Impacts of late-Holocene climate variability and watershed-lake interactions on diatom communities in Lac Brûlé, Québec

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Abstract. A high-resolution diatom analysis of a varved sediment sequence from Lac Brûlé, southwestern Québec, was used to study temporal patterns of environmental change in the late Holocene. Key periods of interest in the record included the Medieval Warm Period (~800–1300 CE), the Little Ice Age (~1450–1850 CE), and post-European settlement (~1850–present). Subfossil diatom assemblages were compared to previously published pollen, cladocera, and sediment records from Lac Brûlé, revealing complex dynamics between terrestrial vegetation succession, nutrient fluxes, and trophic interactions. Generalized additive models showed a response to long-term climate variability in the diatom record, although it was not the most influential driver of community changes at Lac Brûlé. Catchment-mediated processes instead played the largest role in governing the structure of diatom assemblages in the lake. For example, nutrient loading following a local fire in the watershed at 1345 CE led to an abrupt and significant increase in Fragilaria spp. Human activity associated with deforestation and the Wallingford-Back Mine (1924–1972 CE) also had strong impacts on the landscape, which triggered further responses in the aquatic communities of Lac Brûlé.

Key words: bottom-up/top-down; cladocera; diatom; European settlement; generalized additive models (GAMs); Little Ice Age; Medieval Warm Period; mine impact; paleolimnology; pollen; varve.

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INTRODUCTION

There are many complex pathways through which terrestrial and aquatic ecosystems respond to external forcings and their interactions (Winder and Schindler 2004). It is thus challenging to anticipate when and how ecological communities will react to present and future changes in the environment (Johnstone et al. 2016), and to address potential issues regarding ecosystem management. Developing strategies to deal with environmental change requires not only an understanding of the direct and indirect mechanisms influencing current ecosystem responses (Alric et al. 2013), but also an expanded temporal perspective of these changes (Foster et al. 1990). Numerous paleolimnological studies, for example, demonstrate the ability of lake sediment analysis to accurately reconstruct ecosystem responses to external stresses (Smol et al. 2001), especially when sampled at high temporal resolution.

In southwestern Québec and southeastern Ontario, paleo-studies have shown that climate variability in the late Holocene had a significant influence on temperate forests and aquatic communities. Pollen-based inferences indicate that temperature and precipitation were important drivers of vegetation dynamics during well-established climate regimes, namely the Medieval Warm Period (MWP; 800–1300 CE) and the Little
Ice Age (LIA; 1450–1850 CE; Lafontaine-Boyer and Gajewski 2014, Paquette and Gajewski 2013). During these periods, phytoplankton and zooplankton assemblages were responsive to direct climate impacts on lake hydrologic and thermal budgets (Haig et al. 2013, Cooper et al. 2016). However, indirect catchment-mediated processes (e.g., vegetation composition and productivity, fire, soil development) also play an integral role in governing the structure and function of lacustrine ecosystems (Anderson 2000, Fritz and Anderson 2013). Since the settlement of Euro-Canadians in the region (1820s–present), interactions between ongoing climate change and anthropogenic activities have also triggered abrupt shifts in biotic communities (Paquette and Gajewski 2013). Deforestation and agriculture following Euro-Canadian settlement (after the 1820s) in the region was likely limited to the river valleys (Smith 1967), the closest of which (Rivière du Lièvre) is 6 km from Lac Brûlé. The only historical evidence of human impacts in the immediate watershed of the lake is from operations at the Wallingford-Back Mine, which was open from 1924 to 1972 CE (Leroux 2012). The mine is located 300 m north of Lac Brûlé, with a private access road running directly alongside the northern shore. A small stream connecting a pond at the mine to Lac Brûlé may intermittently drain into the lake, though there was no indication of water flow in June of 2016. Currently, several cottages and permanent houses are located around small lakes in the region, but only one cabin exists on Lac Brûlé and it was constructed after the 1980s.

