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

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4

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24

25 **A Abstract**

26 At the end of the last glacial period in the northern hemisphere, meltwater from receding ice sheets  
27 accumulated into large proglacial lakes, potentially limiting postglacial afforestation. We explored  
28 whether former islands of proglacial Lake Ojibway (Canada) (hilltops in the current landscape) could have  
29 acted as migration outposts and thus accelerated the postglacial migration. We extracted sediments  
30 from two small lakes located on “paleo-islands” and used XRF to detect changes in soil erosion and  
31 vegetation biomass. We also used plant macro-remains and wood charcoal to determine if (and which)  
32 tree species colonized the sites and to detect local fire events. Organic sediment accumulation started  
33 around 9657 and 9,947 cal. yr BP at Lakes Perché and Despériers, respectively, before the level of Lake  
34 Ojibway started to decrease and liberate parts of the studied landscape ca 9,400 cal. yr BP. Lithogenic  
35 elements (Ti, K, Sr, Fe, Zr and Rb) decreased between the beginning of organic sediment accumulation  
36 and 8,800-8,700 cal. yr BP, indicating reduced soil erosion, possibly due to soil stabilization by  
37 vegetation. Then, the S/Ti ratio, a proxy of organic matter accumulation increased around 8,800 and  
38 8,400 cal. yr BP. The earliest tree macro-remains (needles of *Larix laricina*, *Picea* spp., and *Pinus* spp., and  
39 seeds of *Betula* spp.) were found between 9,850 and 9,300 cal. yr BP. Local fires were detected around  
40 9,820, 9,360 and 8,362 cal. yr BP. Early afforestation occurred on the islands of Lake Ojibway, 200 and  
41 450 years before its level started to decrease , confirming the hypothesis that some islands acted as  
42 migratory outposts accelerating postglacial migration.

43

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

## 46 **A Introduction**

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

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

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

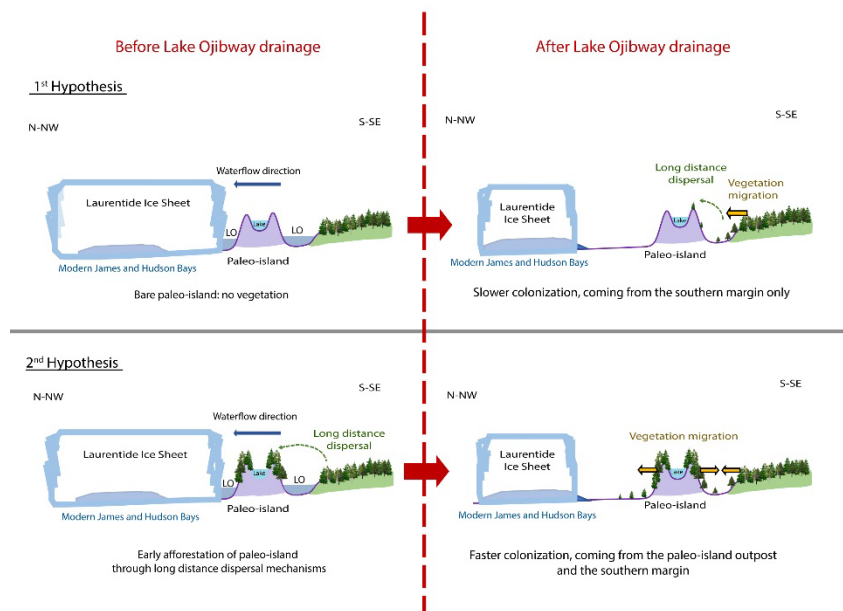
71 The observed postglacial migration of several tree species in western Quebec was faster than the  
72 estimated migration time based on the mean distance dispersal capacities observed nowadays, a  
73 phenomenon called Reid's paradox of rapid plant migration (Clark, 1998). Indeed, several vegetation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

80 During its >2,300 years presence over western Quebec and north-eastern Ontario, Lake Ojibway should  
81 have acted as a barrier slowing down postglacial forest migration, unless its islands were colonized early  
82 and acted as outposts facilitating colonization of lowlands following the drainage of Lake Ojibway into  
83 James Bay. For the islands of Lake Ojibway to be colonized, long-distance dispersal events from the  
84 vegetation front south of the lake were necessary. According to Schurr et al. (2009), long-distance seed  
85 dispersal via abiotic or biotic action happens when  $\leq 1\%$  of seeds travel >1km. Although such events are  
86 rare, they can strongly affect plant biogeography and population dynamics (Cain et al., 2000).

87 If the "paleo-islands" on Lake Ojibway had remained uncolonized, while Lake Ojibway was present, ie., if  
88 no long-distance dispersal events succeeded, colonization following the drainage of the proglacial lake  
89 would have followed a south-north trajectory limited by average seed dispersal distance, as most tree  
90 species in north-eastern Canada are wind-dispersed (Burns and Honkala, 1990) (Fig. 1 – first hypothesis).

91 This scenario does not explain how sites located several hundreds of kilometers north of the migration  
92 front could have been afforested almost immediately after the drainage of Lake Ojibway (Ali et al.,

93 2009). An alternative hypothesis would be that some islands on Lake Ojibway were colonized through  
 94 long-distance seed dispersal before the final drainage of the proglacial lake into James Bay, which would  
 95 explain how sites far from the postglacial migration front could have been afforested quickly, then our  
 96 study would enlighten an early colonization of paleo-islands, ie., while the Lake Ojibway still covered  
 97 Quebec (Fig. 1 – second hypothesis, Fig. 2).



98  
 99 Figure 1: Schematic representation of proglacial Lake Ojibway (LO) creation and hypotheses concerning  
 100 the colonization of paleo-islands before the drainage of Lake Ojibway and implications on postglacial  
 101 migration thereafter.

