

1 **Full title: Driving factors of conifer regeneration dynamics in eastern Canadian boreal old-**
2 **growth forests**

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4 **Short title: Conifer regeneration in boreal old-growth forests**

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33

34 **Abstract**

35 Old-growth forests play a major role in conserving biodiversity, protecting water resources,
36 sequestering carbon, and these forests are indispensable resources for indigenous societies. To
37 preserve the ecosystem services provided by these boreal ecosystems, it becomes necessary to
38 develop novel silvicultural practices capable of emulating the natural dynamics and structural
39 attributes of old-growth forests. The success of these forest management strategies depends on
40 developing an accurate understanding of natural regeneration dynamics. Our goal was therefore
41 to identify the main patterns and the drivers involved in the regeneration dynamics of old-growth
42 forests, placing our focus on boreal stands dominated by black spruce (*Picea mariana* (L.) Mill.)
43 and balsam fir (*Balsam fir* (L.) Mill.) in eastern Canada. We sampled 71 stands in a 2200 km²
44 study area located within Quebec's boreal region. For each stand, we noted tree regeneration
45 (seedlings and saplings), structural attributes (diameter distribution, deadwood volume, etc.), and
46 abiotic (topography and soil) factors. We observed that secondary disturbance regimes and
47 topographic constraints were the main drivers of balsam fir and black spruce regeneration.
48 Furthermore, the regeneration dynamics of black spruce appeared more complex than those of
49 balsam fir. We observed distinct phases of seedling production first developing within the
50 understory, then seedling growth when gaps opened in the canopy, followed by progressive
51 canopy closure. Seedling density, rather than the sapling density, had a major role in explaining
52 the ability of black spruce to fill the canopy following a secondary disturbance. The density of
53 balsam fir seedlings and saplings was also linked to the abundance of balsam fir trees at the stand
54 level. This research helps explain the complexity of old-growth forest dynamics where many
55 ecological factors interact at multiple temporal and spatial scales. This study also improves our

56 understanding of ecological processes within native old-growth forests and identifies the key
57 factors to consider when ensuring the sustainable management of old-growth boreal stands.

58
59 **Keywords:** black spruce, forest ecology, fire, habitat, natural disturbances, population dynamic,
60 seedlings, spruce budworm, succession, sustainable forest management, uneven-aged stands,
61 restoration.

62 **Introduction**

63 The global extent of native old-growth forest has declined markedly over the past few centuries
64 through a cumulative and increasing impact from anthropic activities within these forest
65 landscapes (1–3). The boreal forest, most of which is situated in Canada and Russia, is currently
66 the largest reserve of natural forest on our planet (3). Boreal old-growth forest has also
67 experienced rapid loss over the last centuries (1,4,5). The remaining old-growth forests are
68 critically important to biodiversity, water resources, carbon sequestration and storage, and these
69 stands remain integral elements of indigenous societies and even human health (3,6). The
70 sustainable management of boreal forests has a primary goal of protecting the remaining old-
71 growth forests. Restoring the integrity of intact forests is also an urgent issue; this is especially
72 true in Fennoscandia where old-growth forests have been almost completely eliminated (7). We
73 are therefore facing a critical situation where novel silvicultural practices and restoration
74 strategies are now priorities in the context of the global biodiversity crisis, climate change, and
75 forest sustainability.

76 Effective forest restoration strategies require an accurate understanding of the natural dynamics
77 of old-growth forests. Tree regeneration is an essential process in forest ecosystems to ensure the
78 persistence and resilience of forest stands when subjected to various disturbances (8,9). As such,

79 forest science is placing increased importance on understanding tree regeneration following
80 natural and anthropic disturbance (e.g., 10–16). However, regeneration dynamics in old-growth
81 forests remain an understudied subject in ecology; this absence is particularly true for the boreal
82 biome. Moreover, due to the scarcity of old-growth stands in many boreal regions, conducting
83 studies related to this subject is often challenging, given the lack of reference sites. This need for
84 baseline data underscores the important scientific value of the boreal biome in eastern Canada
85 where some regions still contain large intact stands of forest as intensive forest management
86 practices only began relatively recently, i.e., since the 1960s (17,18). The study of regeneration
87 dynamics in the boreal old-growth forests of eastern Canada thus represents a benefit for all
88 boreal regions, especially those where these ecosystems have been almost completely eliminated.

89 Black spruce (*Picea mariana* (L.) Mill.) and balsam fir (*Abies balsamea* (L.) Mill.) are the two
90 main late-successional species in the eastern Canadian boreal forest (19). Pure black spruce or
91 mixed black spruce–balsam fir stands are the most common old-growth forest types in eastern
92 Canada (19–21). Old-growth forests are also, however, the most logged forest type in this
93 territory, leading to the rapid loss of old-growth forest surfaces (5,22,23). Pure black spruce
94 stands are under even greater pressure as this specific old-growth forest type is most selected for
95 logging given the high economic value of this species (23).

96 Both black spruce and balsam fir are well adapted to long (>150 years) periods of suppressed
97 growth in the understory (24–26). These species are also able to regenerate under their own
98 cover, mostly through vegetative reproduction for black spruce—regeneration by layers—and
99 sexual reproduction, i.e., seed origin, for balsam fir (19). Previous studies have highlighted that
100 the seedling densities of black spruce and balsam fir are similar under gaps or canopy cover (27–
101 29). When a gap in the canopy opens as a result of a secondary disturbance, the gap-fillers will
102 therefore generally be pre-established regeneration rather than seeds or layers that would have

103 established following the disturbance (30,31). Once a gap is created, the regeneration trees of
104 both species increase their vertical growth to reach the overstory relatively quickly (26,32,33).
105 However, black spruce and balsam fir differ in their ecological strategies in terms of growth,
106 sensitivity to disturbance, resistance to fire, and seed dispersal; as such, these differences should
107 vary their specific regeneration dynamics. Balsam fir regeneration is seen as being more
108 competitive than that of black spruce due to balsam fir seedlings' faster and more intense growth
109 response to canopy openings (31,34). Balsam fir, however, is more vulnerable to spruce
110 budworm (*Choristoneura fumiferana* (Mills.)) outbreaks, windthrow, and root rot than black
111 spruce (35–38). Moreover, balsam fir seeds are not adapted to fire, making this species strongly
112 dependent on the proximity of seed trees, as opposed to black spruce that is very well adapted to
113 fire events (39). Black spruce also outcompetes balsam fir on wet soils (39).

