Early afforestation on islands of proglacial Lake Ojibway as evidence of post-glacial migration outposts

Marianne F.S. Vogel[1,2*], Hugo Asselin[3], Sébastien Joannin[2], Yves Bergeron[1,4], Sabrina Leclercq[5], Cécile Latapy[6], Adam A. Ali[2]

[1] Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec, Canada, Canada.

[2] ISEM, Université de Montpellier, CNRS, IRD, Montpellier, France; marianne.vogel@uqat.ca; sebastien.joannin@umontpellier.fr; ahmed-adam.ali@umontpellier.fr

[3] École d'études autochtones, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec, Canada; hugo.asselin@uqat.ca

[4] Département des sciences biologiques, Université du Québec à Montréal, Montréal, Québec, Canada; yves.bergeron@uqat.ca

[5] Faculté des Sciences, Université de Sherbrooke, Sherbrooke, Québec, Canada; sabrina.leclercq@usherbrooke.ca

[6] Université de Montpellier, Montpellier, France; cecile.latapy@etu.umontpellier.fr

*Author for correspondence: marianne.vogel@uqat.ca

ORCID IDs

Marianne F.S. Vogel https://orcid.org/0000-0002-0727-5133

Hugo Asselin https://orcid.org/0000-0002-9542-4994

Sébastien Joannin https://orcid.org/0000-0001-8345-9252

Yves Bergeron https://orcid.org/0000-0003-3707-3687

Adam A. Ali https://orcid.org/0000-0002-6927-6633

A Abstract

At the end of the last glacial period in the northern hemisphere, meltwater from receding ice sheets accumulated into large proglacial lakes, potentially limiting postglacial afforestation. We explored whether former islands of proglacial Lake Ojibway (Canada) (hilltops in the current landscape) could have acted as migration outposts and thus accelerated the postglacial migration. We extracted sediments from two small lakes located on "paleo-islands" and used XRF to detect changes in soil erosion and vegetation biomass. We also used plant macro-remains and wood charcoal to determine if (and which) tree species colonized the sites and to detect local fire events. Organic sediment accumulation started around 9657 and 9,947 cal. yr BP at Lakes Perché and Despériers, respectively, before the level of Lake Ojibway started to decrease and liberate parts of the studied landscape ca 9,400 cal. yr BP. Lithogenic elements (Ti, K, Sr, Fe, Zr and Rb) decreased between the beginning of organic sediment accumulation and 8,800-8,700 cal. yr BP, indicating reduced soil erosion, possibly due to soil stabilization by vegetation. Then, the S/Ti ratio, a proxy of organic matter accumulation increased around 8,800 and 8,400 cal. yr BP. The earliest tree macro-remains (needles of *Larix laricina*, *Picea* spp., and *Pinus* spp., and seeds of *Betula* spp.) were found between 9,850 and 9,300 cal. yr BP. Local fires were detected around 9,820, 9,360 and 8,362 cal. yr BP. Early afforestation occurred on the islands of Lake Ojibway, 200 and 450 years before its level started to decrease , confirming the hypothesis that some islands acted as migratory outposts accelerating postglacial migration.

Keywords: Afforestation, Island biogeography, Plant macro-remains, Postglacial migration, Proglacial Lake Ojibway, XRF analysis

A Introduction

At the end of the Pleistocene, large portions of the northern hemisphere were covered by ice sheets which were progressively retreating to the north. From the beginning of the Holocene (11,700 years ago) to the mid-Holocene (ca 6,000 years ago), the Laurentide Ice Sheet slowly melted over north-eastern Canada (Dalton et al., 2020). As landscapes became free of ice, they were available for colonization by vegetation from forests located at the southern margins of ice sheets.

Meltwater from receding ice sheets sometimes accumulated at their front and created so-called proglacial lakes (Carrivick and Tweed, 2013) that prevented vegetation colonization of deglaciated areas for centuries. Several Holocene proglacial lakes have been identified in Canada, including Lake Ojibway, one of the largest proglacial lakes (115,000 km^3), covering what is currently western Quebec and eastern Ontario (Godbout et al., 2020; Veillette, 1994; Vincent and Hardy, 1977). Lake Ojibway was formed because the crustal depression beneath the ice caused the adjacent terrain to slope down towards the north, which prevented meltwater from leaving the ice front (Fig. 1). The ice sheet produced meltwater, which was prevented from flowing north by the ice itself acting as a wall. Water accumulated at the ice sheet front and created proglacial Lake Ojibway around 10,570 cal. yr BP (calibrated years before present). Then, as the ice sheet continued its northward retreat, the southern end of James Bay was eventually freed from ice and Lake Ojibway gradually drained into it. Different phases of lake level have been recorded before the final drainage of Lake Ojibway. The level of proglacial Lake Ojibway reached its maximum during the Angliers phase ca 9,400 cal. yr BP (Brouard et al., 2021; Godbout et al., 2020). Then, lake level gradually decreased and was ca 65 m lower around 9,000 cal. yr BP when the Kinojévis phase started. As the level of Lake Ojibway decreased, more and more islands emerged. The level of Lake Ojibway had lowered ca 35 m more, at the beginning of the La Sarre phase ca 8,300 cal. yr BP (Brouard et al., 2021). Several dates were proposed for the final drainage of proglacial Lake Ojibway, with most

studies placing it at ca 8,200 cal. yr BP (Brouard et al., 2021; Daubois et al., 2015; Godbout et al., 2020; Roy et al., 2015).

The observed postglacial migration of several tree species in western Quebec was faster than the estimated migration time based on the mean distance dispersal capacities observed nowadays, a phenomenon called Reid's paradox of rapid plant migration (Clark, 1998). Indeed, several vegetation reconstructions based on palynological and macro-remain studies in Western Quebec indicated that afforestation closely followed the drainage of Lake Ojibway (Ali et al., 2008; Carcaillet et al., 2001; Richard, 1980). Such rapid colonization can either be explained (1) by the presence of glacial refugia (Brochmann et al., 2003; Varga, 2010); or (2) by long distance dispersal events (Bullock et al., 2017; Cain et al., 2000). As there is no evidence that glacial refugia were ever present in western Quebec, the second hypothesis can be retained but remains to be supported by empirical data.

During its >2,300 years presence over western Quebec and north-eastern Ontario, Lake Ojibway should have acted as a barrier slowing down postglacial forest migration, unless its islands were colonized early and acted as outposts facilitating colonization of lowlands following the drainage of Lake Ojibway into James Bay. For the islands of Lake Ojibway to be colonized, long-distance dispersal events from the vegetation front south of the lake were necessary. According to Schurr et al. (2009), long-distance seed dispersal via abiotic or biotic action happens when ≤1% of seeds travel >1km. Although such events are rare, they can strongly affect plant biogeography and population dynamics (Cain et al., 2000).
If the "paleo-islands" on Lake Ojibway had remained uncolonized, while Lake Ojibway was present, ie., if no long-distance dispersal events succeeded, colonization following the drainage of the proglacial lake would have followed a south-north trajectory limited by average seed dispersal distance, as most tree species in north-eastern Canada are wind-dispersed (Burns and Honkala, 1990) (Fig. 1 – first hypothesis). This scenario does not explain how sites located several hundreds of kilometers north of the migration front could have been afforested almost immediately after the drainage of Lake Ojibway (Ali et al.,

2009). An alternative hypothesis would be that some islands on Lake Ojibway were colonized through long-distance seed dispersal before the final drainage of the proglacial lake into James Bay, which would explain how sites far from the postglacial migration front could have been afforested quickly, then our study would enlighten an early colonization of paleo-islands, ie., while the Lake Ojibway still covered Quebec (Fig. 1 – second hypothesis, Fig. 2).

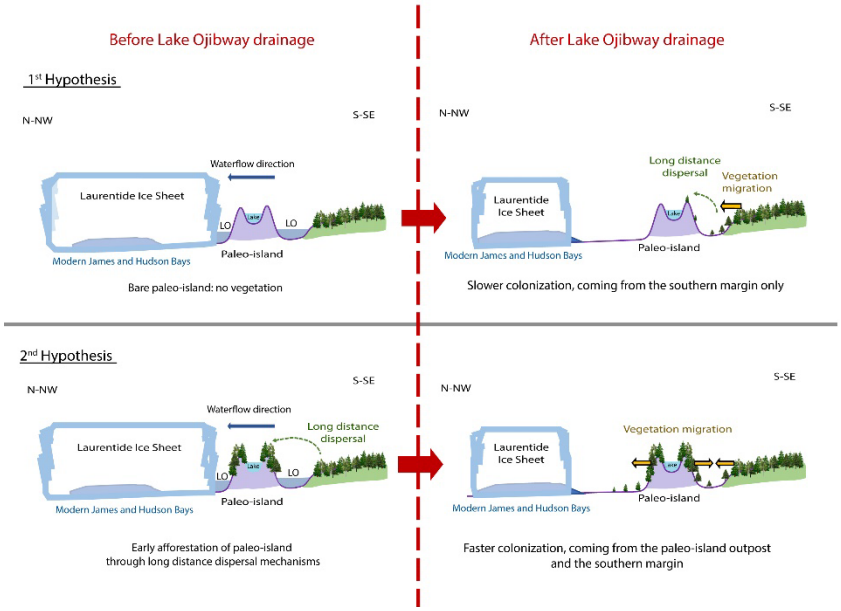


Figure 1: Schematic representation of proglacial Lake Ojibway (LO) creation and hypotheses concerning the colonization of paleo-islands before the drainage of Lake Ojibway and implications on postglacial migration thereafter.

To test the hypothesis of early afforestation of paleo-islands through long-distance dispersal events (second hypothesis), we sampled sediments from two small lakes located on paleo-islands (current hilltops above the maximum shoreline level of Lake Ojibway) (Godbout et al., 2017), and we radiocarbon-dated bulk sediment and macro-remains to build age-depth models. We used multiple proxies to infer afforestation: X-ray fluorescence (XRF) geochemical analysis to detect variations in soil erosion as a proxy for plant cover; plant macro-remain analysis to attest local vegetation presence; and charcoal analysis to reconstruct local wildfire activity as an indicator of biomass burning. Only a few

studies have been conducted so far on the afforestation of sites located near the maximum shoreline levels of proglacial lakes in eastern Canada (Richard, 1980; Richard and Larouche, 1989) and they did not allow to clearly demonstrate the potential role of paleo-islands on postglacial forest migration. Our study documents environmental conditions above the maximum limit of Lake Ojibway, therefore allowing us to test the hypothesis of early colonization of paleo-islands on a proglacial lake.

