

1       **Are marginal balsam fir and eastern white cedar stands relics from once more**  
2                   **extensive populations in north-eastern North America?**

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24 **Abstract**

25 Marginal stands of balsam fir (*Abies balsamea* [L.] Mill.) and eastern white cedar (*Thuja*  
26 *occidentalis* L.) are found north of their limits of continuous distribution in eastern North  
27 America. Regional-scale palaeocological studies have suggested that fir and cedar  
28 populations could have had larger extents in the past. This study aimed at verifying this  
29 hypothesis at the local scale. Wood charcoal fragments were collected from the soils of  
30 two marginal fir and cedar stands as well as from 15 sites in the surrounding forest matrix  
31 where the species are absent currently. Anatomical identification and radiocarbon-dating  
32 showed that fir was more extensive in the study area until about 680 cal BP, representing  
33 up to 31% of the charcoal assemblages at sites where it is currently absent. The evidence  
34 is less conclusive for cedar, however, although some of the charcoal fragments from the  
35 matrix sites could have been either fir or cedar (undistinguishable). Most of the dated  
36 fir/cedar charcoal in the matrix were from the Medieval Warm Period (ca. 1000 cal BP),  
37 suggesting contraction may have occurred at that time. Marginal fir – and possibly cedar  
38 – stands are thus relics of once more extensive populations. Fire is likely the main factor  
39 having contributed to the contraction of the species' distributions. Fir and cedar are now  
40 relegated to areas where fires are less frequent and severe, such as the shores of lakes and  
41 rivers.

42  
43 **Keywords:** boreal forest; wildfire; charcoal; *Abies balsamea*; *Thuja occidentalis*;  
44 outposts

45 **Introduction**

46 In the face of climate change, tree species will either respond by adaptation, migration, or  
47 local extinction (Walther 2002; Aitken et al., 2008; Corlett and Westcott 2013). Climate  
48 models predict that the speed of climate change will require faster migration rates than  
49 those observed during the postglacial period (Malcolm et al. 2002; Corlett and Westcott  
50 2013). Some species, including anemochores (Nathan et al. 2011), will not be able to  
51 keep pace with these changes (Dyer 1995; Clark 1998; Malcolm et al. 2002; Corlett and  
52 Westcott 2013). In such a context, marginal populations could play a key role in  
53 adaptation and migration by acting as dispersal outposts (Lesica and Allendorf 1995;  
54 Thomas et al. 2004; Hampe and Petit 2005).

55 Marginal populations are located beyond a species' limit of continuous distribution. Some  
56 of their characteristics might limit their capacity to act as dispersal outposts. First,  
57 according to the central-marginal hypothesis, marginal populations often have lower  
58 genetic diversity than central populations (Eckert et al. 2008; Pandey and Rajora 2012),  
59 although not always (Gamache et al. 2003; Xu et al. 2012). Second, competition by other  
60 species more adapted to local conditions could constrain the ability of marginal  
61 populations to expand in response to climate change (Case and Taper 2000; Messaoud et  
62 al. 2014). Third, the small size of marginal populations makes them vulnerable to  
63 disturbance, and hence local extinction (Alleaume-Benharira et al. 2006; Kawecki 2008).  
64 To predict how marginal populations will respond to future climate change, it is necessary  
65 to understand how they have responded in the past (Hampe and Petit 2005; Pardi and  
66 Smith 2012).

67 In eastern Canada, the distributions of balsam fir (*Abies balsamea* [L.] Mill.) and eastern  
68 white cedar (*Thuja occidentalis* L.) follow a latitudinal gradient. These species maintain  
69 marginal populations more than 100 km north of their continuous distribution limit,  
70 particularly in areas characterized by low fire incidence, such as the shores of lakes and  
71 rivers (Sirois 1997; Paul et al. 2014). Fir and cedar are late-successional species, poorly  
72 adapted to fire (Frank 1990; Johnston 1990), and wildfires become larger and more  
73 severe from south to north (Bergeron et al. 2004).

74 Palaeoecological studies conducted at large spatial scales have suggested that marginal fir  
75 and cedar stands are relics of formerly more extensive populations (Liu 1990; Richard  
76 1993; Ali et al. 2008; Lucas 2017). Larger and more severe fires during the Neoglacial  
77 period (after ca. 3000 cal BP; Ali et al. 2012; Remy et al. 2017) are being pointed to as  
78 the possible mechanism to explain fir and cedar contraction. While these studies provide  
79 regional information, the holocene dynamics of fir and cedar populations remain to be  
80 explored at the local scale.

81 Given that forest dynamics are not only influenced by the regional climate, but also by  
82 local factors (Cyr et al. 2007; Ali et al. 2009; Senici et al. 2015), regional-scale proxies  
83 (e.g., pollen) can mask the dynamics occurring at the local scale (Davis 2000). For  
84 example, wildfires produce heterogeneous patterns related to variations in local  
85 conditions (Turner and Romme 1994; Kafka et al. 2001; Mansuy et al. 2014).  
86 Consequently, nearby sites are not necessarily subject to the same fire regime and may  
87 have different dynamics (Clarke 2002; Barrett et al. 2013; Ouarmim et al. 2014; El-  
88 Guellab et al. 2015). It is therefore relevant to document past forest dynamics at small  
89 spatial scales, notably to provide a framework for ecosystem-based forest management  
90 (Bergeron et al. 1998; Lindenmayer et al. 2006; Lindbladh et al. 2013).

91 Wood charcoal resulting from forest fires resist degradation and can be preserved in  
92 forest soils for millennia (de Lafontaine and Asselin 2011). Their anatomical  
93 identification to the genus or species level provides information on the composition of  
94 burned stands (Thinon 1992; Scott and Damblon 2010). Hence, soil charcoal are a robust  
95 proxy that can be used to reconstruct the long-term history of vegetation and fire at a fine  
96 spatial scale (Thinon 1992; Figueiral and Mosbrugger 2000; Asselin and Payette 2005;  
97 Talon et al. 2005; Nelle et al. 2013; Payette et al. 2017).

98 This study used charcoal analysis to verify, at the local level, whether marginal fir and  
99 cedar stands in the northern boreal forest of eastern Canada are relics of formerly more  
100 extensive populations. More specifically, it aimed to determine if – and when – fir and  
101 cedar were present at sites where they are currently absent. The potential causes of  
102 fluctuations in fir and cedar abundance in the northern part of their ranges are also  
103 discussed.