114 From the abovementioned observations, stands in the old-growth forests in eastern Canada are
115 expected to shift between black spruce–dominated stands and black spruce–balsam fir mixed
116 stands over time (21,28,40). As well, the structure of these stands varies over time (decades and
117 centuries), even though tree species' composition remains the same (40,41). At a decennial scale,
118 it is therefore likely that the characteristics of the understory, e.g., tree density or tree species
119 composition within the regeneration layer, will change significantly and rapidly due to the
120 succession of tree-mortality and canopy closure phases.

121 Understanding the regeneration process in old-growth forests is therefore critical for developing
122 management strategies and silviculture treatments that limit differences between managed and
123 unmanaged forests (42). Our study objective is to identify the main patterns and factors involved
124 in the regeneration dynamics of black spruce and balsam fir in the eastern Canadian boreal old-
125 growth forests. We hypothesize that (1) for both black spruce and balsam fir, sapling density will
126 increase in relation to the secondary disturbance–related structural changes, such as an opening of

127 the canopy and an increase in deadwood volume, and (2) the main differences between black
128 spruce and balsam fir regeneration dynamics are due to abiotic constraints and the availability of
129 proximal balsam fir seed trees.

130 **Materials and methods**

131 **Study area**

132
133 Our study involved a 2200 km² region of public forest southeast of Lake Mistassini, Québec,
134 Canada, (**Fig 1**) within an area extending between 50°07'23"N to 50°30'00"N and 72°15'00"W to
135 72°30'00"W. The study zone is crossed by the Mistassini, Ouasiemsca, and Nestaocano rivers
136 and lies within the western subdomain of the black spruce–feather moss bioclimatic domain (43).
137 Regional climate is subarctic with a short growing season (120–155 days). Mean annual
138 temperature ranges between –2.5 and 0.0 °C, and mean annual precipitation is 700 to 1000 mm
139 (43). Surficial deposits consist mainly of thick glacial tills, forming a low-lying topography
140 characterized by gentle hills that vary in altitude from 350 to 750 m asl (44). Black spruce and
141 balsam fir dominate the stands across this territory, while jack pine (*Pinus banksiana* Lamb.),
142 white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.), and
143 trembling aspen (*Populus tremuloides* Michx.) are the secondary tree species.
144 Fire is the main driver of stand-replacing disturbances on this territory (45), while spruce
145 budworm outbreaks are the principal agent of secondary disturbance (26). This territory was
146 unmanaged until 1991 when intensive timber exploitation began. The surface area harvested
147 remained relatively low until 2000; however, harvesting increased significantly after this date.

148
149 **Fig 1.** Map of the study territory showing the location of the sample sites (red filled circles). The
150 insert map indicates the location of the study territory in Quebec, Canada (red circle).
151

152 **Experimental design**

153
154 We sampled 71 stands in the study area during 2015 and 2016 and applied a stratified random
155 sampling approach. Site selection considered two main criteria: 1) that sites reflected the six
156 dominant environmental types found within the study area, according to the ecological
157 classification of the Quebec Ministry of Forests, Wildlife and Parks (MFWP) (43), and 2) that sites
158 must contain two minimal stand-age classes (80–200 years and >200 years). Environmental types
159 are defined through a combination of site potential vegetation, slope classes, surface deposits, and
160 drainage classes. The six dominant MFWP environmental types covered more than 72% of the
161 productive forest. They included: 1) balsam fir–white birch potential vegetation having moderate
162 slopes, till deposits, and mesic drainage; 2) black spruce–balsam fir potential vegetation having
163 moderate slopes, till deposits, and mesic drainage; 3) black spruce–feather moss potential
164 vegetation (BSFM) having gentle slopes, sand deposits, and xeric drainage; 4) BSFM having gentle
165 slopes, till deposits, and mesic drainage; 5) BSFM having gentle slopes, till deposits, and subhydic
166 drainage; and 6) BSFM having gentle slopes, organic deposits, and hydric drainage.

167 The age classes correspond to the successional stages of the transition process toward the old-
168 growth stage in Quebec boreal forests (20,46,47): 80–200 years (beginning of the transition toward
169 an old-growth forest) and >200 years (end of the transition to an old-growth forest). Stand age was
170 assessed by surveys in 2015 and 2016, during which we collected cores from the root collar of five
171 dominant or codominant trees per site. Tree age was determined from tree-ring counts of these
172 cores using a binocular microscope.

173 As the study area is very remote and has limited road access, we added additional logistical
174 criteria to the site selection process; we therefore sampled only sites that were accessible via the

175 existing road network. As well, our surveys were systematically placed at 125 m from the stand
176 edge to limit the influence of the edge effect.

177

178 **Plot measurements**

179 At each site, we established a permanent square plot (400 m²) as the basis for all subsequent
180 transects and subplots (**Fig 2**). We sampled all merchantable trees—trees having a diameter at
181 breast height (DBH) ≥ 9 cm—in each 400-m² plot. The attributes sampled were species, DBH and
182 vitality (alive or dead). We then surveyed all saplings—stems having a DBH < 9 cm and height
183 ≥ 1.3 m—within two 100-m² (10 m \times 10 m) subplots within the larger plot (**Fig 2**). The attributes
184 sampled for saplings were species and DBH. To count seedlings and quantify their attributes, we
185 established twenty-five 4-m² circular plots along five 25-m-long transects (5 circular
186 plots/transect) that extended out from the center of the 400-m² plot. The angle between two
187 neighboring 25 m-long transects was equal to 72°. Transect 1 was the transect oriented due north.
188 Along a transect, the first circular plot was placed 5 m from the center of the 400-m² plot, with
189 the following circular plots separated by 5 m. In each 4m² plot, we inventoried all seedlings by
190 tree species. We also measured gap length along the five 25 m-long seedling transects. We
191 defined the size of our study from other similar studies and the forest survey methods of the
192 Quebec provincial government (15,48).

