

1 **Millennial disturbance-driven forest stand dynamics in the Eastern Canadian**
2 **taiga reconstructed from subfossil logs**

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11 Running headline: Fire impacts on boreal landscape diversity

12 **Summary**

13 1. Although wildfire is the main natural disturbance factor driving changes in the
14 North American boreal forest, understanding how the fire history of the last
15 millennium shaped the present-day landscape diversity is a difficult task due to the
16 lack of paleoecological reconstructions with high spatial (few hundreds of square
17 meters) and temporal (annual) resolutions.

18 2. We combined a detailed inventory of the present-day lakeshore forest of two
19 lakes of the Eastern Canadian taiga with the dendrochronological dating of the
20 subfossil logs that accumulated in the littoral zones facing these shores. Our
21 objective was to compare the millennial impact of wildfires among stands of various
22 structures and compositions. Past stem densities and fire years were
23 reconstructed from log recruitment rates and dating of charred logs.

24 3. Multivariate analysis of the present-day lakeshore forest revealed three and two
25 homogeneous shore segments per site (i.e. clusters). Cluster 1 at both sites
26 exhibited denser forest, higher dead wood values and a higher percentage of
27 balsam fir, a fire-sensitive species.

28 4. In total, 426 and 611 subfossil logs (mostly black spruce) were crossdated over
29 the last ~1400 years. Their dendrochronological analysis confirmed that each
30 lakeshore cluster, identified from the traits of the present-day forest, experienced
31 a specific fire history over the last millennium (i.e. 0-5 fires of variable severity) that
32 locally influenced forest composition, tree density and growth. Each fire triggered

33 a specific forest structure trajectory characterized by a different stem density and
34 rate of recovery.

35 5. Climate variability also impacted our sites. Lakeshore trees grew faster during
36 the Medieval Climate Anomaly whereas an early 1800's volcano-induced cold
37 episode coincided with a sharp reduction in tree growth and a peak in tree
38 mortality.

39 6. *Synthesis*: This study provides a long-term perspective that helps explain how
40 the present-day landscape diversity in the Eastern Canadian taiga reflects the site-
41 specific fire history over the last millennium. Fires have caused persistent and
42 cumulative impacts resulting in a progressive opening of the forest cover along
43 with balsam fir exclusion. Present-day landscapes are mosaics of forest stands
44 characterized by different times since fire and different postfire forest structure
45 trajectories.

46 **Key-words**

47 *Abies balsamea*, boreal forest, dendrochronology, determinants of plant
48 community diversity and structure, fire ecology, paleoecology, *Picea mariana*,
49 plant–climate interactions, Quebec, successional trajectory

50 **Introduction**

51 Many ecosystems depend on or are well-adapted to the occurrence of
52 disturbances (Le Goff & Sirois 2004; Brunbjerg et al. 2012; Newbery et al. 2013).
53 However, disturbances may also produce long-term alterations of the natural
54 landscape (He et al. 2002; Vanderwel, Coomes & Purves 2013), as well as a
55 degradation in ecosystem functioning (Villnäs et al. 2013; Zwicke et al. 2013) or a
56 creation of divergent successional pathways (Folke et al. 2004; Johnstone et al.
57 2010; Harvey & Holzman 2013). Spatio-temporal variation in disturbance
58 frequency and severity is an agent of ecological diversity in several biomes
59 (Fraterrigo & Rusak 2008).

60 For example, the North American boreal forest is characterized by large and
61 frequent stand-replacing wildfires (Johnson 1992; Stocks et al. 2003) and is
62 dominated by even-aged communities of fire-adapted species such as black
63 spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.)
64 (Johnson 1992; Sirois 1995). Although spruce and pine stands recover rapidly after
65 fire due to their serotinous cones (i.e. cones that remain closed and disperse seed
66 following a fire), tree density and forest composition vary according to several factors,
67 such as the magnitude of the pre-fire seed banks (Greene & Johnson 1999), the time
68 since the last fire (Morneau & Payette 1989), the severity of the fire (Arseneault
69 2001), and the duration of the fire-free interval preceding the last fire (Lavoie & Sirois
70 1998). In these environments, fire frequency and severity are the dominant drivers
71 of change in forest structure and composition at both the site and landscape levels,

72 and also determine ecosystem net primary production and the regional carbon
73 balance (Bond-Lamberty et al. 2007).

74 In Eastern Canada, these short-term (decadal to secular) fire effects have been
75 superimposed onto a longer-term, large-scale climate-induced decrease in conifer
76 stem density, which was also mediated by fire disturbance (Payette & Gagnon
77 1985). The boreal biome of the region is subdivided into three main latitudinal bands
78 from south to north: the closed-crown forest, the spruce-lichen woodland (hereafter
79 referred to as the taiga) and the forest tundra (Fig. 1; Saucier et al. 2003). In the
80 forest tundra zone, black spruce stands occur mostly in the lowlands, while upland
81 spruce stands systematically failed to recover and shifted to treeless ecosystems
82 after fire over the last 600-900 years, following the Medieval Climate Anomaly
83 (Payette & Gagnon 1985; Payette & Morneau 1993; Payette, Filion & Delwaide
84 2008). Many spruce-lichen woodland and dense forest stands also failed to recover
85 or shifted to more open woodlands after the fires of the 20th century in the closed-
86 crown forest and the taiga zones (Sirois & Payette 1991; Lavoie & Sirois 1998;
87 Girard, Payette & Gagnon 2008; Boiffin & Munson 2013). This generalized fire-
88 climate induced deforestation was accompanied by a decreasing occurrence of
89 fire-sensitive balsam fir (*Abies balsamea* (L.) Mill.) over the last millennia
90 (Arseneault & Sirois 2004; de Lafontaine & Payette 2010). Today, forest stands
91 with abundant fir are scattered in areas less affected by fire, frequently along streams
92 and lakeshores (Sirois 1997; Arseneault, Boucher & Bouchon 2007). It has been
93 hypothesized that these stands are remnants of a previously widespread closed-
94 canopy spruce-fir vegetation zone, similar to that occurring further south, established

95 more than 5000 years ago when fires were less frequent due to a more humid climate
96 (Sirois 1997; Arseneault & Sirois 2004; Boucher, Arseneault & Hétu 2006; Ali et al.
97 2008; de Lafontaine & Payette 2010).

98 The taiga of Eastern Canada (Fig. 1), comprises a mosaic of spruce-lichen
99 woodlands of various postfire ages, stem densities and fir abundance, along with
100 numerous lakes and peatlands in concave landforms (Fig. S1 in Supporting
101 information). Deciphering how these spatially variable forest structures and
102 compositions reflect long-term fire and climate impacts is a difficult task due to the
103 lack of paleoecological records available to reconstruct millennial forest dynamics
104 with both high spatial and temporal resolutions. Dendrochronology can be used to
105 reconstruct forest dynamics at the stand level with an annual resolution, but such
106 reconstructions are limited to a few centuries because of fast decay of dead wood
107 (Bond-Lamberty & Gower 2008). Conversely, pollen and charcoal and plant
108 macroremains allow the reconstruction of long-term vegetation changes and fire
109 histories (e.g. Carcaillet et al. 2010; Payette et al. 2012; Senici et al. 2013), but
110 provide no direct information on past tree density or growth trends and the dating
111 of disturbances relies on radiocarbon methods that are less precise than
112 dendrochronology. Furthermore, contrary to fire impacts, pollen data are not stand-
113 specific because of pollen mobility.

114 In this study, we first conducted a detailed inventory of the present-day lakeshore
115 forest structure and composition of 2.2 kilometres of shoreline situated along two
116 boreal lakes. Subsequently, we used dendrochronology to analyse the large stocks
117 of submerged subfossil logs that accumulated in the littoral zones facing these

118 same shores in order to reconstruct the millennial impacts of wildfires on lakeshore
119 forest stands. Our objective was to verify whether variations in the forest structure
120 and composition of the present-day lakeshore forest at each site can be attributed
121 to varying fire histories during the last millennium. Our hypotheses are that (i) there
122 is a negative correlation between past wildfire frequency and present-day tree
123 density and balsam fir abundance, and that (ii) impacts of past fires have been
124 spatially heterogeneous even within a given site and have persisted over several
125 centuries.

126 **Materials and methods**

127 Study sites and sampling

128 Two lakes, hereafter called L18 (54.25 N, 72.38 W) and L20 (54.56 N, 71.24 W),
129 were the object of this study. They are located at the interface between the taiga and
130 the forest tundra of Northern Quebec in Eastern Canada (Fig. 1). Black spruce is the
131 prevalent tree species and a mosaic of postfire spruce-lichen woodlands
132 characterizes the region (Fig. S1). Other less abundant tree species include balsam
133 fir and tamarack (*Larix laricina* (Du Roi) K. Koch). The regional burn rate is about
134 0.2% per year (Boulanger et al. 2012). The mean annual temperature is -3°C and the
135 average annual precipitation is 760 mm, of which 550 falls as rain (La Grande IV
136 weather station; 22 years of observations, Environment Canada 2014). The region is
137 located in the northern part of the balsam fir range and east of the jack pine range
138 limit. The easternmost jack pine stands are located about 10 kilometres westward of
139 L18.

