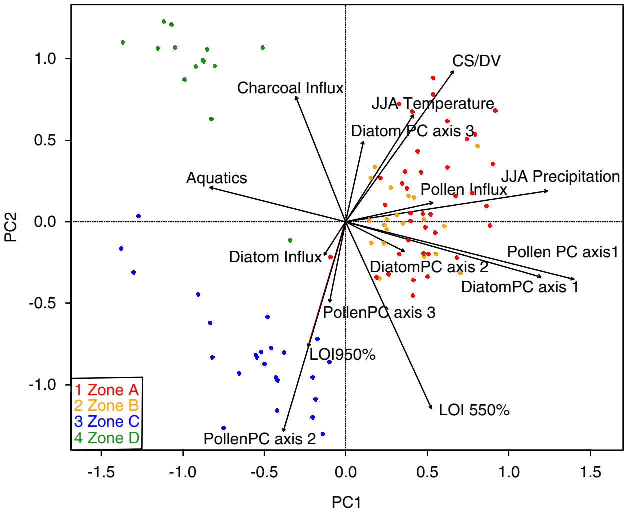

Figure 5. Biplot of a principal components analysis (PCA) of fossil diatom and pollen assemblages (summarized with separate PCAs) and environmental variables from samples in Lac Noir, southwestern Québec. Colored dots represent the biostratigraphic zones defined by the diatom PCA (see Fig. 4). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) CS/DV, chrysophyte scale to diatom valve index; JJA, June, July, August; LOI, loss-on-ignition; PC, principal component.

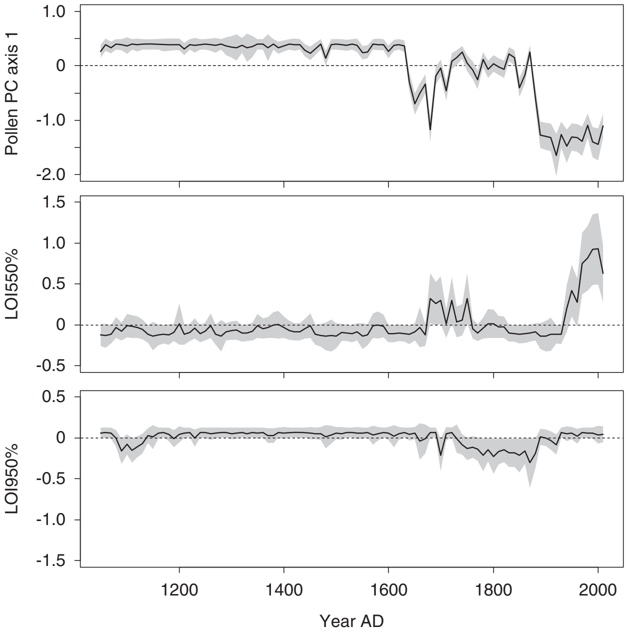

Figure 6. The contributions of environmental variables to the fitted diatom principal component (PC) axis 1 scores in the final generalized additive model for Lac Noir. A 95% pointwise confidence band is shown by the gray band. In the time series, the contribution of the variable is considered significantly different from the intercept when the gray band does not intersect the dashed zero line. LOI, loss-on-ignition.