A Material and methods

B Study area

The study area is located in the Abitibi-Témiscamingue region of western Quebec and is part of the clay belt of Quebec and Ontario created by deposits of proglacial Lake Ojibway (Fig. 2a). The Abijévis hills are located within the Aiguebelle National Park, whereas the Kekeko hills are 50 km southward of the park. Both hill formations originated from marine volcanism and are composed of mafic rocks, ie., mostly non-carbonate rocks such as gabbro and andesite. Surface deposits are glacial till (MERN - Système d'information géominière, 2022; Nutz et al., 2020). The hills were aerially exposed following ice sheet retreat ca 10,650 cal. yr BP (Dyke, 2004; Veillette, 1994). Although they were rounded by ice sheet action, the hills remain among the highest elevations in Abitibi-Témiscamingue, with maximum elevations of 570 m and 488 m above sea level (a.s.l.) for Abijévis and Kekeko, respectively. They are surrounded by a generally flat topography (between 180 and 350 m a.s.l.).

Ancient shorelines of proglacial Lake Ojibway are still visible on hillsides in the current landscape and allowed reconstructions of lake level history (Godbout et al., 2017, 2020) and the identification of several paleo-islands that became hills following the final drainage of Lake Ojibway ca 8,200 cal. yr BP (Richard, 1980; Richard et al., 2020; Veillette, 1994). Lake Ojibway's highest shorelines (ca 9,400 cal. yr BP) are estimated to be slightly below 400 m a.s.l. and 380 m a.s.l. for the Abijévis and Kekeko hills, respectively

(Godbout et al., 2017). Areas above these elevations are therefore considered to have always been paleo-islands (Fig. 2b).

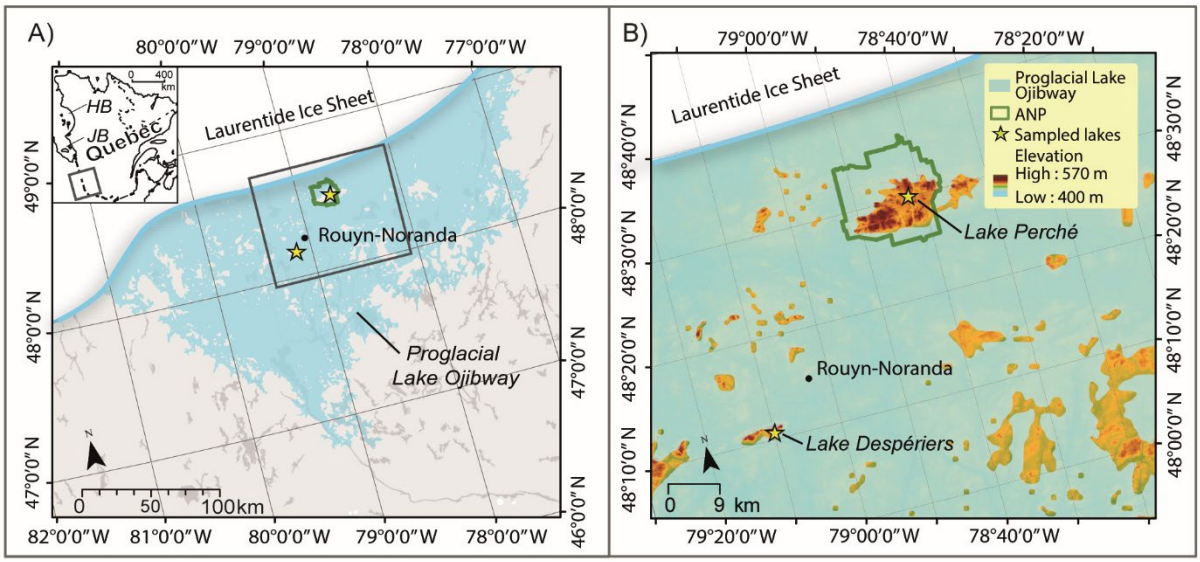


Figure 2: (a) Extent of proglacial Lake Ojibway in western Quebec around 9,600 cal. yr BP (Brooks, 2020), showing the locations of the two studied paleo-islands (yellow stars) according to the lake level at the time. The location of Aiguebelle National Park (ANP) is also shown. The inset shows the location of ANP relative to Hudson Bay (HB) and James Bay (JB), where proglacial Lake Ojibway finally drained around 8,200 cal. yr BP. (b) Close-up of the study area showing paleo-islands (in light to dark orange), including the Abijévis and Kekeko Hills, where Lakes Perché and Despériers were sampled, respectively.

B Site selection and lake sediment sampling

We selected two small headwater lakes surrounded by steep shores to maximize sediment collection: Lake Perché (formerly known as Lake Edrien) in the Aiguebelle National Park (Abijévis hills) and Lake Despériers on the Kekeko hills (Table I; Fig. 2). Lake Perché is located at 380 m a.s.l. While this is slightly below the highest shoreline of Lake Ojibway in the area (400 m a.s.l.), Lake Perché was formed before the complete drainage of proglacial Lake Ojibway and could have recorded part of the paleo-island's history. Lake Despériers is located at 407 m a.s.l., ie. almost 30 m above the highest shoreline of Lake Ojibway in the area (Table I). Current forest vegetation around the sampled lakes is dominated by black spruce (*Picea mariana* [Mill.] BSP), white spruce (*Picea glauca* [Moench] Voss), jack pine (*Pinus*

banksiana Lamb.) and balsam fir (*Abies balsamea* [L.] Mill.). Both lakes are surrounded by rolling hills less than 100 m in height.

Table I: Main characteristics of Lakes Perché and Despériers.

Name	Latitude	Longitude	Elevation (m a.s.l.)	Area (ha)	Organic sediment core length (cm)	Water column depth at sampling location (cm)	Current local vegetation by order of dominance
Lake Perché	48°30'8.10"N	78°41'56.90"W	380	9.70	554	370	*Picea mariana*, *Pinus banksiana*
Lake Despériers	48°11'4.22"N	79° 9'38.80"W	407	8.89	292	750	*Picea mariana*, *Picea glauca, Abies balsamea*

We extracted lake sediment cores from the center of each lake with a 60-mm diameter Livingstone corer. We selected headwater lakes to avoid sediment disturbance by incoming water flows. We collected complete gyttja sequences (organic sediments), from the water-sediment interface to the contact with the underlying mineral glacial sediments. We stored sediments in plastic tubes and kept them in cold conditions (4°C) until further analyses.

B Age-depth models

We built age-depth models with the Bayesian statistics-based 'Bacon' v2.2 package in R (Blaauw and Christen, 2011) for the bottom part of the sediment sequences at each lake, as we wanted to focus on the period corresponding to the beginning of organic sediment accumulation on the paleo-islands. Despite our efforts, we found few macro-remains and we only managed to obtain ^{14}C dates for two levels at lake Perché and one level at lake Despériers (Table II). Hence, we also dated bulk sediment from

three levels from each core to complete the age-depth models (Table II). We calibrated the ^{14}C dates with the IntCal20 calibration curves (Reimer et al., 2020).

Table II: Radiocarbon dates obtained from samples near the bottom of the sediment cores from Lakes Perché and Despériers.

Lake	Sample depth (cm)	^{14}C yr BP	Cal. yr BP	Material dated	Lab. Code
Perché	512.5 - 513	6670 ± 20	7537 ± 30	Bulk sediment	ULA-9479
Perché	537 - 538.5	7225 ± 20	8044 ± 25	Bulk sediment	ULA-9477
Perché	553 - 553.5	7510 ± 30	8341 ± 30	Plant macro-remains[a]	BETA-644328
Perché	555 – 555.5	7680 ± 40	8466 ± 30	Plant macro-remains[b]	BETA-644329
Perché	564 - 564.5	8695 ± 20	9626 ± 30	Bulk sediment	ULA-9478
Despériers	232.5 – 233.5	5975 ± 15	6813 ± 30	Bulk sediment	ULA-10171
Despériers	260 – 261	7055 ± 20	7891 ± 30	Bulk sediment	ULA-10172
Despériers	276 – 277.5	7510 ± 30	8341 ± 30	Plant macro-remains[c]	BETA-638098
Despériers	289 – 289.5	8775 ± 20	9774 ± 40	Bulk sediment	ULA-10173

[a] bark fragment and other unidentified vegetal fragments; [b] bark fragment, *Cristatella mucedo* statoblast and other unidentified vegetal fragments; [c] *Larix laricina* needle fragment and unidentified seed and vegetal fragments.

B Geochemical analyses

We performed XRF analyses on the basal sediments corresponding to the first millennium of the paleo-islands' existence. To detect semi-quantitative variations of geochemical composition, we used the TestAllGeo analysis mode on the Niton XL3t 900SHE portable scanner and continuously scanned the sediments every 0.5 cm along the cores. Changes in the concentration of several major and minor elements can be used as proxies of ecological phenomena (Croudace and Rothwell, 2015). We used K, Ti, Rb, Sr, Zr and Fe (lithogenic elements) as indicators of erosion from the watershed to the lakes, which we expected to decrease following afforestation of the paleo-islands. In addition to being an erosion indicator, low levels of K indicate extensive vegetation presence (Foerster et al., 2012). While S and Ca have various environmental interpretations (Croudace and Rothwell, 2015), we considered S to be

188 indicative of organic matter presence and Ca to be indicative of biogenic carbonate (algae production).
189 As plants fix sulfur (S), we used the S/Ti ratio as an indicator of organic matter presence (Moreno et al.,
190 2007). The fact that S, Ca and the S/Ti ratio are indicators of organic matter presence compensates for
191 our inability to perform loss-on-ignition (LOI) analysis due to lack of material. For each lake, we applied
192 principal component analysis (PCA) with the 'factoextra' package in R (Kassambara, 2017) to differentiate
193 portions of the sediment sequences based on their chemical signature. We used the Kaiser criterion to
194 select significant principal components (PCs), ie., those with eigenvalues >1 (Kaiser, 1960). As variations
195 along the PCs were semi-quantitative because of the XRF scanning method and scanner calibration, we
196 could only compare trends in element dynamics (increase or decrease), and not their absolute values.
197
198 ***B Identification of plant macro-remains***
199 We bathed half of each 0.5-cm slice of basal sediments in a hexametaphosphate ($Na_6P_6O_{18}$) solution for
200 at least 12 hours under agitation, for deflocculation purposes. We then filtered each sample through a
201 250-µm sieve to keep plant macro-remains. We identified plant macro-remains under a dissecting
202 microscope using a published key (Lévesque et al., 1988) and recorded the presence and absence of taxa
203 for each level studied.
204
205 ***B Charcoal extraction and analysis***
206 To perform charcoal extraction, we cut the basal sediments continuously into 0.5-cm-thick slices. We
207 extracted a 1-cm^3 subsample from the middle of each slice to avoid contamination risk (Mustaphi and
208 Pisaric, 2014). We bathed the subsample in a solution of potassium hydroxide (KOH), sodium
209 hexametaphosphate ($Na_6P_6O_{18}$), and sodium hypochlorite (NaClO) for at least 24 hours under agitation to
210 perform deflocculation and to help differentiate charcoal particles from organic matter (Whitlock and
211 Larsen, 2001). We sieved the solution through a 160-µm mesh to extract macro-charcoal particles and

measured their surface area under a dissecting microscope using the WinSEEDLE TM image analysis software (Regents Instruments Inc., https://regent.qc.ca/, August 2021).