Coring and chronology
Sediment cores were retrieved from the deepest basin of Lac Brûlé (43 m depth) in two separate field seasons using freeze-corers. For a previous study (Lafontaine-Boyer and Gajewski 2014), a set of four continuously laminated cores was retrieved in 2012, one of which was sampled for pollen analysis. Lafontaine-Boyer and Gajewski (2014) established a varve-based chronology for the lake sediments by cross-dating the four cores, using distinct marker layers as tie points between the cores. The chronology of the core chosen for pollen analysis (BV13) was also independently validated using 14C dating. In 2013, an additional core (BV14) was retrieved from the same lake basin and analyzed for both cladoceran remains (Cooper et al. 2016) and diatoms. Varve counts from the BV14 core were resolved with those of the four 2012 cores (Appendix S1: Fig. S1), with an estimated error of <1% in the resulting chronology.

Laboratory analysis
Varve thickness of the BV14 core was measured at five-year intervals, using an Acu-Rite linear
encoder and Quick-Check readout with Measure J2X software (VoorTech Consulting, Holderness, New Hampshire, USA). The core was then sectioned at five- or ten-year intervals, with higher sampling resolution taken during significant time periods. Determination of these periods (e.g., the MWP and LIA) was guided in part by the pollen record from the 2012 core. Sediment subsamples of 0.25 cm³ were extracted from each section of the core and processed for diatoms following standard protocols (Battarbee et al. 2001). A microsphere suspension of 5 x 10⁶ spheres/mL was prepared from a stock solution, and a predetermined amount was added to each subsample after cleaning to enable the calculation of fossil diatom concentration and accumulation rates.

**Microscope slide preparation and counting**

A small amount of diatom suspension, diluted with distilled water, was pipetted onto a clean coverslip and left to evaporate at room temperature to attain an even spread of dried diatoms over the coverslip. A drop of Naphrax was then used to mount the coverslips onto permanent slides. A minimum of 500 individual diatom valves (DV) per slide were counted and identified under oil emersion at 1000x magnification, using a Nikon (Minato, Tokyo, Japan) 90i microscope. Identifications were based on Antoniades et al. (2008), Siver et al. (2005), and Patrick and Reimer (1966, 1975). Chrysophyte scales (CS) were counted concurrently for each microscope slide to estimate the relative proportions of scales to DV.

**Statistical analyses**

A total of 21 diatom taxa were selected for statistical analysis, based on the criterion that each individual taxon had >3% relative abundance in at least one of the 194 samples counted. Rare species were grouped into categories of other benthics and other planktonics, and all relative abundance data were Hellinger-transformed prior to data analysis (Legendre and Gallagher 2001). Principal components analysis (PCA) was chosen to summarize patterns of diatom community changes through time (Legendre and Birks 2012). To compare the fossil diatom communities with existing pollen, cladocera, and sediment records from Lac Brulé, samples were aggregated into 10-yr time intervals. This returned 123 continuous samples between 785 and 2005 CE for which all taxonomic and sediment data were available. Changes in the diatom, pollen, and cladocera assemblages at this 10-yr sampling resolution were each quantified with PCAs using the package vegan (Oksanen et al. 2008) in R3.2.5 statistical software (R Development Core Team 2013). Significant principal components (PCs) in each ordination were selected using scree plots of the axis eigenvalues and represented the main taxonomic trends in subsequent analysis.

Using the mgcv package (Wood 2008, 2011) in R, generalized additive models (GAMs) were used to separate and quantify the influences of several independent forcing variables (e.g., climate) on diatom community structure in Lac Brulé. This type of modeling uses a sum of smooth functions to reveal local patterns in the relationships between predictor and response variables (Simpson and Anderson 2009). As such, GAMs are applicable in multi-proxy paleolimnological studies where the effects of variables can often change through time, and are potentially amplified or dampened during significant periods (e.g., the MWP, the LIA, and European settlement).