140 The two sites are part of a network of lakes selected to study the stocks of subfossil
141 logs in boreal lakes and their fluxes across the forest-lake interface (Gennaretti,
142 Arseneault & Bégin 2014), as well as to develop a dendroclimatic reconstruction
143 of the summer temperatures of Eastern Canada over the last millennium
144 (Gennaretti et al. in press). The lakes were selected because they comprise a
145 littoral segment with abundant subfossil logs facing old-growth lakeshore forest
146 vegetation (i.e. time since last fire of about 300-400 years) on a well-drained glacial
147 deposit and on the lakeside protected from dominant winds.

148 To characterize the structure and composition of the present-day lakeshore forest
149 stands, we sampled 39 and 33 plots (10 x 10 m) spaced at 20 m intervals along
150 and adjacent to the selected shore segments at L18 and L20, respectively (Fig. 1).
151 Within each plot we recorded the diameter at breast height (DBH) by species
152 (spruce, fir or tamarack) of all living trees and snags ≥ 2 cm DBH. We also recorded
153 the maximum diameter of all stumps and coarse woody debris pieces on the forest
154 floor, excluding specimens with a maximum diameter < 4 cm. Snags were defined
155 as standing dead trees connected to their roots and taller than breast height,
156 stumps as dead trees connected to their roots and lower than breast height, and
157 coarse woody debris pieces as dead trees on the floor not connected to their roots.
158 The two or three tallest living trees (depending on species diversity) at each plot
159 were cored as close to the collar as possible using a Hagl f increment borer. In
160 the laboratory, tree-ring counting on the increment cores (No. = 165) allowed the
161 minimum time since the last stand-replacing fire at each plot to be determined (i.e.
162 maximum number of tree-rings per tree after applying a correction for coring
163 height). Seedlings and saplings (< 2 cm DBH) were counted within two subplots (1
164 x 10 m) perpendicular to the lakeshore, nested within and on the two opposite
165 edges of each main plot.

166 In the littoral zone facing the lakeshore segments, all subfossil logs with diameter
167 ≥ 4 cm were sampled in the water or in the superficial sediments within 15-20 m
168 from the shores, using the method described by Arseneault et al. (2013). In total,
169 627 and 848 logs were sampled along 1170 and 990 m of shoreline at L18 and L20,
170 respectively. For each subfossil log, the sampling location was mapped with a total

171 station and a cross-section was collected at its maximum diameter for
172 dendrochronological analysis. In the lab, the tree species were identified using wood
173 anatomy characteristics (spruce, fir or tamarack) and tree-ring width measurements
174 and dendrochronological dating were performed with standard procedures as
175 described by Gennaretti, Arseneault & Bégin (2014). In total, 426 (all black spruce)
176 and 611 (595 black spruce and 16 balsam fir) logs could be crossdated over the last
177 ~1400 years at L18 and L20, respectively. Whereas fir and spruce individuals could
178 be crossdated together, no master chronology could be developed for tamarack.

179 These subfossil logs have not been significantly redistributed along the littoral zone
180 after recruitment into the water as proven by the relatively high proportion of
181 specimens oriented perpendicularly to the shore with their base toward the forest and
182 by the contrasting recruitment patterns of logs between consecutive shore segments
183 with different fire histories (Gennaretti, Arseneault & Bégin 2014). Thus, the logs can
184 be used to reconstruct the long term dynamics of the facing forest stands (i.e. past
185 fire years, past fire impacts on tree mortality and regeneration and past changes in
186 stem density and spruce growth; see "Data analysis" below). However, these data
187 do not allow reconstructing past variations in species abundance within the lakeshore
188 forests because very few fir and no tamarack logs were crossdated (Fig. S2). This is
189 due to the fact that fir and tamarack are much less abundant than spruce stems in
190 the studied lakeshore forests, especially within the first line of tall dominant trees near
191 the shoreline, which can generate persistent subfossil samples with a sufficient
192 number of tree-rings for the crossdating procedure (Gennaretti, Arseneault & Bégin
193 2014).

194 Data analysis

195 The data used in this study (living plots and subfossil logs) and the analysis
196 workflow are summarized in Fig. S2. First, triplets of consecutive neighbouring
197 plots in the lakeshore forests were considered, so as to obtain 37 and 31 triplets
198 at L18 and L20, respectively (e.g. triplet 1 comprises plots 1, 2 and 3; triplet 2
199 comprises plots 2, 3 and 4, etc.). Using triplets allowed compiling data within larger
200 and more representative portions of the lakeshore forests and smoothing out the
201 background noise among plots. Several variables were then developed to
202 characterize the forest structure and composition of each triplet (Table 1). When
203 two variables were strongly correlated ($r > 0.8$ or < -0.8), one of them was excluded
204 from the subsequent analyses to limit redundancy (Tables S3 and S4). In this way,
205 "Nliv", "Ntot", "F%reg", "BAliv" and "a" were excluded for L18, while "Nliv", "Ntot",
206 "Nliv6", "BAliv" and "a" were excluded for L20. Correlation between "F%" and
207 "Ndead" was slightly higher than 0.8 at L18, but the two variables were retained as
208 their association is not straightforward.

209 We performed a Principal Component Analysis (PCA) on the triplets of each lake
210 using our set of descriptive variables. All variables were scaled to unit variance.
211 Only principal components with eigenvalues > 1 were retained (Figs 2 and S3 to
212 S6). A hierarchical cluster analysis was subsequently used to detect associations
213 among triplets at each site based on a Euclidean distance matrix obtained from
214 the component scores scaled so as to have variance proportional to their
215 corresponding eigenvalues. Euclidean distance was chosen because it is
216 appropriate with quantitative descriptors and enhances differences among objects

217 by squaring (Legendre & Legendre 1998). Ward's method was applied in clustering
218 because it minimizes variance intra-clusters and maximizes variance inter-
219 clusters. Homogeneous clusters of triplets were then defined for each lake by
220 cutting dendrograms at distance two (Figs S7 and S8). Sensitivity of clustering
221 results to the choice of the method is evaluated in Table S5. Each lakeshore forest
222 plot was finally considered as a part of a cluster if the majority of the triplets in
223 which it was included belonged to that cluster. Two plots (one per lake) could not
224 be assigned to any cluster because their corresponding triplets were equally
225 distributed amongst more than one cluster (Fig. 1).

226 Crossdated spruce and fir logs were subsequently assigned to the nearest
227 lakeshore plot and then to the corresponding cluster. To limit data fragmentation
228 along the shoreline, logs assigned to a series of less than three contiguous plots
229 belonging to the same cluster were discarded from the subsequent analyses (i.e.
230 logs facing plots 9 and 10 at L18, and those facing plot 1 at L20; Fig. 1). Cluster 3
231 at L18 was also divided into two sub-clusters for the analysis of the subfossil logs
232 as, even if today the lakeshore plots are characterized by a similar forest, their
233 histories showed some differences (cluster 3A contains logs assigned to plots 6-8
234 and 11-15, while cluster 3B contains those assigned to plots 24-32; see Figs 1 and
235 3).

236 Tree-ring dating of charred subfossil logs (see Fig. S9 for some examples), along
237 with concurrent variations of log abundance, allowed us to determine when
238 wildfires affected the lakeshore forest of each cluster during the last millennium.
239 Each identified fire was assigned to the date of its most recent evidence

240 considering that some subfossil logs may have lost their charred marks and may
241 have been more or less eroded. Fire evidences are the outermost tree-ring dates
242 of charred logs or of subfossil logs in proximity of a charred specimen and
243 preceding a clear discontinuity in the temporal sequence of outermost tree-ring
244 dates. A detailed analysis of more than 1600 logs from five lakes indicates that our
245 estimated fire dates may precede the actual dates by a few years because an
246 average of three outermost tree-rings per century is lost through decay per log
247 (Gennaretti, Arseneault & Bégin 2014). The relative severity of the detected
248 wildfires was evaluated from their impacts on the number of subfossil logs
249 produced by the lakeshore forest and preserved in the adjacent littoral zone. A
250 typical response to fire includes a peak in subfossil log recruitment (this peak may
251 be attenuated if several killed trees on the shore decompose in an upright position),
252 followed by a recruitment reduction as trees grown up after fire have to reach a
253 minimum height before being available to generate subfossil logs from their upper
254 stem portions (Gennaretti, Arseneault & Bégin 2014). Here, a complete interruption
255 or a strong reduction of log recruitment for several years after a fire were used as
256 an indicator that most of the trees were killed and that the stand developed as an
257 even-aged postfire cohort.