To reconstruct local fire history, ie., fire events that occurred within the lakes' watersheds and thus on the paleo-islands, we applied the Charcoal Size Distribution (CSD) method (Asselin and Payette, 2005; Oris et al., 2014a; Remy et al., 2018) to every fire event detected using the CharAnalysis software v1.1 (Higuera et al., 2008; http://CharAnalysis.googlepages.com). We calculated geometric mean diameters of charcoal particles from the square root of the surface area (Clark and Hussey, 1996) and converted them to log mm. We sorted charcoal particles of each sample according to their size into six classes ranging from -0.9 log mm to 0.3 log mm (every 0.2 log mm). We applied a linear regression to the distribution of the proportion of charcoal particles in each size class (-0.8, -0.6, etc.) for each sample. As large charcoal particles travel less far, local fires are characterized by a greater proportion of large charcoal particles than regional fires, which is reflected by a gentler slope of the size distribution regression (Asselin and Payette, 2005). According to this principle, we classified as local fires (on the paleo-island) the samples with a slope more gentle than a threshold fixed at -1.77 based on a previous study (Oris et al., 2014a). In addition, we considered as local fires only the samples having at least one charcoal particle >-0.3 log mm (Supplemental Figure 1). We considered that other fires (extra-local or regional) did not burn on the paleo-islands.

A Results

B Organic sediment accumulation during Lake Ojibway presence

Basal ^{14}C dates obtained from organic sediments at or close to the contact with the glacial mineral sediments were 9,657 cal. yr BP and 9,947 cal. yr BP for Lakes Perché and Despériers, respectively (Fig. 3). These basal ages are older than the estimated date of Lake Ojibway's final drainage (8,200 cal. yr BP). Radiocarbon dates based on macro-remains that are coeval with the gradual lowering of the level of Lake

Ojibway were recorded 10 cm above the basal dates obtained from bulk sediments. Despite being a little younger than expected, these radiocarbon dates based on macro-remains are the oldest dates obtained for the region. Moreover, they are from the Kinojévis phase (9,000-8,300 cal. yr BP), before the final drainage of Lake Ojibway. Radiocarbon dates based on bulk sediment and on plant macro-remains are consistent, suggesting that no or little reservoir effect altered the age-depth models and basal age estimations (Grimm et al., 2009).

At Lake Perché, the sediment sequence we analyzed spanned from 9,657 to 6,503 cal. yr BP, and at Lake Despériers from 9,947 to 6,850 cal. yr BP (Fig. 3). The mean sedimentation rates were relatively similar at both lakes at the beginning of the Holocene (44 $yr.cm^{-1}$ for Lake Perché and 53 $yr.cm^{-1}$ for Lake Despériers). The mineral sediments found below the gyttja were olive-grey colored silt for both lakes, which was markedly different from the clay characterizing sites located below the shorelines of proglacial Lake Ojibway. Silt is indicative of glacial till associated to the direct action of the ice sheet on the bedrock without a proglacial lake intermediary (Boulton, 1978; Normandeau et al., 2013).

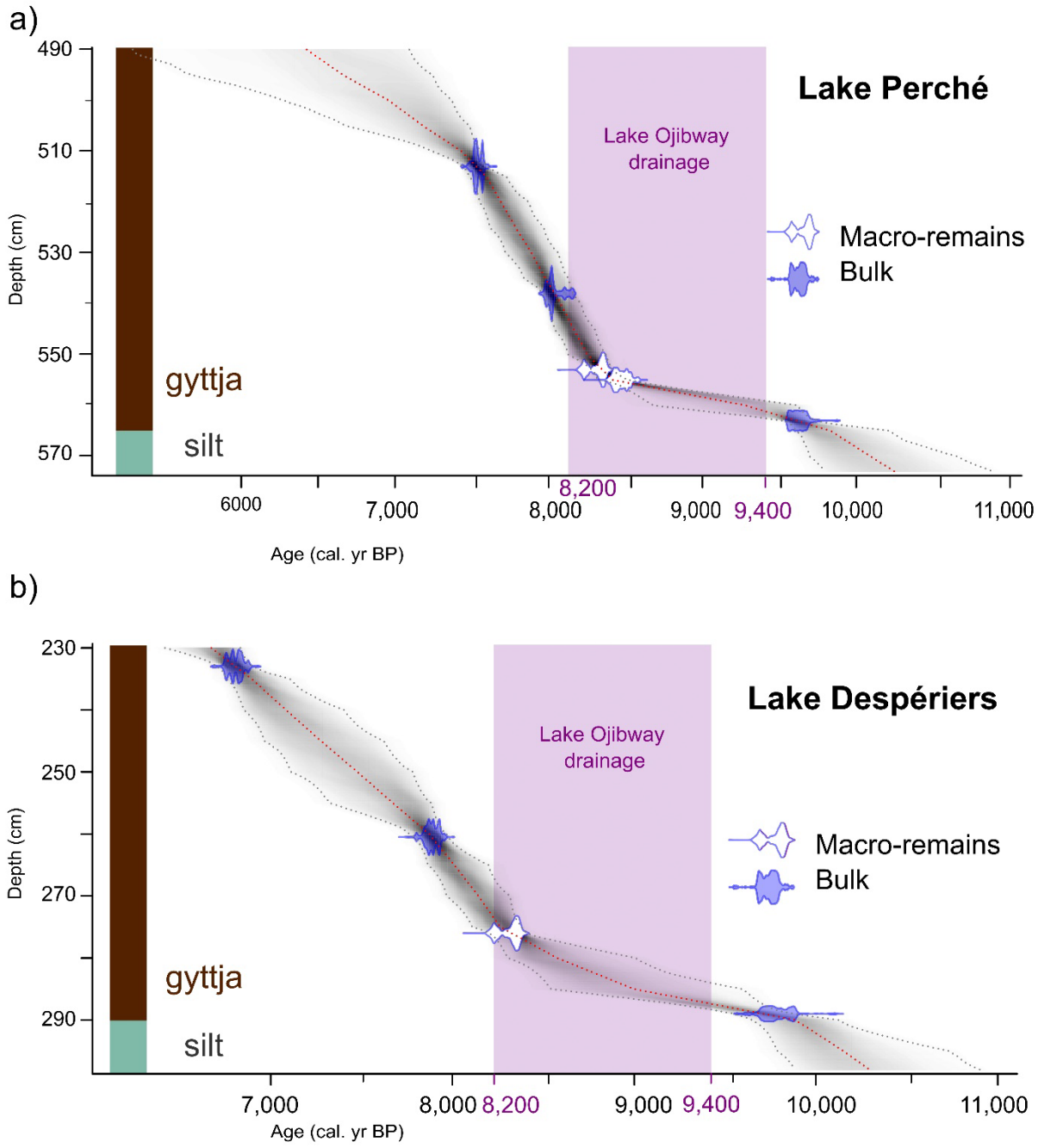


Figure 3: Calibrated age-depth models based on the radiocarbon dates (Table II) obtained from basal sediments (brown = organic sediments and olive-grey = mineralogic sediments) at a) Lake Perché and b) Lake Despériers. The purple rectangle illustrates the period when the level of proglacial Lake Ojibway gradually decreased until its final drainage ca 8,200 cal. yr BP.

B Geochemical signature of the organic sediments

Two groups were detected by the PCA analysis in the gyttja of Lake Perché: (1) from the silt-gyttja transition at 9,600 cal. yr BP to 9,000 cal. yr BP and (2) between 9,000 and 6,500 cal. yr BP (Fig. 4a). The first two principal components explained 88.66% of the variability in the dataset (PC1 = 73.67% and PC2 = 14.99%). PC1 was positively associated to lithogenic elements (K, Ti, Fe, Rb, Zr, Sr) coming from the steep shores surrounding the lake, while PC2 was positively correlated to S. One element (Ca) was positively related to both PCs (Fig. 4a).