104

## 105 **Material and methods**

### 106 *Study area*

107 The study area is located in the black spruce – feather moss bioclimatic domain of  
108 western Quebec (between 49°15'N and 49°55'N and between 78°30'W and 79°15'W). It  
109 is a low-lying area consisting mainly of clay deposits from proglacial lake Ojibway  
110 (Veillette, 1995), and organic deposits in the lower slopes. The climate is of the humid  
111 continental subpolar type. The mean annual temperature and mean annual precipitation at  
112 the nearest weather station (Joutel, 55 km from the study area) were 0 °C and 909 mm,  
113 respectively, for the 1981-2010 period (Environment Canada 2018).

114 The area is dominated by coniferous stands, mainly composed of black spruce (*Picea*  
115 *mariana* [Mill.] B.S.P.). Fir and cedar, while within their range of distribution, are much  
116 more scarce than further south and fail to occupy all suitable sites (Messaoud et al.,  
117 2007b; Paul et al., 2014), and jack pine (*Pinus banksiana* Lamb.) is mostly found on drier  
118 sites. White birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides*  
119 Michx.) are the main deciduous species, mainly found in early successional stands. The  
120 undergrowth is dominated by shrubs of the ericaceous family (*Rhododendron*  
121 *groenlandicum* (Oeder) Kron and Judd., *Kalmia angustifolia* L. var *angustifolia* and  
122 *Vaccinium* spp.).

123

### 124 *Sampling*

125 Two marginal fir and cedar populations accessible by road were identified (TOC and  
126 CDC; hereafter "marginal sites"). Both marginal sites were located on the shores of small  
127 lakes ca. 50 km apart. In addition, 15 sites were randomly selected from the inland forest  
128 of the study area (hereafter "sites in the forest matrix"), representative of the diversity of  
129 tree species composition and edaphic conditions (Table 1).

130 Each site was subdivided into microsites where soil samples were taken (averaging 950  
131 cm<sup>3</sup>). At the marginal sites, microsites were sampled at the corners of three 4 m × 4 m  
132 quadrats (12 microsites in total): one quadrat at the center of the marginal site and two  
133 quadrats 150 m on each side of the central quadrat. Each site in the forest matrix

134 consisted of one quadrat with four microsites sampled at each corner. At each microsite,  
135 charcoal was collected in the mineral soil horizon and at the contact between the organic  
136 and mineral horizons (Payette et al. 2012).

137

#### 138 *Charcoal extraction and identification*

139 Soil samples were immersed in a 2.5% sodium hexametaphosphate solution –  $(\text{NaPO}_3)_6$  –  
140 for 12 hours to disperse aggregates. The samples were then sieved (2 mm mesh) under a  
141 gentle water jet. Charcoal extraction was carried out by flotation and manual sorting  
142 under a binocular microscope (Thinon 1992). Charcoal fragments  $> 2$  mm were selected  
143 for analysis as they represent local information (Asselin and Payette 2005).

144 After extraction, charcoal fragments were identified to the species or genus level  
145 according to a reference collection and to wood anatomy references (Panshin and de  
146 Zeeuw 1980; Schweingruber 1990), and separated into six groups: (1) *Abies balsamea*;  
147 (2) *Thuja occidentalis*; (3) *Abies/Thuja* (the criteria for distinguishing cedar from fir – for  
148 example the parenchyma wall – are not always visible (Jacquiot 1955; Panshin and de  
149 Zeeuw 1980)); (4) *Pinus banksiana*; (5) other gymnosperms and (6) angiosperms. Each  
150 charcoal was weighed and the results are presented as the relative mass for each group  
151 (Ali et al. 2005).

152

#### 153 *Radiocarbon dating*

154 Twenty fir and *Abies/Thuja* charcoal fragments (3 within each marginal site and 14 in the  
155 forest matrix sites) were dated using the Accelerator Mass Spectrometry (AMS)  
156 technique. Samples were prepared for radiocarbon dating at the Centre d'études nordiques  
157 (Laval University, Quebec, Canada) and dates were obtained from the Keck Carbon  
158 Cycle AMS Facility (University of California, Irvine, CA, USA). The radiocarbon dates  
159 were calibrated using the Intcal 13 database (Reimer et al. 2013) of the online Calib  
160 program (version 7.1) (Stuiver et al. 2017).

161

## 162 **Results**

163 Charcoal fragments were found at all sites and a total of 3435 charcoal fragments were  
164 identified. At the marginal sites, fir and cedar (combined percentages of *Abies balsamea*,  
165 *Thuja occidentalis*, and *Abies/Thuja*) accounted for 17-53% of the charcoal assemblages  
166 (Figure 1). Jack pine, still present today around the TOC site, accounted for 6 to 13% of  
167 the charcoal assemblages at this marginal site. Other charcoal taxa at the marginal sites  
168 were mostly other gymnosperms (27-58%), with some angiosperms (2-9%), and 6-29%  
169 of non-identifiable taxa.

170 Fir was present in the charcoal assemblages of nearly half of the sites in the forest matrix  
171 (Figure 2), while cedar has not been identified. However, as cedar is often present in old  
172 fir stands, and given the high proportion of the *Abies/Thuja* category at some sites, cedar  
173 nevertheless could have been present. By combining the relative mass of *Abies balsamea*  
174 and *Abies/Thuja*, we can say that fir – and possibly cedar – used to be present at 12 of the  
175 15 sites in the forest matrix and represented up to 31% of the charcoal assemblages (site  
176 S9). The remaining charcoal fragments were mainly other gymnosperms (13-94%), with  
177 very few angiosperms (0-45%) and 6-44% unidentified fragments. The 12 sites in the  
178 forest matrix with fir and/or cedar in their charcoal assemblages had variable  
179 characteristics. They included both open and closed forests, drainages ranging from very  
180 poor to moderate and various surface deposits.

181 The radiocarbon dates obtained from *Abies/Thuja* charcoal fragments were between 3755  
182 cal. BP and the modern era (1950 AD) (Table 2). The youngest dates (180 cal BP to  
183 modern) were all from marginal sites. In the forest matrix sites, 11 of the 14 dates were  
184 from 679 cal BP to 1283 cal BP.

185

## 186 **Discussion**

187 This study confirmed that fir populations used to have larger extents than today in  
188 northern Quebec, and that a climate-related change in the wildfire regime is responsible  
189 for the contraction of the species' distribution during the Neoglacial period. The evidence  
190 is less conclusive for cedar, however, although some of the charcoal fragments from the

191 matrix sites could have been either fir or cedar (undistinguishable). According to  
192 previous palaeoecological studies, fir and cedar arrived in the study area shortly after the  
193 retreat of proglacial lake Ojibway, in a landscape dominated by black spruce (Richard  
194 1980; Carcaillet et al. 2001; Ali et al. 2008). Fir and cedar proliferated during the  
195 Hypsithermal period (ca. 6000-3000 cal BP), before declining gradually during the  
196 Neoglacial period (Liu 1990; Richard 1993; Viau et al. 2006; Ali et al. 2008). Although  
197 this study does not cover the beginning of the Holocene, the oldest date obtained (3755  
198 cal BP) corresponds to the end of the Hypsithermal period.