258 The subfossil records of both sites were divided into discrete fire-free intervals
259 delineated by the estimated wildfire dates. Three fire-free intervals were identified
260 at both sites: AD 682-1251, 1251-1624 and 1729-1994 at L18, and 728-1207,
261 1207-1592 and 1592-2002 at L20. The recruitment rates of subfossil logs (number
262 recruited per 100 years per 100 m of shoreline based on their outermost tree-ring

263 dates) were computed for each of these intervals in order to compare the relative
264 openness of the lakeshore forest cover between clusters at each site (Figs 3 and
265 4). Assuming that the number of subfossil logs produced by the lakeshore forest
266 in a cluster is directly related to the density of large trees during a fire-free interval,
267 which in turn depends on the pathway of forest recovery following the last fire,
268 regular and high recruitment rates were attributed to a dense mature forest cover
269 and low rates to an open cover. However, because subfossil logs progressively
270 decay, these recruitment rates fade out when moving backward in time and cannot
271 be compared among different fire-free intervals. To allow this comparison, we used
272 the presence at each site of a cluster that has escaped severe fires over the entire
273 study period (see results). For each site, we standardized the number of subfossil
274 logs that were living each year per 100 m of shoreline in each fire-affected cluster
275 by dividing it with the number of logs in the cluster that had escaped severe fires.
276 These ratios show the relative openness of the lakeshore forest cover among fire-
277 free intervals and clusters (Fig. 5).

278 The smoothed average age-related growth curves of the black spruce subfossil
279 logs recruited during different fire-free intervals were compared among clusters
280 and fire-free intervals at each lake. For each interval and cluster, all individual ring
281 width series were aligned according to cambial age and averaged. Firs (16 logs at
282 L20) and specimens with missing pith (seven and 14 logs at L18 and L20,
283 respectively) were discarded. A spline with a 50% frequency cut-off and time-
284 varying response (starting from 10 years and increasing by one each year; Melvin
285 et al. 2007) was then used as smoothing algorithm to generate the smoothed

286 growth curves. These growth curves allowed us to detect the most important
287 temporal and spatial shifts of lakeshore forest growth in response to disturbances
288 and climate change (Figs 6, 7, S10 and S11).

289 **Results**

290 Partitioning of the present-day forest

291 Principal component and cluster analyses identified three and two clusters of
292 homogeneous lakeshore forest stands at L18 and L20, respectively (Figs 1 and 2).
293 At L18, the first principal component (31% of the variance explained) differentiated
294 cluster 1 from clusters 2 and 3, based on its higher percentages of fir, higher
295 densities of snags and stumps, and higher densities of living trees, especially of
296 small size classes (Figs 2 and S3 and Table 2). The second principal component
297 (24% of the variance explained) differentiated cluster 3 from clusters 1 and 2,
298 based on its lower densities of large-sized trees (≥ 12 cm DBH) and higher
299 densities of saplings and seedlings that together influenced the coefficient "b" of
300 the power function models (Figs 2 and S3 and Table 2). Compared to cluster 1
301 and 3, cluster 2 displayed intermediate characteristics and lower densities of
302 saplings and seedlings. At L20, the two clusters differed mainly by their first
303 principal component scores (35% of the variance explained). In comparison to
304 cluster 2, cluster 1 was associated with higher fir percentages, higher basal areas
305 of dead trees and higher densities of regeneration, dead trees and living trees ≥ 2
306 cm DBH (Figs 2 and S4 and Table 2).

307 Past fires, subfossil recruitment and lakeshore tree density

308 At least four wildfires of varying severities affected the lakeshore forest at L18
309 during the last millennium (Fig. 3). Cluster 1, which is today characterized by
310 denser forest with more abundant fir, was clearly less severely affected by these

311 wildfires than clusters 2 and 3, and escaped stand-replacing fires over at least the
312 last 1200 years. A fire event completely interrupted the recruitment of subfossil
313 logs in clusters 2 and 3B and strongly reduced the recruitment in cluster 3A at AD
314 1251, indicating severe tree mortality in the lakeshore environment. The fire may
315 have partially burned the forest of cluster 1, where the recruitment of subfossil logs
316 slightly decreased, but several individuals survived. Because fires generally
317 reduce the recruitment of subfossil logs for about 120 years in these boreal lakes
318 (Gennaretti, Arseneault & Bégin 2014), the interruption/reduction that lasted for at
319 least 200 years at clusters 2 and 3 after the AD 1251 event suggests the
320 occurrence of a second fire before about AD 1400. This presumed fire most likely
321 killed trees established after AD 1251 before they could become tall enough to
322 generate subfossil logs with diameters ≥ 4 cm. Three subsequent closely spaced
323 fires burned across the lakeshore forest of clusters 2 and 3 during the 17th and the
324 first part of the 18th century. The AD 1624 fire was identified from charred subfossil
325 logs preceding a discontinuity in the temporal sequence of *innermost* tree-ring
326 dates (i.e. several lakeshore trees established after this fire), while the AD 1674
327 and 1729 fires were identified from charred subfossil logs and discontinuities in the
328 sequence of *outermost* tree-ring dates (i.e. a break and a sudden increase in log
329 recruitment indicating that several lakeshore trees died during these fires; see
330 cluster 2 in Fig. 3). All these wildfires were less severe than the AD 1251 fire, as
331 the recruitment of subfossil logs was altered but not interrupted. Despite the fact
332 that a charred log with an outermost tree-ring in 1684 was found at the boundary
333 between clusters 1 and 2, the recruitment of subfossil logs remained high and

334 constant in cluster 1, indicating uninterrupted forest development and negligible
335 fire impact.

336 Although all clusters at L18 exhibited similar recruitment rates of subfossil logs
337 prior to the AD 1251 fire, cluster 1, which escaped severe fire disturbances during
338 the last millennium, has been subsequently characterized by much higher and
339 constant rates of recruitment of subfossil logs than clusters 2 and 3 (Fig. 3). This
340 suggests that the density of lakeshore trees was similar among clusters before AD
341 1251 and that the fires produced a long-lasting decrease of stem density at clusters
342 2 and 3. These two clusters seem to have diverged from each other following the
343 fires of the 17th and 18th centuries because cluster 2 has exhibited higher
344 recruitment rates than cluster 3 since the mid 18th century (6.5 vs 2.4 to 2.9 logs
345 per 100 years per 100 meter of shoreline). These higher rates are consistent with
346 the higher present-day density of large-sized trees (≥ 12 cm DBH) in the lakeshore
347 plots of cluster 2 as compared to cluster 3 (Table 2). At L18, an important pulse
348 followed by a reduction of subfossil log recruitment is also coincident with the large
349 Tambora volcanic eruption in AD 1815 (Figs 3 and 8).

350 Fires were less frequent at L20 than at L18, as we detected only two fire events
351 over the last millennium (Fig. 4). The only fire confirmed by charred marks on the
352 logs occurred at AD 1592 and almost completely burned the lakeshore forest of
353 cluster 2, as based on a severe reduction of subfossil log recruitment. The fire
354 probably stopped near plot 20, at the border between clusters 1 and 2, where we
355 found a charred subfossil log. The remaining plots of cluster 1 escaped the fire, as
356 indicated by the very regular and high recruitment rates of subfossil logs. A peak

357 of tree mortality in cluster 2 most likely indicates a previous moderate severity fire
358 at about AD 1207, even if no charred log was discovered.

359 Similarly to L18, dense present-day forest stands with high fir percentages at L20
360 have escaped stand-replacing fires over the last millennium (over at least the last
361 1400 years at cluster 1 of L20). Recruitment rates of subfossil logs have always
362 been higher at cluster 1 than at cluster 2, denoting that stem density has probably
363 been higher at cluster 1 over the entire time period covered by our study (Fig. 4).

364 The yearly ratios of subfossil log abundance in burned relative to unburned clusters
365 at each lake indicate that each fire triggered a specific trajectory of stem density in
366 the burned lakeshore clusters with varying postfire density alterations and rates of
367 recovery (Fig. 5). These effects included prompt and complete recovery to pre-fire
368 stem density (e.g. cluster 2 at L20 after the AD 1592 fire), full but progressive
369 recovery over several centuries (e.g. cluster 2 at L20 after the AD 1207 fire),
370 extremely slow and partial recovery (e.g. clusters 2 and 3A at L18 following the
371 two successive AD 1251 and ~1400 fires), persistent shift to low stem densities
372 (e.g. cluster 3B at L18 following the two successive AD 1251 and ~1400 fires), as
373 well as increased stem densities relative to pre-fire conditions (e.g. cluster 2 at L18
374 after the three fires between AD 1624 and 1729).