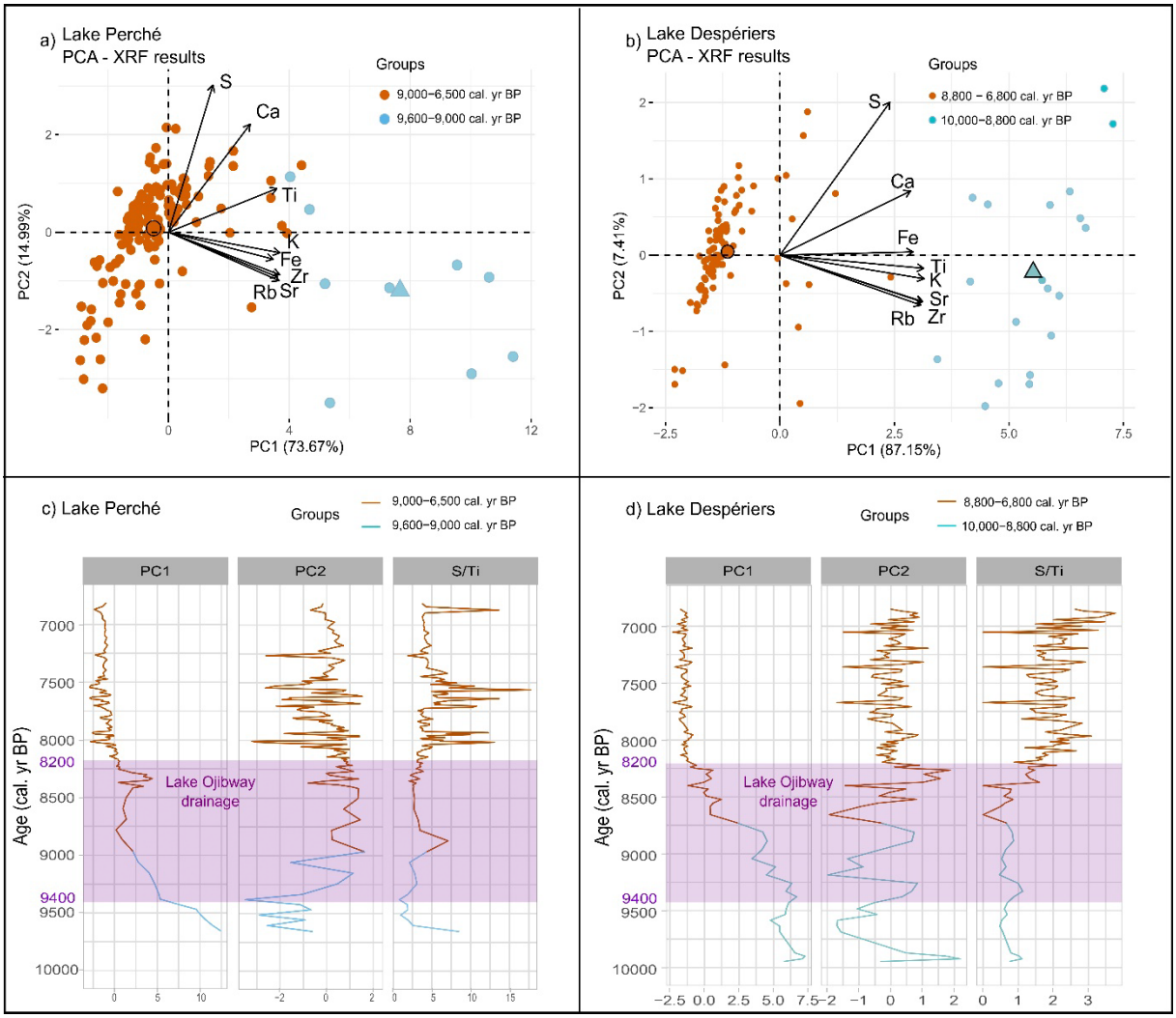


Figure 4: Principal component analysis (PCA) of sediment samples (dots), associated centroids for each cluster (larger dots and triangles), and XRF results (arrows) for a) Lake Perché and b) Lake Despériers. At both sites the sediment samples pre- and post-dating afforestation are clearly separated along PC1.

Variations of PC1 and PC2 loadings, and of the S/Ti ratio across time at c) Lake Perché and d) Lake Despériers. The purple rectangle illustrates the period when the level of proglacial Lake Ojibway gradually decreased until its final drainage ca 8,200 cal. yr BP.. Note that the data for PC2 at Lake Despériers does not respect the Kaiser criterion of eigenvalue >1 and should be interpreted with caution.

The PCA also differentiated two groups in the gyttja of Lake Despériers: (1) from the silt-gyttja transition at 10,000 cal. yr BP to 8,800 cal. yr BP and (2) between 8,800 and 6,800 cal. yr BP (Fig. 4b). The first two principal components explained 94.56% of the variability (PC1 = 87.15% and PC2 = 7.41%). As was the case for Lake Perché, the lithogenic sediments were positively correlated to PC1 at Lake Despériers, S was positively associated to PC2, and Ca was positively related to both PCs.

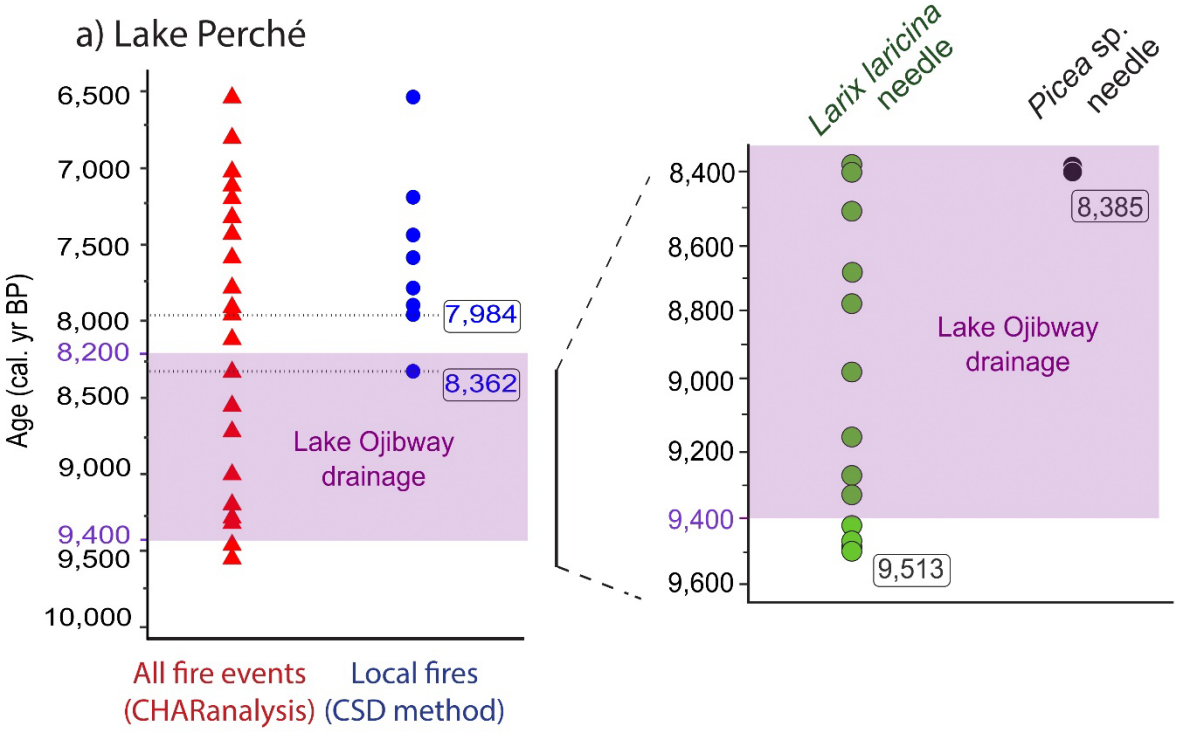
For Lake Perché, PC1 values (associated with lithogenic elements) quickly decreased until 8,800 cal. yr BP, and then increased until 8,300 cal. yr BP. After 8,250 cal. yr BP, values slowly decreased and reached their minimum until the end of the record, ie. 6,500 cal. yr BP. PC2 values (associated with S) increased between 9,350 and 9,000 cal. yr BP (Fig. 4a, c) and then remained relatively stable (despite short-term variations) between 9,000 and 7,900 cal. yr BP (Fig. 4c). The S/Ti ratio slowly increased with peaks around 8,800 cal. yr BP, between 8,000 and 7,800 cal. yr BP, between 7,700 and 7,500 cal. yr BP, and ca 6,900 cal. yr BP (Fig. 4c). The absence of a distinguishable pattern at 8,200 cal. yr BP indicates that the environment remained stable during the drainage of proglacial Lake Ojibway.

For Lake Despériers, PC1 values (associated with lithogenic elements) gradually decreased from the beginning of gyttja accumulation around 10,000 cal. yr BP until 8,700 cal. yr BP, then they strongly decreased around 8700 cal. yr BP to reach minimum values after 8,200 cal. yr BP. (Fig. 4b, d). PC2 did not respect the Kaiser criterion (eigenvalue = 0.59) and therefore could not be interpreted (Supplemental Table 1). The S/Ti ratio remained stable during the early Holocene at Lake Despériers, with peaks at ca 9,900, 9,300 and 8,800 cal. yr BP (Fig. 4d). Then, ca 8,400 cal. yr BP, the S/Ti ratio started to increase until

7,900 cal. yr BP. Around 7,700 cal. yr BP, the S/Ti ratio decreased and remained stable until 7,000 cal. yr BP, then it increased until 6,500 cal. yr BP (Fig. 4d).

B Plant macro-remains: early presence of local trees

Despite the paucity of macro-remains in the sediments, we were able to extract and identify some of them. The earliest tree macro-remains that we found were larch (*Larix laricina [Du Roi]* K. Koch) needles dating from around 9,513 cal. yr BP at Lake Perché (Fig. 5a; Supplemental Figure 2a, b). Spruce (*Picea* spp.) needle fragments were also found ca 8,385 cal. yr BP (Fig. 5a; Supplemental Figure 2c). At Lake Despériers, the earliest tree macro-remains that we found were pine (*Pinus* spp.) needles, dating from around 9,845 cal. yr BP (Fig. 5b; Supplemental figure 2d). Needles of spruce (*Picea* spp.) and larch (*Larix laricina*), as well as birch (*Betula* spp.) seeds were also found ca 9,584-9,300 cal. yr BP (Fig. 5b; Supplemental Figure 2e-i). Trees were therefore present on the studied paleo-islands at least 1,400 years before Lake Ojibway drainage.


a) Lake Perché
Age (cal. yr BP)
6,500
7,000
7,500
8,000
8,200
8,500
9,000
9,400
9,500
10,000
7,984
8,362
Lake Ojibway drainage
All fire events (CHARanalysis)
Local fires (CSD method)
Larix laricina needle
Picea sp. needle
8,400
8,600
8,800
9,000
9,200
9,400
9,600
8,385
9,513
Lake Ojibway drainage