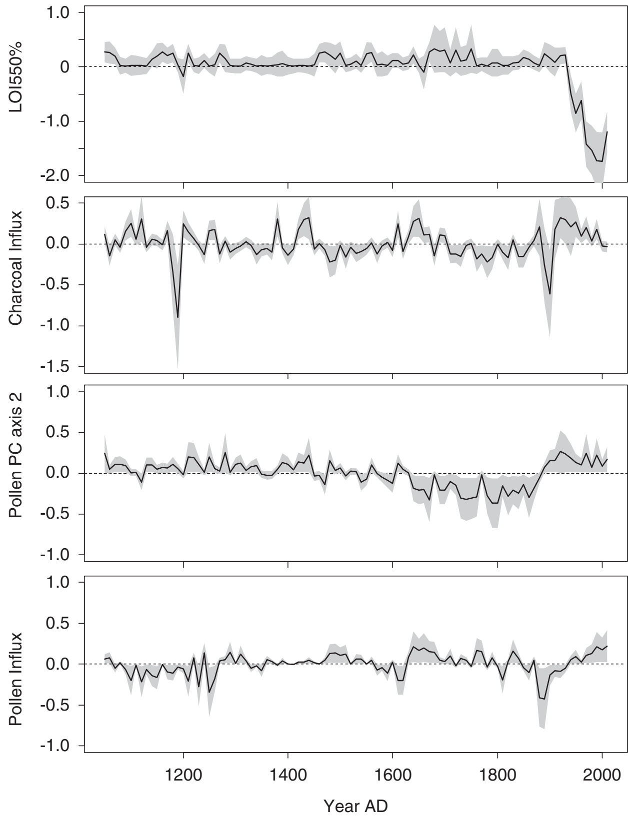

Figure 7. The contributions of environmental variables to the fitted diatom principal component (PC) axis 2 scores in the final generalized additive model for Lac Noir. A 95% pointwise confidence band is shown by the gray band. In the time series, the contribution of the variable is considered significantly different from the intercept when the gray band does not intersect the dashed zero line. LOI, loss-on-ignition.

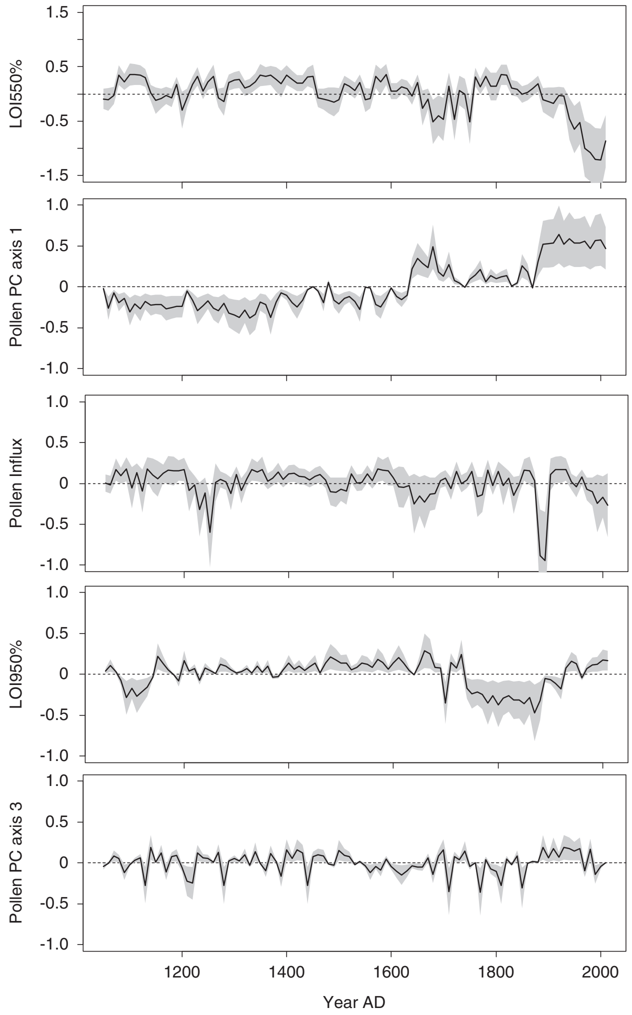

Figure 8. The contributions of environmental variables to the fitted diatom principal component (PC) axis 3 scores in the final generalized additive model for Lac Noir. A 95% pointwise confidence band is shown by the gray band. In the time series, the contribution of the variable is considered significantly different from the intercept when the gray band does not intersect the dashed zero line. LOI, loss-on-ignition.

