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RECEIVED 09 August 2025

REVISED 25 November 2025

ACCEPTED 25 November 2025

PUBLISHED 17 December 2025

## CITATION

Terreux de Félice H, Leclerc M-A and  
Morin H (2025) Was black spruce a good host  
of the spruce budworm in warmer periods of  
the Holocene? a long-term reconstruction.  
*Front. Ecol. Evol.* 13:1682907.  
doi: 10.3389/fevo.2025.1682907

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# Was black spruce a good host of the spruce budworm in warmer periods of the Holocene? a long-term reconstruction

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Understanding the historical variability in the disturbance dynamics of the most important defoliator in eastern Canada, the spruce budworm (SBW), throughout its range will be paramount in anticipating potential changes associated with current climate change. There is growing concerns that black spruce-dominated forests may become increasingly affected by more frequent and severe outbreaks with warmer spring temperatures. Therefore, in this study, we used lepidopteran scales, a novel paleo-proxy found in lake sediments, to reconstruct periods of large spruce budworm populations (LSBP) along a latitudinal gradient and examined the relationship between large population event frequency relative to geographic location over the course of the Holocene in eastern Canada. The synchronous increase in LSBP event frequency in the four lakes observed around 5500 cal. yr BP culminating in maximum event frequency likely resulted from a combination of the northward migration of balsam fir, and low fire frequency. Although favorable Holocene climate conditions appear to have allowed for the expansion of the spruce budworm's range into more northerly black spruce-dominated stands, event frequency remained low suggesting that the most suitable area for the SBW appears to be in more southern balsamfir-dominated stands.

## KEYWORDS

Holocene, outbreak, climate, Québec, lake sediments

## 1 Introduction

In Canada's boreal and mixed-wood forests, fire and insect outbreaks are the two major natural disturbances (Blais, 1965; Morin and Laprise, 1990; Fleming, 2000). In eastern North America, the spruce budworm (*Choristoneura fumiferana* (Clem.)) (SBW) is the major defoliating insect undergoing episodic outbreaks causing significant growth reduction and mortality (Blais, 1958, 1981; Morin, 1994; Krause and Morin, 1995), in its primary host balsam fir (*Abies balsamea* (L.) Mill.) (MacLean, 1980, 1988; Bergeron et al., 1995). Balsam fir has historically been the spruce budworm's preferred host tree because of

the synchronous timing of bud burst and larval emergence (Blais, 1957; Lawrence et al., 1997; Nealis and Régnière, 2004; Fuentealba et al., 2017), along with more nutritious and softer needles (Mattson et al., 1983; Fuentealba and Bause, 2012; Fuentealba et al., 2018), allowing for rapid population growth and maintaining very large populations via accelerated nutrient cycling (De Grandpré et al., 2022). Conversely, in secondary hosts such as black (*Picea mariana* (Mill.)), white (*Picea glauca* (Moench) Voss) and red (*Picea rubens* (Sarg.)) spruce, defoliation and mortality is less important (Hennigar et al., 2008), but large growth reductions are sometimes observed (MacLean, 1984; Nealis and Régnière, 2004). As such, areas of severe defoliation predominantly occur within balsam fir's distribution and in proximity to balsam fir-dominated stands (Blais, 1981; Jardon et al., 2003; Hennigar et al., 2008). Over the past two centuries, major defoliation events have been episodic, and appear to occur every 30 to 40 years at the landscape-scale (Royama, 1984; Krause, 1997; Morin, 1998; Boulanger and Arseneault, 2004).

Although the SBW distribution overlaps with the distribution of black spruce, climate in recent history has limited the insect's proliferation beyond the 50<sup>th</sup> parallel in Québec resulting in outbreaks that are less severe and frequent (Pureswaran et al., 2015), but the question remains whether these dynamics were also valid during the warmer periods of the Holocene. Natural disturbances, such as insect defoliators, are among the most climate-sensitive processes, and current climate change is expected to alter the extent, intensity, frequency, and severity of these disturbances (Gray, 2008; Lindner et al., 2010; Seidl et al., 2017, 2020). Recent work on the effect of warming suggests that secondary hosts, such as black spruce, may become more vulnerable with increasing temperature (Rossi et al., 2015; Pureswaran et al., 2018, 2019; Bellemin-Noël et al., 2021) potentially explaining the greater defoliation observed in black spruce stands during the current outbreak (Bognounou et al., 2017). Such a change in vulnerability would likely alter the dynamics of the black spruce forest, and the ability to observe and reconstruct past long-term variability in spruce budworm disturbance would be of great help in anticipating the future dynamics of the boreal forest ecosystem. Although paleoecological analyses cannot directly test the effects of non-mutually exclusive climate-mediated mechanisms, such as insect survival and development (Régnière et al., 2012; Pureswaran et al., 2015), and/or synchrony between black spruce bud burst and larval emergence (Nealis and Régnière, 2004; Antonucci et al., 2015; Fuentealba et al., 2017; Régnière and Nealis, 2018), these analyses allow for observance of long-term system behavior and trends. The objective of this study was to use lepidopteran scales, a novel spruce budworm paleo-proxy (Navarro et al., 2018a), that is easily identifiable, more abundant, and well-preserved in lake sediment (Montoro Girona et al., 2018; Navarro et al., 2018a) relative to larval head capsules, and frass (Simard et al., 2002, 2006), to reconstruct long-term variability of large spruce budworm population (LSBP) event frequencies during the Holocene within the insect's current range (balsam fir-white birch domain) and at its northern limit (spruce-moss domain). If warm and humid periods were favorable to LBSP events in northern

regions, then we expect greater SBW impacts in black spruce-dominated forests as registered by more frequent LBSP events because these favorable conditions would have enabled the spruce budworm to experience an expansion in host breadth by taking advantage of black spruce a once less preferred secondary host.