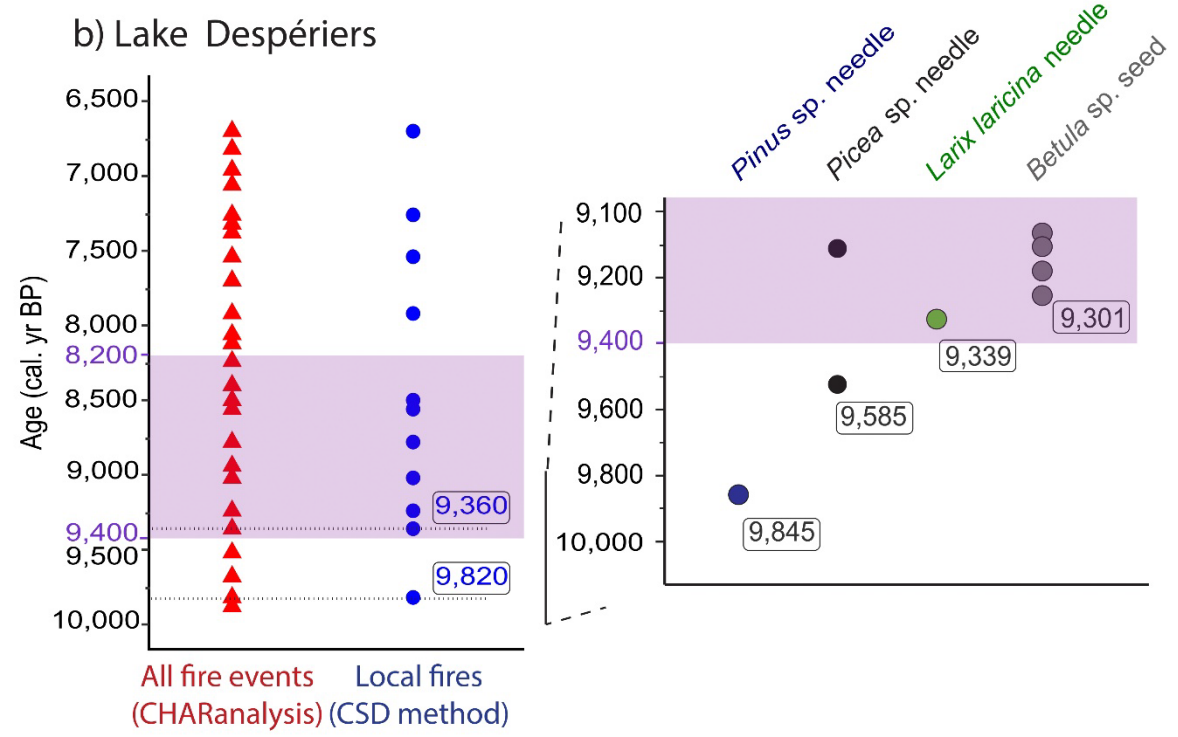

b) Lake Despériers
Age (cal. yr BP)
6,500
7,000
7,500
8,000
8,200
8,500
9,000
9,400
9,500
10,000
9,360
9,820
All fire events (CHARanalysis)
Local fires (CSD method)
Pinus sp. needle
Picea sp. needle
Larix laricina needle
Betula sp. seed
9,100
9,200
9,400
9,600
9,800
10,000
9,301
9,339
9,585
9,845

Figure 5: Fire events detected with CHARanalysis (red triangles), and local fire events detected with the Charcoal Size Distribution (CSD) method (blue circles) and oldest tree macro-remains retrieved from the sediments at (a) Lake Perché and (b) Lake Despériers according to the age-depth models (Fig. 3). The purple rectangle illustrates the period when the level of proglacial Lake Ojibway gradually decreased until its final drainage ca 8,200 cal. yr BP.

B Evidence of local forest fires on a paleo-island

CHARanalysis detected 21 and 25 fire events in the Lake Perché and Lake Despériers sediments, respectively (Fig. 5). At Lake Perché, eight events met the conditions to be considered local fires having burned within the watershed, the earliest local fires were dated at 8,362 (Fig. 5a) when charcoal influx was maximal (Supplemental Figure 3), 7,984 and 7,942 cal. yr BP (Fig. 5a) when charcoal influx was lower (Supplemental Figure 3). The earliest local fire, evidenced by burned needle fragments (possibly *Picea* spp.) (Supplemental Figure 2c), occurred around 160 years before the drainage of proglacial Lake Ojibway. At Lake Despériers, 11 events met the conditions to be considered local fires having burned within the watershed. The earliest local fires at Lake Despériers were dated at 9,820 and 9,360 cal. yr BP, while Lake Ojibway was still present (Fig. 5b).

A Discussion

Our analyses of two sites located 50 km apart revealed that both paleo-islands were colonized by tree species several centuries before the level of Lake Ojibway lowered enough for paleo-islands to become connected with the mainland to the south ca 9,000 cal. yr BP (Godbout et al., 2020; Roy et al., 2015). We used proxies suited to reveal local vegetation establishment, and we avoided proxies such as pollen, which can be influenced by extra-local vegetation inputs.

B Early afforestation of islands on proglacial Lake Ojibway

Gyttja started to accumulate at the bottom of small lakes on paleo-islands while Lake Ojibway was still at its maximum level , ie., about 250-550 years before it started to gradually decrease. The presence of silt rather than clay beneath the gyttja at both sites is evidence that they were never flooded by proglacial Lake Ojibway. Radiocarbon dates obtained from plant macro-remains testify that shrubs and trees were present on the paleo-islands at least 140-260 years before the final drainage of proglacial Lake Ojibway (Table II). According to the age-depth models, the oldest tree macro-remains we found were (indirectly) dated to ca 9,600 cal. yr BP and 9,850 cal. yr BP at Lakes Perché and Despériers, respectively, 200 and 450 years before the level of Lake Ojibway first started to decrease (Brouard et al., 2021; Godbout et al., 2020). Hence, while deglaciation time has been estimated at 10,570 cal. yr BP in the study area (Daubois et al., 2015; Godbout et al., 2020; Roy et al., 2015), our results indicate that the afforestation process needed about 1,000 years to unfold after the glacier retreat. This is much longer than what has been documented at recently deglaciated sites in Alaska, where primary succession took less than 200 years to complete (Fastie, 1995). The difference would likely be due to the distance to seed sources having been much greater at our sites (80 km over mostly water) compared to those in Alaska (<30 km over ground). Furthermore, cold temperatures during the early Holocene (Viau et al., 2006) likely implied lower vegetation productivity, as evidenced in our age-depth models by lower sediment accumulation rates compared to the middle Holocene.

Geochemical analyses showed that lithogenic elements - therefore erosion (Joannin et al., 2022; Lefebvre et al., 2021) - decreased rapidly at both sites from the beginning of gyttja accumulation until 8,800 cal. yr BP (Lake Perché) and 8,700 cal. yr BP (Lake Despériers). As soil cohesion and stabilization are supported by plant root systems (Easterbrook, 1999), it is reasonable to assume that decreasing erosion is an indirect indicator of vegetation colonization on paleo-islands. Indeed, more individual plants produce more roots which stabilize the ground, meaning that less soil erosion is recorded in the lake

sediments. Therefore, PC1 variations suggest the presence of vegetation rapidly after the beginning of gyttja accumulation at both lakes. The plateau PC1 values reached for both lakes around the final drainage of proglacial Lake Ojibway ca 8,200 cal. yr BP likely indicate densification of the vegetation. Increased PC2 values (mostly linked to S fixation by plants) and a peak of the S/Ti ratio around 8,800 cal. yr BP indicate a strong organic matter input and suggest the arrival (or densification) of local vegetation, coherent with the decrease of the level of Lake Ojibway. Therefore, the variations in the concentrations of lithogenic elements and elements indicating organic matter input into the lake sediments provide indirect support of early vegetation establishment before the level of Lake Ojibway started to decrease and possible densification on the paleo-islands before Lake Ojibway's final drainage.

Macro-remains analysis confirmed local presence of trees at both sites, while Lake Ojibway was still present and before it gradually drained. According to the age-depth model, the earliest tree species identified at Lake Perché is *Larix laricina*, possibly indicative of wet conditions around the lake ca 9,500 cal. yr BP (Johnston, 1990). It was followed by *Picea* spp. around 8,400 cal. yr BP, at a time when geochemical analyses indicate that vegetation became denser. At Lake Despériers, *Pinus* spp. was the earliest species found at the paleo-island around 9,850 cal. yr BP and could be indicative of environmental conditions drier than at Lake Perché (Rudolph and Laidly, 1990). Then, between ca 9,585 cal. yr BP and 9,300 cal. yr BP, *Picea* spp., *Larix laricina* and *Betula* spp. were also present, possibly indicating that environmental conditions had become more mesic, as at Lake Perché.

The fact that a local fire was dated at 8,362 cal. yr BP at lake Perché (burned unidentified needle) is yet another confirmation of early afforestation of the paleo-island, as fire ignition and propagation are fuel-dependent (ie., biomass-dependent) (Finney et al., 2021). At Lake Despériers, the earliest local fire around 9,820 cal. yr BP (burned unidentified needle fragment, Fig. S.3.3) confirmed biomass presence and afforestation on the paleo-island (Finney et al., 2021) before the drainage of proglacial Lake Ojibway started.

377

378 ***B The paleo-island colonization process: an answer to Reid's Paradox***

379 For primary succession to be successful on a bare island on a proglacial lake, several biotic and abiotic
380 barriers must be overcome (Crofts and Brown, 2020). Climatic and meteorological factors are at play,
381 substrate characteristics are also important, but distance to seed sources is the main hurdle.

382 At the time of full extension of proglacial lake Ojibway, the distance between the studied paleo-islands
383 and the continental forest margin was about 80 km, with other islands located in between (Fig. 2b).
384 Colonization of the studied paleo-islands could have resulted from seeds coming directly from the
385 colonization front and traveling almost 100 km above water. Such long distance dispersal events have
386 been documented before (Davis et al., 1986). Seeds could also have come from other paleo-islands that
387 could have acted as 'stepping stones' (Harris et al., 2018). In either case, our results support the
388 hypothesis of tree population outposts on paleo-islands, far from the main source population of
389 propagules at the southern margin of the proglacial lake, as previously theorized (Davis et al., 1991).
390 Even with the 'stepping stones' scenario that would have reduced seed traveling distance to steps of ca
391 15-20 km, such dispersal would be considered very long, as the vast majority of boreal tree seeds are
392 dispersed less than 100 m from the parent tree (Asselin et al., 2001; Burns and Honkala, 1990; Greene
393 and Johnson, 1996). Estimating the seed rain at distances longer than a few hundred meters is very
394 difficult technically (Nathan, 2006). A modelling study estimated the proportion of seeds traveling 1-10
395 km (long distance dispersal events) at 0.1% (Higgins and Richardson, 1999). Knowing that yearly seed
396 production of most boreal tree species reaches 1-5 million seeds/ha (Burns and Honkala, 1990), between
397 12,500 and 62,500 seeds could have reached the studied paleo-islands each year. Multiplied by 1000
398 years between deglaciation and vegetation establishment on paleo-islands and adding the probability of
399 germination and survival, the possibility of colonization through long distance dispersal is, after all, not
400 so unlikely. Moreover, as the level of Lake Ojibway gradually decreased from ca 9,400 cal. yr BP, more

401 and more land became available for colonization, which would have decreased the travel distance
402 between mainland and islands, thus gradually increasing the probability of successful dispersal events
403 and colonization of paleo-islands.