Holocene, with relatively high JJA precipitation (Paquette and Gajewski 2013). During the MWP, diatom assemblages in Lac Noir were dominated overall by *T. flocculosa* str. IIIp and *D. stelligera*. In addition to a greater proportion of chrysophytes relative to diatoms (CS/DV), this signaled an oligotrophic, circumneutral to slightly acidic lake, with limited primary productivity (Smol, 1985; Köster et al., 2005; Puusepp and Kangur, 2010; Karmakar et al., 2015).

Throughout the MWP, the GAMs showed that the Lac Noir diatom communities were strongly influenced by the composition of the surrounding forest (pollen PC axis 1), which suggests that there was an overall association of the diatom flora with relatively warm and stable climatic conditions. Broadscale climate forcings (e.g., temperature, precipitation) could be interpreted as key drivers of aquatic responses (Williams et al., 2011), though this is not necessarily reflective of a direct relationship. Instead, shifts in diatom communities are often associated with secondary factors and catchment-mediated processes controlled by climate, such as DOC inputs, water turbidity, pH, nutrient concentrations, and light availability, among others (Morabito et al., 2012; Fritz and Anderson, 2013; Rühland et al., 2015; Neil and Gajewski, 2017). *Tsuga*-dominated forests, for example, are associated with humic-rich soils and greater inputs of dissolved organic carbon (DOC) to nearby lakes (Engstrom and Wright, 1984). These types of environments would favor diatom taxa more tolerant of high DOC such as *T. flocculosa* str. IIIp (Camburn and Charles, 2000; Faulkenham et al., 2003) and *A. tenella* (Haig et al., 2013), both of which were abundant in Lac Noir when *Tsuga* percentages were at their maximum for the late Holocene.

Toward the end of the MWP, several records from southern Ontario and Québec (including Lac Noir), as well as the New England states (United States), showed a relatively synchronous response of diatom communities to gradual climate cooling (Philibert et al., 2003; Köster and Pienitz, 2006; Neil and Gajewski, 2017). In Connecticut (United States), the rise of *A. tenella* in Bates Pond at ~AD 1150 was interpreted as a response to cooling temperatures and reduced thermal stratification (Köster and Pienitz, 2006). This taxon also appeared in Lac

Noir at ~AD 1150 and increased after AD 1300, coinciding with cooling and greater seasonal rainfall reconstructed from the local pollen data (Paquette and Gajewski, 2013). *A. tenella* is a heavily silicified diatom more commonly found in lakes with turbulent waters and high DOC (Harris et al., 2006; Haig et al., 2013; Rühland et al., 2015). In the MWP, high-frequency variations in precipitation may have led to seasonal mixing of Lac Noir as well as greater inputs of humic-rich allogenic sediments and DOC from the catchment (Köster and Pienitz, 2006; Stager et al., 2017), thus creating optimal conditions for *A. tenella*.

Zone B: onset of the LIA (AD 1430–1630)

Subtle changes in the pollen record (e.g., increase in *Pinus* and *Picea*, decline in *Tsuga* and *Fagus*) at AD 1430 were accompanied by an increase in *T. flocculosa* str. IIIp at the expense of *D. stelligera*, suggesting that this marked the initial onset of LIA cooling in the region. An overall increase in the abundance of boreal taxa would result in greater soil acidity and inputs of DOC from the catchment (Fritz and Anderson, 2013) and could explain the slight shift toward more acid-tolerant taxa such as *T. flocculosa* str. IIIp (Faulkenham et al., 2003) at Lac Noir. Lake pH could be affected by weathering processes as well; for instance, an extended period of higher than average JJA precipitation inferred from the Lac Noir pollen record (Paquette and Gajewski, 2013) may have resulted in heavier losses of base cations from the surrounding soils, leading to a slightly more acidic lake environment (Boyle, 2007; Fritz and Anderson, 2013).