## 2 Materials and methods

### 2.1 Site description, selection and sediment coring

The four sampled lakes were located either in the balsam fir-white birch or the black spruce-moss bioclimatic domains (Saucier et al., 2009; Table 1). The earlier domain contains a diversity of tree species, generally composed of balsam fir, white spruce, white birch, and trembling aspen however, poorer sites tend to be dominated by black spruce, meanwhile, the latter domain is generally dominated by black spruce with the presence of jack pine, and balsam fir (Saucier et al., 2009; Table 1). The more southern balsam fir-white birch domain is typically warmer and wetter with a longer growing season relative to the more northern black spruce-moss domain (Saucier et al., 2009; Table 1). In both domains, there is an east-west precipitation gradient with the west being drier than the east resulting in shorter and longer fire return intervals respectively (Saucier et al., 2009). In addition to characterizing current site-level tree species composition (Table 1), long-term changes in forest composition were characterized using the closest available pollen profiles to our lakes from the Neotoma database (<https://www.neotomadb.org>; Table 1, Supplementary Figures S1-S3), along with accessing Holocene August summer temperature data based on chironomid reconstructions from Bajolle et al. (2018) made available in the NOAA Paleoclimatology database (NCEI; <https://www.ncei.noaa.gov/access/paleo-search/study/27330>; Kaufman et al., 2020). The long-term changes in forest composition and temperature were used to provide context for any observed changes in LBSP event frequency.

The four lakes sampled in this study were selected due to their limited inflow and outflow, and a deep water column to avoid sediment mixing, and cored at each lake's maximum depth (Table 1). The core of lake Flévy was collected in 2012 while lake Trouble and Totem were sampled in the summer of 2018, and lake Innu in the summer of 2019. The sediment surface was collected using a gravity corer (Renberg, 1991; Renberg and Hansson, 2008) and sampled at a 1 cm resolution (0.5 cm for lake Totem) in the field. The remainder of the sediment column was sampled using a Livingstone piston corer (Wright et al., 1984) from each lake's deepest point and subsampled at a 1 cm resolution and stored in individual plastic bags to avoid desiccation. The lake Flévy core had already been analyzed in a previous study (Navarro et al., 2018b). The major difference in methodology between Navarro et al. (2018b) and the current study was the amount of sediment assessed at each depth with the earlier study using 5 cm<sup>3</sup> as opposed to the 1 cm<sup>3</sup> used in this study. This difference would not alter the observed trends but could possibly result in higher

TABLE 1 Site-level characteristics of the cored lakes (from north to south) and associated regional climate.

Lake name	Totem	Innu	Trouble	Flévy
Latitude	50°29'52.58"N	50°4'3.19"N	48°52'17.78"N	48°13'2.00"N
Longitude	71°44'40.82"W	68°48'38.45"W	71°34'1.35"W	71°12'59.00"W
Elevation (m.a.s.l)	405	515	198	381
Hillslopes	Moderate	Moderate	Flat	High
Lake surface (ha)	1.10	1.44	0.94	2.33
Coring depth (m)	9.0	3.8	5.2	4.8
Length of organic core (cm)	202	283	636	520
Mean deposition time (yr/cm)	41.8	27.8	11.0	13.3
Bioclimatic domain <sup>1</sup>	Black spruce-moss		Balsam fir-white birch	
Mean annual temperature (°C) <sup>1</sup>	-2.0-0.0		-1.5-1.5	
Growing season length (days) <sup>1</sup>	115-140		125-150	
Growing degree-days ≥5°C (days/year) <sup>1</sup>	850-1150		1050-1300	
Mean annual precipitation (mm) <sup>1</sup>	850-1150		900-1350	
Current approximate tree species composition (%) <sup>2</sup>	Black spruce (70%) Balsam fir (30%)	Black spruce (80-100%) Balsam fir (10%) Tamarack larch (10%)	Black spruce (90-100%) Tamarack larch (10%)	Black spruce (60%) Balsam fir (20%) Trembling aspen (20%)
Pollen profile used for Holocene vegetation reconstruction <sup>3</sup>	LD (50°8'25.00"N, 67°7'54.99"W)	CH2 (49°40'59.99"N, 74°34'59.99"W)	Lac Kénogami (48°21'56.99"N, 71°34'0.99"W)	

<sup>1</sup>Source: Saucier et al. (2009).  
<sup>2</sup>Source: Fourth decadal forest inventory, Québec Ministry of Forests, Fauna, and Parks (2025).  
<sup>3</sup>Source: Neotoma database (<https://www.neotomadb.org>). The pollen profiles for LD, CH2, and Lac Kénogami have been previously published in Mott (1976); Garralla and Gajewski (1992), and Richard (1973, 1977) respectively.

LSBP event frequencies detected at lake Flévy relative to the lakes analyzed in this study. All analyses in this section are for lakes Innu, Totem and Trouble. The lakes Innu and Totem are located in the spruce-moss domain while lakes Trouble and Flévy are found in the balsam fir-white birch domain (Figure 1).

2.2 Lead-210, and radiocarbon dating and sample preparation

The age-depth models for lakes Innu, Trouble, Totem were derived from a combination of Lead-210 (<sup>210</sup>Pb) to reconstruct recent history (approximately last 150 years), and deep history using radiocarbon (<sup>14</sup>C) dates (Table 2). Recent history was derived from bulk sediment samples that were sent and analyzed for <sup>210</sup>Pb activity at Flett Research Ltd (Winnepeg, MN, Canada). A more detailed methodology is provided in Supplementary Material section 1.1, but in short, a dry mass was obtained from samples that were dried, homogenized, and then digested in nitric acid to help isolate the Polonium-210 (<sup>210</sup>Po) which provides an indirect measurement of the total <sup>210</sup>Pb present in the sample (Eakins and Morrison, 1978). Also, samples were spiked with a tracer to measure and identify any potential losses (Eakins and Morrison, 1978), and the <sup>210</sup>Po was isolated using spontaneous auto-deposition on silver planchets (Flynn, 1968). Supported <sup>210</sup>Pb was derived from Radon-

226 (<sup>226</sup>Ra; Mathieu et al., 1988) from which excess lead-210 could be calculated and Constant Rate of Supply models (Appleby and Oldfield, 1978; Appleby and Oldfieldz, 1983) could be applied to estimate the ages of the sediment in recent history.