199 The Neoglacial period was characterized by cool, wet summers in eastern North America  
200 (Carcaillet and Richard 2000; Ali et al. 2012). Studies in several lakes 0.2-60 km from  
201 the study area suggested that the cooler and wetter climate after 3000 cal BP would have  
202 led to less frequent, but larger fires (Ali et al. 2012; Oris et al. 2014; Remy et al. 2017),  
203 probably more severe. As fire size and severity play a key role in long-term vegetation  
204 trajectories (Bergeron et al. 2004; Remy et al. 2017), the shift from frequent small fires to  
205 infrequent large fires likely explains the contraction of fir – and maybe also cedar –  
206 distribution during the Neoglacial period. A similar shift in fire regime was also  
207 suggested to have caused balsam fir to disappear from taiga sites located north of the  
208 study area (Arseneault and Sirois 2004; Gennaretti et al. 2014). Fir and cedar do not have  
209 an aerial seed bank (Rowe and Scotter 1973; Greene et al. 1999) and have low dispersal  
210 capacity (Frank 1990; Johnston 1990; Cornett et al. 1997). Furthermore, seed production  
211 by cedar is low in the northern part of its range, where this study took place (Visnadi,  
212 2014). To recolonize burned sites, fir and cedar must count on the seed rain from a  
213 nearby remnant stand or from surviving mature individuals within the burn (Zasada et al.  
214 1992; Asselin et al. 2001). Large, severe Neoglacial fires would have thus limited fir and  
215 cedar postfire recruitment.

216 The contraction of fir – and possibly cedar – distribution seems to have accelerated  
217 around 1000 cal BP, during the Medieval Warm Period (Hunt, 2006; Viau and Gajewski  
218 2009). Indeed, most of the dated *Abies/Thuja* charcoal fragments in the forest matrix  
219 were concentrated in a ca. 500-yr period centered on 1000 cal yr BP (Figure 3), a period

220 well known in the area for its increased fire activity (Ali et al. 2009; Oris et al. al. 2014;  
221 El-Guellab et al. 2015; Remy et al. 2017).

222 The role of local factors in the fire regime is well documented (Bergeron et al. 2004;  
223 Parisien and Moritz 2009; Mansuy et al. 2010, 2014; Parks et al. 2012). In this study,  
224 evidence of past fir/cedar populations was found at sites with varied topography, surface  
225 deposit, drainage and species composition. Therefore, disappearance of the two species  
226 from these sites suggests that regional climatic factors might have supplanted the effects  
227 of local factors on the fire regime (Senici et al. 2015). For example, sites S9 and S15 had  
228 the highest proportion of fir/cedar in their charcoal assemblages (31 and 28%,  
229 respectively). Site S9 is an old spruce stand with a thick *Sphagnum* carpet, while site S15  
230 is in a topographic depression. These features are known to limit fire spread and severity  
231 (Cyr et al. 2007; Mansuy et al. 2014; Ouarmim et al. 2015). Being firebreaks, these sites  
232 succeeded in maintaining a high portion of fir – and possibly cedar – during the first half  
233 of the Neoglacial. But firebreaks were ineffective against the large and severe fires of the  
234 Medieval Warm Period.

235 In addition to fire, other potential factors have been suggested to explain the decline in  
236 fir/cedar in northern Quebec: reproductive failure, competition from black spruce, and  
237 lack of safe sites for germination (Gauthier et al. 2000; Messaoud et al. 2007a,b, 2014;  
238 Paul et al. 2014; Visnadi 2014). Nevertheless, fire seems to be the overarching limiter to  
239 fir and cedar spread north of their continuous range (Ali et al. 2008; Paul et al. 2014). The  
240 historical presence of fir/cedar in the forest matrix sites up to about 680 cal BP suggests  
241 that these species can grow in the study area. This corroborates the results of previous  
242 studies having shown that many sites theoretically favorable to fir/cedar are not occupied  
243 currently (Messaoud et al. 2007b; Paul et al. 2014), as fire kills mature trees, thus limiting  
244 regeneration, paving the way for black spruce to take advantage (Messaoud et al. 2007b,  
245 2014). Today, fir and cedar are found in areas with low fire incidence (Sirois 1997;  
246 Denneler et al. 2008; Ouarmim et al. 2015).

247 Interestingly, marginal sites burned during the last two centuries, but were recolonized by  
248 fir and cedar afterwards. This would tend to confirm the role of outposts that marginal  
249 sites could play in response to climate change in northern Quebec. In general, the high

250 humidity or poorly drained areas such as wetlands and shores of lakes and rivers limit fire  
251 propagation or reduce severity (Cyr et al. 2005; Senici et al. 2015; Araya et al. 2016;  
252 Nielsen et al. 2016). Reduced fire severity in marginal sites means that some mature  
253 individuals survive and serve as seed sources for post-fire recruitment (Zasada et al.  
254 1992; Asselin et al. 2001). However, for fir and cedar to expand beyond the area of  
255 influence of lakes and rivers, climatic conditions will have to be wetter, which does not  
256 seem to be part of the predictions for the coming decades (Flannigan et al. 2009; Hély et  
257 al. 2010). It is therefore possible that fir and cedar will remain confined to marginal sites.

258

### 259 **Conclusion**

260 The presence of fir – and possibly cedar – in holocene charcoal assemblages from sites  
261 where they are currently absent confirms formerly more extensive distributions in the  
262 northern part of their current range in Quebec. This study thus corroborates, at the local  
263 scale, the results of previous regional-scale palaeoecological studies. Wildfire appears to  
264 be the main factor responsible for range contraction of both species by eliminating seed  
265 sources, hence relegating fir and cedar to sites protected from severe and recurring fires,  
266 such as the shores of lakes and rivers. However, for these sites to act as outposts for the  
267 northern expansion of fir and cedar in response to climate change, climatic conditions  
268 will have to favor the establishment of a regime of light and infrequent fires, which is  
269 unlikely given predictions.