In this study, changes in the scores of each significant diatom PC axis were considered as the response variable in the GAMs (four individual models). The following predictor variables were introduced in each model: pollen PC axes 1–3, the ratio of CS to DV, and cladocera PC axes 1–3. These variables were chosen as indicators of watershed disturbances, climate, lake trophic status, and trophic interactions between aquatic primary producers and consumers. The GAMs were fit using restricted maximum likelihood smoothness selection, and thin-plate splines with a value of $k = 9$ for each basis dimension. A shrinkage method approach was also used to place a second penalty on each smooth term (Marra and Wood 2011). Evidence of autocorrelation was seen in the models explaining diatom PC axes 1 and 4; however, fitting generalized additive mixed models with various autoregressive processes failed to resolve the correlation structure in the residuals. We therefore used the models without correcting for autocorrelation, but recognize that this potentially led to poorer function estimates (Kohn et al. 2000).
RESULTS

Diatom assemblage zones

The diatom record from Lac Brulé was dominated by planktonic species (~40–80%), including Discostella stelligera (Cleve & Grunow) Houk & Klee 2004, and other Cyclotella species, Asterionella formosa Hassal 1850, and Aulacoseira spp. Fragilaroids and benthic diatoms were less abundant throughout most of the record (15–60%) and were mainly represented by Fragilaria spp., Achmannanthidium minutissimum (Kützing) Czarnecki 1994, and Tabellaria flocculosa (Roth) Kützing 1844 (Fig. 1). The fossil diatom percentage diagram was divided into three major zones (and four sub-zones) based on a PCA of the main taxa (Fig. 2).

Discostella stelligera was relatively abundant at the beginning of zone A (715–1350 CE), but declined rapidly from ~55% to 25% of the total diatom sum around 850 CE (Fig. 1). This marked the transition between zones A1 and A2 and was associated with an increase in Cyclotella bodanica var. intermedia Manguin ex Kociolek & Reviers 1996 and A. formosa, as well as the near disappearance of Aulacoseira spp. Species such as Cyclotella rossi Håkansson 1990 and T. flocculosa maintained relatively consistent abundances throughout zone A (~10% and 5%, respectively). In zone A1, the summed abundance of all planktonic species was greater than the average for the whole record. Planktonic species percentages fell below average from 850 CE to 1100 CE and remained close to average for the remainder of zone A2.

Zone B (1350 CE–1875 CE) was divided into two subzones, based on several transitions in the diatom assemblages. In zone B1, D. stelligera increased slightly, while C. bodanica var. intermedia and C. rossi declined rapidly from 20% to under 5% of the total diatom sum. Fragilaria spp. had a prominent peak (~13.5%) in 1375 CE, but returned to lower abundances of <5% for the remainder of zone B. At the end of zone B1, T. flocculosa decreased to <1% relative abundance. In zone B1, benthic and fragilaroid species were still outnumbered by planktonic species, though they did increase to above average values in comparison with the rest of the record. Discostella stelligera abruptly increased at the beginning of zone B2, reaching a maximum abundance of ~75% of the total diatom sum in 1460 CE. Following this peak, D. stelligera decreased again to ~50%. An increase in Aulacoseira spp. was also seen at around 1650 CE. Throughout the zone, both C. bodanica var. intermedia and C. rossi...
gradually increased in abundance toward percentages seen earlier in the record. Abundances of planktonic species were consistently above average in zone B2.

Zone C (1875 CE–2010 CE) was characterized by high abundances of *Cyclotella michiganiana* Skvortzov [Skvortzov] 1937, *Fragilaria* spp., and *A. minutissimum* in comparison with the earlier record. The relative abundances of these three species peaked at ~15%, 40%, and 8.5% of the total diatom sum, respectively. At the beginning of the zone, *D. stelligera* represented roughly 20–45% of the diatom assemblage. At 1970 CE, *D. stelligera* increased abruptly to ~65%, and reached a peak in 2010 CE. When *Fragilaria* spp. peaked in 1935 CE, benthic and fragilarioid species outnumbered planktonic species in the diatom record by a ratio of 3:2. Following this, planktonic species began to increase in abundance, reaching around 80% of the total diatom sum at the top of the record.

