

**Title: Linking radial growth patterns and post-disturbance dynamics in boreal old-growth forests driven by recurrent insect outbreaks: a tale of opportunities, successes, and failures**

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## 16    **Abstract**

17    In boreal landscapes, emphasis is currently placed on close-to-nature management  
18    strategies, which aim to maintain the biodiversity and ecosystem services related to old-  
19    growth forests. The success of these strategies, however, depends on an accurate  
20    understanding of the dynamics within these forests. This study aims to reconstruct the  
21    disturbance and post-disturbance dynamics in boreal old-growth forests that are driven by  
22    recurrent moderate-severity disturbances. We studied eight old-growth forests in Québec,  
23    Canada, that has recorded recurrent and moderate to severe spruce budworm  
24    (*Choristoneura fumiferana* [Clem.]) outbreaks over the 20th century. To reconstruct the  
25    disturbance history and the post-disturbance dynamics of the study sites, we used  
26    dendrochronological data and k-means clustering to identify growth releases and growth  
27    patterns in the studied trees. We identified nine growth patterns; these patterns represented  
28    trees differing in age, size, and canopy layer, and indicated different tree histories. Spruce  
29    budworm outbreaks caused recurrent moderate-severity disturbances within the study sites.  
30    The canopy gaps created by these disturbances were filled mainly by understory trees,  
31    which responded by single and significant increases in radial growth and height. In  
32    contrast, overstorey trees had little influence on gap filling; thus, trees were mostly from  
33    the dominant and codominant canopy layers. Our study underlines the resistance of boreal  
34    old-growth forests to recurrent and moderate-severity disturbances, as understory trees  
35    can rapidly fill the resulting gaps. However, trees that are unable to attain the canopy  
36    following the disturbance then tend to remain in the lower canopy layers. Therefore,  
37    reaching the canopy represents a once-in-a-lifetime opportunity, where success or failure  
38    depends on a relatively short window of time. This gap-filling dynamic produces, however,

39 a vertical structure that is often similar to the expected structure in even-aged forests. Our  
40 results highlight the efficacy of identifying tree growth patterns to reconstruct stand  
41 disturbance dynamics and contribute to developing closer to nature forest management  
42 strategies.

### 43 **Résumé**

44 Dans les paysages boréaux, l'accent est désormais mis sur des stratégies de gestion proches  
45 de la nature afin de maintenir la biodiversité et les services écosystémiques liés aux vieilles  
46 forêts. Le succès de ces stratégies dépend toutefois d'une compréhension fine de la  
47 dynamique de ces forêts. Par conséquent, l'objectif de cette étude est de reconstruire les  
48 dynamiques de perturbation et post-perturbation dans les vieilles forêts boréales causées  
49 par des perturbations récurrentes de sévérité modérée. Nous avons étudié huit vieilles forêts  
50 au Québec, Canada, ayant enregistré des épidémies de tordeuse des bourgeons de l'épinette  
51 (*Choristoneura fumiferana* [Clem.]) récurrentes et de sévérité modérée à élevée au cours  
52 du 20ème siècle. Nous avons utilisé des données dendrochronologiques et des analyses de  
53 groupement par k-moyennes pour identifier les patrons généraux de croissance et les  
54 reprises de croissance abruptes des arbres étudiés, afin de reconstituer l'historique des  
55 perturbations et la dynamique post-perturbation des sites d'étude. Nous avons identifié neuf  
56 patrons de croissance, observés dans des arbres d'âge, de taille ou de strate de canopée  
57 différents, indiquant des dynamiques particulières. Les épidémies de tordeuse des  
58 bourgeons de l'épinette ont provoqué des perturbations récurrentes de sévérité modérée sur  
59 les sites étudiés. Les trouées créées à la suite de ces perturbations ont été principalement  
60 comblées par des arbres du sous-étage en un unique et significatif accroissement de