Although the timing of the LIA at Lac Noir is in phase with intervals commonly used to define the period in eastern North America (Gajewski, 1988; Viau et al., 2006, 2012; Mann et al., 2008), the PCA of combined environmental variables (Fig. 5) showed that diatom assemblages from zone A (the MWP) and zone B (the onset of the LIA) overlapped. This indicates that there was a smooth transition from one period to the next, and changes within the lake and in its surrounding catchment were not pronounced. The GAMs (Figs. 6, 7, and 8) confirmed that this transition was indistinct and revealed only slight responses in diatom communities to vegetation changes and/or disturbances (pollen PC axis 1 and 2), which was expected given minimal changes in local pollen assemblages at this time (Supplementary Fig. 1).

Zone C: peak of the LIA (AD 1630–1870)

At AD 1630, the Lac Noir pollen record showed a decline in pollen influx (Fig. 3), as well as the replacement of *Tsuga* and *Fagus* by *Betula*, *Pinus strobus*, and *Alnus* in the catchment (Supplementary Fig. 1), which was interpreted as a rapid shift to a cool climate and dry conditions associated with the peak of the LIA (Paquette and Gajewski, 2013). Within the lake, there was a decline in *T. flocculosa* str. IIIp percentages and CS/DV values and increases in *A. formosa*, *F. crotonensis*, *D. stelligera*, and *S. pinnata*, as well as total diatom influx; overall this indicated a shift to a slightly more nutrient-rich lake with relatively higher productivity (Smol, 1985; Köster et al., 2005; Wolin and Stoermer, 2005; Pappas, 2010; Puusepp and Kangur, 2010) in comparison with that of the earlier record.

The GAMs showed sharp breaks in the time series representing the influences of vegetation and disturbances on diatom communities in Lac Noir (pollen PC axis 1 and 2; Figs. 6–8), signaling that changes in the surrounding forest were abrupt and had significant impacts on the diatom flora of the lake. For instance, deteriorating climatic conditions triggered disturbances and openings in the forest canopy, as evidenced by increasing abundances of *Alnus*, *Pinus strobus*, and other shrubs in local and regional pollen records (Paquette and Gajewski, 2013; Lafontaine-Boyer and Gajewski, 2014). The initial opening of the forest in addition to enhanced soil erosion in the LIA (Stevenson et al., 1990) likely facilitated transport of nutrients to nearby lakes (Hall and Smol, 1993), promoting primary productivity. Changes in terrestrial vegetation composition have been shown to affect leaf litter quality and nutrient availability within lakes (Rawlence, 1992). Forests composed of broad-leaved taxa (e.g., *Betula* and *Alnus*) contribute more nitrates (NO_3^-) and phosphorus (P) to lakes through erosion and runoff than those dominated by conifers (e.g., *Tsuga*), favoring diatoms indicative of meso-eutrophic lake conditions (Hall and Smol, 1993; Beck et al., 2016). Diatoms such as *A. formosa* and *F. crotonensis* are more competitive than *Tabellaria* sp. in lakes with moderate to high levels of N and silica (Saros et al., 2005; Arnett et al., 2012) and are indicators of eutrophication in temperate lakes (Lotter, 1998). Increases in these taxa at Lac Noir thus support an inference of higher nitrogen concentrations (likely the primary limiting nutrient) and overall lake productivity during the peak of the LIA.

In contrast to the MWP, declining percentages of *Tsuga* as well as cooler and dry climatic conditions at the peak of the LIA (Paquette and Gajewski, 2013) may have led to less acidic waters and low DOC inputs, evidenced by an increase in *D. stelligera* and benthic alkaphilous taxa (e.g., *S. pinnata*) at the expense of *T. flocculosa* str. IIIp (Faulkenham et al., 2003; Lavery et al., 2014). Studies of Arctic and temperate lakes report conflicting findings in regard to optimal lake and/or climatic conditions for *D. stelligera*, even in sites within close proximity to one another (Saros and Anderson, 2015). Some studies suggest that *D. stelligera* is more abundant in warm conditions with greater thermal stratification (Perren et al., 2009; Rühland et al., 2015); however, at Lac Noir, as well as at other sites, there seems to be a definitive association of this small centric taxon to N concentrations (Fritz and Anderson, 2013; Neil and Gajewski, 2017) or even climate cooling as was described by Saros and Anderson (2015) in relation to neoglaciation.