Total diatom accumulation rates (DAR; also known as influx) for Lac Brûlé were relatively low until 1700 CE when they increased slightly, and reached maximum values in 2005 CE (Fig. 2). High-frequency oscillations of DAR in zone B2 were interpreted as a function of batch number during processing, possibly resulting from slight differences in concentrations of microspheres added to sample vials on different dates. Long-term trends spanning the entire record, however, did not appear to be affected by this variance. The CS/DV in Lac Brûlé was highest near the beginning of zone A2, with a long-term trend of decreasing values from 925 CE to present date (Fig. 2).

**Principal components analysis**

Approximately 52% of the total variance in diatom assemblages was explained on the first four axes of a PCA (Fig. 2; Appendix S1: Fig. S2; component 1: 19.4%; component 2: 13.2%; component 3: 11.4%; component 4: 8.0%). The first component represented changes in the composition of *D. stelligera*, *Fragilaria* spp., and *Staurisirella pinnata* (Ehrenberg) D.M. Williams &
Round 1988, with negative scores in zones A1 and A2, positive scores in zone B2, and large positive scores in zone C after 1950 CE. The second component was positively loaded on *C. rossi* and negatively loaded on *C. michiganiana* and *A. minutissimum*. This component had high positive scores in zone A1 and negative scores in zones B1 and C. The third component was correlated with rarer taxa, including positive contributions of *Cymbopleura* spp. and *A. minutissimum* vs. those of *Aulacoseira* spp. and *Achnanthes microcephala* (Kützing) Grunow 1880. This component showed a trend of positive scores in zone A2 and highly variable (though mostly negative) scores from 1430 CE to present. The fourth component was correlated with *Fragilaria* spp., having positive scores in zones B1 and C.

**Generalized additive models**

Generalized additive models were used to show the contributions of seven forcing variables on fitted diatom PC axis scores at Lac Brulé: pollen PC axes 1 and 3 (Fig. 2; Appendix S1; Fig. S3; interpreted as watershed disturbances), pollen PC axis 2 (climate), CS/DV ratio (lake trophic status), and cladocera PC axes 1, 2, and 3 (Fig. 2; Appendix S1; Fig. S4; trophic interactions). In each of the four GAMs (Figs. 3–6), cladocera PC axis 3 had zero contribution to the fitted scores and is therefore not shown in the figures. Together, the seven variables explained 63.0%, 60.7%, 49.2%, and 57.6% of the variance in the fitted diatom PC axis 1–4 scores, respectively (Fig. 7).

In the first GAM explaining the fitted diatom PC axis 1 scores, watershed disturbances (pollen PC axis 1) contributed the most to the fitted...
values ($P$-value $< 0.001$). At ~1345 CE, there was an abrupt shift from positive to negative values in the time series representing the effects of watershed disturbance on diatom PC axis 1 scores (Fig. 8A), signaling an important disturbance event in the record. Another shift toward greater negative values at around 1900 CE indicated a second disturbance event with similar consequences for the diatom community. Climate (pollen PC axis 2) also had significant influences on the fitted diatom PC axis 1 scores, though not as consistently throughout the record. Fig. 8B, however, shows changes from positive to negative $y$-axis values (and vice versa) that marked three important climatic periods in the mid- to late Holocene: 800–1450 CE, 1450–1900 CE, and 1900–2010 CE. Finally, lake trophic status (CS/DV) was only significant after 1675 CE.

In the second GAM explaining the fitted diatom PC axis 2 scores, trends were influenced by several covariates. Pollen PC axis 1 again showed a sudden shift at ~1345 CE, interpreted as a response to disturbance in the watershed (Fig. 9A). However, unlike in the first model, pollen PC axis 3 showed a significant change to positive $y$-axis values at ~1860 CE, again indicating an abrupt disturbance event (Fig. 9C). Climate (pollen PC axis 2) was the most influential contributor to the fitted diatom PC axis 2 scores, and showed the same climatic periods identified in the first GAM (Fig. 9B). Trophic interactions were mostly significant for brief periods in the oldest and most recent sediments of the record (cladocera PC axis 1; Fig. 9E), but also showed similarities to the pollen PC axis 2 time series (cladocera PC axis 2; Fig. 9F).
Only lake trophic status (CS/DV) was significant in contributing to the fitted diatom PC axis 3 scores, where y-axis values became more positive at \(-1345\) CE, and again at \(-1700\) CE (Fig. 10D). In the fourth GAM, climate (pollen PC axis 2) and trophic interactions (cladocera PC axis 1) were the only significant contributors to fitted diatom PC axis 4 scores (Fig. 11B, E).