61 circonférence et de hauteur. En revanche, les arbres déjà situés dans la canopée ont eu peu  
62 d'influence sur la fermeture de ces trouées. En conséquence, les arbres dominants et  
63 codominants étaient les plus fréquents dans la canopée. Les résultats de cette étude  
64 soulignent la résistance des vieilles forêts boréales aux perturbations récurrentes et de  
65 sévérité modérée, car les arbres de sous-étage peuvent rapidement combler les trouées qui  
66 en résultent. Cependant, les arbres incapables d'atteindre le sommet de la canopée à la suite  
67 d'une perturbation resteront ensuite souvent dans les strates inférieures de la canopée.  
68 Atteindre le sommet de la canopée est souvent une opportunité unique, dont le succès  
69 dépend d'une très courte fenêtre temporelle. Cette dynamique de fermeture de canopée  
70 crée cependant une structure verticale qui est généralement plus proche de ce qui est  
71 attendu dans les forêts équiennes. Globalement, cette étude souligne que l'identification  
72 des patrons de croissance des arbres permet de reconstituer aisément la dynamique des  
73 perturbations naturelles. Nos résultats peuvent contribuer ainsi à développer des stratégies  
74 de gestion forestière plus proches des dynamiques naturelles.

75 **Keywords:** spruce budworm (*Choristoneura fumiferana* [Clem.]); old-growth forest;  
76 disturbance severity; ecosystem-based management; radial growth pattern; disturbance  
77 dynamics; forest dynamics; dendrochronology

## 79 **Introduction**

80 Anthropogenic activities over the last centuries have increased pressure on forest  
81 ecosystems, causing a significant loss of natural forest surfaces (Achard et al., 2009;  
82 Aksenov, Karpachevskiy, Lloyd, & Yaroshenko, 1999; Watson et al., 2018). Forest

artificialization, fragmentation, and deforestation threaten numerous species and ecosystem services, including carbon sequestration and water supply (Karjalainen, Sarjala, & Raitio, 2010; Watson et al., 2018). Climate change is expected to increase the frequency and severity of natural disturbances and extreme weather conditions, thereby further stressing forest ecosystems (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015; Jandl, Spathelf, Bolte, & Prescott, 2019; Seidl et al., 2017). To address these issues, emphasis is now placed on forest management strategies that aim to mimic natural forest structures and dynamics (Gauthier et al., 2009; Kuuluvainen, 2009; Puettmann, Coates, & Messier, 2009). Reducing differences between managed and natural forests is expected to offset the loss of biodiversity and ecosystem services while increasing the resistance and the resilience of forest ecosystems to climate change (Park et al., 2014; Puettmann et al., 2009).

In this context, old-growth forests—forests at the final stage of forest succession, driven by secondary disturbances (Oliver & Larson, 1996; Wirth, Messier, Bergeron, & Frank, 2009)—have become a major subject of attention. These forests are often the most threatened by human activities, their area greatly reduced through deforestation and intensive forest management (Achard et al., 2009; Aksenov et al., 1999; Östlund, Zackrisson, & Axelsson, 1997). Many of the structural attributes that generally define these ecosystems, such as structural complexity, large trees, or high deadwood volume, are rare, if not absent, in younger or managed forests (Martin, Fenton, & Morin, 2018; Paillet et al., 2015; Wirth et al., 2009). These features, however, provide many essential habitats for species (Boudreault, Paquette, Fenton, Pothier, & Bergeron, 2018; Tremblay et al., 2018; Winter & Möller, 2008). Similarly, the temporal continuity of old-growth forests, where