193

194 **Fig 2.** Schematic representation of the experimental design used for the sample sites. N: north;
195 CWD: coarse woody debris.

196

197 In addition to these sapling transects, we surveyed coarse woody debris along four 20 m-long
198 transects that followed the edges of the 400-m² plot. We surveyed the diameter of any coarse
199 woody debris intersecting with the transect. We recorded this information for only debris having

200 a diameter >9 cm at the transect intersection. Debris items buried in the organic layer at a depth
201 >15 cm were not sampled. We determined the soil and topographic parameters by digging a soil
202 profile at the center of the 400-m² plot. We used a clinometer to measure slope.

203 **Data compilation**

204

205 We applied the following equation to estimate regeneration attributes, i.e., seedling and sapling
206 density, for black spruce and balsam fir:

$$207 \quad D = \sum_{i=1}^n R \times \frac{10\,000}{\sum_{i=1}^n S},$$

208 where D corresponds to the density per hectare, R is the number of seedlings or saplings sampled
209 in each of the n plots surveyed, and S represents the surface (in m²) of each of the n plots.

210 (40) had previously computed several structural and environmental attributes for each of the
211 sampled sites used in this study (**Table 1**). Some of these attributes relate to stand structure,
212 including merchantable tree density, basal area, Weibull's shape parameter of diameter
213 distribution (49), and gap fraction, i.e., the ratio between gap length and total transect length,
214 sensu (50). Other attributes relate to stand composition, such as the basal area proportion of
215 balsam fir. For estimating deadwood, (40) computed the volume of coarse woody debris per
216 hectare using the formula of Marshall et al. (51); however for this study, we also calculated the
217 basal area of snags, i.e., merchantable dead trees, at each study site, an attribute absent from the
218 earlier (40) study. We evaluated forest succession from the minimum time since the last fire, i.e.,
219 the age of the oldest tree sampled, and the cohort basal area proportion (CBAP; sensu 52). The
220 latter attribute is an indicator of the stand transition from an even-aged to old-growth stage, i.e.,
221 the stage where almost all trees of the first cohort following the last stand-replacing disturbance
222 have disappeared. A CBAP ≈ 0 indicates a stand where all trees belong to the first cohort, and a
223 CBAP = 1 indicates a stand where the first cohort has been entirely replaced by a new shade-

224 tolerant cohort. Finally, we detailed the topographic and pedologic characteristics of the studied
225 stands using slope and the depth of the organic horizon.

226

227 **Table 1** Description of the regeneration, stand structure, and abiotic attributes sampled at the
228 study sites as adapted from (40). “*” indicates attributes computed by (40).

229

230 **Data analysis**

231

232 First, we performed k-means clustering (53) on black spruce and balsam fir regeneration
233 attributes to identify the main patterns driving the regeneration dynamics of these two tree
234 species in eastern Canadian boreal old-growth forests. To highlight the differences between the
235 two species, we ran k-means clustering for each species separately. The clustering of black
236 spruce regeneration relied on black spruce seedling and sapling densities of all 71 sites. Similarly,
237 clustering of balsam fir regeneration also relied on balsam seedling and sapling densities;
238 however, balsam fir seedlings and saplings were absent in 24 sites. We thus removed these sites
239 for the clustering of balsam fir (47 plots remaining) to eliminate any influence from sites lacking
240 this balsam fir regeneration. For each cluster analysis, we determined the optimal number of
241 regeneration clusters using the simple structure index (SSI; 54) criterion. Separately for both
242 species, we compared regeneration as well as the structural and environmental attributes within
243 the clusters. We used analysis of variance (ANOVA) when the ANOVA conditions were fulfilled
244 (data normality and homoscedasticity) or Kruskal-Wallis nonparametric analysis of variance
245 when these conditions were not met. When ANOVA or the Kruskal-Wallis tests were
246 significant, we performed a Tukey posthoc test (55) or a Fisher’s least significant difference test
247 (56), respectively. Moreover, we also calculated Spearman’s rank correlation coefficient between
248 the regeneration and structural/environmental attributes. This latter analysis aimed to provide

249 valuable information for interpreting our results by highlighting the strength of the relationship
250 between regeneration and these various attributes.
251 All analyses were performed using R software, version 3.3.1 (57) and the *vegan* (58), *Hmisc* (59),
252 and *agricolae* (60) packages, applying a p -threshold of 0.05.

253 **Results**

254 **Black spruce and balsam fir regeneration**

255

256 For cluster analysis of black spruce regeneration, we determined eight as being the optimal
257 number of clusters (SSI = 2.23; **Fig 3**). Black spruce seedling and sapling densities differed
258 significantly between the black spruce regeneration clusters (BS; **Table 2A**). Black spruce
259 seedling density was more than 8× higher in cluster BS8, having the highest density (26 543
260 seedlings/ha), than in cluster BS1, characterized by the lowest seedling density values (3 008
261 seedlings/ha). Black spruce seedling density did not differ between clusters BS4, BS5, and BS6.
262 Regarding the density of black spruce saplings, cluster BS1—having the lowest values at 322
263 saplings/ha—contained a sapling density 12× less than cluster BS5, which had the highest density
264 of black spruce seedlings at 3 783 saplings/ha. The remaining clusters, characterized by
265 intermediate values of black spruce sapling density, aligned along a gradient. We also observed
266 significant differences in balsam fir seedling density between clusters. Concerning balsam fir
267 seedling density within the clusters of black spruce regeneration, we observed significant
268 differences, ranging from 873 seedlings/ha (lowest value, cluster BS7) to 9 720 seedlings/ha
269 (highest value, cluster BS1); however, balsam fir sapling density did not differ significantly
270 between the clusters.

271

272 **Fig 3.** (A) Density of black spruce seedlings and saplings at the 71 studied sites, grouped by
273 black spruce regeneration clusters. (B) Value of the SSI criterion according to the number of
274 clusters for black spruce using k-means clustering. Filled circle in (B) indicates the highest value
275 of the SSI criterion.