During the peak of the LIA, the Lac Noir diatom record again closely resembled that of Bates Pond in Connecticut (Köster and Pienitz, 2006). At Bates Pond, increased abundances of benthic *Fragilaria* spp. (*S. pinnata* included) at AD 1640 were interpreted as a response to cooling climate

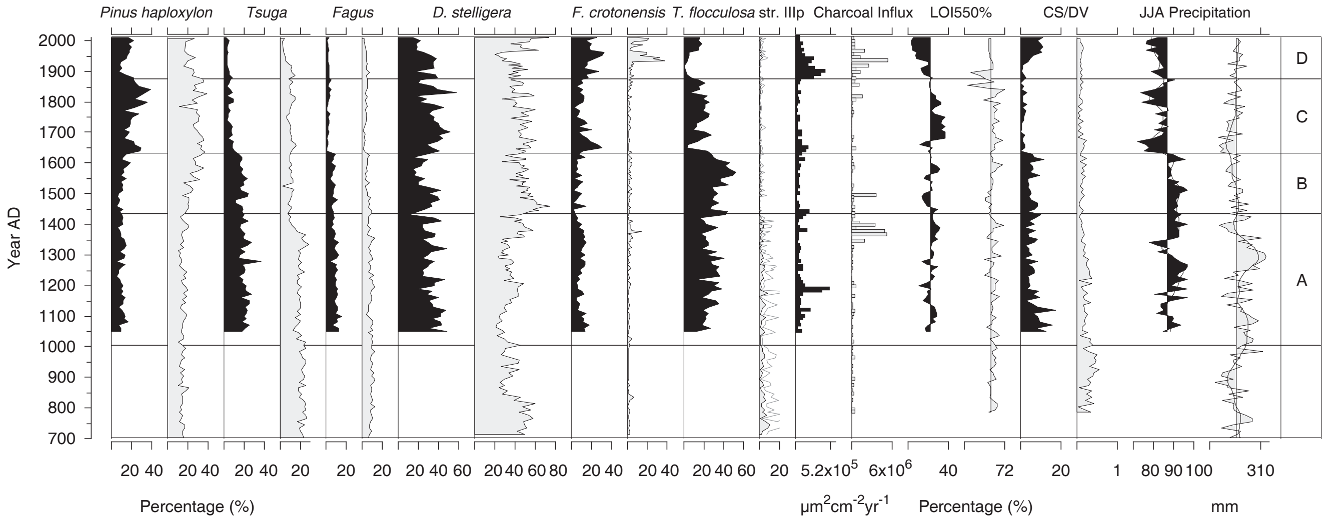

Figure 9. A comparison of selected pollen and diatom percentages and environmental variables from Lac Noir (black; this study; Paquette and Gajewski, 2013) and Lac Brûlé (grey; Lafontaine-Boyer and Gajewski, 2014; Neil and Gajewski, 2017).). CS/DV, chrysophyte scale to diatom valve index; JJA, June, July, August; LOI, loss-on-ignition.

conditions and prolonged seasonal ice cover. At other sites, extended ice cover has been shown to trigger internal releases and mobilization of P from lake sediments (Kirilova et al., 2009). *S. pinnata* has a slightly higher weighted average for TP and TN than other diatom taxa such as *Tabellaria flocculosa* str. IIIp (Hall and Smol, 1996; Christie and Smol, 1993), and thus increases in this taxon at Lac Noir may have signaled either internal or external nutrient loading during the cool, dry phase of the LIA. Increased abundances of small benthic *Fragilaria* spp. could indicate an expansion of the littoral zone as well (Karst and Smol, 2000); at Lac Noir, low inferred JJA precipitation and greater abundances of aquatic macrophytes during the peak of the LIA (Fig. 3; Paquette and Gajewski, 2013) may have therefore led to optimal conditions for *S. pinnata*.