375 Age-related growth curves of the subfossil logs

376 The analysis of the average growth curves of the subfossil logs showed important
377 climate- and fire-induced impacts on the lakeshore forest growth during the last
378 millennium. Fires reduced lakeshore stem density and, as a consequence, the

379 juvenile growth of trees (i.e. for young cambial ages) was faster in the burned
380 lakeshore clusters than in the unburned ones (i.e. cluster 1 at both sites) during
381 the subsequent fire-free intervals (see the juvenile growth of the subfossil logs of
382 clusters 2 or 3 in comparison to that of logs of cluster 1 in Figs 6 and 7).
383 Furthermore, the average growth curves showed that, in clusters that escaped
384 severe fire disturbances over the entire time period covered by the study (i.e.
385 cluster 1 at both sites), trees grew faster during Medieval times than afterward,
386 suggesting the influence of a warmer climate (Figs S10 and S11).

387 **Discussion**

388 *Fire vs. trajectories of forest structure and composition*

389 The long-term perspective, along with the high spatial and temporal resolutions
390 provided by this study, allowed the verification of whether or not variations in the
391 present-day structure and composition of contiguous lakeshore forest stands in the
392 Eastern Canadian taiga correspond to their respective fire histories during the last
393 millennium. Our multivariate analysis of the current lakeshore forest vegetation
394 revealed three and two homogeneous clusters with different forest compositions
395 and structures at L18 and L20, respectively, even if these forests only face 1170
396 and 990 m of shore (Figs 1 and 2 and Table 2). The dendrochronological analysis
397 of the subfossil logs collected in the littoral zone facing these clusters confirmed
398 that they experienced site-specific fire histories over the last millennium that locally
399 influenced tree density and tree growth (Figs 3 to 7), thus shaping the present-day
400 landscape diversity. Unfortunately, our results do not allow reconstructing past
401 variations in species abundance within the studied lakeshore forests (see "Study
402 sites and sampling"). However, all the lakeshore segments that were affected by
403 fire during the last millennium are today characterized by more open forests with
404 less dead wood and lower percentages of balsam fir than the unburned stands
405 (Table 2), even despite the most recent fire occurring about 300 to 400 years ago.
406 Consequently, our results support the hypothesis that fire impacts may persist for
407 several centuries in the Eastern Canadian taiga and that present-day landscapes
408 are the outcome of the progressive fire-induced breakup (i.e. forest cover opening
409 and balsam fir exclusion) of a previously closed-crown spruce-fir vegetation zone

410 (Sirois 1997; Arseneault & Sirois 2004; Ali et al. 2008; de Lafontaine & Payette
411 2010).

412 An important result of this study is the large variability in the postfire forest structure
413 trajectories in the lakeshore environment over the last millennium. Although it is
414 generally assumed that black spruce is a fire-adapted species due to its serotinous
415 cones, our results suggest that the classical model of postfire forest recovery in
416 black spruce forests (i.e. fast recovery to pre-fire stem densities) is over-simplistic
417 because each fire can trigger a specific forest structure trajectory characterized by
418 a different stem density reduction and a different rate of recovery. Despite the fact
419 that an increase in stem density relative to pre-fire conditions occurred at cluster 2
420 of L18 following the three low to moderate severity fires between AD 1624 and
421 1729, all other fires decreased stem densities or maintained the low densities
422 triggered by previous fires and the rates of recovery were extremely variable (Fig.
423 5). All time periods of fire-induced low stem densities reconstructed from low
424 recruitment rates of subfossil logs (i.e. AD 1207-1592 at cluster 2 of L20 and AD
425 1251-1994 at clusters 2 and 3 of L18) are confirmed by concomitant faster juvenile
426 growth of spruce trees in burned clusters (Figs 6 and 7). Indeed, black spruce
427 grows faster in open postfire woodlands than in dense postfire or old-growth
428 forests stands due to less intense competition (Fourrier, Pothier & Bouchard 2013).

429 Although we could not identify the processes that have influenced the variability of
430 the postfire forest trajectories, several circumstances may have contributed to
431 hamper rapid postfire recovery to pre-fire stem densities, especially in the taiga
432 context where severe climate conditions may limit spruce growth and reproduction

433 and may lead to significant tree mortality events (Bond-Lamberty et al. 2014). For
434 example, high fire severity and a short time interval between the severe AD 1251
435 fire and the subsequent supposed fire prior to AD 1400 may explain the low stem
436 densities that have characterized the last 750 years in the clusters 2 and 3 of L18
437 (Fig. 5). Unfavourable conditions for seed maturation during the Little Ice Age may
438 also have contributed to these low postfire tree densities. Once such open stands
439 are initiated due to insufficient postfire regeneration, tree density is likely to remain
440 low until at least the next fire because a continuous lichen mat subsequently
441 develops at the soil surface and inhibits seedling establishment (Morneau &
442 Payette 1989).

443 Contrary to black spruce, balsam fir does not retain its seeds in serotinous cones
444 and thus must re-establish from fire survivors outside burned areas (Asselin, Fortin
445 & Bergeron 2001). Consequently, balsam fir abundance and dominance increase
446 with decreasing fire recurrence across its distribution range. Paleoecological
447 studies have already suggested that balsam fir migrated northward more than
448 5000 years ago under the low-frequency fire regime of the mid-Holocene
449 (Carcaillet & Richard 2000) and that an increased fire frequency subsequently
450 reduced its abundance in the taiga of Eastern Canada (Sirois 1997; Arseneault &
451 Sirois 2004; Boucher, Arseneault & Héту 2006; Ali et al. 2008; de Lafontaine &
452 Payette 2010). Indeed, subfossil trunks buried in peat and alluvial deposits revealed
453 that balsam fir occurred much more frequently prior to 4000 BP than afterward (Sirois
454 1997; Arseneault & Sirois 2004; Boucher, Arseneault & Héту 2006). Our results did
455 not allow the reconstruction of past variations in fir abundance from direct field

456 evidence because very few firs were found among the subfossil logs (see "Study
457 sites and sampling" and Fig. S2). However, at both of our study sites, all lakeshore
458 clusters that experienced at least one severe fire exhibited low fir percentages (0-
459 8%) and all clusters with abundant fir (i.e. more than 20%; Table 2) had escaped
460 fire or were only marginally affected by fire over remarkably long time intervals of
461 more than 1200 years (Figs 3 and 4). This exclusive and systematic high fir
462 abundance in the present-day unburned forest remnants strongly supports the idea
463 that balsam fir is out of phase with the late Holocene fire regime and the associated
464 climate and that fir has persisted mainly in unburned refugia.

465 *Climate change impacts*

466 Despite the fact that fire disturbance has been the dominant driver of change in
467 forest stem density and growth over the past millennium, climate variability was
468 also important. Recent climate reconstructions indicate that a well-defined
469 Medieval Climate Anomaly occurred at about AD 900-1250 in the North American
470 taiga and forest tundra, followed by a progressive decrease of summer
471 temperatures down to the coldest period of the last millennium, which occurred
472 during the first half of the 19th century (Viau, Ladd & Gajewski 2012; Pages 2k
473 Consortium 2013). A reconstruction of summer temperatures from tree-ring widths
474 of more than 1700 subfossil logs collected in six lakes of our study area, including
475 L18 and L20 (Gennaretti et al. in press), closely reproduces these trends, also
476 indicating that the cold period of the early 1800's was triggered by the successive
477 AD 1809 (unknown volcano) and AD 1815 (Tambora) volcanic eruptions (see also
478 Fig. 8). Both of these opposed climate anomalies influenced forest dynamics at

479 our study sites. At the unburned clusters (i.e. cluster 1), where age-related growth
480 trends have not been disturbed by fire events and consequent changes in forest
481 density, spruce trees grew faster during the Medieval Anomaly than afterward,
482 reflecting its warmer climate (Figs S10 and S11). This period was also
483 characterized by relatively high stem density at all clusters of both sites (Fig. 5).
484 However, our data do not allow the differentiation of the role of the warmer climate
485 or of the possible absence of previous fire disturbances on these high stem
486 densities for this older period. At the other extreme of the climatic gradient, the
487 precise correspondence between the AD 1809-1815 eruptions, a sharp tree growth
488 reduction, and a peak in lakeshore tree mortality at our sites (Fig. 8), confirms that
489 volcanoes forced this cold episode and influenced forest dynamics. At L18, this
490 episode of tree mortality was less severe in cluster 2 than in clusters 1 and 3 (Fig.
491 3), possibly reflecting its more sheltered position along concave lakeshore
492 segments (Fig. 1). At L18, the subsequent decrease of subfossil log recruitment
493 over the 1820-1870 time period also suggests that, at this site, the most vulnerable
494 lakeshore trees died rapidly in less than about 10 years after the two eruptions,
495 thus attenuating later mortality (Fig. 8).