Deep history was reconstructed using radiocarbon dates derived from terrestrial plant macrofossils (leaves, needles, and seeds) sampled along the sediment cores, that were sent and analyzed at the André E. Lalonde AMS Laboratory at the University of Ottawa (Table 2). Briefly, macrofossils underwent pretreatment, combustion, graphitization, followed by accelerator mass spectrometry measurement (Crann et al., 2017; St-Jean et al., 2017). Plant macrofossils were inspected for contaminants, and sonicated in Milli-Q water when needed, underwent an acid-alkali-acid wash, and freeze-dried overnight (Brook et al., 2010; Crann et al., 2017). Samples were then combusted in a Thermoflash 1112 Elemental Analyzer in CN mode to trap pure carbon dioxide (CO<sub>2</sub>; Crann et al., 2017). The pure CO<sub>2</sub> was converted to elemental carbon in semi-automated graphitization lines in the presence of iron and hydrogen then pressed into targets with a pneumatic press (Crann et al., 2017; St-Jean et al., 2017). Accelerator Mass Spectrometry measurements were done using a 3 MV Tandem Accelerator Mass Spectrometer built by High Voltage Engineering (The Netherlands; Kieser et al., 2015). A terminal voltage of 2.5 MV with Ar stripping was used to measure the <sup>14</sup>C<sup>3+</sup> ions (Crann et al., 2017). The fraction of modern carbon (F<sup>14</sup>C) was calculated

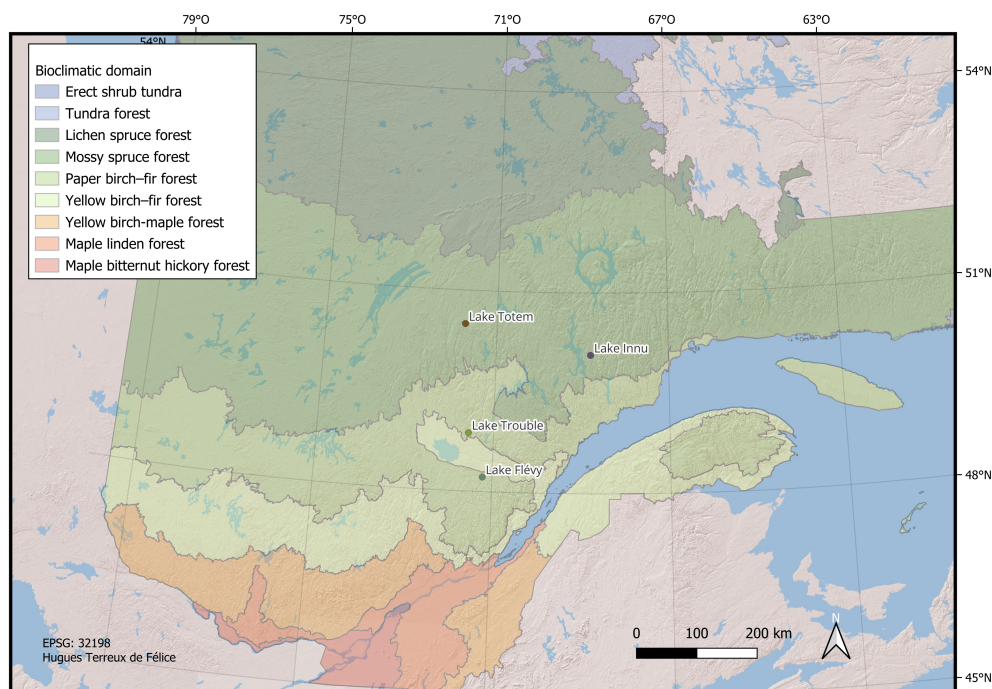


FIGURE 1  
Location of the study sites within the bioclimatic domains of Québec (Canada).

following Reimer et al. (2004) by using the ratio of the sample  $^{14}\text{C}/^{12}\text{C}$  to the standard  $^{14}\text{C}/^{12}\text{C}$  in the same data block (Crann et al., 2017). Noting that all ratios were background corrected using corresponding process, oxalic acid-II, iron-only blanks along with secondary references (Crann et al., 2017). Results were also corrected for spectrometer and preparation and normalized to  $\delta^{13}\text{C}$  and finally  $^{14}\text{C}$  ages were calculated following Stuiver and Polach (1977). Further procedural and instrument details are provided in Supplementary Material section 1.2.

In the R software environment (R core team, 2020), Bayesian age-depth models for lake Innu, Trouble, and Totem were obtained using the IntCal20 calibration curve (Reimer et al., 2020) and the package Rbacon 2.5.8 with default settings (Blaauw et al., 2022) as these settings best reflected the sediment accumulation rate of the cores (see Results). The age-depth model for lake Flévy was derived by reanalyzing the radiocarbon dates in Navarro et al. (2018b) using Rbacon 2.5.8 and the IntCal20 calibration curve (Reimer et al., 2020; Blaauw et al., 2022). Broadly, this age-depth modelling package subdivided the respective sediment cores into sections of equal thickness within which linear accumulation rates, constrained by the provided  $^{210}\text{Pb}$  and radiocarbon dates, were estimated using Markov Chain Monte Carlo iterations (Blaauw et al., 2022).

For scale extraction we used a punch to collect exactly  $1\text{ cm}^3$  of wet sediment and placed it in a 30 milliliter (mL) vial. Twenty mL of 20% KOH solution was added and the sample was placed in an autoclave (Amsco unit by Steris) at  $121^\circ\text{C}$ , 17 psi for 30 minutes (Leclerc et al., 2024) for complete deflocculation (Frey and Pamini, 1986). The slurry was then sieved through a mesh of  $53\text{ }\mu\text{m}$  to retain most of the scales (Navarro et al., 2018a). Fifteen mL of sugary solution at  $1.24\text{ g/L}$  was added to further separate sediment particles

and isolate the scales, and then centrifuged at 4500 RPM for 20 minutes to concentrate sediment and reduce sample volume. The supernatant was removed with a Pasteur pipet and samples were stored at  $4^\circ\text{C}$ . The entire pellet of each sample was analyzed under a microscope (Leica DM 4000 B) with a digital camera (Leica DFC 425) at 100x magnification, and all scales were photographed.