276
277 **Table 2** Mean and standard error of the regeneration attributes for (A) black spruce regeneration
278 clusters and (B) balsam fir regeneration clusters. Different letters indicate significant differences
279 at $p < 0.05$, following $a > b > c > d > e$. BS: black spruce; BF: Balsam fir

280 Regarding balsam fir regeneration, two and four clusters produced an identical SSI criterion
281 value of 1.14; **Fig 4.** Nonetheless, to obtain a more detailed evaluation of the dynamics of balsam
282 fir regeneration, we chose to use four clusters (BF; **Table 2B**). Balsam fir seedling and sapling
283 density varied markedly between clusters, and we identified significant differences for every
284 attribute between the clusters. For example, the density of balsam fir seedlings within cluster
285 BF4, marked by the highest seedling density at 18 740 seedlings/ha, was almost 20× that of the
286 cluster having the lowest density of balsam fir seedlings (957 seedlings/ha; cluster BF1).
287 Similarly, the highest density of balsam fir saplings (7 442 saplings/ha; cluster BF3) was 33× that
288 of the cluster having the lowest density (223 saplings/ha; cluster BF1). Differences between
289 clusters in terms of black spruce seedling or sapling density were less striking, although both
290 attributes differed significantly between the clusters. Black spruce seedling density varied from 1
291 900 to 14 379 seedlings/ha, whereas black spruce sapling density ranged from 470 to 1 670
292 saplings/ha (clusters BF4 and BF1, respectively, for both cases).

293
294 **Fig 4.** (A) Density of balsam fir seedlings and saplings at the 48 studied sites of the balsam fir
295 regeneration portion of the study, grouped by balsam fir regeneration clusters. (B) Value of the
296 SSI criterion according to the number of clusters for balsam fir using k-means clustering. Filled
297 red circles in (B) indicate the highest value of the SSI criterion.

298

299 **Structural and environmental attributes**

300

301 Densities of black spruce seedlings and saplings both correlated positively with gap fraction,
302 cohort basal area proportion, minimum time since the last fire, and depth of the organic horizon;
303 both correlated negatively with slope (**Table 3**). Black spruce seedling density correlated
304 negatively with basal area, balsam fir proportion, and maximum height. Balsam fir seedling and
305 sapling densities correlated positively with balsam fir proportion, coarse woody debris volume,
306 snag basal area, maximum height, and slope. Balsam fir seedling density also correlated
307 significantly with basal area. In general, correlation coefficients tended to be relatively low even
308 when significant; this was especially true for black spruce as no correlation coefficient between
309 sapling density and gap fraction exceeded 0.5. These relatively low coefficient values indicate a
310 relatively weak relationship between black spruce regeneration and the structural and
311 environmental attributes. We observed, however, elevated correlation coefficients (≥ 0.5) for
312 balsam fir in relation to several structural and environmental attributes, including balsam fir
313 proportion, slope, coarse woody debris volume (saplings only), and snag basal area (seedlings
314 only).

315
316 **Table 3** Spearman correlation coefficients between regeneration attributes and structural and
317 environmental attributes. “*” indicates significance at $p < 0.05$, “**” at $p < 0.01$, and “****” at $p <$
318 0.001.

319
320 Black spruce regeneration clusters differed significantly from each other for many attributes,
321 including basal area, gap fraction, minimum time since the last fire, slope, and depth of the
322 organic horizon (**Table 4**). We identified marked differences between the study attributes and
323 clusters; for example, basal area differed two-fold between cluster BS8 and cluster BS7, gap
324 fraction values of cluster BS1 were more than double those of cluster BS5, the minimum time
325 since the last fire varied from 146 (cluster BS1) to 249 years (cluster BS8), cluster BS8 has a 5×

326 higher slope than that of cluster BS1 (4.0% versus 23.4%, respectively), organic horizon depth
327 varied from 16.0 cm (cluster BS1) to 47.9 cm (cluster BS8). Overall, clusters BS1 and BS8 were
328 the most distinct clusters; the other clusters fell along a gradient between this pair of clusters.
329 Cluster BS1 grouped stands located on steeper sites, characterized by a shallow organic horizon,
330 a dense canopy, a high basal area, and relatively young trees. In contrast, cluster BS8 grouped
331 stands having a gentle slope as well as a thick organic horizon, open canopy, low basal area, and
332 older trees. The remaining clusters represented intermediate values between these two boundary
333 clusters.

334 **Table 4** Mean and standard error of the structural and environmental attributes for black spruce
335 regeneration clusters (BS). Different letters indicate significant differences at $p < 0.05$, following
336 $a > b > c > d$. BS: black spruce; BF: Balsam fir
337

338 We noted significant differences between balsam fir regeneration clusters in terms of balsam fir
339 proportion, coarse woody debris volume, snag basal area, and slope (**Table 5**). As with the black
340 spruce regeneration clusters, two balsam fir regeneration clusters—clusters BF1 and BF4—
341 represented opposite extremes along a gradient. Balsam fir proportion was almost 14× higher in
342 cluster BF4 (56.7%) than in cluster BF1 (4.12%). Coarse woody debris volume in cluster BF3
343 was more than double that of cluster BF1, at 61.6 and 155 m³/ha, respectively. Cluster BF4
344 contained a snag basal area that was more than triple that of cluster BF1 (14 versus 3.9 m²/ha,
345 respectively). Slope in cluster BF4 (28.4%) was also 4× higher than that in cluster BF1 (8.14%).
346 All told, cluster BF1 represented sites having a gentle slope and lower balsam fir proportion, as
347 well as a moderate coarse woody debris volume and snag basal area. Cluster BF3, on the other
348 hand, grouped sites marked by steeper slopes, as well as higher values of balsam fir proportion,
349 coarse woody debris volume, and snag basal area. As above, the remaining clusters fell between
350 these two extreme clusters. Relative to the black spruce results, however, these two balsam fir
351 clusters differed much less from each other; for example, we observed no significant differences

352 in coarse woody debris volume for clusters BF2, BF3, and BF4. This pattern implies that the
353 structural differences within the balsam fir regeneration clusters were less noticeable than those
354 observed in the black spruce stands.