404 Catabatic winds blowing from the ice sheet to the south could have slowed down the migration process
405 (Richard and Larouche, 1989). Reconstructions of paleo-wind directions indicate a dominant wind
406 blowing towards the east or south-east (Veillette, 1996), but do not indicate a predominance of catabatic
407 winds (Nutz et al., 2020). Active (biotic) dispersal (eg, by birds) could have contributed to long-distance
408 dispersal, even if most boreal tree species are generally dispersed by wind (Higgins et al., 2003; Nathan
409 et al., 2008; Wilkinson, 1997). Indeed, nonstandard dispersal of wind-dispersed seeds by omnivorous
410 birds has been hypothesized and later confirmed by empirical data (Nogales et al., 2012; Rumeu et al.,
411 2014). We do not have palaeoecological proxies confirming or denying bird presence or passage on the
412 paleo-island, but they could have facilitated tree seed dispersal. In the winter, secondary seed dispersal
413 over snow or ice, or on ice rafts in the spring, could have also favored long-distance dispersal (Alsos et
414 al., 2016; Greene and Johnson, 1997). Paleo-island plant colonization could also have occurred with
415 seeds from the Lake Ojibway free water at Lake Perché, as it was located close to the proglacial lake's
416 shoreline. In the spring, melting snow would have flushed plant material (including seeds) into Lake
417 Ojibway, and windrows would have facilitated their buoyancy and transport by wind up to the paleo-
418 island shores (Glaser, 1981).
419 Simulation studies have estimated the migration rate of *Picea* spp. at about 50 $m.yr^{-1}$ (Snell and Cowling,
420 2015; Sulphur et al., 2016), which would mean that trees would have needed ca 4,000 years to migrate
421 the 200 km from south to north of the area covered by proglacial Lake Ojibway following its final
422 drainage around 8,200 cal. yr BP, if it were not for paleo-islands. However, basal dates of bulk sediments
423 sampled in lakes located at the northern end of the area yielded ages very close to drainage time (Ali et
424 al., 2009; El-Guellab et al., 2015; Oris et al., 2014b). Our demonstration of early afforestation of two

paleo-islands implies that they could have acted as migration outpost following the drainage of proglacial Lake Ojibway, hence accelerating colonization of the lowlands. The total area covered by paleo-islands represented ca 3,600 km^2, ie., about 10% of the area covered by proglacial Lake Ojibway at its maximal extent (Fig. 2a). This means that several possible outposts were available for early afforestation, from near the colonization front in the south, up to the ice sheet margin in the north (Fig. 2b). The contribution of paleo-islands as migration outposts is the most likely mechanism that could explain Reid's paradox of rapid plant migration in western Quebec (Clark et al., 1998).

A Acknowledgements

We thank Thibaut Petry and his team at Aiguebelle National Park for their help and support. We also thank Mary Robles, Raynald Julien and Danielle Charron for their help with fieldwork and data processing. We are grateful to the Institut de recherche en mines et en environnement (UQAT) for letting us use their XRF scanner, and to Yvan Poirier and Mathieu Villeneuve for their help with the scanner. We thank Nils Ambec and Alayn Larouche for their help to identify plant macro-remains. We also thank Jean J. Veillette for constructive discussions, and Raphaël Chavardès, Dorian Gaboriau and the proofreading committee "Corrige-moi" who provided helpful comments on a first draft. We thank the anonymous reviewers, whose comments improve our manuscript. This is a contribution of the Laboratoire International de Recherche sur les Forêts Froides and ISEM contribution No XXX.

A Conflict of interest

The authors declare no conflict of interest.

A Funding

This work was supported by Mitacs Acceleration in partnership with Aiguebelle National Park [grant number IT25924].

A Data availability statement

Data used for this article are available online:

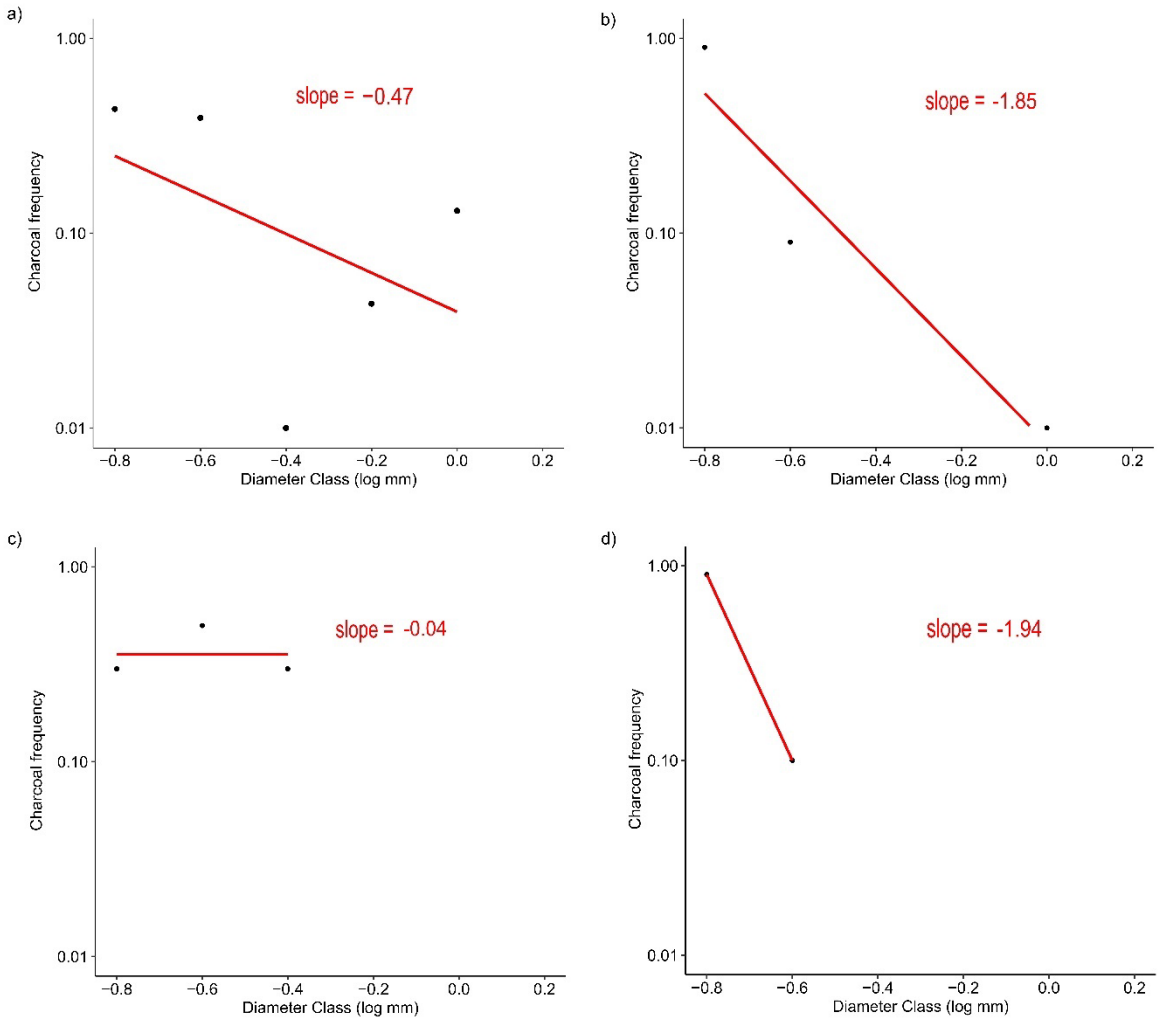
https://data.mendeley.com/datasets/k8b2t978hd/draft?a=bcbf8880-3a2a-4638-aa92-14aac331ac35

A Supplementary Material

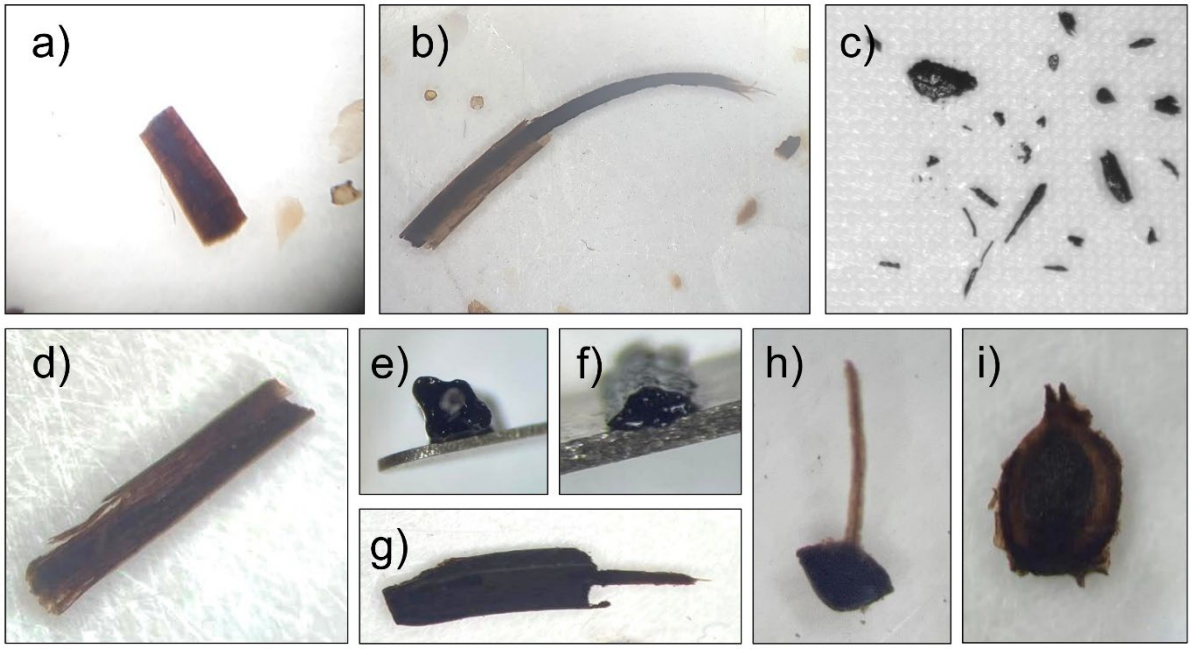
Supplemental Table 1: Eigenvalues for principal components 1 and 2 following principal component analysis on the data for Lake Perché and Lake Despériers (Fig. 3). Eigenvalues >1 met the Kaiser criterion for significance and are indicated in bold.