102  
 103 To test the hypothesis of early afforestation of paleo-islands through long-distance dispersal events  
 104 (second hypothesis), we sampled sediments from two small lakes located on paleo-islands (current  
 105 hilltops above the maximum shoreline level of Lake Ojibway) (Godbout et al., 2017), and we  
 106 radiocarbon-dated bulk sediment and macro-remains to build age-depth models. We used multiple  
 107 proxies to infer afforestation: X-ray fluorescence (XRF) geochemical analysis to detect variations in soil  
 108 erosion as a proxy for plant cover; plant macro-remain analysis to attest local vegetation presence; and  
 109 charcoal analysis to reconstruct local wildfire activity as an indicator of biomass burning. Only a few

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

115

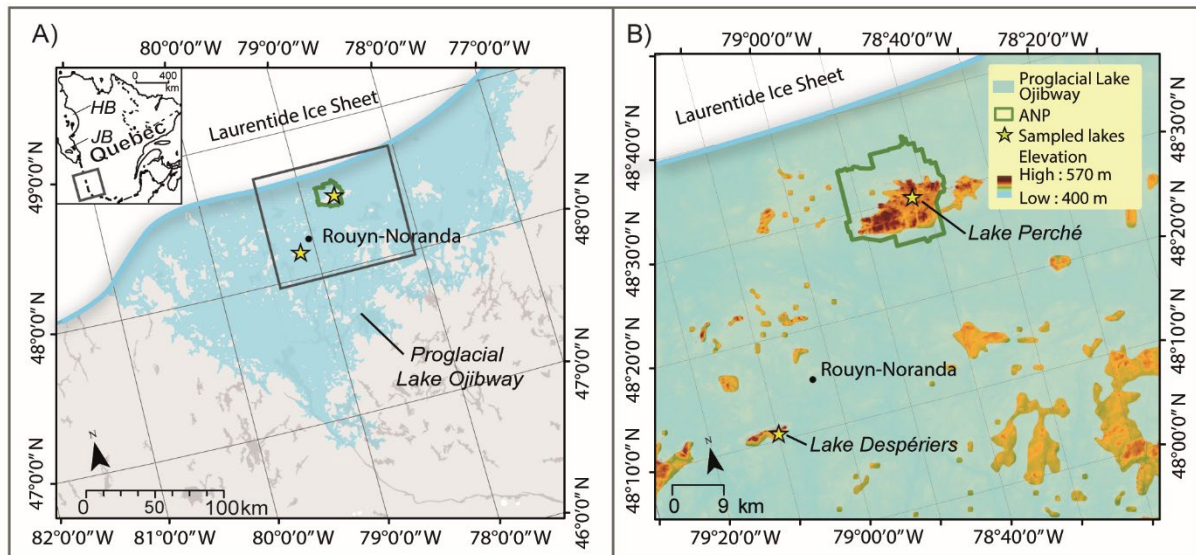
## 116 **A Material and methods**

### 117 ***B Study area***

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

128 Ancient shorelines of proglacial Lake Ojibway are still visible on hillsides in the current landscape and  
129 allowed reconstructions of lake level history (Godbout et al., 2017, 2020) and the identification of several  
130 paleo-islands that became hills following the final drainage of Lake Ojibway ca 8,200 cal. yr BP (Richard,  
131 1980; Richard et al., 2020; Veillette, 1994). Lake Ojibway's highest shorelines (ca 9,400 cal. yr BP) are  
132 estimated to be slightly below 400 m a.s.l. and 380 m a.s.l. for the Abijévis and Kekeko hills, respectively

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



135  
136 Figure 2: (a) Extent of proglacial Lake Ojibway in western Quebec around 9,600 cal. yr BP (Brooks, 2020),  
137 showing the locations of the two studied paleo-islands (yellow stars) according to the lake level at the  
138 time. The location of Aiguebelle National Park (ANP) is also shown. The inset shows the location of ANP  
139 relative to Hudson Bay (HB) and James Bay (JB), where proglacial Lake Ojibway finally drained around  
140 8,200 cal. yr BP. (b) Close-up of the study area showing paleo-islands (in light to dark orange), including  
141 the Abijévis and Kekeko Hills, where Lakes Perché and Despériers were sampled, respectively.

142

### 143 **B Site selection and lake sediment sampling**

144 We selected two small headwater lakes surrounded by steep shores to maximize sediment collection:

145 Lake Perché (formerly known as Lake Edrien) in the Aiguebelle National Park (Abijévis hills) and Lake

146 Despériers on the Kekeko hills (Table I; Fig. 2). Lake Perché is located at 380 m a.s.l. While this is slightly

147 below the highest shoreline of Lake Ojibway in the area (400 m a.s.l.), Lake Perché was formed before

148 the complete drainage of proglacial Lake Ojibway and could have recorded part of the paleo-island's

149 history. Lake Despériers is located at 407 m a.s.l., ie. almost 30 m above the highest shoreline of Lake

150 Ojibway in the area (Table I). Current forest vegetation around the sampled lakes is dominated by black

151 spruce (*Picea mariana* [Mill.] BSP), white spruce (*Picea glauca* [Moench] Voss), jack pine (*Pinus*



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

154

155 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	<i>Picea mariana</i> , <i>Pinus banksiana</i>
Lake Despériers	48°11'4.22"N	79° 9'38.80"W	407	8.89	292	750	<i>Picea mariana</i> , <i>Picea glauca</i> , <i>Abies balsamea</i>

156

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

162

### 163 ***B Age-depth models***

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

169 three levels from each core to complete the age-depth models (Table II). We calibrated the <sup>14</sup>C dates  
170 with the IntCal20 calibration curves (Reimer et al., 2020).