355 **Table 5** Mean \pm standard deviation of structural and environmental attributes for balsam fir
356 regeneration clusters (BF). Letters indicate significant differences at $p < 0.05$, following a > b >
357 c.
358

359 **Discussion**

360 Old-growth forests are critical habitats for biodiversity and ecosystem services. A better
361 understanding of their functioning is therefore necessary for developing sustainable management
362 strategies. The results of our study highlight that regeneration in boreal old-growth forests
363 involves complex processes (non-linear, self-organized, disturbance-driven, structurally-
364 dependent, etc.) that cannot be summarized along a single linear chronosequence of forest
365 succession or by using a limited number of structural attributes as proxies. In general, we
366 observed secondary disturbance regimes and topographic constraints as the main drivers of
367 balsam fir and black spruce regeneration in our study stands. Temporal and spatial scales are
368 therefore two important factors to explain the dynamics of tree regeneration in the boreal old-
369 growth forests of eastern Canada.

370 **Dynamics of black spruce regeneration**

371
372 The dynamics of black spruce regeneration in boreal old-growth forests involve highly complex
373 processes. We observed highly variable seedling and sapling densities within the study stands,
374 and specific structural attributes defined each black spruce regeneration cluster. These
375 observations may explain the low Spearman correlation coefficients observed for black spruce, as
376 its regeneration density depends on multiple and interrelated factors (10,15,61). Moreover, the

377 black spruce regeneration clusters present no significant differences in their cohort basal area
378 proportions; therefore, differences between clusters did not result from succession toward an old-
379 growth stage. We observed a significant difference between clusters in relation to minimum time
380 since the last fire; however, this value generally exceeded 150 years, i.e., the threshold beyond
381 which tree age becomes a poor indicator of stand age in boreal forests (62,63). As such, changes
382 in stand structure due to secondary disturbance are more relevant for explaining regeneration
383 dynamics rather than invoking the process of forest succession.

384 For black spruce, differences in the structural attributes between regeneration clusters testify to
385 the influence of disturbance on seedling and sapling density (**Fig 5A**). As a starting point, cluster
386 BS7 grouped dense old-growth forest stands found on gentle to medium slopes (0–7% and 8–
387 24%, respectively). The stands in this cluster contained a moderate gap fraction and a high basal
388 area, i.e., stands that have neither been recently nor significantly disturbed. Indeed, due to their
389 narrow canopy, even dense old-growth black spruce stands can be characterized by a relatively
390 high gap fraction (41). At this cluster’s successional stage, a low black spruce sapling density and
391 high seedling density indicated a dense understory waiting for a canopy opening. This
392 distribution of trees, saplings, and seedlings agrees with previous results (41,63) that identified a
393 low suppressed tree density in old-growth stands that had a dense canopy and that were
394 dominated by black spruce. It is quite likely that most of the black spruce seedlings sampled in
395 the study sites represented layers rather than seeds. Indeed, this regeneration strategy is more
396 effective on soils where most of the organic horizon is covered by a layer of mosses and organic
397 matter (65). Moreover, these layers generally remain connected to the mother tree at this seedling
398 stage and, thus, these layers likely remain under hormonal control with the process of apical
399 dominance inhibiting their growth (lateral growth) (66–68).

400

401 **Fig 5.** Dynamics of (A) black spruce and (B) balsam fir regeneration according to secondary
402 disturbance regime and topography as derived from the identified regeneration clusters. Water
403 paintings by Valentina Buttò.
404

405 Overstory trees aged progressively and became increasingly sensitive to secondary disturbances
406 and senescence-induced mortality (69–71). Cluster BS7 became cluster BS6, and black spruce
407 sapling density began to increase. Overstory trees eventually died, creating gaps and decreasing
408 the stand basal area. Black spruce regeneration individuals, including layers, are efficient gap-
409 fillers (26,30,33), and these layers are no longer subject to apical control upon the death of the
410 mother tree. Hence, most seedlings benefited from these openings to produce to a high sapling
411 density, i.e., cluster BS6 shifted to cluster BS5. Saplings eventually reached the overstory and
412 progressively closed the canopy. The result was a significant decrease in sapling density.

413 However, we observed two different pathways depending on stand topography: gentle slopes
414 (clusters BS4 and BS3, sapling growth and canopy closure, respectively) and moderate slopes
415 (cluster BS2, sapling growth and canopy closure). Canopy closing finally led to an increased
416 stand basal area, i.e., clusters BS2 and BS3 shifted toward cluster BS7, reinitiating the cycle.

417 While we observed few changes in black spruce sapling density during this last transition,
418 seedling density increased sharply, indicating the re-establishment of a dense understory layer
419 awaiting the next canopy opening.

420 The two remaining black spruce regeneration clusters both represented two specific abiotic
421 conditions and dynamics. BS8 was defined by a gentle slope, a thick organic horizon, a high gap
422 fraction, and a low basal area. These characteristics typify stands undergoing paludification—the
423 accumulation of soil organic matter due to insufficient drainage resulting in a decreased stand
424 productivity (72,73). Paludification inhibits tree growth, but not black spruce regeneration. As a
425 result, black spruce sapling and seedling densities are often dense in paludified black spruce

426 stands, but these saplings and seedlings are unable to close the gaps caused by overstory tree
427 death (29). Paludification, however, is a process limited to specific conditions, i.e., poor drainage
428 and low temperatures; this process is not observed within well or moderately well-drained soils,
429 i.e., stands having a minimum slope (74–76), explaining, therefore, the particularity of this
430 cluster.

431 BS1, on the other hand, was defined by a shallow organic horizon, a steep slope, and a low gap
432 fraction. This cluster presented the lowest black spruce seedling and sapling densities; this pattern
433 matches prior observations in the study area that the abundance of black spruce decreases
434 progressively as slope increases, eventually being replaced by balsam fir and northern hardwoods
435 (40,45). Competition with balsam fir could explain the limited regeneration of black spruce on
436 these steepest sites. However, another factor could be the thin organic horizon that reduces the
437 survival of black spruce layers due to insufficient moisture, especially in the summer (77).
438 Nonetheless, in sufficiently drained sites of more moderate slope, black spruce regeneration in
439 old-growth forests presented a dynamic having four phases: 1) development of a dense seedling
440 bank under a closed canopy; 2) rapid seedling growth once the overstory was disturbed and
441 causing a decrease in seedling density and an increase in sapling density; 3) progressive canopy
442 closure, implying a decrease in sapling density as saplings become merchantable trees; and 4) a
443 return to phase 1.