the last primary disturbance often occurred centuries ago, is vital for many low-dispersal or disturbance-sensitive species (Barbé, Fenton, & Bergeron, 2017; Fenton & Bergeron, 2011). Old-growth forests also play a key role in the offering of ecosystem services, such as carbon storage and water flux (Keeton, 2019; Kenina, Jaunslaviete, Liepa, Zute, & Jansons, 2019; Warren, Keeton, Bechtold, & Kraft, 2019). Maintaining remnant old-growth forests or enhancing old-growth attributes in managed stands has become, therefore, a common priority for forest and environmental managers (Bauhus, Puettmann, & Messier, 2009; Kuuluvainen, 2009; Thom & Keeton, 2019). The success in achieving conservation objectives related to old-growth forests depends, however, heavily on fine-scale knowledge of the dynamics of these ecosystems; more specifically, we need to understand how old-growth forests respond to recurrent and moderate-severity disturbances. Moderate-severity disturbances—also known as intermediate-severity disturbances; a disturbance that exceeds the gap scale without being catastrophic (Hart & Kleinman, 2018)—are an inherent part of the natural disturbance regime of old-growth forests (Kuuluvainen & Aakala, 2011; Martin, Morin, & Fenton, 2019; Meigs et al., 2017). Therefore, a better understanding of the consequences of moderate-severity disturbances on old-growth forests will improve the evaluation of the resilience of these ecosystems to direct or indirect anthropogenic stresses.

The boreal forests of eastern Canada offer an ideal territory for addressing questions related to moderate-severity disturbances because remnant primary forests remain abundant and are dominated by stands at the old-growth stage (Cyr, Gauthier, Bergeron, & Carcaillet, 2009; Grondin et al., 2018; Watson et al., 2018). As well, these stands continue to be driven by natural disturbances, in particular by spruce budworm (*Choristoneura fumiferana*

[Clem.]) outbreaks, which occur over an approximate 30-year cycle (Jardon & Morin, 2003; Martin et al., 2019; Morin, Laprise, Simon, & Amouch, 2009). Although boreal old-growth forests are abundant in eastern Canada, they are nonetheless highly threatened by human activities. Forest management based on short-rotation clearcutting is the main cause of old-growth forest loss because these stands are harvested first and at rate greater than that of primary disturbances (Barrette, Tremblay, & Auger, 2018; Bergeron et al., 2017; Martin, Boucher, Fenton, Marchand, & Morin, 2020a). In the boreal regions, climate change is also expected to increase the recurrence and severity of disturbances, in particular spruce budworm outbreaks (De Grandpré, Kneeshaw, et al., 2018; Bouzidi et al., 2019; Pureswaran et al., 2019). Hence, a better understanding of the resistance and resilience of boreal old-growth forests in eastern Canada to recurrent moderate-severity disturbances is vital to better evaluate the projected consequences of climate change and propose alternatives to clearcut-based forest management. This knowledge would also add to existing research on old-growth forests and therefore contribute to finding relevant management solutions, including for forests situated outside of the boreal regions of eastern Canada.

Dendrochronological analysis is an effective tool for reconstructing the disturbance dynamics and response of the understorey to disturbances, usually by identifying growth releases, i.e. abrupt changes in tree-ring width (Fraver & White, 2005; Nowacki & Abrams, 1997; Trotsiuk et al., 2014). The study of a tree's growth patterns, i.e. the changes in tree-ring width from the pith to the last formed ring, makes it possible to identify growth releases and also determine how the tree reacted to this release (Martin, Krause, Fenton, & Morin, 2020b; Trotsiuk et al., 2016). The identification of growth patterns has tended,

however, to be, at least partially, based on a subjective process, limiting its use (Frelich, 2002; Lorimer & Frelich, 1989; Niukkanen & Kuuluvainen, 2011). Martin et al. (2020b) highlighted that the use of machine-learning algorithms provides an effective solution for identifying growth patterns accurately and objectively. The combined analysis of both growth releases and growth patterns therefore offers much promise for reconstructing the dynamics of old-growth forests driven by natural disturbances.

This study focused on the boreal forests of eastern Canada, and more specifically, within a territory subjected to severe spruce budworm outbreaks over the 20th century (Morin, 1994; Morin & Laprise, 1990; Navarro, Morin, Bergeron, & Montoro Girona, 2018). Dendrochronological analyses, combining the study of growth releases and growth patterns, will be used to reconstruct the disturbance regime of the studied stands and evaluate the success of understorey and overstorey trees in filling the gaps created by secondary disturbances. This study aims to reconstruct the disturbance and post-disturbance dynamics in boreal old-growth forests driven by moderate-severity disturbances. We hypothesize that (1) radial growth in the studied trees can be divided into several distinct growth patterns shaped by the secondary disturbance regime, and (2) each of these growth patterns corresponds to trees defined by specific characteristics (e.g. age, canopy layer), making it possible to reconstruct the post-disturbance dynamics of the forests that they constitute.