171

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

Lake	Sample depth (cm)	<sup>14</sup> 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 <sup>a</sup>	BETA-644328
Perché	555 - 555.5	7680 ± 40	8466 ± 30	Plant macro-remains <sup>b</sup>	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 <sup>c</sup>	BETA-638098
Despériers	289 - 289.5	8775 ± 20	9774 ± 40	Bulk sediment	ULA-10173

174 <sup>a</sup> bark fragment and other unidentified vegetal fragments; <sup>b</sup> bark fragment, *Cristatella mucedo* statoblast  
175 and other unidentified vegetal fragments; <sup>c</sup> *Larix laricina* needle fragment and unidentified seed and  
176 vegetal fragments.

177

## 178 **B Geochemical analyses**

179 We performed XRF analyses on the basal sediments corresponding to the first millennium of the paleo-  
180 islands' existence. To detect semi-quantitative variations of geochemical composition, we used the  
181 TestAllGeo analysis mode on the Niton XL3t 900SHE portable scanner and continuously scanned the  
182 sediments every 0.5 cm along the cores. Changes in the concentration of several major and minor  
183 elements can be used as proxies of ecological phenomena (Croudace and Rothwell, 2015). We used K, Ti,  
184 Rb, Sr, Zr and Fe (lithogenic elements) as indicators of erosion from the watershed to the lakes, which we  
185 expected to decrease following afforestation of the paleo-islands. In addition to being an erosion  
186 indicator, low levels of K indicate extensive vegetation presence (Foerster et al., 2012). While S and Ca  
187 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 ( $\text{Na}_6\text{P}_6\text{O}_{18}$ ) solution for  
200 at least 12 hours under agitation, for deflocculation purposes. We then filtered each sample through a  
201 250- $\mu\text{m}$  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<sup>3</sup> 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 ( $\text{Na}_6\text{P}_6\text{O}_{18}$ ), and sodium hypochlorite ( $\text{NaClO}$ ) 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- $\mu\text{m}$  mesh to extract macro-charcoal particles and

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

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

229

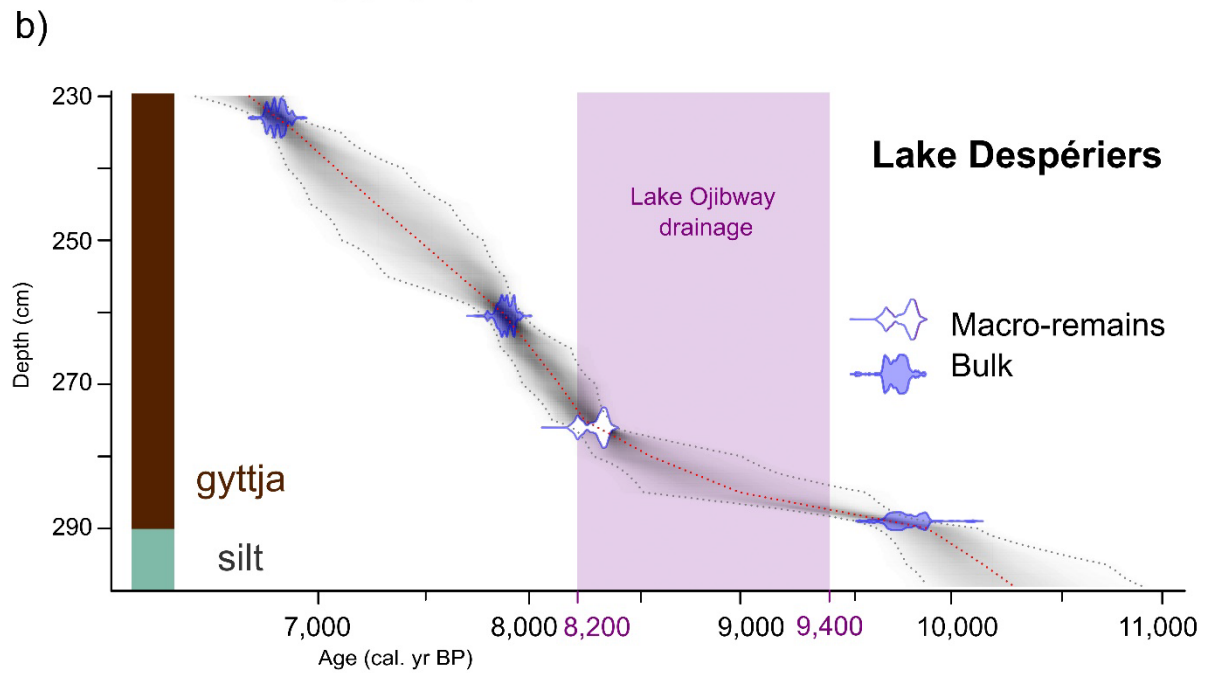
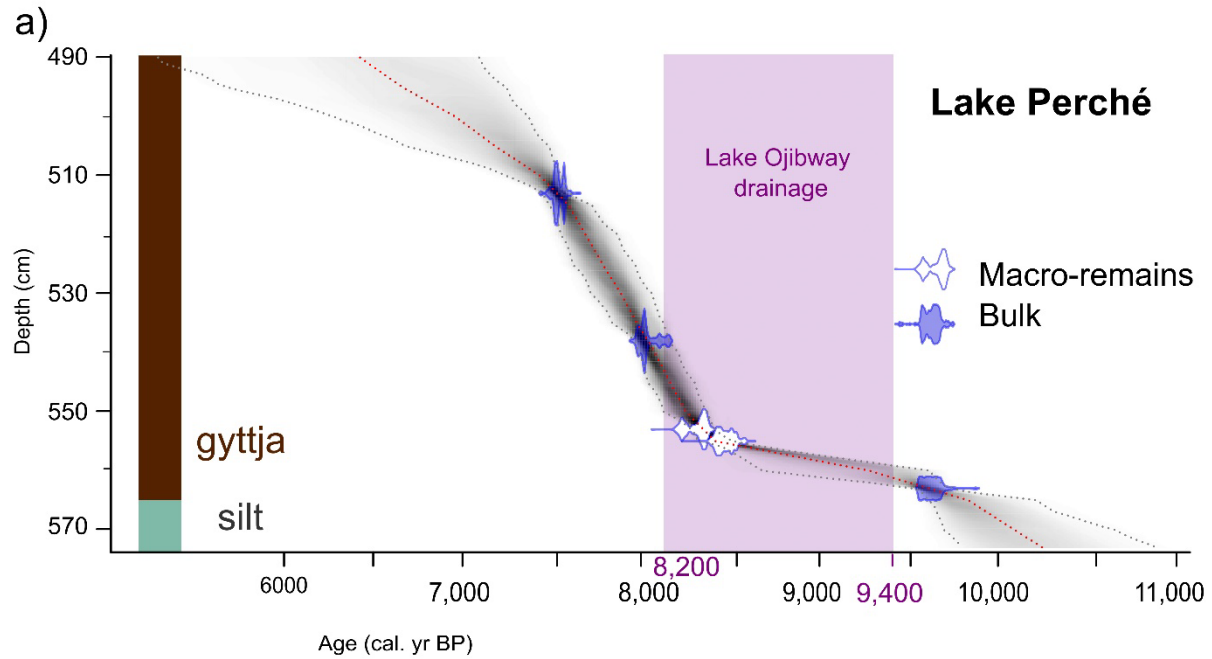
## 230 **A Results**