270

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281 **References cited**

- 282 Aitken SN, Yeaman S, Holliday JA, Wang T and Curtis-McLane S (2008) Adaptation,  
283 migration or extirpation: climate change outcomes for tree populations.  
284 *Evolutionary Applications* 1(1): 95-111.
- 285 Ali A, Carcaillet C, Talon B, Roiron P and Terral J-F (2005) *Pinus cembra* L. (arolla  
286 pine), a common tree in the inner French Alps since the early Holocene and above  
287 the present tree line: a synthesis based on charcoal data from soils and travertines.  
288 *Journal of Biogeography* 32(9): 1659-1669.
- 289 Ali A, Asselin H, Larouche AC, Bergeron Y, Carcaillet C and Richard PJ (2008)  
290 Changes in fire regime explain the Holocene rise and fall of *Abies balsamea* in the  
291 coniferous forests of western Québec, Canada. *Holocene* 18(5): 693-703.
- 292 Ali A, Carcaillet C and Bergeron Y (2009) Long term fire frequency variability in the  
293 eastern Canadian boreal forest: the influences of climate vs. local factors. *Global*  
294 *Change Biology* 15(5): 1230-1241.
- 295 Ali A, Blarquez O, Girardin MP, Hély C, Tinquaut F, El-Guellab A, Valsecchi V, Terrier  
296 A, Bremond L and Genries A (2012) Control of the multimillennial wildfire size  
297 in boreal North America by spring climatic conditions. *Proceedings of the*  
298 *National Academy of Sciences* 109(51): 20966-20970.
- 299 Alleaume-Benharira M, Pen I and Ronce O (2006) Geographical patterns of adaptation  
300 within a species' range: interactions between drift and gene flow. *Journal of*  
301 *Evolutionary Biology* 19(1): 203-215.
- 302 Araya YH, Rimmel TK and Perera AH (2016) What governs the presence of residual  
303 vegetation in boreal wildfires? *Journal of Geographical Systems* 18(2): 159-181.
- 304 Arseneault D and Sirois L (2004) The millennial dynamics of a boreal forest stand from  
305 buried trees. *Journal of Ecology* 92(3): 490-504.
- 306 Asselin H, Fortin M-J and Bergeron Y (2001) Spatial distribution of late-successional  
307 coniferous species regeneration following disturbance in southwestern Quebec  
308 boreal forest. *Forest Ecology and Management* 140(1): 29-37.

309 Asselin H and Payette S (2005) Late Holocene deforestation of a tree line site: estimation  
310 of pre-fire vegetation composition and black spruce cover using soil charcoal.  
311 *Ecography* 28(6): 801-805.

312 Barrett CM, Kelly R, Higuera PE and Hu FS (2013) Climatic and land cover influences  
313 on the spatiotemporal dynamics of Holocene boreal fire regimes. *Ecology* 94(2):  
314 389-402.

315 Bergeron Y, Richard PJ, Carcaillet C, Gauthier S, Flannigan M and Prairie YT (1998)  
316 Variability in fire frequency and forest composition in Canada's southeastern  
317 boreal forest: a challenge for sustainable forest management. *Conservation*  
318 *Ecology* 2(2).

319 Bergeron Y, Gauthier S, Flannigan M and Kafka V (2004) Fire regimes at the transition  
320 between mixedwood and coniferous boreal forest in northwestern Quebec.  
321 *Ecology* 85(7): 1916-1932.

322 Carcaillet C and Richard PJH (2000) Holocene changes in seasonal precipitation  
323 highlighted by fire incidence in eastern Canada. *Climate Dynamics* 16(7): 549-  
324 559.

325 Carcaillet C, Bergeron Y, Richard PJH, Fréchette B, Gauthier S and Prairie YT (2001)  
326 Change of fire frequency in the eastern Canadian boreal forests during the  
327 Holocene: does vegetation composition or climate trigger the fire regime? *Journal*  
328 *of Ecology* 89(6): 930-946.

329 Case TJ and Taper ML (2000) Interspecific competition, environmental gradients, gene  
330 flow, and the coevolution of species' borders. *American Naturalist*, 155(5): 583-  
331 605.

332 Clark JS (1998) Why trees migrate so fast: confronting theory with dispersal biology and  
333 the paleorecord. *American Naturalist* 152(2): 204-224.

334 Clarke PJ (2002) Habitat islands in fire-prone vegetation: do landscape features influence  
335 community composition? *Journal of Biogeography* 29(5-6): 677-684.

336 Corlett RT and Westcott DA (2013) Will plant movements keep up with climate change?  
337 *Trends in Ecology and Evolution*, 28(8): 482-488.

338 Cornett MW, Reich PB and Puettmann KJ (1997) Canopy feedbacks and  
339 microtopography regulate conifer seedling distribution in two Minnesota conifer-  
340 deciduous forests. *Ecoscience* 4(3): 353-364.

341 Cyr D, Bergeron Y, Gauthier S and Larouche AC (2005) Are the old-growth forests of  
342 the Clay Belt part of a fire-regulated mosaic? *Canadian Journal of Forest*  
343 *Research* 35(1): 65-73.

344 Cyr D, Gauthier S and Bergeron Y (2007) Scale-dependent determinants of heterogeneity  
345 in fire frequency in a coniferous boreal forest of eastern Canada. *Landscape*  
346 *Ecology* 22(9): 1325-1339.

347 Davis MB (2000). Palynology after Y2K—understanding the source area of pollen in  
348 sediments. *Annual Review of Earth and Planetary Sciences* 28(1): 1-18.

349 de Lafontaine G and Asselin H (2011) Soil charcoal stability over the Holocene across  
350 boreal northeastern North America. *Quaternary Research* 76(2): 196-200.

351 Denneler B, Asselin H, Bergeron Y and Begin Y (2008) Decreased fire frequency and  
352 increased water levels affect riparian forest dynamics in southwestern boreal  
353 Quebec, Canada. *Canadian Journal of Forest Research* 38(5): 1083-1094.

354 Dyer JM (1995) Assessment of climatic warming using a model of forest species  
355 migration. *Ecological Modelling* 79(1-3): 199-219.

356 Eckert CG, Samis KE and Loughheed SC (2008) Genetic variation across species  
357 geographical ranges: the central-marginal hypothesis and beyond. *Molecular*  
358 *Ecology* 17(5): 1170-1188.

359 El-Guellab A, Asselin H, Gauthier S, Bergeron Y and Ali AA (2015) Holocene variations  
360 of wildfire occurrence as a guide for sustainable management of the northeastern  
361 Canadian boreal forest. *Forest Ecosystems* 2(15): 1-7.

362 Environnement Canada (2018) Données des stations pour le calcul des normales  
363 climatiques au Canada de 1971 à 2000. Available at:  
364 [http://climate.weather.gc.ca/climate\\_normals/index\\_e.html#1981](http://climate.weather.gc.ca/climate_normals/index_e.html#1981) (accessed 3  
365 March 2018).