## **Materials and methods**



## Study territory

Our study took place in the natural boreal forest stands in the Monts-Valin region of Québec, Canada (**Figure 1**). The studied area ranges from 48°61'N to 49°30'N and from 70°34'W to 70°82'W in the balsam fir (*Abies balsamea* (L.) Mill.)–white birch (*Betula papyrifera* Marsh.) and the eastern black spruce (*Picea mariana* (Mill.) B.S.P.)–feather moss bioclimatic zones (Saucier et al., 2009). In the balsam fir–white birch bioclimatic domain, mean annual temperatures are approximately 0°C, the length of the growing season ranges from 130 to 150 days, and mean annual precipitation varies between 1,100 and 1,300 mm (Blouin & Berger, 2004). In the black spruce–feather moss bioclimatic domain, mean annual temperatures range between -2.5°C and 1°C, the length of the growing season is approximately 140 days, and mean annual precipitation varies between 900 and 1,300 mm (Morneau & Landry, 2007). Regional topography is dominated by a hilly relief, and the elevation ranges between 400 and 1,000 m a.s.l. Forest is the main form of vegetation cover across this territory; black spruce, balsam fir, white birch, and aspen (*Populus tremuloides* Michx.) are the most common tree species.

## Sampling

We randomly selected eight old-growth forests across the study territory using a stratified random sampling protocol. We based our sampling criteria on attributes derived from forest survey maps, and these attributes were then verified in the field. We aimed to sample old-growth forests that had been markedly disturbed by spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks in this region between 1972 and 1984 (Krause, 1997; Morin & Laprise, 1990). We initially identified stands classified as old (i.e. >100 years old),

coniferous-dominated, and defined by a canopy containing at least 20% gaps; we considered this last factor as an indicator of relatively recent disturbances.

Sampling occurred in 2009. In each selected stand, we established a 400-m<sup>2</sup> (20 × 20 m) plot within which we surveyed all merchantable trees (diameter at breast height [DBH] ≥ 9 cm), alive or dead. For each tree, we identified the attributes of species, DBH, height, vitality (alive or dead), and crown status (intact or broken). We then felled all merchantable trees within the 400-m<sup>2</sup> plots to obtain a more accurate measurement of height and sample basal disks for subsequent dendrochronological analysis. We only selected basal disks from living coniferous trees, and we rejected any disks marked by substantial amounts of decay that prevented tree-ring analysis. We obtained 381 basal disks: 290 black spruce and 91 balsam fir. For each living tree, we also defined its canopy layer (i.e. dominant, codominant, intermediary, and suppressed) following the methodology of Québec Ministry of Forests, Wildlife and Parks (MRNF, 2008). The canopy layers are based on the dominant height (DH), i.e. the mean height of the 100 tallest trees per hectare; therefore, in our case, we used the four tallest trees in each 400-m<sup>2</sup> plot. Dominant trees are defined by a height greater or equal to DH, whereas codominant trees have a height less than DH but greater or equal to 2/3 DH. Intermediary trees are defined by a height less than 2/3 DH but greater than 1/2 DH, and suppressed trees have a height less than 1/2 DH. Finally, we also sampled saplings (living trees with a DBH <9 cm and a height ≥1.3 m) in two square 5-m<sup>2</sup> plots situated at opposite edges of each 400-m<sup>2</sup> plot. For each sapling, we recorded its species, DBH, and height.

216 *Data preparation*

217 The 381 basal disks were air-dried and mechanically sanded in preparation for tree-ring  
218 measurements. We measured tree rings along two radii (radius series) to the nearest 0.01  
219 mm, using a manual Henson micrometer (Fred C. Henson, Mission Viejo, CA, USA), or a  
220 LINTAB measurement table and TsapWin software (Rinntech, Heidelberg, Germany). We  
221 used a combination of visual cross-dating and the COFECHA computer program (Holmes,  
222 1983) to correct the tree-ring series. We then obtained a single tree-ring series for each tree  
223 (tree series) by taking the mean value of each tree ring measured in the radius series of the  
224 corresponding tree.