### 231 ***B Organic sediment accumulation during Lake Ojibway presence***

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

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

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



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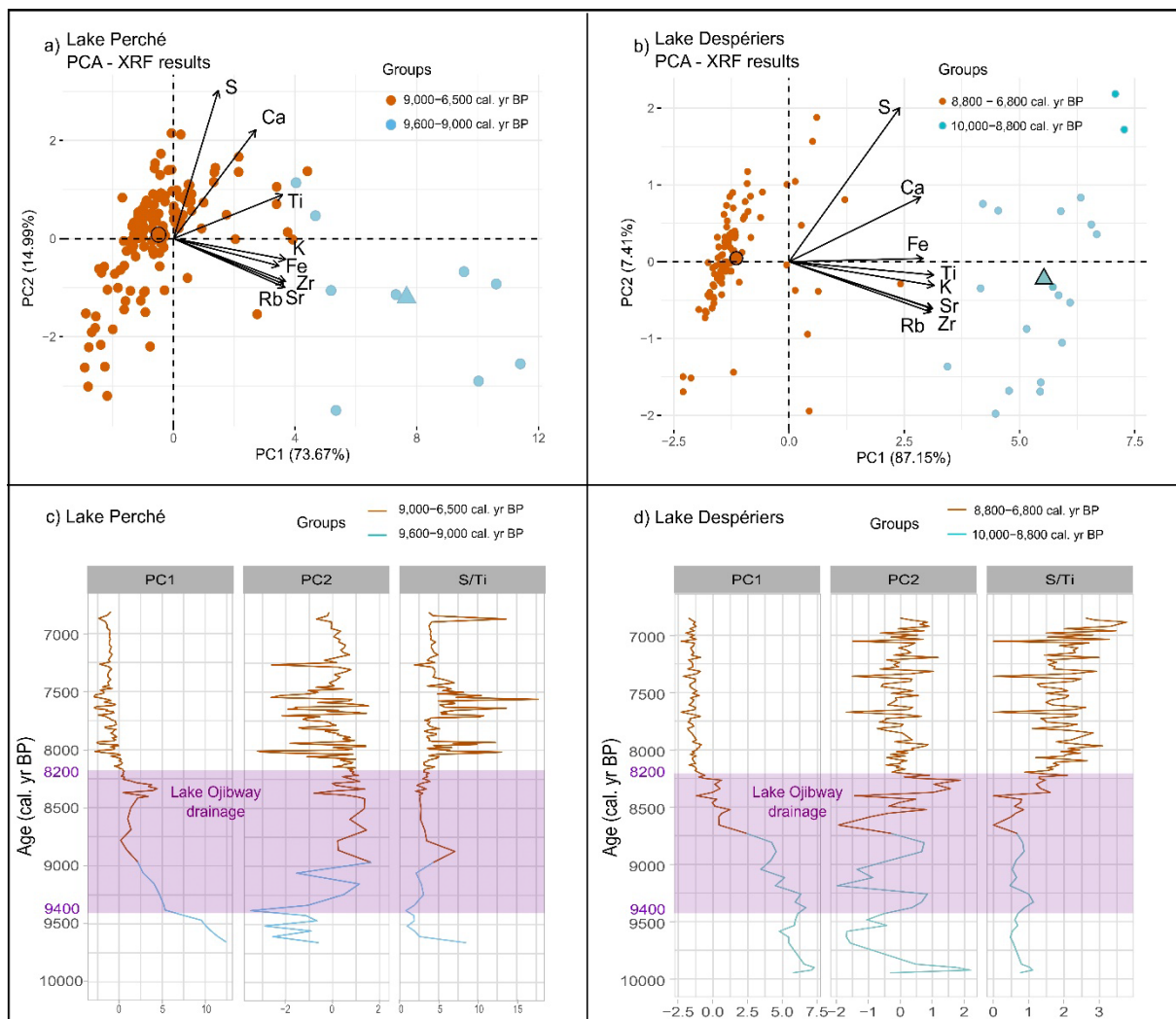
250 Figure 3: Calibrated age-depth models based on the radiocarbon dates (Table II) obtained from basal  
 251 sediments (brown = organic sediments and olive-grey = mineralogic sediments) at a) Lake Perché and b)  
 252 Lake Despériers. The purple rectangle illustrates the period when the level of proglacial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

254

255

256 **B Geochemical signature of the organic sediments**

257 Two groups were detected by the PCA analysis in the gyttja of Lake Perché: (1) from the silt-gyttja  
258 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  
259 first two principal components explained 88.66% of the variability in the dataset (PC1 = 73.67% and PC2  
260 = 14.99%). PC1 was positively associated to lithogenic elements (K, Ti, Fe, Rb, Zr, Sr) coming from the  
261 steep shores surrounding the lake, while PC2 was positively correlated to S. One element (Ca) was  
262 positively related to both PCs (Fig. 4a).