## 2.3 Lepidopteran scale peak identification

Identification of scale peaks was done with CharAnalysis software (<https://github.com/phiguera/CharAnalysis>) (Higuera et al., 2009). This software was originally developed to identify, and extract charcoal peak accumulations that correspond to wildfire events, and the same methodology was applied to determine peak lepidopteran scale accumulations (Navarro et al., 2018a, b). These detected peak scale accumulations strongly agree with commonly used, reliable, and modern spruce budworm proxies (Leclerc et al., 2024, 2025) and are therefore assumed to accurately reflect spruce budworm populations around a lake. Indeed, a LSBP event would be related to an increase and a peak in the number of scales found in the sediment, noting however, that peak scale accumulations may encompass one or more outbreaks, and are interpreted as periods in time where SBW populations were elevated, and not as a count of individual outbreak events. To distinguish large population events from background scale accumulation rates, we obtained a constant time-step by interpolating each lake's accumulations using its corresponding median temporal resolution (28, 40, 10, and 5 years for lakes Totem, Innu, Trouble, and Flévy respectively):  $C_{\text{int}}$ , and defined two components:  $C_{\text{back}}$  and  $C_{\text{peak}}$ . The  $C_{\text{back}}$



TABLE 2 Sampling depth, material, median ( $\pm$  standard deviation) calibrated ages of lakes Totem, Innu, and Trouble.

Lake	Lab ID	Depth (cm)	Dated material	$^{210}\text{Pb}$ cal. year BP/ $^{14}\text{C}$ year BP	$\pm$	cal. BP (associated probability)
Totem	$^{210}\text{Pb}$	1-2	Bulk sediment	-53	2	-13- (-92)
	UOC-14230	29-30	Organic macrofossils	1361	28	1342 - 1330 (2.6%) 1312 - 1262 (79.6%) 1209 - 1177 (13.2%)
	UOC-8723	86-87	Organic macrofossils	1903	19	1894-1817 (95.4%)
	UOC-8724	102-103	Organic macrofossils	2320	23	2358-2317 (95.4%)
	UOC-14229	177-178	Organic macrofossils	4219	27	4851 - 4799 (40.1%) 4759 - 4695 (43.7%) 4676 - 4646 (11.7%)
	UOC-8725	266-267	Organic macrofossils	6274	43	7294-7154 (96.1%) 7115-7025 (9.3)
	UOC-8726	286-287	Organic macrofossils	7228	32	8159-8082 (28.7%) 8075-7971 (66.7%)
Innu	$^{210}\text{Pb}$	4-5	Bulk sediment	36	30	2-71
	UOC-14231	41-42	Organic macrofossils	1687	33	1693 - 1669 (14.2%) 1620 - 1530 (81.2%)
	UOC-14225	93-94	Organic macrofossils	3824	29	4395-4373 (2.0%) 4354-4327 (4.6%) 4299-4145 (83.9%) 4122-4095 (5.0%)
	UOC-14226	115-116	Organic macrofossils	4721	31	5578-5506 (29.0%) 5486-5441 (22.8%) 5411-5324 (43.7%)
	UOC-14227	180-181	Organic macrofossils	6617	37	7570-7528 (32.5%) 7522-7430 (63.0%)
	UOC-14228	210-211	Organic macrofossils	7864	41	8974-8957 (1.3%) 8940-8918 (1.8%) 8892-8885 (0.4%) 8861-8832 (3.3%) 8780-8545 (88.5%)
Trouble	$^{210}\text{Pb}$	2-3	Bulk sediment	-65	1	-62-(-66)
	UOC-14232	91-92	Organic macrofossils	1467	33	1394 - 1302 (95.4%)
	UOC-8716	166-167	Organic macrofossils	1550	20	1523-1391(95.4%)
	UOC-8717	256-257	Organic macrofossils	2389	25	2490-2346 (95.4%)
	UOC-8718	346-347	Organic macrofossils	2788	26	2956-2841 (88.6%) 2827-2797 (6.8%)
	UOC-8719	438-439	Organic macrofossils	3466	26	3830-3685 (86.3%) 3665-3644 (9.1%)
	UOC-8720	528-529	Organic macrofossils	4338	25	4966-4850 (95.4%)
	UOC-8722	635-636	Organic macrofossils	6283	26	7262-7167 (85.4%)

component was identified using a LOWESS smoother robust to outliers in conjunction with the smallest possible smoothing window that yielded a Signal-to-Noise ratio (SNI) above 3.  $C_{\text{peak}}$  was obtained by subtracting  $C_{\text{back}}$  from  $C_{\text{int}}$ . Further, a Gaussian mixture model was used to discriminate LSBPs within  $C_{\text{peak}}$  from noise resulting from sediment mixing (Gavin et al., 2006; Higuera et al., 2010). We did not conduct the minimum count test; the final step used in CharAnalysis to avoid missing any LSPB events. Normally after  $C_{\text{peak}}$  values are identified as being above a

threshold value defined by the Gaussian mixture model, these potential LSPB events undergo the minimum count criterion test. This test determines if two detected events were generated from a single event by determining whether the two events belong to the same Poisson distribution and comparing the accumulation of scales in the event relative to the previous 75 years. Only peaks with a probability  $\alpha < 0.05$  are considered LSPB events. However, during periods of large spruce budworm populations, the SBW numbers gradually increase to a maximum and then decreases,

likely translating into gradual accumulations of scales in the sediment and therefore would more likely resemble a Normal and not a Poisson distribution.

## 2.4 Large spruce budworm population event frequency

LSBP event frequency was calculated from kernel rate occurrence estimation (Blarquez et al., 2014). This is a powerful approach because it is flexible, supports nonlinear trends, and produces a reliable statistical error (Mudelsee et al., 2004). The years of LSBP events identified by the Gaussian mixture model were used to run a bootstrap resampling analysis. LSBP event frequency was based on each lake's median time-step and then estimated using a bandwidth of 1000 years and resampled 1000 times to ensure statistical robustness. To prevent over-representation of rare events, the bootstrap resampling was constrained to select between 1 and 10% of the total number of events, thereby reducing the likelihood of generating outlier reconstructions where a single event could be sampled multiple times (Blarquez et al., 2013). Finally, to compare LSBP event frequencies between northern (Totem and Innu) and southern (Flévy and Trouble) lakes we used an orthogonal contrast matrix coupled with an ANOVA. The event frequency values were logarithmically transformed to respect the assumption of normality.

Three contrast pairs were tested: 1) southern vs. northern lakes, 2) Flévy vs. Trouble and 3) Innu vs. Totem.