366 Figueiral I and Mosbrugger V (2000) A review of charcoal analysis as a tool for  
367 assessing Quaternary and Tertiary environments: achievements and limits.  
368 *Palaeogeography, Palaeoclimatology, Palaeoecology* 164(1): 397-407.

369 Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM and Gowman LM (2009)  
370 Implications of changing climate for global wildland fire. *International Journal of*  
371 *Wildland Fire* 18(5):, 483-507.

372 Frank RM (1990) *Abies balsamea* (L.) Mill. In: Burns RM and Honkala BH (eds) *Silvics*  
373 *of North America. I. Conifers*. Washington DC: United States Department of  
374 Agriculture (USDA), Forest Service, Agriculture Handbook 654, pp. 26-35.

375 Gamache I, Jaramillo-Correa JP, Payette S and Bousquet J (2003) Diverging patterns of  
376 mitochondrial and nuclear DNA diversity in subarctic black spruce: imprint of a  
377 founder effect associated with postglacial colonization. *Molecular Ecology* 12(4):  
378 891-901.

379 Gauthier S, De Grandpré L and Bergeron Y (2000) Differences in forest composition in  
380 two boreal forest ecoregions of Quebec. *Journal of Vegetation Science* 11(6):  
381 781-790.

382 Gennaretti F, Arseneault D and Bégin Y (2014) Millennial disturbance-driven forest  
383 stand dynamics in the Eastern Canadian taiga reconstructed from subfossil logs.  
384 *Journal of Ecology* 102(6): 1612-1622.

385 Greene D, Zasada JC, Sirois L, Kneeshaw D, Morin H, Charron I and Simard M-J (1999)  
386 A review of the regeneration dynamics of North American boreal forest tree  
387 species. *Canadian Journal of Forest Research* 29(6): 824-839.

388 Hampe A and Petit RJ (2005) Conserving biodiversity under climate change: the rear  
389 edge matters. *Ecology Letters* 8(5): 461-467.

390 Hély C, Girardin MP, Ali AA, Carcaillet C, Brewer S and Bergeron Y (2010). Eastern  
391 boreal North American wildfire risk of the past 7000 years: A model-data  
392 comparison. *Geophysical Research Letters* 37(14): L14709.

393 Hunt BG (2006) The Medieval Warm Period, the Little Ice Age and simulated climatic  
394 variability. *Climate Dynamics* 27(7-8): 677-694.

395 Jacquot C (1955) *Atlas d'anatomie des bois des Conifères*. Paris: Centre Tech. Bois.

- 396 Johnston WF (1990) *Thuja occidentalis* L. Northern White-Cedar In: Burns RM and  
397 Honkala BH (eds) *Silvics of North America. I. Conifers*. Washington DC: United  
398 States Department of Agriculture (USDA), Forest Service, Agriculture Handbook  
399 654, pp. 580-589.
- 400 Kafka V, Gauthier S and Bergeron Y (2001) Fire impacts and crowning in the boreal  
401 forest: study of a large wildfire in western Quebec. *International Journal of*  
402 *Wildland Fire* 10(2): 119-127.
- 403 Kawecki TJ (2008) Adaptation to marginal habitats. *Annual Review of Ecology,*  
404 *Evolution, and Systematics* 39: 321-342.
- 405 Lesica P and Allendorf FW (1995) When are peripheral populations valuable for  
406 conservation? *Conservation Biology* 9(4): 753-760.
- 407 Lindbladh M, Fraver S, Edvardsson J and Felton A (2013) Past forest composition,  
408 structures and processes - How paleoecology can contribute to forest  
409 conservation. *Biological Conservation* 168: 116-127.
- 410 Lindenmayer DB, Franklin JF and Fischer J (2006) General management principles and a  
411 checklist of strategies to guide forest biodiversity conservation. *Biological*  
412 *Conservation* 131(3): 433-445.
- 413 Liu K-B (1990) Holocene paleoecology of the boreal forest and Great Lakes-St.  
414 Lawrence forest in northern Ontario. *Ecological Monographs* 60(2) 179-212.
- 415 Lucas A (2017) *Dynamique holocène de Thuja occidentalis L. dans la partie nord de son*  
416 *aire de répartition*. MSc thesis. Rouyn-Noranda: Université du Québec en  
417 Abitibi-Témiscamingue.
- 418 Malcolm JR, Markham A, Neilson RP and Garaci M (2002) Estimated migration rates  
419 under scenarios of global climate change. *Journal of Biogeography* 29(7): 835-  
420 849.
- 421 Mansuy N, Gauthier S, Robitaille A and Bergeron Y (2010) The effects of surficial  
422 deposit–drainage combinations on spatial variations of fire cycles in the boreal  
423 forest of eastern Canada. *International Journal of Wildland Fire* 19(8): 1083-  
424 1098.

425 Mansuy N, Boulanger Y, Terrier A, Gauthier S, Robitaille A and Bergeron Y (2014)  
426 Spatial attributes of fire regime in eastern Canada: influences of regional  
427 landscape physiography and climate. *Landscape Ecology* 29(7): 1157-1170.

428 Messaoud Y, Bergeron Y and Asselin H (2007a) Reproductive potential of balsam fir  
429 (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) at  
430 the ecotone between mixedwood and coniferous forests in the boreal zone of  
431 western Quebec. *American Journal of Botany* 94(5): 746-754.

432 Messaoud Y, Asselin H, Bergeron Y and Grondin P (2014) Competitive advantage of  
433 black spruce over balsam fir in coniferous boreal forests of Eastern North  
434 America revealed by site index. *Forest Science* 60(1): 57-62.

435 Messaoud Y, Bergeron Y and Leduc A (2007b) Ecological factors explaining the location  
436 of the boundary between the mixedwood and coniferous bioclimatic zones in the  
437 boreal biome of eastern North America. *Global Ecology and Biogeography* 16(1):  
438 90-102.

439 Nathan R, Horvitz N, He Y, Kuparinen A, Schurr FM and Katul GG (2011) Spread of  
440 North American wind-dispersed trees in future environments. *Ecology Letters*  
441 14(3): 211-219.

442 Nelle O, Robin V and Talon B (2013) Pedoanthracology: Analysing soil charcoal to  
443 study Holocene palaeoenvironments. *Quaternary International* 289: 1-4.

444 Nielsen S, DeLancey E, Reinhardt K and Parisien M-A (2016) Effects of lakes on  
445 wildfire activity in the boreal forests of Saskatchewan, Canada. *Forests* 7(11):  
446 265.