263  
264 Figure 4: Principal component analysis (PCA) of sediment samples (dots), associated centroids for each  
265 cluster (larger dots and triangles), and XRF results (arrows) for a) Lake Perché and b) Lake Despériers. At  
266 both sites the sediment samples pre- and post-dating afforestation are clearly separated along PC1.

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

271  
272 The PCA also differentiated two groups in the gyttja of Lake Despériers: (1) from the silt-gyttja transition  
273 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  
274 principal components explained 94.56% of the variability (PC1 = 87.15% and PC2 = 7.41%). As was the  
275 case for Lake Perché, the lithogenic sediments were positively correlated to PC1 at Lake Despériers, S  
276 was positively associated to PC2, and Ca was positively related to both PCs.

277 For Lake Perché, PC1 values (associated with lithogenic elements) quickly decreased until 8,800 cal. yr  
278 BP, and then increased until 8,300 cal. yr BP. After 8,250 cal. yr BP, values slowly decreased and reached  
279 their minimum until the end of the record, ie. 6,500 cal. yr BP. PC2 values (associated with S) increased  
280 between 9,350 and 9,000 cal. yr BP (Fig. 4a, c) and then remained relatively stable (despite short-term  
281 variations) between 9,000 and 7,900 cal. yr BP (Fig. 4c). The S/Ti ratio slowly increased with peaks  
282 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  
283 6,900 cal. yr BP (Fig. 4c). The absence of a distinguishable pattern at 8,200 cal. yr BP indicates that the  
284 environment remained stable during the drainage of proglacial Lake Ojibway.

285 For Lake Despériers, PC1 values (associated with lithogenic elements) gradually decreased from the  
286 beginning of gyttja accumulation around 10,000 cal. yr BP until 8,700 cal. yr BP, then they strongly  
287 decreased around 8700 cal. yr BP to reach minimum values after 8,200 cal. yr BP. (Fig. 4b, d). PC2 did not  
288 respect the Kaiser criterion (eigenvalue = 0.59) and therefore could not be interpreted (Supplemental  
289 Table 1). The S/Ti ratio remained stable during the early Holocene at Lake Despériers, with peaks at ca  
290 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

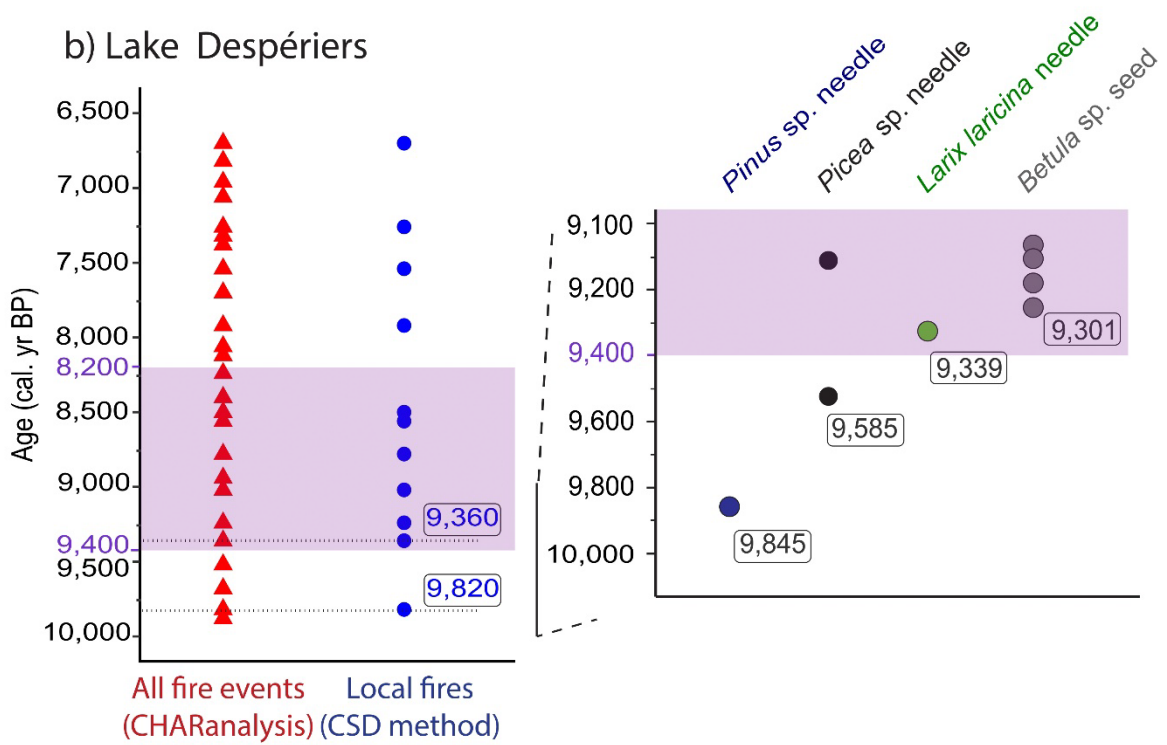
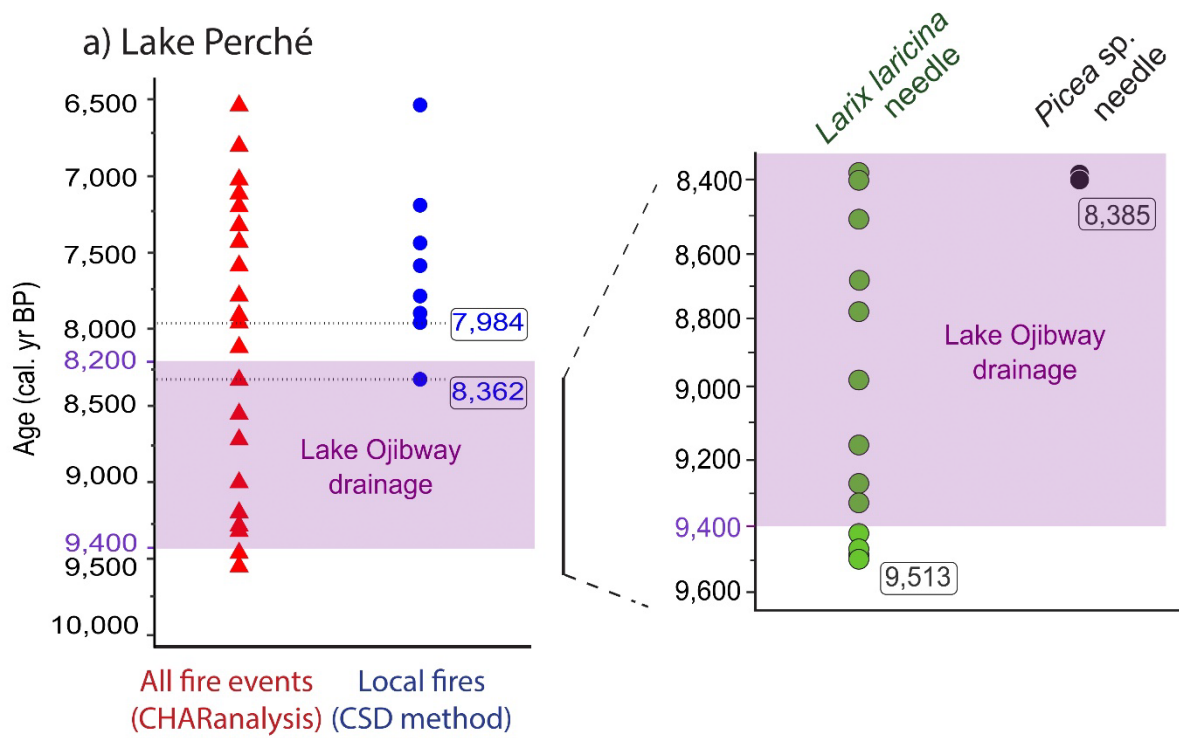