## 3 Results

Innu and Totem lake cores were composed of homogenous gyttja, and relatively short, 202 and 283 cm respectively, likely explaining the particularly high sediment accumulation rates expressed in years/cm (Innu: mean = 41.63, median = 40, max = 57, min = 21; Totem: mean = 26.72, median = 28, max = 59, min = 6). Lake Trouble's core was longer with a relative constant sediment accumulation rate (mean = 11.08, median = 10, max = 21, min = 3), and was composed of homogeneous gyttja until 5700 cal. yr BP (570 cm depth), where a large amount of sand was present limiting LSBP event data analysis beyond this point as microscopic observation of the scales was impossible. Finally, lake Flévy's core was also long with a relatively constant sediment accumulation rate (mean = 19.02, median = 19, max = 42, min = 6) (Figure 2) and was composed of homogeneous gyttja (Navarro et al., 2018b). Markov Chain Monte Carlo simulations for all cores resemble white noise, and the posteriors for sediment accumulation rates, along with the variability in sediment accumulation rates overlap with the priors (Figure 2). Further, the age-depth models do not exhibit any strange elbows and generally resemble smooth curves (Figure 2). A total of

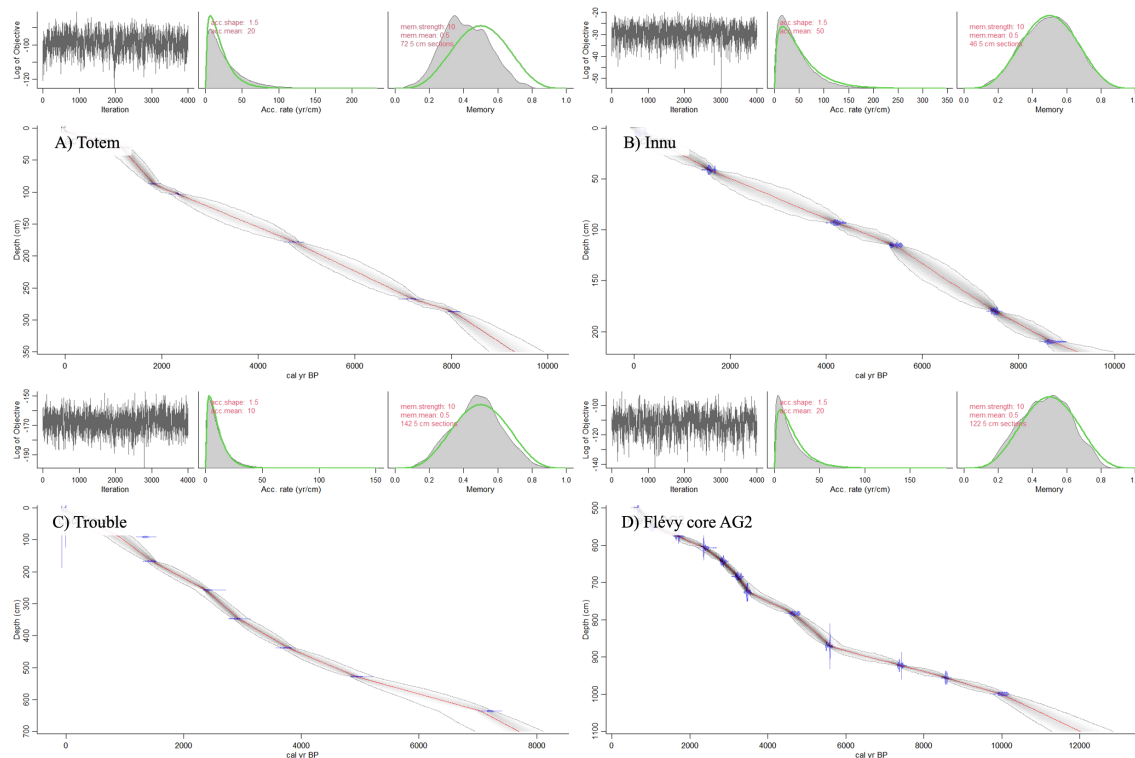


FIGURE 2

Lake sediment core age-depth models for lakes (A) Totem (B) Innu (C) Trouble (D) Flévy core AG2. Main panel: Red dashed line and dashed grey curves represent the mean model with 95% confidence interval, with calibrated  $^{14}\text{C}$  dates are shown in blue. Upper left: Markov Chain Monte Carlo simulations estimating accumulation rates of each core section. Upper center: Modelled accumulation rates compared to a gamma distribution (green line). Upper right: Variation in sediment accumulation through time (Memory) relative to a beta distribution (green line).

33 peaks were identified at Totem, 25 peaks at Innu, 43 at Trouble, and 93 at Flévy (Figures 3, 4).

Variability in outbreak frequency was less important in northern lakes relative to southern lakes. Maximum peak frequency for lake Innu and Totem were respectively 4.471 and

5.974 kyr<sup>-1</sup> and 9.712 and 20.391 kyr<sup>-1</sup> for lake Trouble and Flévy (Figure 4). Large spruce budworm population event frequencies were somewhat synchronous prior to 5500 cal. yr BP, however, synchrony is most clearly observed and pronounced between lakes from 5500 cal. yr BP to the present. An increase and then a