444 **Balsam fir regeneration dynamics**

445

446 Disentangling balsam fir regeneration dynamics in the study stands presented a greater challenge
447 than that for black spruce dynamics as balsam fir regeneration was absent for 24 plots and sparse
448 for the 28 sites belonging to cluster BF1. Several factors may explain the scarcity of balsam fir
449 regeneration in most of the studied stands, such as soils being too wet or the stands having a

450 limited seed bank. In the sites characterized by relatively poor drainage, very wet and cold soils
451 inhibit balsam fir seed germination and favor black spruce layering (78,79). In the study region,
452 the fire cycle is shorter in the valley bottoms than on the hilltops (45), probably due to a later
453 snowmelt at higher elevations. Balsam fir is not a fire-adapted species, and this tree often requires
454 decades if not centuries to recolonize a burned area (80). Moreover, the dispersal of balsam fir
455 seeds is relatively limited, and its occurrence requires proximal seed trees (15,39) as evidenced
456 by the strong correlation observed between the proportion of balsam fir and the balsam fir
457 regeneration density. Shorter fire cycles in the valley bottoms may thus inhibit the colonization of
458 balsam fir in these areas of the study territory. Nevertheless, the absence of balsam fir in boreal
459 old-growth stands is common in eastern Canada (19,20,40) because of all the factors explained
460 previously; as such, sampling bias does not account for the results in our study.

461 We observed no significant difference between the balsam fir regeneration clusters in terms of
462 the minimum time since the last fire and the cohort basal area proportion. As with the black
463 spruce clusters, all balsam fir clusters represented the old-growth successional stage. Previous
464 research of balsam fir regeneration dynamics in the boreal forests of eastern Canada focused on
465 stands at the beginning of the transition toward the old-growth stage (e.g., 27,80,81). Our results
466 underscore that once the old-growth stage is attained, and if seed trees are present nearby, the
467 existing seed bank is sufficient to provide continuous regeneration of balsam fir (28,83).

468 Moreover, we observed significantly different stand slopes between the clusters, highlighting the
469 importance of topography in explaining balsam fir stand dynamics (40). These results imply that
470 as in the case of black spruce, secondary disturbance dynamics and topographic constraints drive
471 balsam fir regeneration in the old-growth forests of eastern Canada.

472 For sites located on gentle slopes (0–8%), we observed two different balsam fir regeneration
473 clusters. One cluster represented sites where balsam fir was almost absent from the canopy

474 (BF1), whereas the other cluster represented stands where balsam fir accounted for around 30%
475 of the basal area (BF2). As a result, there was almost no balsam fir regeneration in BF1, while
476 seedling and sapling densities were of moderate levels in BF2. Coarse woody debris volume was,
477 however, higher in BF2 than BF1, suggesting more recent disturbances (**Fig 5B**). This involves a
478 dynamic where boreal old-growth species composition switches between a pure black spruce
479 stand and a mixed black spruce and balsam fir stand, possibly with the presence of white birch at
480 a very low abundance (27,28). This type of dynamic is consistent with previous observations
481 (28,40). Balsam fir is a competitive species that can quickly reach the upper canopy following a
482 secondary disturbance (28,31). It is also very sensitive to disturbance, especially spruce budworm
483 outbreaks, the main secondary disturbance agent in eastern Canadian boreal forests (37,84,85).
484 Outbreaks of this insect heighten balsam fir mortality as spruce budworm larvae emergence is
485 well synchronized with balsam fir budburst. In contrast, black spruce mortality during spruce
486 budworm outbreaks is relatively low as black spruce budburst and larval emergence are poorly
487 synchronized (86). The most severe budworm outbreaks cause significant mortality of the
488 regeneration, in particular that of balsam fir (38,87,88). As a result, balsam fir abundance may
489 decrease significantly in formerly mixed black spruce–balsam fir stands following an outbreak,
490 although balsam fir may, with time, progressively recolonize the stand (20,21).

491 We observed no difference between the balsam fir regeneration clusters BF2 and BF3 in terms of
492 coarse woody debris volume and proportion of balsam fir; this pattern represents dynamics in
493 sites of moderate slope (i.e., 9–28%). However, the snag basal area was significantly higher in
494 BF3. Relative to black spruce, balsam fir is also more vulnerable to windthrow and fungal rot
495 (35,36). The presence of an important coarse woody debris volume in stands with an elevated
496 balsam fir proportion in the canopy is therefore consistent with balsam fir ecology. However, a
497 higher snag basal area can also indicate a relatively recent disturbance, as black spruce and

498 balsam fir snags often fell in the twenty years following a tree death (89). Hence, cluster BF3
499 may group recently disturbed stands marked by a dynamic balsam fir regeneration that quickly
500 fills the canopy (27,28,31). Once the canopy is closed, stand structure shifts to BF2, defined by a
501 dense seedling bank.

502 Finally, BF3 and BF4 grouped stands on steep slopes (>28%), yet that no had significant
503 structural differences between the two clusters. This result may reflect the low number of sites
504 sampled for both clusters (3 and 5 sites, respectively). However, it is also probable that they
505 represented a balsam fir regeneration dynamic similar to that observed on moderate slopes, with
506 BF3 grouping recently disturbed stands and the BF4 grouping the resilient stands. On
507 intermediate slopes, black spruce regeneration continued to compete with balsam fir, thereby
508 explaining the intermediate balsam fir seedling density in BF2. On steep slopes, however, balsam
509 fir dominated the canopy. It is therefore likely that these stands were driven by regular small- and
510 moderate-scale disturbances (26), resulting in recurrent deadwood inputs and active
511 regeneration/mortality phases.

512 **Conclusion**

513 This study determined how secondary disturbance regimes and topographic constraints explain
514 the dynamics of black spruce and balsam fir regeneration in old-growth forests. Thus, our study
515 refutes a classic assumption in forest science by demonstrating that the standard linear and
516 theoretical paradigms (successional stages) are not able to explain the complexity of old-growth
517 forest dynamics where many ecological factors interact at multiple temporal and spatial scales.
518 Second, this study provides a better acknowledgment of the importance of regeneration dynamics
519 in the boreal old-growth forests of eastern Canada. Disturbance dynamics in these ecosystems
520 are, however, defined by disturbances that vary in terms of type, frequency, and severity (26,71).