496 Long-term fire imprints on landscape diversity

497 Our study provides a long-term perspective that helps explain how fire disturbance
498 and time since fire have shaped the present-day landscape diversity in the Eastern
499 Canadian taiga, in the context of the generalized decrease in conifer stem density
500 that has characterized the northern boreal zone over the last 600-900 years (Payette
501 & Gagnon 1985; Sirois & Payette 1991; Payette & Morneau 1993; Lavoie & Sirois

502 1998; Girard, Payette & Gagnon 2008; Payette, Filion & Delwaide 2008). The high
503 variability in the postfire stem density reduction and in its rate of recovery displayed
504 by our lakeshore clusters since the first detected fire at about AD 1207 (Fig. 5)
505 suggests that present-day landscapes (see Fig. S1) are mosaics of forest patches
506 representing different times since fire along specific postfire forest structure
507 trajectories. In the taiga, open woodlands would have experienced at least one
508 severe fire since the Medieval Climate Anomaly, often reducing tree densities or
509 maintaining low densities triggered by previous fires and excluding balsam fir from
510 stands where the species was still present. In addition some important implications
511 can be deduced from the fact that present-day forest stands reflect the past fire
512 history even if the last fire occurred at least 300-400 years ago. First, it indicates that
513 several centuries are needed for stem density and forest composition to converge
514 between forest stands that experienced or escaped fire. Second, it proves that the
515 taiga contains two types of old-growth forest stands (i.e. some centuries old) on well-
516 drained soils (dense vs open old-growth forest stands) depending on whether or not
517 they burned during the last 800 years.

518 It has already been observed that the long-term absence of severe disturbances
519 can lead to the decline of forest ecosystems and to the reduction of forest biomass
520 in several biomes (Wardle, Walker & Bardgett 2004). In this study, we observed
521 rather that sites that did not severely burn during the last 1200 years had higher
522 stem density, tree basal area and tree species diversity than sites that burned 2-5
523 times over the same time period. Even if these dense stands are relict from
524 previous more favourable climate conditions, they nevertheless indicate that

525 relatively high stem densities can be maintained over at least a millennium in
526 absence of fire. Extrapolating the recent regional burn rate of about 0.2% per year
527 (based on the 1980-2010 fire data; Boulanger et al. 2012) to the last millennium,
528 and assuming that stand age distribution is negative exponential (Johnson 1992),
529 stands older than 1000 years would represent only about 15% of the present-day
530 landscape. We conclude that the forest decline stage linked to the absence of
531 disturbances is uncommon in the northern taiga of Eastern Canada.

532 The increase in fire occurrence and area burned that is expected for the Eastern
533 Canadian taiga over the 21st century (Boulanger et al. 2013) is likely to impact
534 landscape diversity in our study area. Our data suggest that higher burn rates will
535 accelerate the regression of balsam fir and will increase the abundance of more
536 open woodlands, unless climactic thresholds that once allowed the development
537 of dense spruce-fir stands are surpassed, improving the forest regeneration
538 processes (Sirois, Bonan & Shugart 1994). In addition, considering that the jack
539 pine eastern range limit is located only 10 km west of site L18, and that pine has
540 faster juvenile growth, earlier sexual maturity, and higher seed retention in
541 serotinous cones than black spruce (Rudolph & Laidly 1990), jack pine is likely to
542 expand into our study region with an increased fire frequency. If a pine expansion
543 occurs, then open spruce woodlands will be likely shift to denser pine-spruce
544 stands after fire with pine abundance increasing after repeated fires, as observed
545 within the current pine range limit (Lavoie & Sirois 1998; Le Goff & Sirois 2004).

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554 **Data Accessibility**

555 All data from the manuscript will be archived in "Figshare" (the DOI is still to be
556 obtained).

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719 **Tables**

720 **Table 1.** Variables used to describe present-day forest structure and composition
 721 in triplets of sampling plots at the sites L18 and L20

Variable ID	Unit	Description
Nliv	No. ha ⁻¹	Density of living trees comprising saplings and seedlings
Ntot	No. ha ⁻¹	Density of living trees comprising saplings and seedlings plus snags and stumps
Nreg	No. ha ⁻¹	Density of saplings and seedlings
Nliv2	No. ha ⁻¹	Density of living trees ≥ 2 cm DBH
Nliv6	No. ha ⁻¹	Density of living trees ≥ 6 cm DBH
Nliv12	No. ha ⁻¹	Density of living trees ≥ 12 cm DBH
Ndead	No. ha ⁻¹	Density of snags and stumps
Ncwd	No. ha ⁻¹	Density of coarse woody debris pieces on the floor
BAliv	m ² ha ⁻¹	Basal area of living trees ≥ 2 cm DBH
MeanBAliv	m ² tree ⁻¹	Average basal area per living tree ≥ 2 cm DBH
BAdead	m ² ha ⁻¹	Basal area of snags and stumps
MeanBAdead	m ² tree ⁻¹	Average basal area per snag or stump
F%reg	%	Percentage of fir in the sapling and seedling
F%	%	Percentage of fir among living trees ≥ 2 cm DBH
T%	%	Percentage of tamarack among living trees ≥ 2 cm DBH
Age	years	Average minimum time since the last stand-replacing fire of the three plots
a	-	Coefficient "a" of the power function model describing the stand size structure of living trees*
b	-	Coefficient "b" of the power function model*

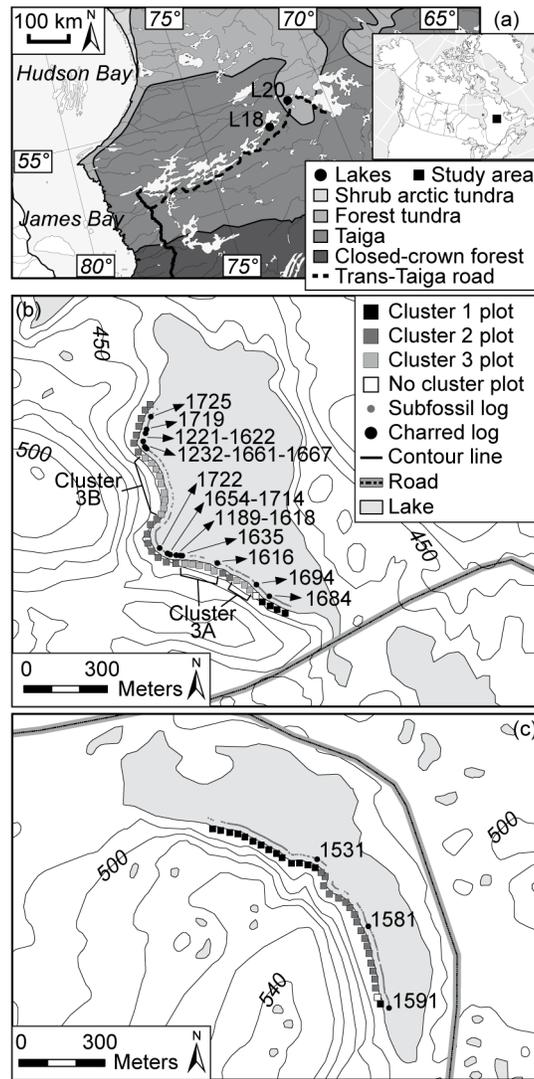
* $y = a * x^{(b)}$ where y is the number of individuals per hectare and x is the central value of 2-cm size classes (Tables S1 and S2)

722

723 **Table 2.** Description of the lakeshore forest of each cluster at L18 and L20.
724 Distinguishing traits are in bold (i.e. values of the variables contributing the most
725 to the discrimination of the clusters of homogeneous lakeshore forest according to
726 our multivariate analysis; see Figs 2, S3 and S4). Standard deviations (SD) refer
727 to variability among triplets of sampling plots. Variables are described in Table 1