447 Oris F, Asselin H, Finsinger W, Hely C, Blarquez O, Ferland ME, Bergeron Y and Ali  
448 AA (2014) Long-term fire history in northern Quebec: implications for the  
449 northern limit of commercial forests. *Journal of Applied Ecology* 51(3): 675-683.

450 Ouarmim S, Asselin H, Hely C, Bergeron Y and Ali AA (2014) Long-term dynamics of  
451 fire refuges in boreal mixedwood forests. *Journal of Quaternary Science* 29(2):  
452 123-129.

453 Ouarmim S, Ali AA, Asselin H, Hely C and Bergeron Y (2015) Evaluating the  
454 persistence of post-fire residual patches in the eastern Canadian boreal  
455 mixedwood forest. *Boreas* 44(1): 230-239.

456 Pandey M and Rajora OP (2012) Genetic diversity and differentiation of core vs.  
457 peripheral populations of eastern white cedar, *Thuja occidentalis* (Cupressaceae).  
458 *American Journal of Botany* 99(4): 690-699.

459 Panshin AJ and de Zeeuw C (1980) *Textbook of wood technology: structure,*  
460 *identification, properties and use of the commercial woods of the United States*  
461 *and Canada*. New York: McGraw-Hill Book Co.

462 Pardi MI and Smith FA (2012) Paleoecology in an era of climate change: how the past  
463 can provide insights into the future. In: Louys J (ed) *Paleontology in ecology and*  
464 *conservation*. New York: Springer-Verlag, pp. 93-115.

465 Parisien M-A and Moritz MA (2009) Environmental controls on the distribution of  
466 wildfire at multiple spatial scales. *Ecological Monographs* 79(1): 127-154.

467 Parks SA, Parisien M-A and Miller C (2012). Spatial bottom-up controls on fire  
468 likelihood vary across western North America. *Ecosphere* 3(1): 12.

469 Paul V, Bergeron Y and Tremblay F (2014) Does climate control the northern range limit  
470 of eastern white cedar (*Thuja occidentalis* L.)? *Plant Ecology* 215(2): 181-194.

471 Payette S, Delwaide A, Schaffhauser A and Magnan G (2012) Calculating long-term fire  
472 frequency at the stand scale from charcoal data. *Ecosphere* 3(7): 1-16.

473 Payette S, Delwaide A, Couillard P-L and Pilon V (2017) Disjunct jack pine (*Pinus*  
474 *banksiana*) populations of the boreal forest in eastern Canada: expanding,  
475 declining, or stable? *Botany* 95(7): 697-707.

476 Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE,  
477 Cheng H, Edwards RL and Friedrich M (2013) IntCal13 and Marine13  
478 radiocarbon age calibration curves 0-50,000 years cal BP. *Radiocarbon* 55(4),  
479 1869–1887.

480 Remy CC, Lavoie M, Girardin MP, Hély C, Bergeron Y, Grondin P, Oris F, Asselin H  
481 and Ali AA (2017). Wildfire size alters long-term vegetation trajectories in boreal  
482 forests of eastern North America. *Journal of Biogeography* 44(6): 1268-1279.

483 Richard P (1980) Histoire postglaciaire de la végétation au sud du lac Abitibi, Ontario et  
484 Québec. *Géographie physique et Quaternaire* 34(1): 77-94.

485 Richard P (1993) The origin and postglacial dynamics of the mixed forest in Quebec.  
486 *Review of Palaeobotany and Palynology* 79(1-2): 31-68.

487 Rowe JS and Scotter GW (1973) Fire in the boreal forest. *Quaternary Research* 3(3):  
488 444-464.

489 Schweingruber FH.(1990) *Anatomy of European woods*. Bern: Paul Haupt.

490 Scott AC and Damblon F (2010) Charcoal: Taphonomy and significance in geology,  
491 botany and archaeology. *Palaeogeography, Palaeoclimatology, Palaeoecology*  
492 291(1): 1-10.

493 Senici D, Chen HY, Bergeron, Y and Ali AA (2015) The effects of forest fuel  
494 connectivity on spatiotemporal dynamics of Holocene fire regimes in the central  
495 boreal forest of North America. *Journal of Quaternary Science* 30(4): 365-375.

496 Sirois L (1997) Distribution and dynamics of balsam fir (*Abies balsamea* [L.] Mill.) at its  
497 northern limit in the James Bay area. *Ecoscience* 4(3): 340-352.

498 Stuiver M, Reimer PJ and Reimer RW (2017) CALIB 7.1 Available at: <http://calib.org>  
499 (accessed 3 August 2017).

500 Talon B, Payette S, Filion L and Delwaide A (2005) Reconstruction of the long-term fire  
501 history of an old-growth deciduous forest in Southern Québec, Canada, from  
502 charred wood in mineral soils. *Quaternary Research* 64(1): 36-43.

503 Thinon M (1992) *L'analyse pédoanthracologique- Aspects méthodologiques et*  
504 *applications*. Dissertation, Marseille: Université d'Aix-Marseille III.

505 Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC,  
506 Erasmus BF, De Siqueira MF, Grainger A and Hannah L (2004) Extinction risk  
507 from climate change. *Nature* 427(6970): 145-148.

508 Turner M and Romme W (1994) Landscape dynamics in crown fire ecosystems.  
509 *Landscape Ecology* 9(1): 59-77.

510 Veillette JJ (1995) Evolution and paleohydrology of glacial Lakes Barlow and Ojibway.  
511 *Quaternary Science Reviews* 13(9-10): 945-971.

- 512 Viau A and Gajewski K (2009) Reconstructing millennial-scale, regional paleoclimates  
513 of boreal Canada during the Holocene. *Journal of Climate* 22(2): 316-330.
- 514 Viau AE, Gajewski K, Sawada MC and Fines P (2006) Millennial-scale temperature  
515 variations in North America during the Holocene. *Journal of Geophysical*  
516 *Research: Atmospheres* 111(D9): D09102.
- 517 Visnadi I (2014) *Régénération et dynamique des populations marginales de Thuja*  
518 *occidentalis L. en forêt boréale*. MSc thesis. Rouyn-Noranda: Université du  
519 Québec en Abitibi-Témiscamingue.
- 520 Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M,  
521 HoeghGuldberg O and Bairlein F (2002) Ecological responses to recent climate  
522 change. *Nature* 416(6879): 389-395.
- 523 Xu H, Tremblay F, Bergeron Y, Paul V and Chen C (2012) Genetic consequences of  
524 fragmentation in “arbor vitae,” eastern white cedar (*Thuja occidentalis L.*),  
525 toward the northern limit of its distribution range. *Ecology and Evolution* 2(10):  
526 2506-2520.
- 527 Zasada JC, Sharik TL and Nygren M (1992) The reproductive process in boreal forest  
528 trees. In: Shugart HH, Leemans R and Bonan GB (eds) *A system analysis of the*  
529 *global boreal forest*. Cambridge: Cambridge University Press, pp. 85-125.