Zone D: post–Euro-Canadian settlement (AD 1870 to present)

The initial settlement and subsequent expansion of Euro-Canadian activities in southern Québec (~AD 1820–1875; Smith, 1967; Neil and Gajewski, 2017) corresponded broadly with the end of the LIA in the region (Gajewski, 1988). The impacts of human-induced land clearance and burning of forests for agriculture in the region were prominent in the Lac Noir record after AD 1870; there was an abrupt increase in herbaceous pollen (*Ambrosia*, Poaceae, Plantaginaceae, *Rumex*) coinciding with an influx of microcharcoal in the lake sediments (Paquette and Gajewski, 2013). Disturbance associated with the colonization, such as logging or burning, may have increased the inputs of minerogenic materials to the lake (Rosén and Hammarlund, 2007), possibly evidenced by a decline in organic matter content (Fig. 3).

Abrupt changes in the GAMs at AD 1870 confirm significant responses of the diatom flora to direct and indirect impacts of catchment disturbances (pollen PC axis 1 and LOI 550%; Figs. 6–8). Both climate (pollen PC axis 2) and terrestrial productivity (pollen influx) were also influencing factors on the lake ecosystem, although their contributions to diatom trends were gradual and subtler. Peaks in *A. minutissimum* and *S. minutulus* were recorded at Lac Noir from AD 1870–1930, slightly after initial settlement when anthropogenic activities and associated impacts on the landscape were high (Smith, 1967). Regional deforestation as a result of land clearance and logging likely triggered the release of nutrients, particularly N, within the catchment (Vitousek et al., 1997; Neil and Gajewski, 2017), which ultimately caused the changes seen in the diatom flora at Lac Noir during this period; for instance, *A. minutissimum* is known to be responsive to nitrogenous influxes and pollution (Pappas, 2010). Multiple mechanisms related to human activities further contribute to the loading of P in lake ecosystems, including the use of fertilizers and manure in agricultural fields (presently located as close as 1 to 2 km east of Lac Noir), septic leaching into local groundwater and surface water, or atmospheric deposition of dust particles (Riemersma et al., 2006). Diatom calibration sets of lakes in southern Ontario and Québec suggest that *S. minutulus* has a weighted average (optima) of 549.5 µg/L for TN (Christie and Smol, 1993) and 17.0 µg/L for TP (Tremblay et al., 2014). The peak in *S. minutulus* between AD 1870 and 1930 at Lac Noir was therefore reflective of meso-eutrophic conditions associated with anthropogenic activities and indicated TN and TP values that were roughly double those observed in the modern surface sample collected from Lac Noir soon after the core was retrieved (Cooper et al., 2016).

Greater atmospheric N deposition caused by fossil fuel combustion, agricultural practices, and other anthropogenic activities have been noted in recent decades, as evidenced by a rise in *A. formosa* and *F. crotonensis* in North American lakes (Hall and Smol, 1996; Saros et al., 2005; Arnett et al., 2012; Sheibley et al., 2014). Similar increases in these taxa were seen at Lac Noir after Euro-Canadian settlement, suggesting that this activity has had substantial influences on lakes in southern Québec. After AD 1930, the Lac Noir diatom record showed signs of progression toward a less productive ecosystem (e.g., disappearance of *S. minutulus,* higher CS/DV values, an increase in *T. flocculosa* str. IIIp), similar to that observed during the MWP. Human impacts on vegetation were less pronounced, and regional temperatures were once again warmer than the long-term average for the late Holocene (Paquette and Gajewski, 2013; Lafontaine-Boyer and Gajewski, 2014). The more recent change in lake trophic state could be explained by a reduction in phosphorus concentrations resulting from better management practices (Riemersma et al., 2006) or perhaps the ability of early successional forests to better retain nutrients (Hall and Smol, 1996).