**DISCUSSION**

**The Medieval Warm Period (~800–1450 CE)**

In this study, very few samples from the earliest section of the core (subzone A1) were available for input in the GAMs; this restricted interpretations of terrestrial and aquatic assemblages to the past 1200 yr of the late Holocene, beginning with the onset of the MWP at \(-800\) CE in southwestern Québec. In the MWP, terrestrial vegetation in southwestern Québec was characterized as temperate conifer–hardwood forest dominated by hemlock, white pine, maple, beech (*Fagus*), and birch (Paquette and Gajewski 2013, Lafontaine-Boyer and Gajewski 2014). At Lac Brulé, this led to a pollen-based reconstruction of generally warmer climatic conditions (Lafontaine-Boyer and Gajewski 2014) consistent with sites across eastern North America (Gajewski 1988, Viau et al. 2012) and formed the basis of the interpretation of the PC axes (above). Regional aridity and droughts associated with the MWP were recorded by multiple lake-level studies west of Lac Brulé (Booth et al. 2006, 2012, Haig et al. 2013). In contrast, the Lac Brulé pollen record indicated variability in reconstructed precipitation values throughout the MWP; conditions were
relatively dry until ~1000 CE, after which they became predominantly wetter (Lafontaine-Boyer and Gajewski 2014). There is therefore little evidence to suggest that droughts were occurring in the MWP further east, in southwestern Québec or in southeastern Ontario (Keizer et al. 2015).

The GAMs showed a defined period from ~800 CE to 1450 CE where climate (PC axis 2) in the MWP was a significant contributor to fitted diatom trends (Fig. 8B). At the onset of the MWP, increased abundances of *Cyclotella bodanica* var. *intermedia* and *Cyclotella rossi* in Lac Brulé (Fig. 1) signaled lower available nutrient concentrations associated with the warming summer temperatures (Findlay et al. 1998, Bracht et al. 2008). During this period, the high ratio of chrysophytes to diatoms (Fig. 2; Smol 1985), as well as the relatively high percentages of *Tabellaria flocculosa* (Fig. 1; Puusepp and Kangur 2010), indicated oligotrophic conditions in the lake. As temperatures rose above average for the late Holocene, increased thermal stability may have favoured lighter planktonic diatoms (e.g., *Cyclotella*) over more heavily silicified *Aulacoseira* spp. (Harris et al. 2006). As conditions became wetter toward the end of the MWP, erosion of the soils in the Lac Brulé catchment area and subsequent nutrient loading would have been more prominent. This is evidenced by a gradual decline of chrysophytes in relation to diatoms after 1000 CE (Fig. 2).

The cladoceran assemblages of Lac Brulé during the MWP also revealed relatively high abundances of *Bosmina longirostris*, a species commonly correlated with warmer temperatures (Cooper et al. 2016). However, the presence of
B. longirostris would also typically indicate lake eutrophication (Luoto et al. 2008), contradicting the diatom- and chrysophyte-based inferences of nutrient poor conditions in the MWP. If cladoceran assemblages were responding to changes in lake trophic status (through bottom-up controls), we would have expected to see a positive correlation between B. longirostris and CS/DV values. The lack of such a relationship suggests that top-down influences on cladoceran assemblages (e.g., changes in temperature affecting cladocera metabolism and/or fish predation pressures) may have been more relevant in governing community structure during this period.