530 Table 1. Characteristics of marginal sites and sites in the forest matrix.

531

	Tree species	Density index (%)	Distance from marginal stand (km)	Surface deposit	Drainage	Slope
<b><i>Marginal sites</i></b>						
CDC	Pm, Ab, Bp, To, Bp	61-80	-	Interlobar moraine	Good	Moderate
TOC	Pm, Ab, To, Pb	41-60	-	Esker	Good	Gentle
<b><i>Sites in the forest matrix</i></b>						
S1	Pm, Ll	41-60	3.4	Till with clay matrix	Poor	Gentle
S2	Pm	25-40	0.7	Till with clay matrix	Poor	Null
S3	Pm	25-40	0.6	Thick organic	Very poor	Null
S4	Pm, Bp	81-100	1.3	Interlobar moraine	Moderate	Gentle
S5	Pm	81-100	1.2	Interlobar moraine	Moderate	Gentle
S6	Pm, Ll	81-100	1.1	Interlobar moraine	Moderate	Gentle
S7	Pm	81-100	1.4	Till with clay matrix	Poor	Null
S8	Pm	25-40	1.2	Interlobar moraine	Imperfect	Null
S9	Pm	25-40	1.3	Interlobar moraine	Moderate	Gentle
S10	Pm	41-60	3.3	Till with clay matrix	Poor	Null
S11	Pm, Ll	41-60	3.2	Till with clay matrix	Poor	Null
S12	Pm, Ll	41-60	3.8	Till with clay matrix	Poor	Null
S13	Pm	41-60	3.7	Interlobar moraine	Poor	Null
S14	Pm, Ll	41-60	3.6	Till with clay matrix	Poor	Null
S15	Pm	41-60	4.1	Interlobar moraine	Poor	Null

Ab: *Abies balsamea*, Pm: *Picea mariana*, Bp: *Betula papyrifera*, Pt: *Populus tremuloides*, Ll: *Larix laricina*, To: *Thuja occidentalis*, Pb: *Pinus banksiana*

532 Table 2. Radiocarbon dates for 20 *Abies/Thuja* charcoal fragments from marginal  
 533 sites and from sites in the forest matrix.

Site	Interface/ Mineral	Species	Age (cal BP)	Cal BP (2σ)	Reference (UCIAMS)
<b><i>Marginal sites</i></b>					
TOC	Mineral	<i>Abies</i>	Modern		190366
TOC	Mineral	<i>Thuja</i>	50 ± 30		190378
TOC	Interface	<i>Thuja</i>	90 ± 30	108 (22-265)	190365
CDC	Mineral	<i>Abies</i>	90 ± 30	108 (22-265)	190382
CDC	Interface	<i>Thuja</i>	95 ± 30	110 (20–267)	190361
CDC	Interface	<i>Abies</i>	185 ± 30	180 (0 – 300)	190360
<b><i>Sites in the forest matrix</i></b>					
S6	Interface	<i>Abies</i>	735 ± 30	679 (656–726)	190371
S9	Mineral	<i>Abies/Thuja</i>	755 ± 30	688 (666–728)	190373
S1	Interface	<i>Abies/Thuja</i>	830 ± 30	737 (688–789)	190367
S9	Interface	<i>Abies</i>	835 ± 30	742 (688–792)	190380
S1	Interface	<i>Abies</i>	890 ± 30	810 (733–909)	190377
S15	Interface	<i>Abies/Thuja</i>	930 ± 30	853 (786-924)	190374
S5	Mineral	<i>Abies</i>	1030 ± 40	947 (801-1054)	190370
S5	Interface	<i>Abies</i>	1055 ± 30	960 (926-1051)	190376
S3	Interface	<i>Abies</i>	1125 ± 30	1024 (959-1172)	190368
S3	Mineral	<i>Abies</i>	1150 ± 30	1061 (979-1174)	190369
S15	Interface	<i>Abies/Thuja</i>	1345 ± 30	1283 (1185-1309)	190375
S7	Interface	<i>Abies</i>	1805 ± 30	1741 (1626-1821)	190372
S7	Interface	<i>Abies</i>	1835 ± 30	1772 (1704-1864)	190379
S6	Mineral	<i>Abies</i>	3475 ± 30	3755 (3645-3834)	190381

534

535 **Figure captions**

536

537 Figure 1. Relative mass (%) for each charcoal category within marginal sites (CDC and  
538 TOC) and 150 m on each side of the center of the marginal sites (A, B).