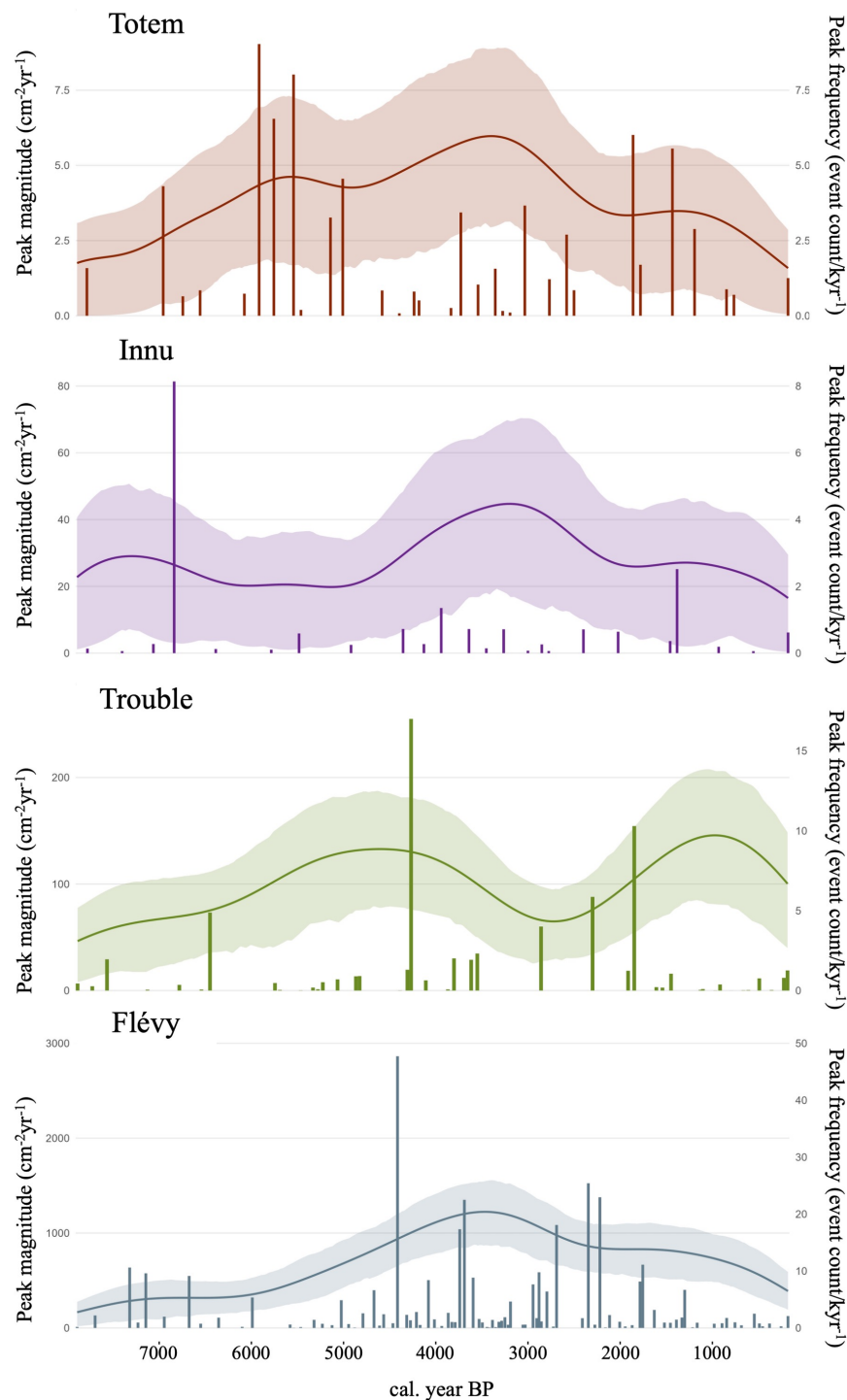


FIGURE 3

Large spruce budworm population event frequency (smooth curves) and associated uncertainty (shading) for each lake. Bars depict the retained lepidopteran scale peaks (C<sub>fire</sub>) along with their respective magnitudes.

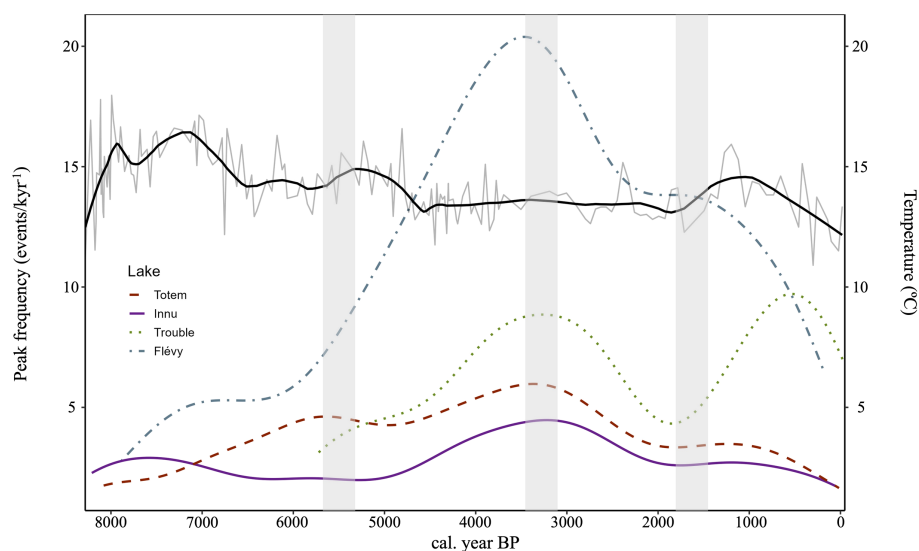


FIGURE 4

Large spruce budworm population event frequencies for the lakes after Kernel density bootstrap and chironomid-reconstructed August summer (grey) and smoothed temperatures (black). Vertical grey bands highlight the approximate timing of synchronous change in event frequency at 5500, 3100, and 1900 cal. year BP.

maximum was reached for all lakes around 3100 cal. yr BP followed by a particularly low period around 1900 cal. yr BP. Further, all lakes, except Innu, also showed a decrease in LSBP event frequency close to the present. The ANOVA indicated that means in event frequency differed between lakes ( $F(3,1677) = 1065.6, p \leq 0.001$ ) (Figure 5). Specifically, event frequencies in the northern lakes differed from those in the southern lakes ( $F(1,1677) = 2726.8, p \leq 0.001$ ), between lakes Trouble and Flévy ( $F(1,1677) = 330.5, p \leq 0.001$ ), and between lakes Innu and Totem ( $F(1,1677) = 139.7, p \leq 0.001$ ).

## 4 Discussion

### 4.1 Attribution of scale peaks to SBW

The regional consistency after 5500 cal. yr BP. suggests that the scales found in the sediment are mostly attributable to the SBW. The sampled sites are located in continental Québec, and in the boreal forest composed predominantly of coniferous tree species either at the core or at the northern periphery of the spruce budworm's distribution (Pureswaran et al., 2015; Nealis, 2016).