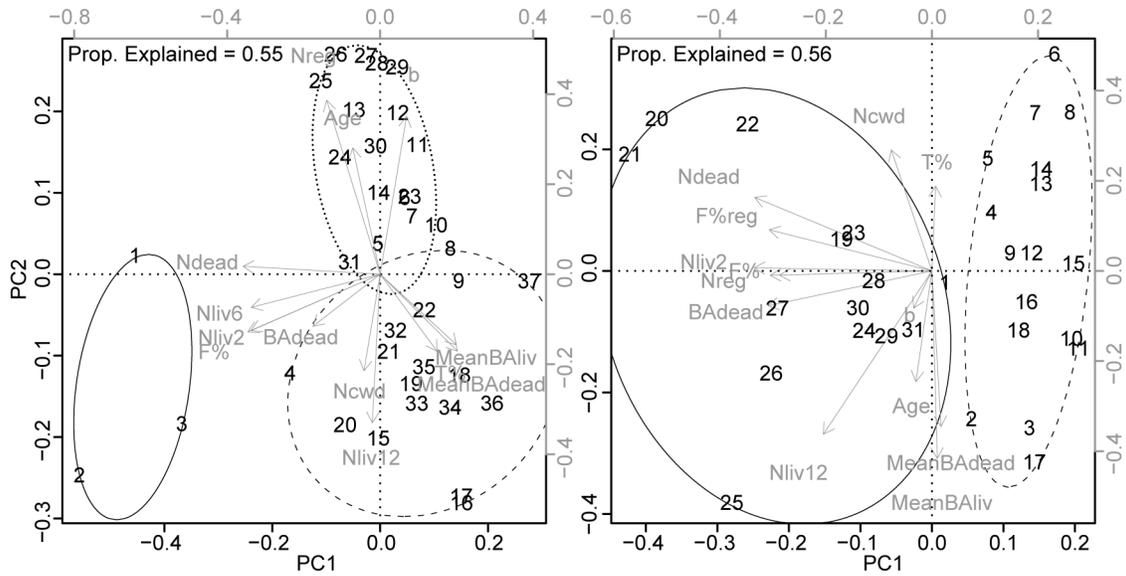
Variable	L18			L20	
	Cluster 1 (mean ± SD)	Cluster 2 (mean ± SD)	Cluster 3 (mean ± SD)	Cluster 1 (mean ± SD)	Cluster 2 (mean ± SD)
Nliv (No. ha ⁻¹)	22578 ± 9255	11671 ± 2640	25806 ± 6088	24393 ± 5432	15396 ± 4337
Ntot (No. ha ⁻¹)	23778 ± 9103	12171 ± 2714	26457 ± 6120	25671 ± 5672	16135 ± 4370
Nreg (No. ha ⁻¹)	17889 ± 9083	9225 ± 2367	23500 ± 5931	19964 ± 5156	12608 ± 4197
Nliv2 (No. ha ⁻¹)	4689 ± 435	2445 ± 758	2306 ± 548	4429 ± 418	2788 ± 488
Nliv6 (No. ha ⁻¹)	2244 ± 271	1182 ± 262	1237 ± 308	2036 ± 385	1351 ± 250
Nliv12 (No. ha ⁻¹)	544 ± 19	482 ± 207	296 ± 142	421 ± 103	273 ± 123
Ndead (No. ha ⁻¹)	1200 ± 219	500 ± 166	651 ± 95	1279 ± 379	739 ± 166
Ncwd (No. ha ⁻¹)	811 ± 84	757 ± 335	580 ± 254	610 ± 100	590 ± 116
Baliv (m ² ha ⁻¹)	18.6942 ± 1.9140	14.8115 ± 4.9150	10.8277 ± 2.6050	18.1739 ± 2.8759	11.4771 ± 2.4030
MeanBALiv (m ² tree ⁻¹)	0.0040 ± 0.0001	0.0067 ± 0.0031	0.0049 ± 0.0013	0.0041 ± 0.0005	0.0041 ± 0.0006
Badead (m ² ha ⁻¹)	10.8140 ± 1.6916	6.7733 ± 1.7550	6.9507 ± 2.1521	10.4133 ± 2.4791	6.0797 ± 1.9972
MeanBAdead (m ² tree ⁻¹)	0.0090 ± 0.0002	0.0142 ± 0.0037	0.0109 ± 0.0038	0.0085 ± 0.0020	0.0085 ± 0.0027
F%reg (%)	3 ± 3	0 ± 0	0 ± 0	42 ± 21	9 ± 16
F% (%)	22 ± 4	1 ± 2	0 ± 0	28 ± 13	8 ± 9
T% (%)	0 ± 0	2 ± 2	1 ± 1	1 ± 2	2 ± 1
Age (years)	245 ± 32	226 ± 15	252 ± 13	217 ± 15	207 ± 17
a	17871 ± 9090	9220 ± 2367	23497 ± 5932	19949 ± 5159	12597 ± 4201
b	2.0 ± 0.4	2.2 ± 0.5	3.1 ± 0.5	2.2 ± 0.2	2.2 ± 0.4

728



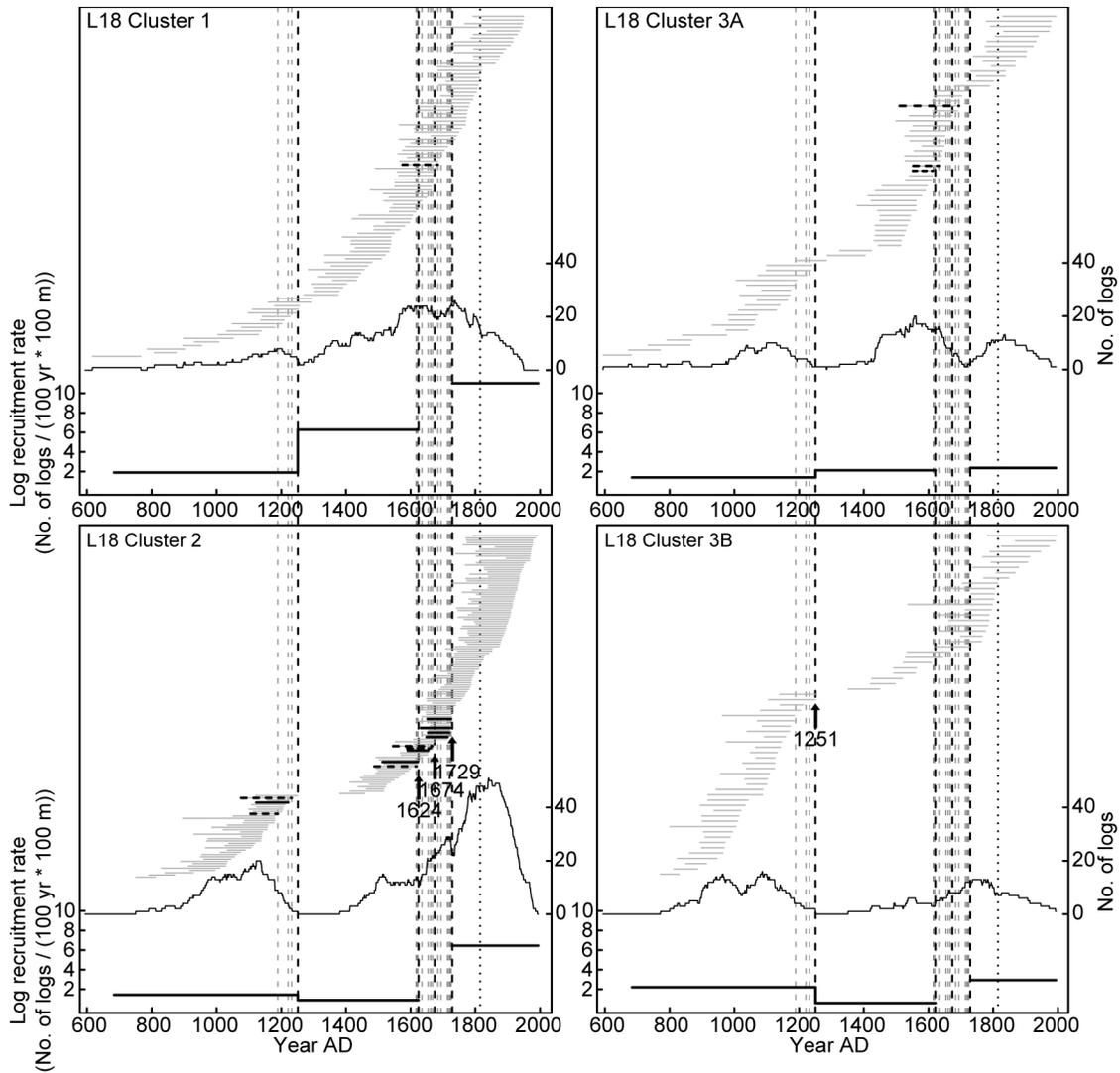
730

731 **Fig. 1.** Map of the study area in the northern taiga of Eastern Canada (a) and of
 732 lake L18 (b) and L20 (c) with plots assigned to the corresponding cluster. In b and
 733 c, the outermost tree-ring dates of charred subfossil logs are also shown. If two or
 734 more charred logs are facing the same plot, their outermost tree-ring dates are
 735 separated by a minus sign.