291 7,900 cal. yr BP. Around 7,700 cal. yr BP, the S/Ti ratio decreased and remained stable until 7,000 cal. yr  
292 BP, then it increased until 6,500 cal. yr BP (Fig. 4d).

293

294 ***B Plant macro-remains: early presence of local trees***

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



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

310

### 311 ***B Evidence of local forest fires on a paleo-island***

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

321

### 322 **A Discussion**

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

328

329 ***B Early afforestation of islands on proglacial Lake Ojibway***

330 Gyttja started to accumulate at the bottom of small lakes on paleo-islands while Lake Ojibway was still at  
331 its maximum level , ie., about 250-550 years before it started to gradually decrease. The presence of silt  
332 rather than clay beneath the gyttja at both sites is evidence that they were never flooded by proglacial  
333 Lake Ojibway. Radiocarbon dates obtained from plant macro-remains testify that shrubs and trees were  
334 present on the paleo-islands at least 140-260 years before the final drainage of proglacial Lake Ojibway  
335 (Table II). According to the age-depth models, the oldest tree macro-remains we found were (indirectly)  
336 dated to ca 9,600 cal. yr BP and 9,850 cal. yr BP at Lakes Perché and Despériers, respectively, 200 and  
337 450 years before the level of Lake Ojibway first started to decrease (Brouard et al., 2021; Godbout et al.,  
338 2020). Hence, while deglaciation time has been estimated at 10,570 cal. yr BP in the study area (Daubois  
339 et al., 2015; Godbout et al., 2020; Roy et al., 2015), our results indicate that the afforestation process  
340 needed about 1,000 years to unfold after the glacier retreat. This is much longer than what has been  
341 documented at recently deglaciated sites in Alaska, where primary succession took less than 200 years to  
342 complete (Fastie, 1995). The difference would likely be due to the distance to seed sources having been  
343 much greater at our sites (80 km over mostly water) compared to those in Alaska (<30 km over ground).  
344 Furthermore, cold temperatures during the early Holocene (Viau et al., 2006) likely implied lower  
345 vegetation productivity, as evidenced in our age-depth models by lower sediment accumulation rates  
346 compared to the middle Holocene.