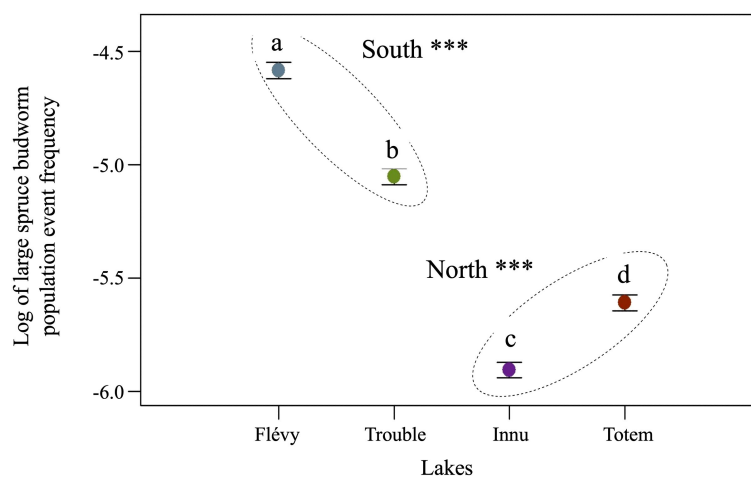


FIGURE 5

Orthogonal matrix contrast of mean large spruce budworm population event frequency after log transformation and ANOVA. Significant differences between localities are indicated by dashed circles with stars and significant differences between lakes are indicated by differing letters using a threshold of 0.05.



Moreover, historical spruce budworm outbreak epidemiology suggests that it is the only North American insect that can outbreak and simultaneously infest such large areas over several years (Morin and Laprise, 1990; Morin, 1998; Jardon, 2001; Jardon et al., 2003). Since 1975, 95% of the area defoliated in Québec has been affected by SBW, and among identified peak accumulations in the sediment using scale morphological features, more than 60% belonged to the SBW (Navarro et al., 2018a, b). Further, multi-proxy comparisons support the use of lepidopteran scales to reconstruct periods of large spruce budworm populations (Leclerc et al., 2024, 2025). It is therefore less likely that scales found in the sediment belong to other moths such as the hemlock looper (*Lambdina fiscellaria* (Guénée)), which tends to affect coastal areas, and have very patchy outbreaks that last only 1–2 years (Otvos et al., 1971, 1979) or the forest tent caterpillar (*Malacosoma disstria* Hübner) which outbreaks mainly in deciduous-dominated forests (Cooke and Lorenzetti, 2006; Cooke et al., 2012). Nevertheless, it is possible that these other species may contribute to the total of analyzed scales as scales from different species are likely equally well preserved in the sediment (Shorohova et al., 2011; Navarro et al., 2018a), and broken and hidden scales along with somewhat similar scale morphology may lead to identification errors (Navarro et al., 2018a). However, in this study, the location of the lakes, the surrounding forest composition, past spruce budworm epidemiology, scale morphology, and multi-proxy comparisons strongly suggests that the analyzed scales do belong to the SBW.

The low LSBP event frequency observed in the northern lakes may reflect the low host-tree availability limiting spruce budworm population build-ups, and their extent relative to the southern lakes prior to 7000 cal yr. BP (Mott, 1976; Garralla, 1991; Garralla and Gajewski, 1992; Figures 3, 4; Supplementary Figures S1–S3). Lakes Innu and Totem were likely surrounded by tundra dominated by grasses and shrubs with patches of spruce, larch, and poplar (Saarnisto, 1974; Mcandrews, 1988; Heide, 1984; MacDonald et al., 1991) as the postglacial recolonization was slow during this period (Richard, 1973, 1975; Richard et al., 1992; Lavoie and Filion, 2001). Nevertheless, LSBP events would have likely occurred in spruce patches (Garralla, 1991).

## 4.2 Mid-Holocene increase and host availability

The warmest period of the Holocene (6000 to 3000 cal yr. BP) was characterized by a synchronous increase in LSBP event frequency (Figure 4) likely linked to the post-glacial recolonization by balsam fir (King, 1986; Remy et al., 2017) around 6000–5500 cal yr. BP as demonstrated by an increase in the proportion of the primary host in the pollen profiles (Supplementary Figures S1–S3). After the fragmentation of the Laurentian Ice Cap and deglaciation of the Hudson Bay (Dyke, 2005), the beginning of the warmest period of the Holocene generally exhibited low event frequencies despite mild climate and the boreal forest being continuous to 52°N (Viau and

Gajewski, 2009). However, later on, the relatively warm, and humid mid-Holocene period likely resulted in a low fire frequency (Edwards et al., 1996; Ali et al., 2009; Blarquez et al., 2015). The low fire frequency during this period likely allowed late-successional species such as balsam fir to increase in density (Bergeron and Dubue, 1988, Supplementary Figure S1–S3). The greater density in primary host-tree species in conjunction with fewer fires in the northern parts of the SBW range would increase connectivity between trees and favor the establishment of periods of large populations over larger areas (James et al., 2011; Harper et al., 2002).

The combined effect of low fire frequency and increased host-tree density likely explains the maximum LSBP event frequency reached by all lakes around 3100 cal. yr BP (Figures 3, 4). The recurrent presence of the budworm in a stand is assumed to be dependent on temperature but especially on high balsam fir density (Morin et al., 2021). From around 5500 cal. yr BP, the scale signal appears to reflect regional variation (Figure 4). We believe that warm and humid periods would be most favorable to high LSBP event frequencies and the mid-Holocene period of the studied chronologies support this prediction via the possible mechanism of low fire frequencies. Synchronous variations in event frequency from 5500 cal. yr BP in several lakes located in different ecosystems is suggestive of the regional influence of large SBW populations along with the importance of the presence of balsam fir on the landscape.