The Little Ice Age (~1450–1850 CE)

At approximately 1450 CE, the expansion of white pine, spruce, and alder (Alnus), as well as a decline in beech, marked the onset of regional cooling associated with the LIA in southwestern Québec (Lafontaine-Boyer and Gajewski 2014) and southeastern Ontario (Keizer et al. 2015). Deteriorating climatic conditions during this period favoured coniferous species adapted to colder and moister conditions, while hindering
the regeneration of hemlock after a major fire in the lake catchment area (discussed below). After 1600 CE, there was an abrupt decline in the accumulation of beech and maple pollen at Lac Brûlé (Lafontaine-Boyer and Gajewski 2014) and also around a second lake within 25 km of the study site (Paquette and Gajewski 2013). This event was interpreted as a rapid cooling in the region that persisted for approximately 100 yr.

Fig. 9. The contribution of watershed disturbances (panels A, C), climate (panel B), lake trophic status (panel D), and trophic interactions (panels E, F) to the fitted diatom principal component (PC) axis 2 scores in the final generalized additive model for Lac Brûlé. The gray band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept.

Fig. 10. The contribution of watershed disturbances (panels A, C), climate (panel B), lake trophic status (panel D), and trophic interactions (panels E, F) to the fitted diatom principal component (PC) axis 3 scores in the final generalized additive model for Lac Brûlé. The gray band is an approximate 95% pointwise confidence interval on the contribution. Where the band encompasses the dashed zero line, the contribution of the variable is not statistically significantly different from the intercept.
The timing of the LIA (~1450–1850 CE) as well as a considerable influence of climate on fitted diatom trends was demonstrated by the GAMs. The diatom record of Lac Brulé showed an increase in the abundance of *Discostella stelligera* at the onset of the LIA cooling (Fig. 1), though this species would typically be linked with warmer climates (Perren et al. 2009). Fritz and Anderson (2013) proposed that an expansion of *D. stelligera* prior to 20th-century warming may have resulted from climate-induced mixing of the water column, or nutrient loading from catchment-driven processes. As Lac Brulé is surrounded by steep and high hills, it is unclear whether changes in wind regimes would have had significant influences on diatom assemblages in the lake. However, nutrient enrichment in the LIA was evidenced by relatively low abundances of *C. bodanica* var. *intermedia* and *T. flacculosa* (Wolin and Stoermer 2005), as well as the continued decline of chrysophytes relative to diatoms (Smol 1985). Given the uncertainty associated with interpretations of *Cyclotella* (or *Discostella*) patterns in paleolimnological studies, future work would benefit from improved knowledge of the ecological preferences of individual species within this genus (Saros and Anderson 2015). During the coldest and driest period reconstructed from the Lac Brulé pollen record (1600–1700 CE; Lafontaine-Boyer and Gajewski 2014), the only significant change in the diatom assemblages was a brief peak in *A. formosa* (Fig. 1). This suggests that worsening conditions in the LIA did not have strong adverse effects on aquatic assemblages; instead, climate during this cold period may have been a hindrance primarily to terrestrial plant production (Lafontaine-Boyer and Gajewski 2014).

The cooler temperatures associated with the LIA favoured the presence of cold-tolerant cladocera species, as evidenced by an increase in the representation of *Daphnia longispina* (Cooper et al. 2016). Furthermore, percentage abundances of the smaller-sized *B. longirostris* decreased in relation to larger-sized species (*Eubosmina longispira* and *D. longispina*). Lower temperatures in the LIA may have caused a top-down cascading effect in the ecosystem; extended ice-cover could have caused oxygen depletion in the lake, leading to higher fish kills and reduced predation pressures on larger cladocera species, which would have been more easily detected by predators (Luoto et al. 2008, Cooper et al. 2016).

**Impacts of fire disturbance in the Lac Brulé watershed**

As interpreted in Lafontaine-Boyer and Gajewski (2014), a large influx of charcoal in the Lac...
19th Regional and local anthropogenic influences in the Brulé sediment record at around 1345 CE signaled a local fire in the watershed. Several changes were seen in the pollen record at this time, most notably a rapid decline in hemlock percentages which subsequently failed to recover to levels found prior to the fire.