521 Thus, our results highlight the overall trends of regeneration dynamics in old-growth forests, and
522 further research is required to determine how these trends may change depending on disturbance
523 characteristics.

524 Third, sustainable forest management aims to develop new silvicultural treatments to minimize
525 differences between natural and managed stands. For this, partial cuttings offer a promising
526 solution to adapt forestry practices to act in a similar manner as secondary disturbance regimes.

527 These treatments, however, must be adapted to conditions within the eastern Canadian forest (90–
528 93). The results of our study provide new guidelines for a forest management approach that
529 brings the regeneration dynamics within managed stands closer to those of boreal old-growth
530 forests.

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778 **Tables and figures**

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780 **Table 1** Description of the regeneration, stand structure, and abiotic attributes sampled at the study sites as
 781 adapted from Martin et al. (2018). “*” indicates attributes computed by Martin et al. (2018).

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Category	Attribute	Unit	Description
Regeneration	Black spruce seedling density	n/ha	Number of living black spruce seedlings per hectare
	Black spruce sapling density	n/ha	Number of living black spruce saplings per hectare
	Balsam fir seedling density	n/ha	Number of living balsam seedlings per hectare
	Balsam fir sapling density	n/ha	Number of living balsam fir saplings per hectare
Stand structure	Tree density*	n/ha	Number of living merchantable stems per hectare
	Basal area*	m ² /ha	Basal area of the living merchantable trees per hectare
	Balsam fir proportion*	%	Proportion of balsam fir in the basal area
	Coarse woody debris volume*	m ³ /ha	Coarse woody debris volume per hectare
	Snag basal area	m ² /ha	Basal area of the dead merchantable trees per hectare
	Gap fraction*	%	Mean percentage of the canopy under gaps
	Stand height*	m	Mean height value of the dominant trees sampled at each site
	Weibull's shape parameter*	-	Weibull's function shape parameter (WSP, Bailey and Dell 1973), based on the diameter distribution of saplings and merchantable trees. A WSP of ≥ 1.5 represents a Gaussian distribution of the diameters, $1 \leq \text{WSP} < 1.5$ reflects an irregular distribution, and $\text{WSP} < 1$ describes a reverse J-shaped distribution
Cohort basal area proportion*	-	Replacement index of the even-aged cohort by old-growth cohorts, as defined by Kneeshaw and Gauthier (2003), and values range from 0 to 1. CBAP = 0 indicates a stand having a single even-aged cohort, and CBAP = 1 indicates a stand where old-growth cohorts have replaced all of the even-aged cohort	
Abiotic	Minimum time since last fire*	years	Age of the oldest tree
	Slope	%	Mean slope value along the 400 m ² square plot
	Depth of the organic horizon*	cm	Mean depth of the organic horizon along the soil profile

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Table 2 Mean and standard error of the regeneration attributes for (A) black spruce regeneration clusters and (B) balsam fir regeneration clusters. Different letters indicate significant differences at $p < 0.05$, following $a > b > c > d > e$. BS: black spruce; BF: Balsam fir

A: Black spruce regeneration

Cluster	BS1 (n=10)	BS2 (n = 11)	BS3 (n = 17)	BS4 (n = 6)	BS5 (n = 3)	BS6 (n = 11)	BS7 (n = 6)	BS8 (n = 7)
Black spruce seedling density (n/ha)	3 080 ± 1 959 e	4 882 ± 2 177 d	10 906 ± 2 096 c	9 683 ± 2 048 c	11 267 ± 1 582 c	17 836 ± 2 777 b	21 850 ± 3 365 a	26 543 ± 4 295 a
Black spruce sapling density (n/ha)	322 ± 257 f	1 175 ± 251 d	1 019 ± 286 d	2 233 ± 353 bc	3 783 ± 484 a	1 773 ± 269 c	742 ± 277 e	3 082 ± 532 ab
Balsam fir seedling density (n/ha)	9 720 ± 7 920 a	5 773 ± 7 621 ab	1 835 ± 4 253 c	1 917 ± 4 224 c	3 333 ± 5 687 ac	873 ± 2 039 c	6 317 ± 8 655 ab	2 357 ± 5 474 bc
Balsam fir sapling density (n/ha)	1 492 ± 1 499	2 516 ± 3 374	228 ± 495	500 ± 765	608 ± 1 032	125 ± 357	592 ± 668	200 ± 416

B: Balsam fir regeneration

Cluster	BF1 (n = 28)	BF2 (n = 11)	BF3 (n = 3)	BF4 (n = 5)
Black spruce seedling density (n/ha)	14 379 ± 7 824 a	10 773 ± 9 688 ab	1 900 ± 794 b	9 180 ± 7 258 ab
Black spruce sapling density (n/ha)	1 670 ± 1 025 a	1 282 ± 1 131 ab	1 283 ± 388 ab	470 ± 151 b
Balsam fir seedling density (n/ha)	957 ± 1 520 c	9 827 ± 3 243 b	1 6267 ± 5 460 ab	1 8740 ± 2 756 a
Balsam fir sapling density (n/ha)	223 ± 397 c	1 464 ± 683 b	7 442 ± 1 934 a	2 590 ± 1 066 ab

Table 3 Spearman correlation coefficients between regeneration attributes and structural and environmental attributes. “*” indicates significance at $p < 0.05$, “**” at $p < 0.01$ and “***” at $p < 0.001$.