## 4.3 Northward migration of the SBW

Recent studies on budworm phenology have shown that a reduction in asynchrony or an increase in synchrony between larval hatching and bud break of its secondary hosts (black, white spruce) and/or favorable larval development induced by climate could allow the insect to move north towards the edge of its historical range (Pureswaran et al., 2015; De Grandpré et al., 2019). If this is the case, black spruce stands at the edge of the spruce budworm's range are expected to undergo greater defoliation, and should record more frequent LSBP events when conditions are favorable. However, in this study, LSBP event frequency over the course of the Holocene differed significantly between northern and southern lakes, and further, frequencies in the north never exceeded those in the south (except lake totém around 6000 cal. yr BP; Figure 5). Interestingly, a significant difference in LSBP event frequency between all lakes was detected. The difference between the southern lakes may be due to site-level productivity due to a slightly dissimilar current species composition, despite a similar past composition (Supplementary Figure S3). More likely however, is the influence of differences in lake basin shape (Lehman, 1975; Bennett and Buck, 2016) along with surrounding topography, and catchment basin size (e.g., Smith et al., 2010). It is also possible that the difference observed may stem from the fact that scale accumulations were not standardized between the lakes sampled in this study, and Navarro et al. (2018b). The difference observed between the northern lakes,

Innu and Totem, is somewhat surprising given similar current (Table 1) and past vegetation composition (Richard et al., 2020; Fréchette et al., 2018, 2021, Supplementary Figures S1, S2). This difference may also most likely stem from site-level variability particularly lake basin shape (Lehman, 1975; Bennett and Buck, 2016) along with surrounding topography, and catchment basin size (e.g., Smith et al., 2010). Although the moth was able to establish itself homogeneously over the landscape as evidenced by the seemingly synchronous event peak frequency at 5500 cal. yr BP, the climatic and environmental conditions do not appear to have been sufficient to drastically alter northern event frequencies.

Understanding the relatively attenuated change in LSBP event frequencies observed in the northern lakes during favorable Holocene climate conditions may be elucidated by contrasting the northern and southern ecosystems by considering factors that may differ between the two systems. First, in the balsam fir-white birch domain host-insect phenological synchrony along with fir regeneration allows for the establishment of a feedback loop (Baskerville, 1975; Morin, 1994). Spruce budworm defoliation on balsam fir results in canopy tree mortality creating canopy gaps allowing for the release of the pre-established fir seedlings and saplings in the understory to replace the overstory (Morin and Laprise, 1997; Doucet and Blais, 2000; Lemay et al., 2018) predisposing the stand to subsequent outbreaks (Baskerville, 1975; Bouchard et al., 2006, 2007). This interaction is likely possible due to the low fire frequency in this domain (Couillard et al., 2012, 2013, 2021).

In contrast, aspects of nutrient cycling and foliage quality, regeneration, growth, and phenological synchrony in the black spruce system likely differ from those of the balsam fir-spruce budworm system. The higher nutrient quality of fir needles in the balsam fir system allows for the establishment of a positive feedback loop: defoliation by larvae results in greater nutrient availability to surviving trees through litterfall and frass, and these trees can then produce needles of higher nutritional quality allowing populations to increase favoring further defoliation (De Grandpré et al., 2022). This feedback ultimately allows for the build-up of spruce budworm populations permitting populations to move from endemic to epidemic levels. Conversely, defoliation by the insect did not appear to alter nutrient cycling and leaf nutritional quality in the black spruce system (De Grandpré et al., 2022). Further, and to a lesser extent, frequent periods of large budworm populations may be limited by the slower growth rates of black spruce at higher latitudes (Rossi et al., 2009, 2010), complex regeneration dynamics (Martin et al., 2019, 2020) affected by feeding on reproductive structures prior to bud flush (Schooley, 1980; Syme, 1981; Prévost et al., 1988; Wanner et al., 1997), and by previous disturbances (Paquin et al., 1999; Greene et al., 1999; Simard and Payette, 2005; Baltzer et al., 2021). As a result, the black spruce system may have sustained low endemic populations, and only during 'spill-over' events from more southern primary host-dominated regions could populations become large enough to affect northern sites.

## 4.4 Implications for future climate change

Alternatively, it is possible that black spruce remained a poor host even during favorable Holocene climate conditions as the warming was not enough to ameliorate synchrony between bud burst and larval emergence as has been observed in recent history (Pureswaran et al., 2015, 2019; Fuentealba et al., 2017). Indeed, recent warming in northern regions appears to exceed the temperatures experienced during the last 2000 years (Mayewski and Maasch, 2006; Viau et al., 2012; Pei et al., 2017) and even over the course of most of the Holocene (Viau et al., 2006; Viau and Gajewski, 2009; Marcott et al., 2013; Marsicek et al., 2018). Thus, it is likely that past Holocene warming may not serve as an analogue for the recent warming (Mitchell, 1990; Kaufman and Broadman, 2023) suggesting that past event frequencies observed in this study may not be indicative of future event behavior.

## 5 Conclusion

Our results are the first comparing SBW activity between the spruce-moss and balsam fir-white birch domains. Apparent synchronicity in LSBP event frequency was observed at a regional and supra-regional scale. The post-glacial recolonization of balsam fir around 5500 cal. yr BP likely allowed the SBW to spread more widely over the landscape. Black spruce does not appear to have been a preferred host of the SBW during the climatic variations of the last 8000 years. Nevertheless, current climate change is unmatched in terms of warming rates during the Holocene (Marsicek et al., 2018). Moreover, the average temperature of the Holocene is nearly 1.7 °C lower than that recorded in 2016, so our results are only suggestive of potential future LSBP event frequency behavior and not an accurate prediction.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Author contributions

HT: Formal Analysis, Investigation, Visualization, Software, Validation, Conceptualization, Writing – review & editing, Data curation, Writing – original draft, Methodology. M-AL: Writing – review & editing. HM: Funding acquisition, Project administration, Supervision, Investigation, Writing – review & editing, Methodology, Conceptualization, Resources.

## Funding

The author(s) declared financial support was received for this work and/or its publication. Funding was provided by the Natural Sciences and Engineering Research Council (NSERC) of Canada Industrial Research Chair on black spruce growth and the effect of the spruce budworm on landscape heterogeneity in the boreal forest grant number 499381-15. Funding was obtained by HM.

## Acknowledgments

The authors would like to thank the 2 reviewers for their suggestions and feedback greatly improving the manuscript. Prior to an abrupt career change, Dr. Olivier Blarquez provided advice on methods, analysis, and interpretation. Thanks to Dr. Louis De Grandpré for providing comments on an earlier version of the manuscript and providing thoughts relating to our results. Thank you to Marika Tremblay and Guillaume Vigneault for help in the laboratory. Thanks to Claire Fournier, and Mireille Boulianne for preparing sucrose solution and providing lab equipment.

## Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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