In the GAMs, there was an abrupt shift in the contribution of watershed disturbances (pollen PCA axis 1) to fitted diatom scores at 1345 CE (Figs. 8, 9; panel A); this confirmed that external forcing in the catchment area (a fire) played a significant role in governing diatom community structure in Lac Brulé. An abrupt increase in varve thickness immediately following the fire indicated heavier accumulation of allochthonous materials in the lake basin as a result of increased erosion in the watershed (Lafontaine-Boyer and Gajewski 2014). Additionally, high charcoal and dissolved organic carbon (DOC) inputs into the lake caused more shading and lower light penetration through the water column (Philibert et al. 2003). These poor light conditions favoured the more tolerant *Fragilaria* spp. (Anderson et al. 2008), which showed a peak in relative abundance at this time. Reduced light availability was also marked by a decline in planktonic diatom abundance, particularly for species with more heavily silicified valves (e.g., *C. bodanica* var. *intermedia*; Gall 2015).

Cladoceran assemblages showed more subtle changes associated with the fire at 1345 CE; the GAMs also indicated that trophic interactions (cladocera PC axes 1 and 2) did not contribute significantly to fitted diatom scores at this time (Figs. 8–10). However, small increases in the accumulation rates of littoral cladoceran species (*Alonella excisa, Chydrorus brevilabris*, and *Sida undiff.*) after the fire signaled greater nutrient inputs and DOC in the lake (Cooper et al. 2016), consistent with the inferences made from both the pollen and diatom records.

Regional and local anthropogenic influences in the 19th–21st century

The first European settlement along the Ottawa River and its tributary valleys occurred in the early 1820s, increasing toward the middle of the century as the lumber trade expanded (Smith 1967). The impacts of anthropogenic land-use changes on regional forest ecosystems were reflected as a rise in *Ambrosia* pollen in Lac Brulé sediments at 1860 CE (Lafontaine-Boyer and Gajewski 2014), slightly after initial colonization of the region. Historical records describe logging activities along the Rivière du Lièvre (approximately 6 km from the study site) and in the surrounding Lièvre valley (Smith 1967), although the extent and proximity of these activities to Lac Brulé remains unclear. Regardless, the pollen record showed decreased pollen accumulation rates of white pine, beech, and hemlock after 1860 CE, reflecting selective logging of these species within the region. In the mid- to late 19th century, fire associated with logging and the practice of burning forests for agriculture (Johnstone et al. 2016) was evidenced by increased charcoal accumulation rates in the sediment record, as well as an increase in the relative abundance of shrub and herbaceous pollen as the forest canopy opened (Lafontaine-Boyer and Gajewski 2014). Human-induced fire activity in the immediate watershed of Lac Brulé, however, was unlikely due to the steep sloping topography surrounding the lake, making it unsuitable for extensive use.

Regional-scale anthropogenic activities thus led to significant impacts on vegetation composition, which ultimately exerted bottom-up controls on the primary producers (diatoms) of Lac Brulé. For example, land clearance and conversion led to the mobilization of previously fixed nitrogen compounds (Vitousek et al. 1997), effectively altering the water chemistry of nearby lake ecosystems. The Lac Brulé diatom record showed an increase in the abundance of *Achnanthidium minutissimum* after 1860 CE (Fig. 1), indicating a response to an influx of nitrogen and DOC associated with Euro-Canadian settlement in the general area (Pappas 2010). Diatom assemblages also showed a post-settlement pattern of succession from *C. bodanica* var. *intermedia* to *C. michiganiana*, similar to several other diatom records from the upper Great Lakes (Garrison and Wakeman 2000, Wolin and Stoermer 2005). Increased nutrient loading as a result of regional deforestation activities in the late 19th century likely drove this shift in diatom species, as higher total nitrogen (TN) favoured *C. michiganiana* over *C. bodanica* var. *intermedia* (Wolin and Stoermer 2005).