Category	Attribute	Black spruce		Balsam fir	
		Seedlings	Saplings	Seedlings	Saplings
Structure	Tree density (n/ha)	0.18	-0.09	0.14	0.10
	Basal area (m ² /ha)	-0.09	-0.49***	0.36*	0.17
	Balsam fir proportion (%)	-0.21	-0.26*	0.80***	0.86***
	Gap fraction (%)	0.34**	0.51***	-0.17	-0.02
	Weibull's shape parameter	0.05	0.16	-0.19	-0.09
	Coarse woody debris volume (m ³ /ha)	-0.11	-0.07	0.44**	0.61***
	Snag basal area (m ² /ha)	-0.21	-0.21	0.55***	0.48***
	Maximum height (m)	-0.12	-0.31**	0.39**	0.33*
	Cohort basal area proportion	0.32**	0.24*	0.08	0.07
Abiotic	Minimum time since the last fire (years)	0.43***	0.32**	-0.19	-0.22
	Slope (%)	-0.29*	-0.37**	0.59***	0.56***
	Depth of the organic horizon (cm)	0.41***	0.32**	-0.17	-0.10

Table 4 Mean and standard error of the structural and environmental attributes for black spruce regeneration clusters (BS). Different letters indicate significant differences at $p < 0.05$, following $a > b > c > d$. BS: black spruce; BF: Balsam fir

Cluster	BS1	BS2	BS3	BS4	BS5	BS6	BS7	BS8
Tree density (n/ha)	790.00 ± 332.00	950.00 ± 392.00	899.00 ± 283.00	925.00 ± 569.00	600.00 ± 563.00	1 068.00 ± 382.00	1 162.00 ± 423.00	832 ± 399
Basal area (m ² /ha)	23.20 ± 9.93 ab	18.10 ± 5.16 abc	17.20 ± 5.83 bc	12.40 ± 7.47 cd	10.40 ± 8.84 cd	16.60 ± 5.85 bcd	25.10 ± 7.01 a	11.10 ± 4.32 d
Balsam fir proportion (%)	35.20 ± 34.30	20.00 ± 23.90	3.60 ± 7.64	6.91 ± 12.80	8.79 ± 12.40	3.99 ± 10.10	22.30 ± 30.70	1.16 ± 1.52
Gap fraction (%)	42.70 ± 23.70 c	61.60 ± 25.00 ab	49.80 ± 21.10 bc	83.40 ± 26.40 a	85.30 ± 25.40 a	66.60 ± 15.50 ab	71.30 ± 23.80 ab	84.80 ± 17.10 a
Weibull's shape parameter	1.11 ± 0.68	1.07 ± 0.46	1.03 ± 0.43	1.09 ± 0.17	1.06 ± 0.22	1.05 ± 0.20	0.80 ± 0.45	0.98 ± 0.16
Coarse woody debris volume (m ³ /ha)	82.30 ± 69.10	92.00 ± 69.50	33.20 ± 22.70	27.60 ± 29.20	113.00 ± 101.00	51.00 ± 34.10	60.70 ± 48.50	41.90 ± 25.40
Snag basal area (m ² /ha)	5.80 ± 4.68	7.27 ± 6.00	3.57 ± 2.36	2.71 ± 1.17	5.17 ± 4.59	2.72 ± 1.52	4.42 ± 1.97	2.93 ± 1.54
Maximum height (m)	19.30 ± 3.88	20.00 ± 2.77	18.10 ± 3.37	17.10 ± 2.78	15.60 ± 6.78	18.10 ± 1.22	20.00 ± 1.98	16.80 ± 2.78
Cohort basal area proportion	0.37 ± 0.33	0.53 ± 0.37	0.48 ± 0.35	0.58 ± 0.35	0.34 ± 0.29	0.78 ± 0.25	0.45 ± 0.42	0.83 ± 0.34
Minimum time since the last fire (years)	146.00 ± 45.60 c	190.00 ± 65.40 bc	179.00 ± 52.90 bc	181.00 ± 53.00 bc	159.00 ± 61.60 bc	239.00 ± 49.70 a	209.00 ± 56.40 ab	249.00 ± 71.60 a
Slope (%)	23.40 ± 10.80 a	13.20 ± 10.30 b	6.35 ± 8.03 c	4.33 ± 4.84 c	8.67 ± 7.51 bc	6.27 ± 6.33 bc	8.17 ± 6.21 bc	4.00 ± 3.37 c
Depth of the organic horizon (cm)	16.00 ± 9.73 c	27.10 ± 11.80 b	35.10 ± 14.30 ab	27.70 ± 13.00 b	37.00 ± 25.00 ab	29.90 ± 15.40 b	37.20 ± 16.00 ab	47.90 ± 18.80 a

Table 5 Mean \pm standard deviation of structural and environmental attributes for balsam fir regeneration clusters (BF). Letters indicate significant differences at $p < 0.05$, following $a > b > c$.

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Cluster	BF1	BF2	BF3	BF4
Tree density (n/ha)	880.00 \pm 332.00	927.00 \pm 277.00	892.00 \pm 104.00	810.00 \pm 326.00
Basal area (m ² /ha)	17.50 \pm 7.27	20.80 \pm 7.64	14.90 \pm 1.92	21.70 \pm 6.94
Balsam fir proportion (%)	4.12 \pm 6.95 b	28.80 \pm 19.10 a	55.00 \pm 5.10 a	56.70 \pm 35.40 a
Gap fraction (%)	64.10 \pm 26.00	57.10 \pm 29.80	72.70 \pm 14.80	64.00 \pm 27.10
Weibull's shape parameter	0.87 \pm 0.29	1.15 \pm 0.62	0.88 \pm 0.12	0.81 \pm 0.13
Coarse woody debris volume (m ³ /ha)	61.60 \pm 47.00 b	84.00 \pm 35.60 a	155.00 \pm 62.90 a	121.00 \pm 60.00 a
Snag basal area (m ² /ha)	3.90 \pm 3.05 c	5.09 \pm 2.00 bc	14.00 \pm 5.58 a	7.97 \pm 4.40 ab
Maximum height (m)	18.90 \pm 3.05	20.70 \pm 2.06	19.70 \pm 2.23	21.20 \pm 1.75
Cohort basal area proportion	0.60 \pm 0.35	0.63 \pm 0.36	0.82 \pm 0.30	0.74 \pm 0.16
Minimum time since the last fire (years)	213.00 \pm 66.50	193.00 \pm 50.60	188.00 \pm 50.10	204.00 \pm 41.40
Slope (%)	8.14 \pm 9.11 c	12.50 \pm 10.5 bc	18.70 \pm 5.03 ab	28.40 \pm 6.02 a
Depth of the organic horizon (cm)	31.60 \pm 16.00	26.10 \pm 14.00	29.00 \pm 15.10	21.60 \pm 9.29