Lac Noir and Lac Brûlé: a regional comparison of diatom/pollen records

A comparison of the paleorecords from Lac Brûlé and Lac Noir (25 km apart) showed that the vegetation surrounding each of the two sites responded to environmental changes similarly in timing and direction of change, with some exceptions (Lafontaine-Boyer and Gajewski, 2014). Diatom community composition was more unique to each lake as a result of local catchment-scale characteristics, including basin morphometry, habitat availability, water chemistry, and disturbances (Blanco, 2014). Regardless, most of the pollen taxa and several of the abundant diatom species were common to both sites and were directly comparable (Fig. 9).

Inconsistency in the pollen records of the two lakes was mainly attributed to a decline in *Tsuga* that occurred earlier in Lac Brûlé at AD 1345, in response to a fire in the catchment (Fig. 9; indicated by a peak in charcoal influx). This disturbance was considered to be local, as there was no equivalent response in the Lac Noir record, despite the relatively close proximity of the two lakes (Lafontaine-Boyer and Gajewski, 2014). At Lac Brûlé, the *Tsuga* decline triggered an influx of nutrients and DOC into the lake, also resulting in poor light penetration through the water column (Cooper et al., 2016; Neil and Gajewski, 2017). This was reflected in the diatom assemblages as a decrease in the relative abundance of *T. flocculosa* str. IIIp. However, the overall nutrient status of Lac Brûlé did not appear to be greatly affected by the fire in the catchment area, as CS/DV values did not show any major changes at this time (Neil and Gajewski, 2017).

In the absence of a local fire at Lac Noir, a similar decrease in *Tsuga* only occurred later in the record at AD 1630 and coincided with the deteriorating conditions at the peak of the LIA. At this time, most of the plant taxa represented in both lakes (e.g., *Pinus strobus*, *Fagus*) declined in abundance after exceeding a threshold that reduced growth and reproductive success. The Lac Noir record also revealed a tight coupling between diatom assemblages and abrupt, climate-driven vegetation responses in the catchment area. Greater nutrient availability associated with the shift in forest composition may have resulted in a more productive lake ecosystem, again evidenced by a decline in *T. flocculosa* str. IIIp and a peak in the percentages of *A. formosa* and *F. crotonensis*. As the decline in *Tsuga* was accompanied by additional changes in terrestrial vegetation at Lac Noir, such as a decline in *Fagus*, there were greater consequences for the nutrient status of the lake (e.g., a rapid decline in CS/DV values that was absent from the Lac Brûlé record).

Local forcings were responsible for triggering site-specific changes in the diatom records of Lac Brûlé and Lac Noir. For example, in both lakes, diatom assemblages in the uppermost samples representing the last 100 yr were dissimilar as they responded individually to changes in their respective environments. At Lac Brûlé, diatoms responded abruptly to impacts associated with the Wallingford-Back Mine (AD 1924–1972), located approximately 300 m north of the lake (Neil and Gajewski, 2017). Mining operations did not significantly affect the surrounding vegetation, though increases in the percentages of *F. crotonensis* at Lac Brûlé to well above previous values indicated nutrient enrichment of the lake associated with human activity. Diatom assemblages from Lac Noir were relatively undisturbed in comparison, with major changes only occurring concurrently with vegetation shifts in the catchment after AD 1870.

CONCLUSIONS

The timing of zone boundaries delineated by the diatom assemblages of Lac Noir, southwestern Ontario, match major shifts in pollen relative abundance and influx, as well as peaks in charcoal input to the sediment and, to a certain extent, transitions in sediment organic matter and carbonates. This indicates a close coupling of the lake ecosystem to terrestrial vegetation dynamics in the catchment and surrounding region. Multiproxy paleolimnological studies with sampling at high resolution are thus necessary to unraveling the intricate dynamics of climatic and terrestrial influences on lake aquatic communities. These types of studies not only provide necessary details regarding the succession of past communities, but also represent a key component in forecasting future responses to climate variability and human-induced disturbances.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit https://doi.org/10.1017/qua.2018.99

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