225 To identify a tree's radial growth pattern, i.e. the main radial growth trends over time, we  
226 used the methods established by Martin et al. (2020b). Each tree series was divided into 20  
227 segments (20-segment series), each containing a similar number of tree rings—the  
228 difference in the number of rings per segment for a same tree never exceeded one ring. The  
229 first segment began at the first ring after the pith, and the last segment ended at the last ring  
230 produced by the tree. This method allowed comparing trees of different ages by smoothing  
231 interannual growth changes and keeping only the overall trend in radial thickness. The age  
232 of sampled trees ranged from 55 to 271 years (mean:  $143 \pm 39.2$  years), and the mean  
233 number of tree rings per section was  $7.13 \pm 2$  rings.

234 For each tree, we also computed the following growth attributes based on the tree series:  
235 age, mean tree-ring width, ring-width standard deviation, 5th percentile ring width, and  
236 95th percentile ring width. To reconstruct the disturbance history of the sample sites, we

used the methods of Nowacki & Abrams (1997) to identify the annual percentage of growth change (%GC) of the 381 tree series, using the equation

$$\%GC = \{(M_2 - M_1)/M_1 \times 100\},$$

where  $M_1$  is the mean ring width for the first 10-year period, and  $M_2$  is the mean ring width for the subsequent 10-year period. We defined a major release when  $\%GC \geq 50\%$ , a minor release when  $\%GC = ]50;25\%$ , a minor suppression when  $\%GC = [-25;-50\%$ , and a major suppression when  $\%GC$  was lower or equal to  $-50\%$ . For each site, we then computed the percentage of trees in major release, minor release, minor suppression, and major suppression for each year covered by the chronologies. Changes in the annual percentage of growth release between sites were then observed using a locally weighted regression (Trexler & Travis, 1993) smoothed with a 50% span using the *ggplot* package (Wickham, 2016) in *R* software, version 3.3.1 (R Core Team, 2019).

### *Analysis*

To answer our hypothesis that radial growth in the studied stands can be divided into several distinct growth patterns, we first identified tree-ring growth patterns using a k-means clustering algorithm (Hartigan & Wong, 1979) on the 381 20-segment series by applying the Martin et al. (2020b) methodology. We based the k-means clustering on the mean ring width for each of the 20 segments, preliminarily scaled and centred, with each segment considered to be a different explanatory variable. To ensure the robustness of the obtained clusters, we performed 1,000 iterations of the k-means algorithm. We determined the optimal number of clusters (radial growth patterns) using the simple structure index

(SSI; Dolnicar, 1999) criterion, with the highest SSI value indicating the optimal k-means partition.

To answer our second hypothesis that each of these growth patterns corresponds to specific layers of the canopy, we then compared the differences in growth attributes, DBH, and height between the growth patterns using linear mixed-effects models (LMM). The fixed effects were the growth attributes, DBH, and tree height; we used sample sites as the random effect. We used LMM to limit the influence of the sites (e.g. in terms of stand fertility) on the analysis. When necessary, we log-transformed the data or removed outliers (i.e. values below the 1st percentile and above the 99th percentile) to respect the requirements of LMM (i.e. homoscedasticity and the normality of the independent variable for each group). In the case of tree height, we considered broken tree canopies as a possible source of bias because the measured height was, in our case, not the actual tree height. We therefore only considered trees having an intact canopy when comparing tree height between the various growth patterns. When the LMM produced significant results, we performed a Tukey post hoc test (Tukey, 1977). The distributions of the species and the canopy layers were also compared between the growth patterns using Fisher's tests.