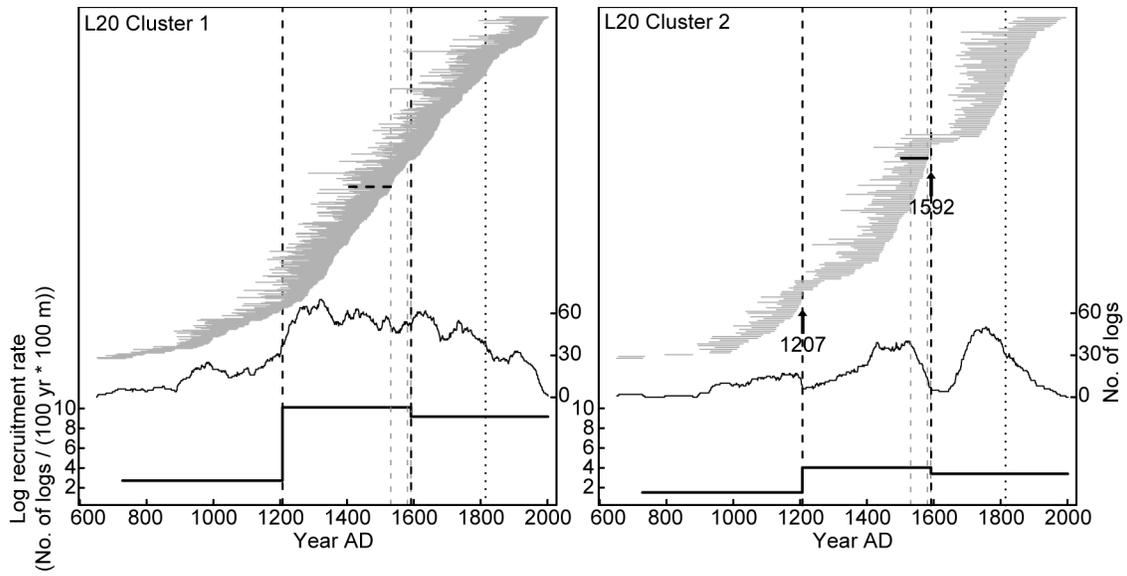
736

737 **Fig. 2.** Biplots of the first two principal components of the L18 (left) and L20 (right)
 738 PCAs. Variables (see Table 1) are in grey and triplets of plots are in black. Triplets
 739 belonging to the same cluster are enclosed in minimum spanning ellipses (solid:
 740 cluster 1; dashed: cluster 2; dotted: cluster 3).



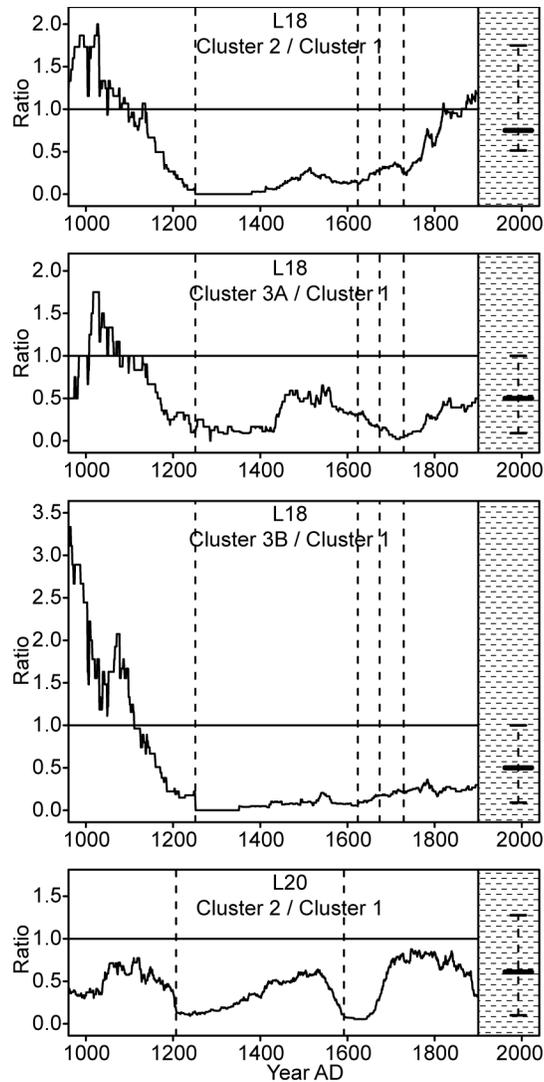
741

742 **Fig. 3.** Life spans, abundance and recruitment rate of L18 subfossil logs
 743 crossdated to the calendar year and assigned to the corresponding cluster
 744 according to their location. Each horizontal grey solid line refers to the life span of
 745 one log. Charred logs facing plots at the boundary between two cluster (horizontal
 746 black dashed lines) and other charred logs (horizontal black solid lines) are also
 747 shown, as well as the recruitment date of all charred logs in the littoral zone (based
 748 on their outermost tree-ring date; vertical grey dashed lines), the estimated wildfire
 749 dates (vertical black arrows on the most recent fire evidence and vertical black
 750 dashed lines) and the date of the Tabora eruption (AD 1815; vertical black dotted
 751 line). The thin black line at the middle of each panel shows the number of logs that
 752 were living each year. The thick black line at the bottom of each panel shows the
 753 average recruitment rate of logs during the identified fire-free interval (number
 754 recruited per 100 years per 100 m of shoreline based on the outermost tree-ring
 755 dates).



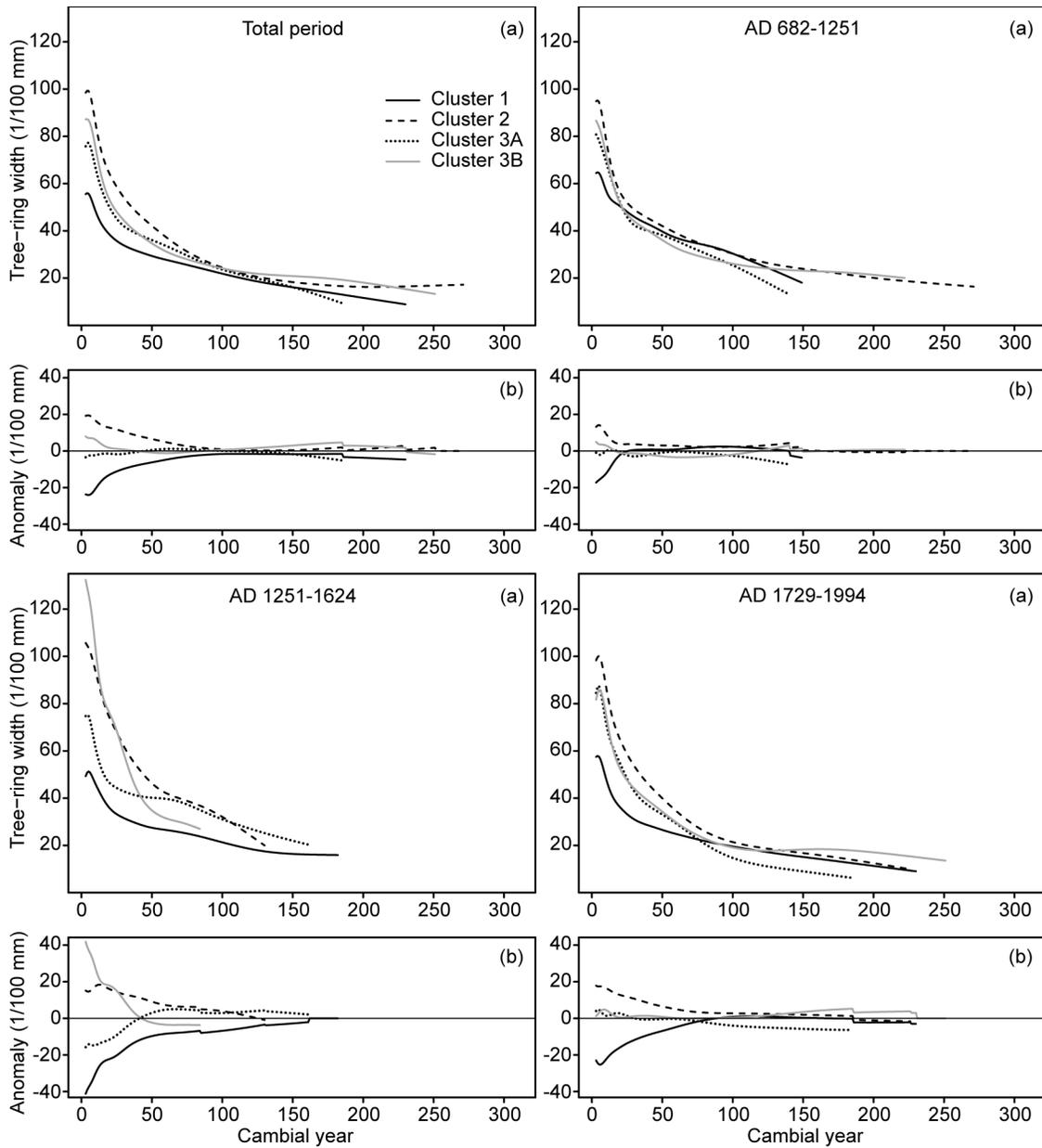
756

757 **Fig. 4.** Life spans, abundance and recruitment rate of L20 subfossil logs
 758 crossdated to the calendar year and assigned to the corresponding cluster
 759 according to their location. All symbols are as in Fig. 3.