In contrast to the rather distinct shifts seen in both the pollen and diatom assemblages during the 19th century, the primary consumers (cladocera) of Lac Brulé showed minimal responses to these anthropogenic impacts. This could be
explained by weaker bottom-up controls on the lake ecosystem toward the top of the food web (McQueen et al. 1989). Given the wide range of ecological tolerance of the two dominant cladocera species in the record (B. longirostris and E. longispina), they also would have been more resilient against environmental changes associated with early human settlement.

Anthropogenic impacts in the immediate watershed of Lac Brulé also affected the aquatic communities of the lake, most notably during the operation of the Wallingford-Back Mine from 1924 to 1972 CE (Leroux 2012). Immediately following the opening of the mine, the diatom record showed an abrupt increase in benthic Fragilaria species (Fig. 1), which were able to out-compete the previously dominant D. stelligera for resources (Köster et al. 2005). Small peaks in A. formosa and Aulacoseira spp. at this time indicated nutrient enrichment (Wolin and Stoermer 2005), potentially through a connection between the tailing pond of the mine and Lac Brulé, and/or incoming dust from the nearby access road. Furthermore, the relative abundance of cladocera species B. longirostris in the 20th century showed an almost identical profile to that of Fragilaria. This substantiated the inference of increased nutrients and inputs of DOC associated with exploitation of the Wallingford-Back Mine (Cooper et al. 2016). After the closure of the mine in 1972 CE, the relative abundance of Fragilaria and B. longirostris dropped, again very abruptly. The GAMs also showed a change in the contribution of watershed disturbances (pollen PC axis 1) to diatom trends at this time (Fig. 8A), further indicating that the mine was a significant factor influencing lake community structure.

The abrupt responses of diatom assemblages to late-Holocene climate variability, natural watershed disturbances (e.g., fire), and anthropogenic stressors demonstrate the importance of paleolimnological studies with high-resolution sampling. More generally, the ecosystems of southwestern Québec have shown significant responses to past climatic changes and local forcings on a timescale similar to that of the current global warming. The coherent, immediate, and coupled responses of watershed dynamics and lake communities to the fire in 1345 CE coincidentally occurred as the climate was deteriorating in the LIA. The impacts of the fire on both terrestrial and aquatic systems thus lasted longer than would otherwise be predicted given the nature of this disturbance. The rapid response and subsequent recovery of the lake to impacts from the Wallingford-Back Mine would also have been difficult to predict without the long-term perspective offered by paleoecological studies. Finally, the methodology we have applied here permitted the identification of the different and interacting forcings on Lac Brulé and its surroundings, on a timescale particularly relevant to the understanding of current climate change and land-use impacts.

**Conclusions**

1. Integrating paleo-records of terrestrial (pollen) and aquatic (diatoms, cladocera) biota in paleolimnological studies provides insight into the complexities of watershed-lake interactions, as well as the functioning of aquatic ecosystems at different trophic levels.

2. At Lac Brulé, the diatom record showed trends associated with two distinct millennial-scale climate variations in the late Holocene. In the MWP, oligotrophic conditions and thermal stratification in the lake were associated with pollen-based inferences of warmer summer temperatures. The expansion of Discostella stelligera at the onset of regional cooling in the LIA was thought to be primarily driven by catchment-mediated processes (nutrient loading), rather than direct climatic influences.

3. Watershed-lake interactions were thus important drivers of change for aquatic communities; in this study, GAMs revealed that diatoms responded most strongly to disturbances in the Lac Brulé catchment area. For example, at around 1345 CE a local fire triggered an abrupt response in the vegetation of the surrounding watershed (a rapid decline in hemlock), which consequently impacted the diatom community of the lake. The fire occurred concurrently with the transition from the MWP to the LIA; replication of paleolimnological studies in the region is thus needed to identify the response of diatoms (and other proxies) to this change in climate regimes in the absence of major disturbances in the watershed.
4. Regional deforestation as a result of Euro-Canadian settlement in the region in the early to mid-1800s had a strong influence on the water chemistry of Lac Brulé, which in turn affected the diatom assemblages. This is further evidence to support the conclusion that terrestrial vegetation dynamics are strongly correlated with aquatic community structure.

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