For all analyses, we used R software, version 3.3.1, and the *vegan* (Oksanen et al., 2018), *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016), *emmeans* (Russel, 2018), *sjPlot* (Lüdecke, 2020), and *TRADER* (Altman, Fibich, Dolezal, & Aakala, 2014) packages, applying a  $p$ -threshold for significance of 0.05.

## **Results**

### *Overall stand characteristics*

In general, black spruce dominated the sampled stands with a minor (<10%) contribution of balsam fir (**Table 1**). The exceptions were Site 5, where balsam fir dominated, and Site 8, where both species had a similar abundance. The mean tree age of the stands ranged between 122 and 207 years, corresponding to the general range of longevity for both black spruce and balsam fir (Burns & Honkala, 1990). Tree age varied considerably within stands, with several trees older than 200 years; this age pattern indicates a complex age structure, typical of old-growth forests. The diametric structure was generally complex, with sapling density 1.75× to 7.5× that of trees. Dominant height ranged between 13.6 and 17.1 m, and mean tree height ranged between 9.4 and 12.7 m.

### *Radial growth patterns*

The SSI criterion reached a maximum at nine clusters (SSI criterion = 1.04; **Figure 2B**) for the 20-segment series. We therefore divided the 20-segment series into nine clusters (**Figure 2A**), which could be, in turn, grouped into four categories: 1) narrow and constant radial increments along all the sections (linear); 2) increasing or large radial increments along the first half of the chronology, followed by decreasing radial increments for the remaining portion (bell); 3) narrow radial increments over the first half of the chronology, followed by increasing radial increments within the remaining portion (ascending); and 4) narrow radial increments over the first third of the chronology, then an increase in radial increments within the second third, and finally a decrease in radial increments over the last third (sine). Growth patterns belonging to the ascending and sine groups were divided into three growth patterns distributed along a mean ring-width gradient (narrow, moderate, and large). For the bell group, we identified two growth

patterns, one marked by a low growth rate (low-bell) and the other by a high growth rate (high-bell). The number of trees per growth pattern generally exceeded 20; the sole exception was for the high-bell, a pattern that we only observed for seven trees. Due to the high specificity of this growth pattern relative to the others, however, we kept this pattern for the further analyses.

We observed significant differences between patterns for all growth and tree attributes (**Figure 3**). There was, however, little difference between the ranges of tree age per growth pattern, although trees defined by low-ascending, low-sine, and high-sine patterns were, on average, significantly older than trees defined by the linear pattern. Trees defined by the high-bell and high-sine patterns included the larger and taller trees. In contrast, the linear, low-bell, low-ascending, and moderate-ascending patterns contained the smallest trees, both in terms of DBH and height. High-bell, high-ascending, and high-sine patterns were defined by the largest mean ring width, ring-width standard deviation, 5th percentile ring width (high-ascending excepted), and 95th percentile ring width. In contrast, the low-ascending pattern was generally characterized by the smallest mean ring width, ring-width standard deviation, 5th percentile ring width, and 95th percentile ring width. The other growth patterns presented intermediate results. The largest trees (DBH >15 cm) were generally defined by a mean tree-ring width >1 mm/year but also by an age <200 years (**Figure 4**). We observed almost all the high-sine, high-ascending, high-bell, and moderate-sine patterns in these trees. In contrast, trees older than 200 years were uncommon and variable in size and growth, with the low-ascending pattern being most frequent. Trees younger than 200 years and having a DBH <15 cm were characterized by diverse growth patterns and variable mean ring widths. Finally, we

observed no significant differences in growth pattern occurrence between black spruce and balsam fir (Fisher's  $p = 0.132$ ; **Appendix B**).

*Distribution of the radial growth patterns in the canopy*

The occurrence of specific growth patterns differed significantly between the various canopy layers (Fisher's  $p < 0.001$ ; **Figure 5**). In the dominant layers, growth patterns from the sine group were the most common, with the high-sine pattern being observed the most often, followed by growth patterns from the bell group. In the codominant layer, sine patterns were again the most abundant (with the low-sine pattern most dominant), but ascending patterns were the second most common group. For the intermediary and suppressed layers, the ascending patterns dominated, particularly the low- and moderate-ascending patterns. In the suppressed layer, however, the low-bell and linear patterns were the second and third most common patterns, with sine patterns almost absent.