539

540 Figure 2. Relative mass (%) for each charcoal category in sites in the forest matrix.

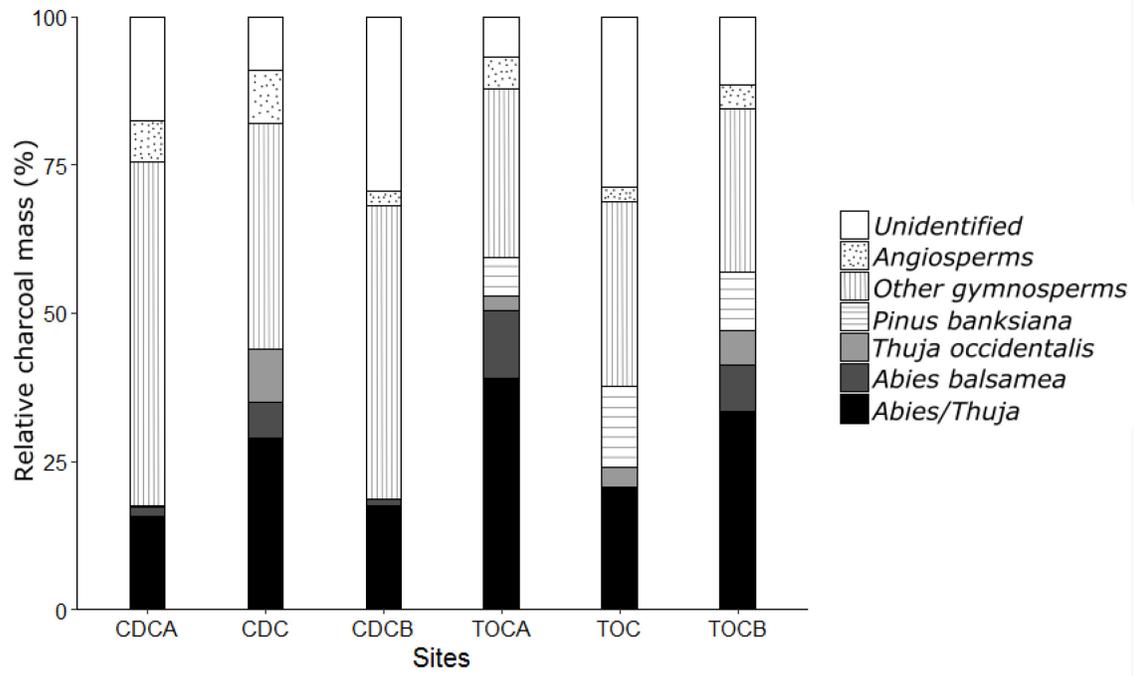
541

542 Figure 3. Dates when fir/cedar were present in marginal sites (stars) and in sites in the  
543 forest matrix (dots).

544

545 Figure 1

546

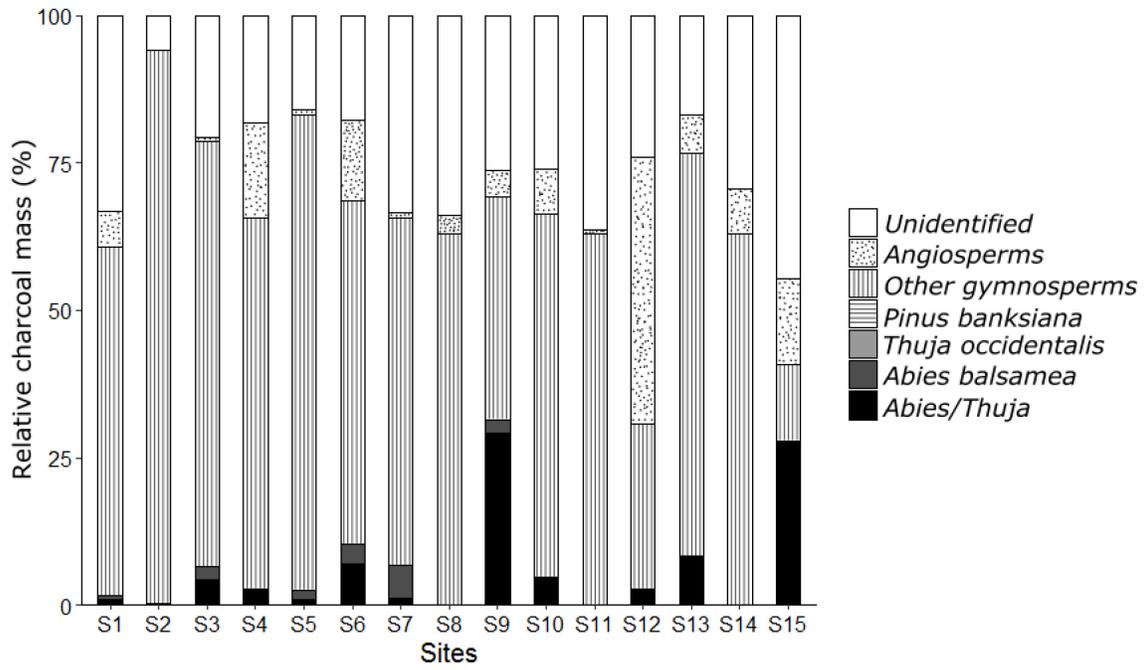


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549 Figure 2

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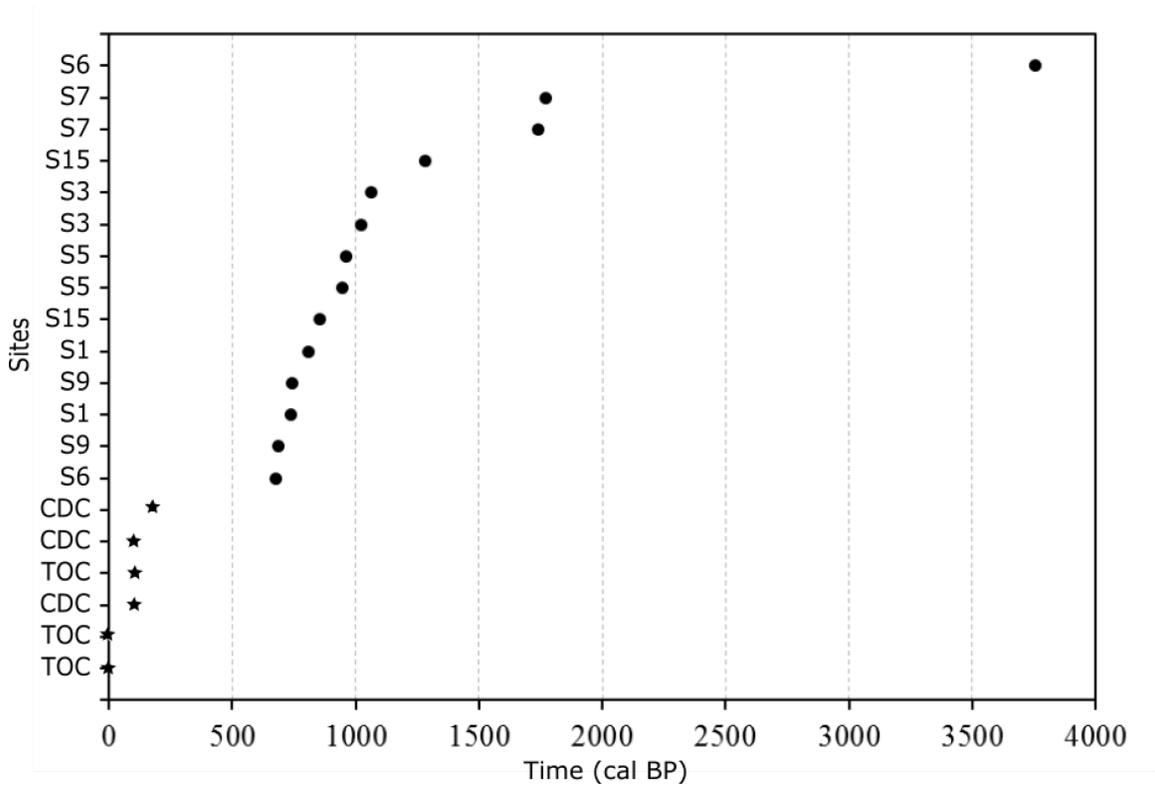


551

552

553 Figure 3

554



555

556