347 Geochemical analyses showed that lithogenic elements - therefore erosion (Joannin et al., 2022;  
348 Lefebvre et al., 2021) - decreased rapidly at both sites from the beginning of gyttja accumulation until  
349 8,800 cal. yr BP (Lake Perché) and 8,700 cal. yr BP (Lake Despériers). As soil cohesion and stabilization are  
350 supported by plant root systems (Easterbrook, 1999), it is reasonable to assume that decreasing erosion  
351 is an indirect indicator of vegetation colonization on paleo-islands. Indeed, more individual plants  
352 produce more roots which stabilize the ground, meaning that less soil erosion is recorded in the lake

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

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

371 The fact that a local fire was dated at 8,362 cal. yr BP at lake Perché (burned unidentified needle) is yet  
372 another confirmation of early afforestation of the paleo-island, as fire ignition and propagation are fuel-  
373 dependent (ie., biomass-dependent) (Finney et al., 2021). At Lake Despériers, the earliest local fire  
374 around 9,820 cal. yr BP (burned unidentified needle fragment, Fig. S.3.3) confirmed biomass presence  
375 and afforestation on the paleo-island (Finney et al., 2021) before the drainage of proglacial Lake Ojibway  
376 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<sup>-1</sup> (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

425 paleo-islands implies that they could have acted as migration outpost following the drainage of  
426 proglacial Lake Ojibway, hence accelerating colonization of the lowlands. The total area covered by  
427 paleo-islands represented ca 3,600 km<sup>2</sup>, ie., about 10% of the area covered by proglacial Lake Ojibway at  
428 its maximal extent (Fig. 2a). This means that several possible outposts were available for early  
429 afforestation, from near the colonization front in the south, up to the ice sheet margin in the north (Fig.  
430 2b). The contribution of paleo-islands as migration outposts is the most likely mechanism that could  
431 explain Reid's paradox of rapid plant migration in western Quebec (Clark et al., 1998).

432

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443

### 444 **A Conflict of interest**

445 The authors declare no conflict of interest.

446



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450

451 **A Data availability statement**

452 Data used for this article are available online:

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

454

455 **A Supplementary Material**

456

457

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

	PC1 eigenvalue	PC2 eigenvalue
Lake Perché	<b>5.65</b>	<b>1.38</b>
Lake Despériers	<b>6.97</b>	0.59

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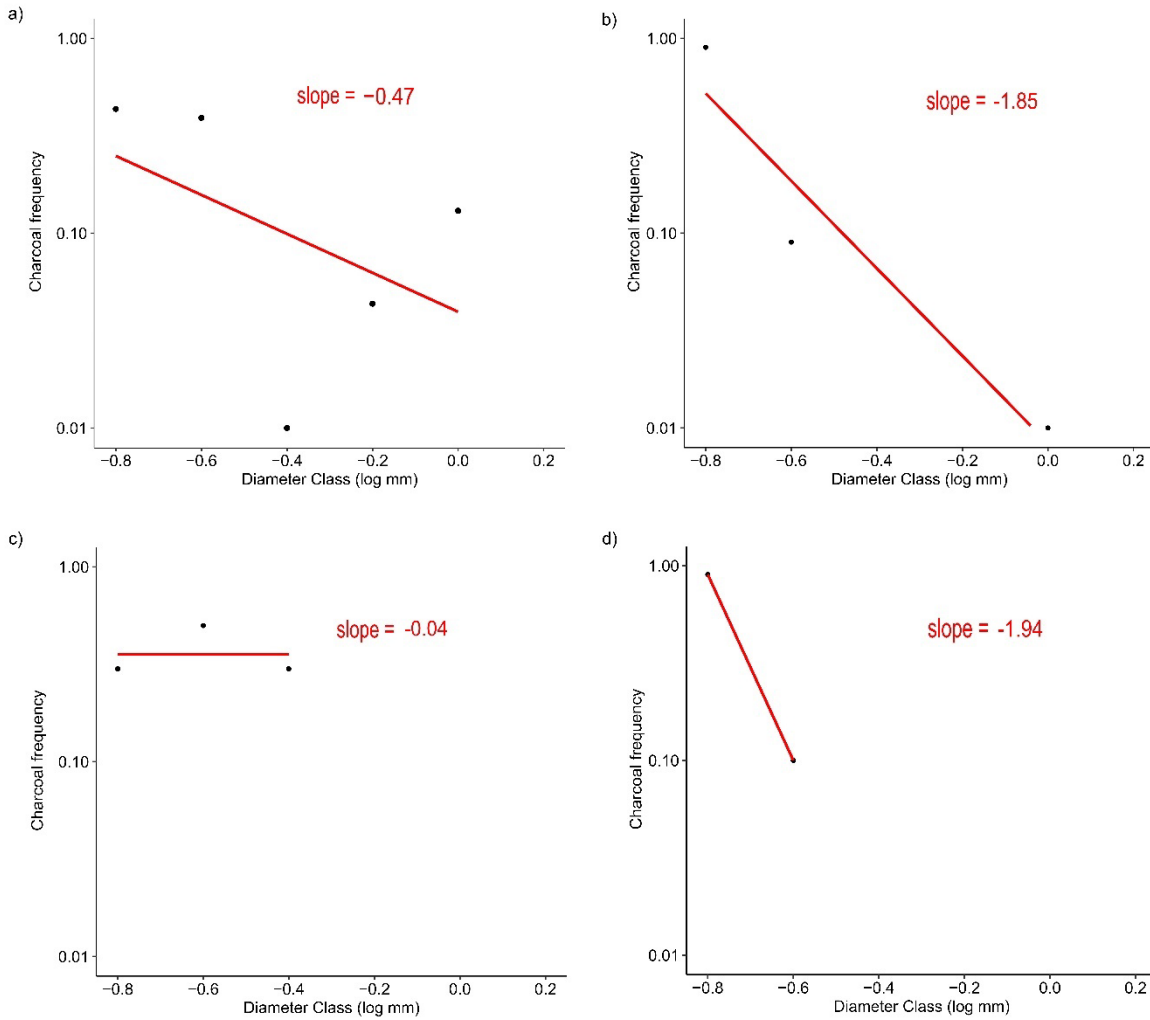
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486 Supplemental figures