Overall, the codominant layer was the most common layer ( $53.2 \pm 14\%$  of the sampled trees; **Table 2**). For five of the sample sites (sites 1, 2, 4, 5, and 7), the majority of trees belonged to the codominant layer. At the other sites, the intermediary and suppressed layers contained more than half of the sampled trees. Nonetheless, codominant and dominant trees still represented at least one third of living trees within the stands. Moreover, saplings were always more abundant than trees (**Table 1**), indicating a dense regeneration in the understorey.



## *Disturbance dynamics*

At all sites, we observed four distinct peaks of growth release (1870–1890, 1910–1940, 1950–1960, 1975–1990) between 1850 and 1999 (**Figure 6**). All peaks occurred during or after a spruce budworm outbreak period and were preceded by a period of suppression. The 1870–1890 peak was the least distinct, characterized by many simultaneously suppressed trees and marked differences in the percentage of released trees between sites. In contrast, the highest and longest peak was that of 1910–1940, when approximately 75% of the trees presented a growth release, two thirds of these considered as major growth releases. This period was, however, preceded by the second-highest peak of trees experiencing suppression; these suppressions were, however, generally minor. The 1950–1960 and 1975–1990 peaks shared similar percentages of trees undergoing release (approximately 40%); however, most releases for the 1975–1990 peak were major, whereas the majority in the 1950–1960 peak were minor. The 1975–1990 peak was preceded by the highest suppression peak (approximately 35% of trees), whereas the percentage of suppressed trees before the 1950–1960 peak was relatively low (approximately 20% of trees). The study sites therefore appeared mainly driven by recurrent spruce budworm outbreaks, particularly related to a high mortality caused by the outbreak that occurred between 1910 and 1924 in this region.

## **Discussion**

Tree radial growth was divided into nine distinct growth patterns. These patterns corresponded to four dominant groups that each contained one to three growth patterns, organized generally along a forest productivity gradient. This result supported our first

hypothesis, highlighting that secondary disturbances have diverse impacts on overstorey tree growth. Canopy layers were each defined by specific radial growth patterns, thereby supporting our second hypothesis. Overall, spruce budworm was the main driver of secondary disturbance within the study sites. Therefore, our study clarifies how secondary disturbance dynamics shape the vertical structure of boreal old-growth forests that are driven by recurrent and severe insect outbreaks.

*Reaching the top of the canopy: a once-in-a-lifetime opportunity*

Most of the studied trees were defined by a sine or ascending growth pattern, indicating that black spruce and balsam fir reacted vigorously to the canopy openings caused by spruce budworm outbreaks. Both patterns are generally defined by a major increase in radial growth, a phenomenon observed in coniferous-dominated old-growth forests in North America and Europe (Martin et al., 2020b; Morin, 1994; Trotsiuk et al., 2016). Trees defined by a linear pattern were generally the smaller and younger individuals, reflecting suppressed trees that did not benefit from a canopy opening (Rossi, Tremblay, Morin, & Savard, 2009; Trotsiuk et al., 2016). Trees defined by a low-bell pattern were similar in size to those presenting a linear pattern, albeit slightly older than the low-bell-pattern individuals. The minimal and short-duration increases in radial growth observed for this pattern related to trees failing to significantly increase their growth following a disturbance. Finally, the high-bell pattern was highly specific, characterized by a marked growth and no identified juvenile suppression. This pattern was, however, very rare (7 occurrences within 381 studied trees), testifying to its limited influence on stand dynamics and structure.