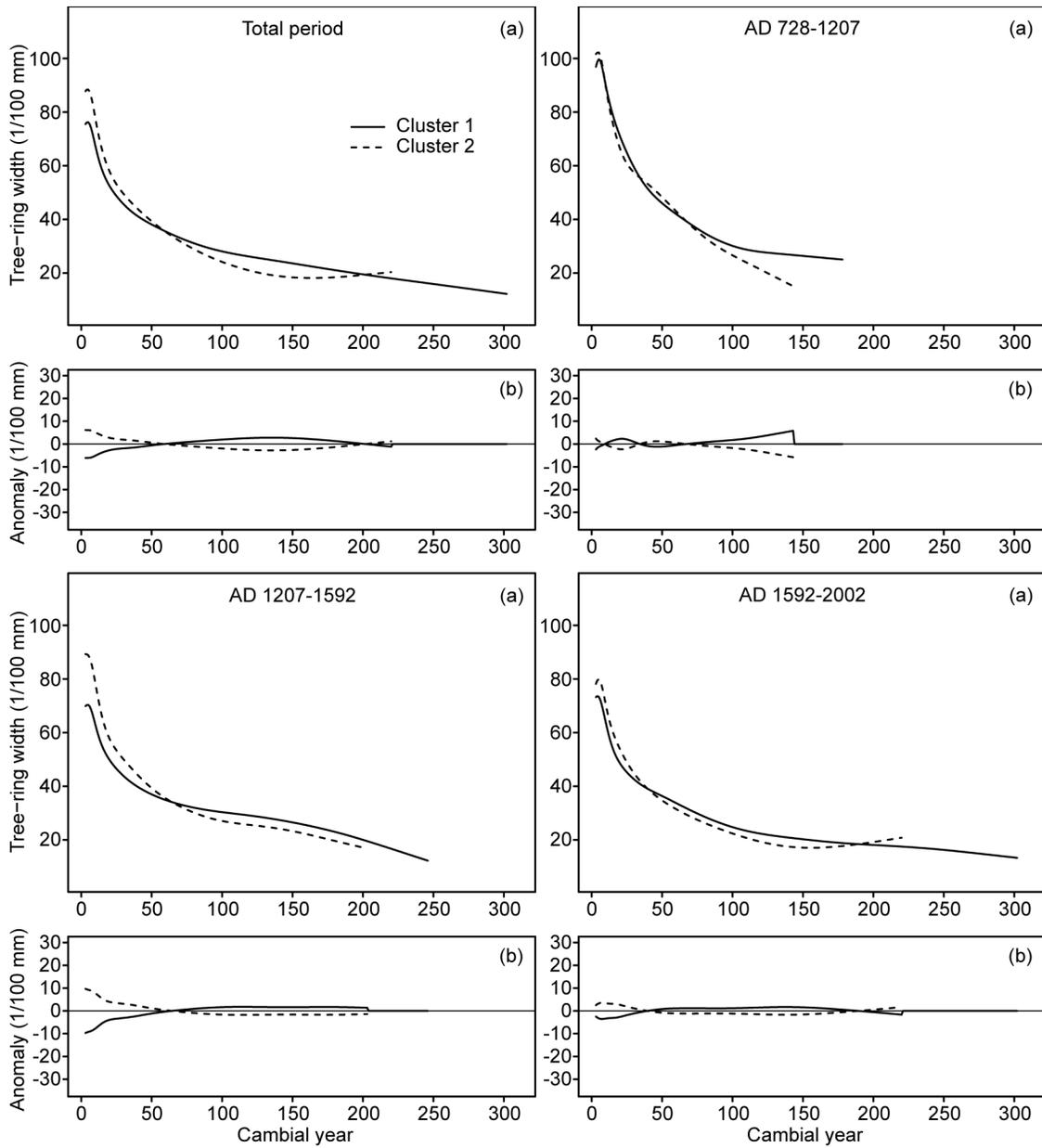
760

761 **Fig. 5.** Ratio between the number of subfossil logs that were living each year per
 762 100 m of shoreline in the cluster 2 or 3 and the number of logs living in the cluster
 763 1 at L18 (three upper panels) and L20 (bottom panel). Values older than AD 1000
 764 or more recent than AD 1900 are not shown because they are influenced by
 765 relevant losses of subfossil logs through decomposition and burial (Gennaretti,
 766 Arseneault & Bégin 2014) or by the fact that the recruitment of subfossil logs in the
 767 littoral zones is still ongoing, respectively. The estimated wildfire dates at each lake
 768 (vertical dashed lines) and the 5th, 50th and 95th percentiles of the ratios between
 769 the density of living trees ≥ 12 cm DBH (Nliv12) in the triplets of sampling plots
 770 belonging to the corresponding clusters (bold horizontal line and whiskers) are
 771 shown.



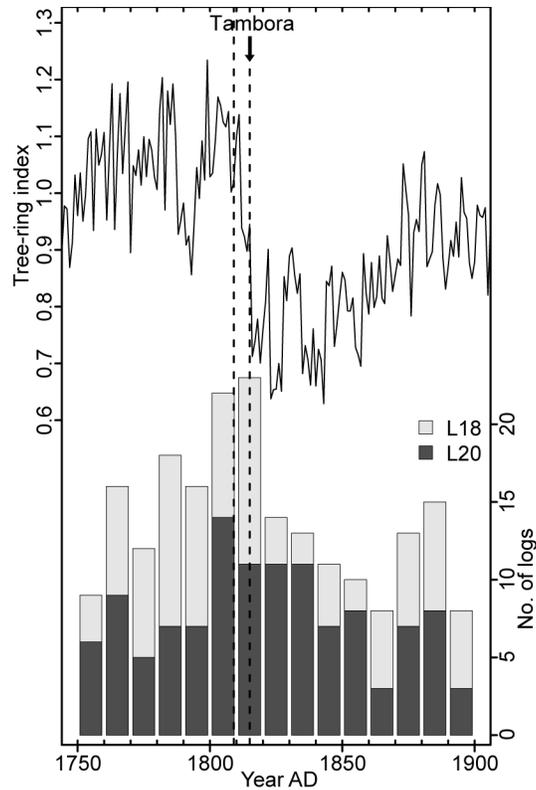
772

773 **Fig. 6.** Comparison among all clusters at L18 of the smoothed average growth
 774 curves for the subfossil logs recruited during different fire-free intervals. The "a"
 775 plots show the smoothed average growth curves, while the "b" plots show the
 776 growth anomalies calculated by subtracting the average of all clusters from the
 777 curve of each cluster. The legend in the first "a" plot refers to the other plots as
 778 well.



779

780 **Fig. 7.** Comparison between the two clusters at L20 of the smoothed average
 781 growth curves for the subfossil logs recruited during different fire-free intervals.
 782 The plots "a" and "b" are as in Fig. 6.



783

784 **Fig. 8.** Effect of the Tambora eruption on tree-growth and mortality at L18 and L20.
 785 The plot shows the average of the two local tree-ring chronologies (RCS-
 786 standardized; Esper et al. 2003) developed with the ring-width series of the L18
 787 and L20 subfossil logs (black solid line), as well as the dates of the Tambora and
 788 of the earlier AD 1809 eruptions (vertical dashed lines), and the number of
 789 subfossil logs recruited at L18 and L20 (based on their outermost tree-ring dates)
 790 per each 10-year class over the analyzed time period.

791 **Supporting information**

792 Additional supporting information may be found in the online version of this article:

793 **Table S1.** Power function models describing the stand size structure of triplets of
794 plots at L18.

795 **Table S2.** Power function models describing the stand size structure of triplets of
796 plots at L20.

797 **Table S3.** Correlation matrix of the variables used to characterize the lakeshore
798 forest at L18.

799 **Table S4.** Correlation matrix of the variables used to characterize the lakeshore
800 forest at L20.

801 **Table S5.** Sensitivity of clustering results to the choice of the method.

802 **Fig. S1.** Photo from a helicopter of a typical area of the taiga zone.

803 **Fig. S2.** Flowchart highlighting data and analyses.

804 **Fig. S3.** Component loadings for L18 PCA.

805 **Fig. S4.** Component loadings for L20 PCA.

806 **Fig. S5.** L18 PCA biplots.

807 **Fig. S6.** L20 PCA biplots.

808 **Fig. S7.** Cluster dendrogram for L18 triplets of plots.

809 **Fig. S8.** Cluster dendrogram for L20 triplets of plots.

810 **Fig. S9.** Examples of charred subfossil logs.

811 **Fig. S10.** Comparison among fire-free intervals of the growth curves of the
812 subfossil logs for each cluster at L18.

813 **Fig. S11.** Comparison among fire-free intervals of the growth curves of the
814 subfossil logs for each cluster at L20.