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

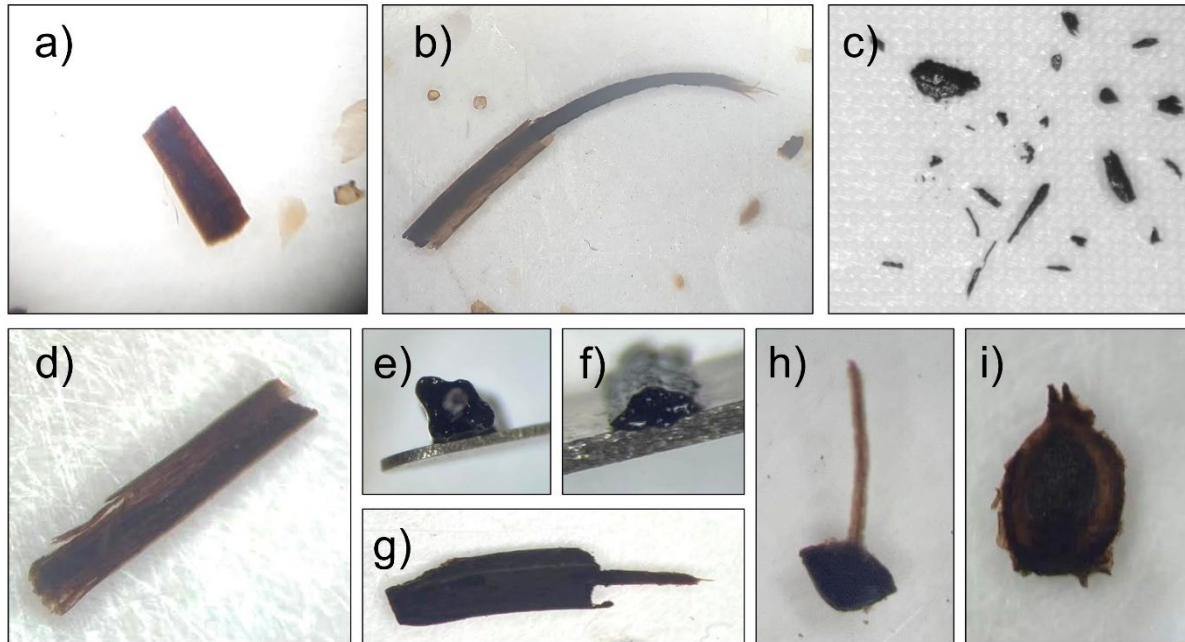
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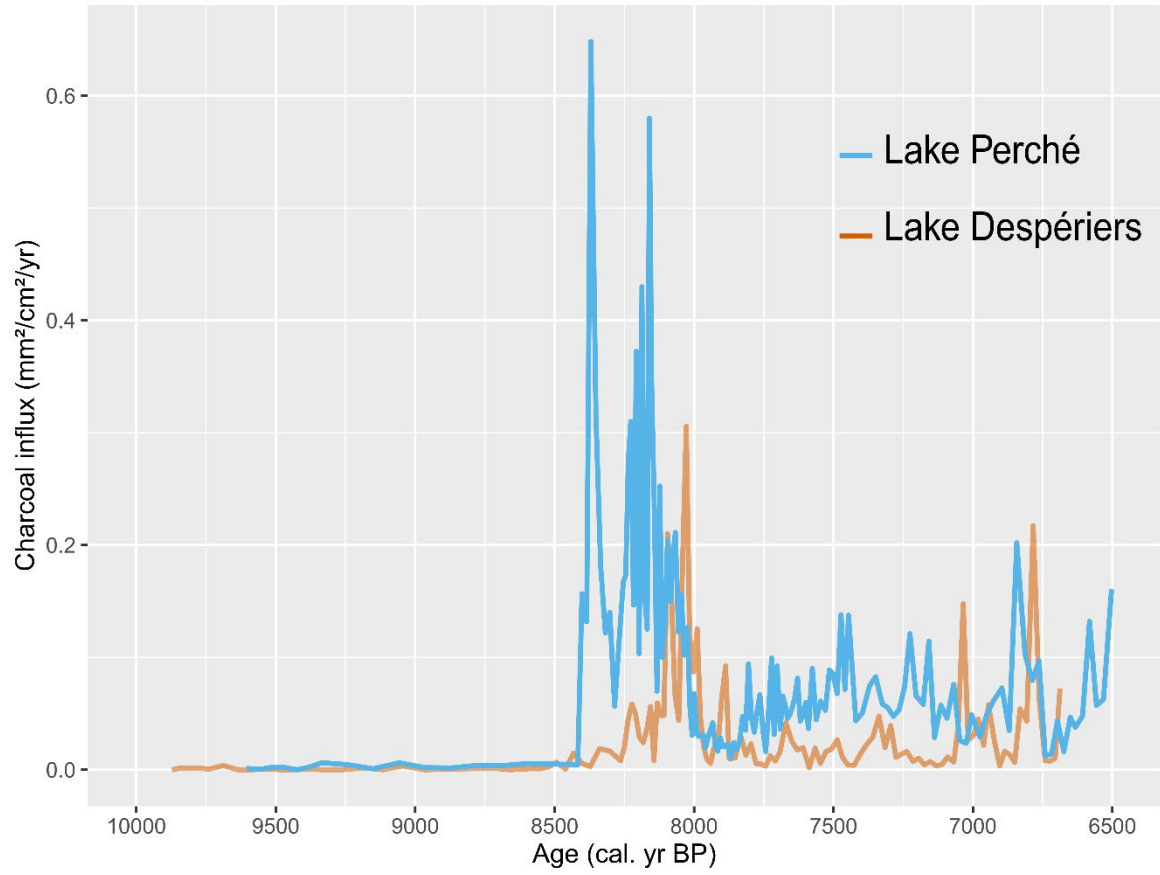
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Supplemental Figure 2: Nine of the oldest macro-remains found in the basal sediments of Lake Perché: (a-  
 b) *Larix laricina* needles, c) Possible *Picea* sp. needle (charcoal particles); and Lake Despériers: d) *Pinus* sp.  
 needle, (e-f) *Picea*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



511

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

513

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