	PC1 eigenvalue	PC2 eigenvalue
Lake Perché	**5.65**	**1.38**
Lake Despériers	**6.97**	0.59

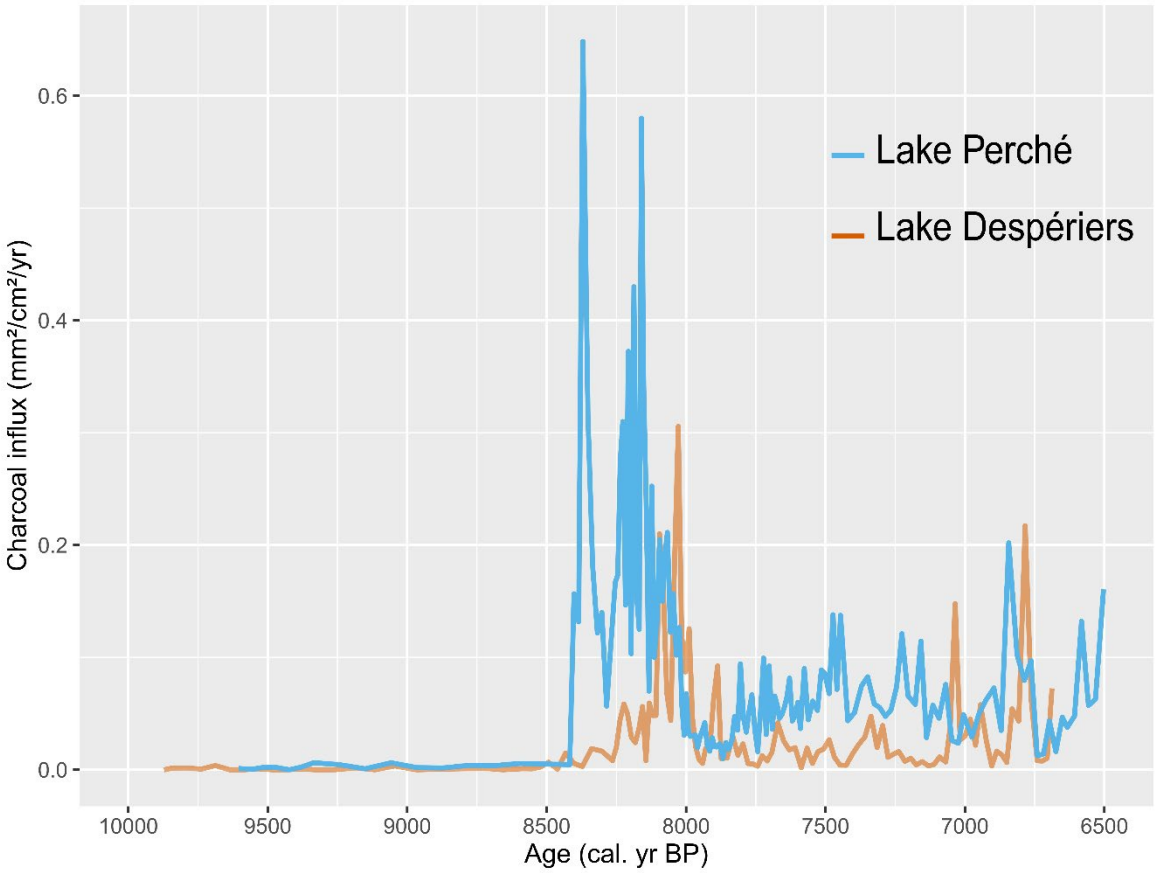
Supplemental figures



Supplemental Figure 1: Four examples of linear regressions performed on charcoal distributions and their associated slopes. a) Local fire, as both criteria are respected (slope less steep than the -1.77 threshold and presence of charcoal particles >-0.3 log mm), b) Regional fire as the slope is steeper than the threshold, c) Regional fire as no charcoal particle >-0.3 log mm was found, and d) Regional fire as none of the criteria is respected.



Supplemental Figure 2: Nine of the oldest macro-remains found in the basal sediments of Lake Perché: (a-b) *Larix laricina* needles, c) Possible *Picea* sp. needle (charcoal particles); and Lake Despériers: d) *Pinus* sp. needle, (e-f) *Picea* sp. needle, (g-h) *Larix laricina* needles and i) *Betula* sp. seed. Magnification x40 under a dissecting microscope (see Methods).



Supplemental Figure 3: Charcoal influx for Lake Perché in blue and Lake Despériers in orange.

A References

Ali AA, Asselin H, Larouche AC, Bergeron Y, Carcaillet C and Richard PJH (2008) Changes in fire regime explain the Holocene rise and fall of *Abies balsamea* in the coniferous forests of western Québec, Canada. *The Holocene* 18(5): 693–703: doi:10.1177/0959683608091780.

Ali AA, Carcaillet C and Bergeron Y (2009) Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology* 15(5): 1230–1241: doi:10.1111/j.1365-2486.2009.01842.x.

Alsos IG, Ehrich D, Seidenkrantz M-S, Bennike O, Kirchhefer AJ and Geirsdottir A (2016) The role of sea ice for vascular plant dispersal in the Arctic. *Biology Letters* 12(9): 4: doi:http://dx.doi.org/10.1098/rsbl.2016.0264.

Asselin H, Fortin M-J and Bergeron Y (2001) Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *Forest Ecology and Management* 9.

Asselin H and Payette S (2005) Detecting local-scale fire episodes on pollen slides. *Review of Palaeobotany and Palynology* 137(1–2): 31–40: doi:10.1016/j.revpalbo.2005.08.002.

Blaauw M and Christen J (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6: doi:10.1214/ba/1339616472.

Boulton GS (1978) Boulder shapes and grain-size distributions of debris as indicators of transport paths through a glacier and till genesis. *Sedimentology* 25(6): 773–779: doi:https://doi.org/10.1111/j.1365-3091.1978.tb00329.x.

Brochmann C, Gabrielsen TM, Nordal I, Landvik JY and Elven R (2003) Glacial survival or tabula rasa? The history of North Atlantic biota revisited. *TAXON* 52(3): 417–450: doi:10.2307/3647381.

Brooks GR (2020) Evidence of a strong paleoearthquake in ~9.1 ka cal BP interpreted from mass transport deposits, western Quebec – northeastern Ontario, Canada. *Quaternary Science Reviews* 234: 106250: doi:10.1016/j.quascirev.2020.106250.

Brouard E, Roy M, Godbout P-M and Veillette JJ (2021) A framework for the timing of the final meltwater outbursts from glacial Lake Agassiz-Ojibway. *Quaternary Science Reviews* 274: 107269: doi:10.1016/j.quascirev.2021.107269.

Bullock JM, Mallada González L, Tamme R, Götzenberger L, White SM, Pärtel M, et al. (2017) A synthesis of empirical plant dispersal kernels. *Journal of Ecology* 105(1): 6–19: doi:10.1111/1365-2745.12666.

Burns RM and Honkala BH (1990) *Silvics of North America*. Forest Service, Washington, DC: US Department of Agriculture. Available at: https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_1/silvics_vol1.pdf.

549 Cain ML, Milligan BG and Strand AE (2000) Long-distance seed dispersal in plant populations.
550 *American Journal of Botany* 87(9): 1217–1227: doi:10.2307/2656714.

551 Carcaillet C, Bergeron Y, Richard PJH, Fréchette B, Gauthier S and Prairie YT (2001) Change of
552 fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation
553 composition or climate trigger the fire regime? *Journal of Ecology* 89(6): 930–946:
554 doi:10.1111/j.1365-2745.2001.00614.x.

555 Carrivick JL and Tweed FS (2013) Proglacial lakes: character, behaviour and geological
556 importance. *Quaternary Science Reviews* 78: 34–52: doi:10.1016/j.quascirev.2013.07.028.

557 Clark JS (1998) Why trees migrate so fast: confronting theory with dispersal biology and the
558 paleorecord. *The American Naturalist* 152(2): 204–224: doi:10.1086/286162.

559 Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, et al. (1998) Reid's Paradox of
560 rapid plant migration. *BioScience* 48(1): 13–24: doi:10.2307/1313224.

561 Clark JS and Hussey TC (1996) Estimating the mass flux of charcoal from sedimentary records:
562 effects of particle size, morphology, and orientation. *The Holocene*. SAGE Publications Ltd 6(2):
563 129–144: doi:10.1177/095968369600600201.

564 Crofts AL and Brown CD (2020) The importance of biotic filtering on boreal conifer recruitment
565 at alpine treeline. *Ecography* 43(6): 914–929: doi:10.1111/ecog.04899.

566 Croudace IW and Rothwell RG (eds) (2015) *Micro-XRF studies of sediment cores: applications*
567 *of a non-destructive tool for the environmental sciences*. Dordrecht: Springer.

568 Dalton AS, Margold M, Stokes CR, Tarasov L, Dyke AS, Adams RS, et al. (2020) An updated
569 radiocarbon-based ice margin chronology for the last deglaciation of the North American Ice
570 Sheet Complex. *Quaternary Science Reviews* 234: 106223: doi:10.1016/j.quascirev.2020.106223.

571 Daubois V, Roy M, Veillette JJ and Ménard M (2015) The drainage of Lake Ojibway in
572 glaciolacustrine sediments of northern Ontario and Quebec, Canada: The drainage of Lake
573 Ojibway, Canada. *Boreas* 44(2): 305–318: doi:10.1111/bor.12101.

574 Davis MB, Schwartz MW and Woods K (1991) Detecting a species limit from pollen in
575 sediments. *Journal of Biogeography* 18(6): 653: doi:10.2307/2845547.

576 Davis MB, Woods KD, Webb SL and Futyma RP (1986) Dispersal versus climate: Expansion of
577 *Fagus* and *Tsuga* into the Upper Great Lakes region. *Vegetatio* 67(2): 93–103.

578 Dyke AS (2004) An outline of North American deglaciation with emphasis on central and
579 northern Canada. *Developments in Quaternary Sciences*. Elsevier, 373–424. Available at:
580 https://linkinghub.elsevier.com/retrieve/pii/S1571086604802094: doi:10.1016/S1571-
581 0866(04)80209-4.

582 Easterbrook DJ (1999) *Surface processes and landforms*. Prentice Hall, Upper Saddle River, NJ:
583 Pearson College Div.

El-Guellab A, Asselin H, Gauthier S, Bergeron Y and Ali AA (2015) Holocene variations of wildfire occurrence as a guide for sustainable management of the northeastern Canadian boreal forest. *Forest Ecosystems* 2(1): 15: doi:10.1186/s40663-015-0039-2.

Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76(6): 1899–1916: doi:10.2307/1940722.

Finney MA, McAllister SS, Forthofer JM and Grumstrup TP (2021) *Wildland fire behaviour: dynamics, principles and processes*. Csiro Publishing.

Foerster V, Junginger A, Langkamp O, Gebru T, Asrat A, Umer M, et al. (2012) Climatic change recorded in the sediments of the Chew Bahir basin, southern Ethiopia, during the last 45,000 years - ScienceDirect. *Quaternary International* 274: 25–37.

Glaser PH (1981) Transport and deposition of leaves and seeds on tundra: A late-glacial analog. *Arctic and Alpine Research* 13(2): 173–182: doi:10.2307/1551193.

Godbout P-M, Roy M and Veillette JJ (2020) A detailed lake-level reconstruction shows evidence for two abrupt lake drawdowns in the late-stage history of the eastern Lake Agassiz-Ojibway basin. *Quaternary Science Reviews* 238: 106327: doi:10.1016/j.quascirev.2020.106327.

Godbout P-M, Roy M, Veillette JJ and Schaefer JM (2017) Cosmogenic ^{10}Be dating of raised shorelines constrains the timing of lake levels in the eastern Lake Agassiz-Ojibway basin. *Quaternary Research* 88(2): 265–276: doi:10.1017/qua.2017.40.

Greene DF and Johnson EA (1996) Wind dispersal of seeds from a forest into a clearing. *Ecology* 77(2): 595–609: doi:10.2307/2265633.

Greene DF and Johnson EA (1997) Secondary dispersal of tree seeds on snow. *The Journal of Ecology* 85(3): 329–340: doi:10.2307/2960505.

Harris A, Ickert-Bond S and Rodríguez A (2018) Long distance dispersal in the assembly of floras: A review of progress and prospects in North America. *Journal of Systematics and Evolution* 56(5): 430–448: doi:10.1111/jse.12422.

Higgins SI, Nathan R and Cain ML (2003) Are long-distance events in plants usually caused by nonstandard means of dispersal? *Ecology* 84(8): 1945–1956: doi:10.1890/01-0616.

Higgins SI and Richardson DM (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *The American Naturalist* 153(5): 464–475: doi:10.1086/303193.

Higuera PE, Brubaker LB, Anderson PM, Brown TA, Kennedy AT and Hu FS (2008) Frequent fires in ancient shrub tundra: implications of paleorecords for Arctic environmental change. *PLoS ONE* 3(3): e0001744: doi:10.1371/journal.pone.0001744.

Joannin S, Capit A, Ollivier V, Bellier O, Brossier B, Mourier B, et al. (2022) First pollen record from the Late Holocene forest environment in the Lesser Caucasus. *Review of Palaeobotany and Palynology* 304: 104713: doi:10.1016/j.revpalbo.2022.104713.

Johnston WF (1990) *Larix laricina* (Du Roi) K. Koch – Tamarack. *Sylvics of North America*, 141–151.

Kaiser HF (1960) The application of electronic computers to factor analysis. *Educational and Psychological Measurement* 20(1): 141–151: doi:10.1177/001316446002000116.

Kassambara A (2017) *Practical guide to Principal Component Methods in R: PCA, M(CA), FAMD, MFA, HCPC, factoextra*. STHDA.

Lefebvre P, Sabatier P, Mangeret A, Gourgiotis A, Le Pape P, Develle A-L, et al. (2021) Climate-driven fluxes of organic-bound uranium to an alpine lake over the Holocene. *Science of The Total Environment* 783: 146878: doi:10.1016/j.scitotenv.2021.146878.

Lévesque PEM, Dinel H and Larouche A (1988) *Guide to the identification of plant macrofossils in Canadian peatlands*. Ottawa, Ont: Land Resource Research Centre, Research Branch, Agriculture Canada.

MERN - Système d'information géominière (2022) Zones morphosédimentologiques indicatives de la géologie du Quaternaire en Abitibi (Québec). Carte interactive. . Available at: https://sigeom.mines.gouv.qc.ca/signet/classes/I1108_afchCarteIntr?l=F&m=B&ll=48.48231,-78.77259&z=16&c=z_morph_qc%7C36&op=mspQc%7Call%7C.

Moreno A, Giralt S, Valero-Garcés B, Sáez A, Bao R, Prego R, et al. (2007) A 14kyr record of the tropical Andes: The Lago Chungará sequence (18°S, northern Chilean Altiplano). *Quaternary International* 161(1): 4–21: doi:10.1016/j.quaint.2006.10.020.

Mustaphi CJC and Pisaric MFJ (2014) A classification for macroscopic charcoal morphologies found in Holocene lacustrine sediments. *Progress in Physical Geography: Earth and Environment* 38(6): 734–754: doi:10.1177/0309133314548886.

Nathan R (2006) Long-distance dispersal of plants. *Science*. American Association for the Advancement of Science 313(5788): 786–788: doi:10.1126/science.1124975.

Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A and Tsoar A (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution* 23(11): 638–647: doi:10.1016/j.tree.2008.08.003.

Nogales M, Heleno R, Traveset A and Vargas P (2012) Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* 194(2): 313–317: doi:10.1111/j.1469-8137.2011.04051.x.

Normandeau A, Lajeunesse P and Philibert G (2013) Late-Quaternary morphostratigraphy of Lake St-Joseph (southeastern Canadian Shield): Evolution from a semi-enclosed glacimarine basin to a postglacial lake. *Sedimentary Geology* 295: 38–52: doi:10.1016/j.sedgeo.2013.07.005.

Nutz A, Lajeunesse P, Ghienne J-F, Schuster M, Brouard E, Dietrich P, et al. (2020) Deglacial to paraglacial history of the Lake Saint-Jean lowlands: A geomorphological perspective. In: Slaymaker O and Catto N (eds) *Landscapes and Landforms of Eastern Canada*. Cham: Springer

655 International Publishing, 145–158. Available at: https://doi.org/10.1007/978-3-030-35137-3_5:
656 doi:10.1007/978-3-030-35137-3_5.

657 Oris F, Ali AA, Asselin H, Paradis L, Bergeron Y and Finsinger W (2014a) Charcoal dispersion
658 and deposition in boreal lakes from 3 years of monitoring: Differences between local and
659 regional fires: Monitoring charcoal deposition in lakes. *Geophysical Research Letters* 41(19):
660 6743–6752: doi:10.1002/2014GL060984.

661 Oris F, Asselin H, Finsinger W, Hély C, Blarquez O, Ferland M-E, et al. (2014b) Long-term fire
662 history in northern Quebec: implications for the northern limit of commercial forests. *Journal of*
663 *Applied Ecology* 51(3): 675–683: doi:10.1111/1365-2664.12240.

664 Reimer PJ, Austin WEN, Bard E, Bayliss A, Blackwell PG, Bronk Ramsey C, et al. (2020) The
665 IntCal20 Northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon*
666 62(4): 725–757: doi:10.1017/RDC.2020.41.

667 Remy CC, Fouquemberg C, Asselin H, Andrieux B, Magnan G, Brossier B, et al. (2018)
668 Guidelines for the use and interpretation of palaeofire reconstructions based on various archives
669 and proxies. *Quaternary Science Reviews* 193: 312–322: doi:10.1016/j.quascirev.2018.06.010.

670 Richard P (1980) Histoire postglaciaire de la végétation au sud du lac Abitibi, Ontario et Québec.
671 *Géographie physique et Quaternaire* 34(1): 77–94: doi:10.7202/1000385ar.

672 Richard PJH, Fréchette B, Grondin P and Lavoie M (2020) Histoire postglaciaire de la végétation
673 de la forêt boréale du Québec et du Labrador. *Le Naturaliste canadien* 144(1): 63:
674 doi:10.7202/1070086ar.

675 Richard PJH and Larouche AC (1989) La végétation postglaciaire du Témiscamingue, Québec,
676 durant l'épisode glaciolacustre Barlow. *Canadian Journal of Botany* 67(2): 544–558:
677 doi:10.1139/b89-076.

678 Roy M, Veillette JJ, Daubois V and Ménard M (2015) Late-stage phases of glacial Lake Ojibway
679 in the central Abitibi region, eastern Canada. *Geomorphology* 248: 14–23:
680 doi:10.1016/j.geomorph.2015.07.026.

681 Rudolph TD and Laidly PR (1990) *Pinus banksiana* Lamb. jack pine. *Silvics of North America*.
682 U.S. Government Printing Office, 280–290.

683 Rumeu B, Afonso V, Fernández-Palacios JM and Nogales M (2014) Diversity, distribution and
684 conservation status of island conifers: a global review. *Diversity and Distributions* 20(3): 272–
685 283: doi:10.1111/ddi.12163.

686 Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A and Nathan R (2009) Long-distance
687 seed dispersal. *Fruit Development and Seed Dispersal*, 204–237.

688 Snell RS and Cowling SA (2015) Consideration of dispersal processes and northern refugia can
689 improve our understanding of past plant migration rates in North America. *Journal of*
690 *Biogeography* 42(9): 1677–1688: doi:10.1111/jbi.12544.

691 Sulphur KC, Goldsmith SA, Galloway JM, Macumber A, Griffith F, Swindles GT, et al. (2016)
692 Holocene fire regimes and treeline migration rates in sub-arctic Canada. *Global and Planetary*
693 *Change* 145: 42–56: doi:10.1016/j.gloplacha.2016.08.003.

694 Varga Z (2010) Extra-Mediterranean refugia,post-glacial vegetation history and area dynamics in
695 Eastern Central Europe. In: Habel JC and Assmann T (eds) *Relict Species*. Berlin, Heidelberg:
696 Springer Berlin Heidelberg, 57–87. Available at: http://link.springer.com/10.1007/978-3-540-
697 92160-8_3: doi:10.1007/978-3-540-92160-8_3.

698 Veillette JJ (1994) Evolution and paleohydrology of glacial lakes Barlow and Ojibway.
699 *Quaternary Science Reviews* 13: 945–971.

700 Vincent J-S and Hardy L (1977) L'évolution et l'extension des lacs glaciaires Barlow et Ojibway
701 en territoire québécois. *Géographie physique et Quaternaire* 31(3–4): 357:
702 doi:10.7202/1000283ar.

703 Whitlock C and Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM,
704 Bradley RS and Alverson K (eds) *Tracking Environmental Change Using Lake Sediments*.
705 Dordrecht: Kluwer Academic Publishers, 75–97. Available at:
706 http://link.springer.com/10.1007/0-306-47668-1_5: doi:10.1007/0-306-47668-1_5.

707 Wilkinson DM (1997) Plant colonization: are wind dispersed seeds really dispersed by birds at
708 larger spatial and temporal scales? *Journal of Biogeography* 24(1): 61–65: doi:10.1111/j.1365-
709 2699.1997.tb00050.x.

710