389 The identified growth patterns separated among the various canopy layers. Sine patterns  
390 were observed most commonly in the dominant and codominant layers, whereas ascending  
391 patterns were most frequent in the intermediary and suppressed layers. This distribution of  
392 patterns implies that trees defined by sine patterns had reached the top of the canopy  
393 already for several years, whereas trees sharing the ascending pattern continue to attempt  
394 to attain the highest layers. Considering the size and the age of the trees, those defined by  
395 the high-ascending or moderate-ascending patterns were likely to eventually reach the  
396 dominant and codominant layers. However, trees in the lower canopy layers and defined  
397 by a slow growth were unlikely to benefit from the death of taller trees to access the upper  
398 layers (Montoro Girona, Morin, Lussier, & Walsh, 2016). Therefore, trees defined by a  
399 low-ascending or low-bell pattern had missed out on the opportunity of reaching the top of  
400 the canopy; these trees remain as part of the intermediary or suppressed layers.

401 Identifying the factors that determine a tree's success or failure in reaching the upper  
402 canopy is challenging because these factors are dependent on conditions at the tree, stand,  
403 and disturbance levels. For example, local variations in microsite quality significantly  
404 influence regeneration growth and density (Jayen, Leduc, & Bergeron, 2017; Leroy, Leduc,  
405 Thiffault, & Bergeron, 2016). Similarly, the spatial patterns of mortality caused by  
406 secondary disturbances are often complex, leaving survivor trees in the canopy (De  
407 Grandpré, Waldron, et al., 2018; Hart & Kleinman, 2018; Hytteborn & Verwijst, 2014)  
408 that may compete with understorey trees. We also observed little difference in species  
409 composition between the growth patterns, testifying to the similar behaviours of black  
410 spruce and balsam fir regeneration under moderate secondary disturbances. Our results  
411 therefore highlight that black spruce and balsam fir regeneration can significantly increase

their growth after a secondary disturbance and rapidly fill the created gaps. Nonetheless, the time window for attaining the upper layers of the canopy is short, and trees unable to grow sufficiently fast are generally confined to the lower layers. In general, the dynamics observed in this study slightly differ from those identified in broadleaved or mixed temperate forests, where growth patterns can be more complex; for example, trees may access the canopy over several steps (Frelich, 2002; Lorimer & Frelich, 1989; Nowacki & Abrams, 1997). Our results therefore highlight how moderate-severity disturbances are a once-in-a-lifetime opportunity for suppressed coniferous trees to access the top of the canopy in boreal old-growth forests.

*Recurrent moderate-severity disturbances are an intrinsic part of old-growth forest dynamics*

The impact of spruce budworm outbreaks on boreal landscapes is highly heterogeneous, ranging from the punctual death of isolated trees to the death of large and continuous forest areas (Kneeshaw et al., 2009; Kulha et al., 2019; Morin et al., 2009). Hence, some regions are marked by significantly higher mortality rates than other areas for a given outbreak (Pureswaran et al., 2015; Navarro et al., 2018). The three 20th-century spruce budworm outbreaks that occurred within the study territory are characterized by their severity (Morin, 1994; Morin & Laprise, 1990; Navarro et al., 2018), which produced a recurrent and significant mortality in the study stands. The peaks in the percentage of trees undergoing release following these outbreaks ranged between 50% and 75% across the study territory, with 20% to 55% of the trees presenting major releases. In contrast, for the same outbreaks, old-growth forests situated approximately 150 km to the north experienced a percentage of

trees in release between 20% and 40%, with 15% to 25% of these trees presenting a major release (Martin et al., 2019). Martin et al. (2019) determined, therefore, that true old-growth forests in this territory were driven almost equally by low-severity and moderate-severity secondary disturbances. In contrast, spruce budworm outbreaks in our study territory were twice as severe as the outbreaks documented by Martin et al. (2019), suggesting that all our study stands were driven primarily by secondary disturbances of moderate severity (Hart & Kleinman, 2018; Martin et al., 2019). In some cases, recurrent and severe secondary disturbances may override stand resistance, thereby reinitiating forest succession (De Grandpré, Waldron, et al., 2018; Donato, Campbell, & Franklin, 2012; Meigs et al., 2017). Yet, the structural attributes of the study stands matched those observed in other boreal old-growth forests in eastern Canada (Harper, Bergeron, Drapeau, Gauthier, & De Grandpré, 2005; Martin et al., 2018; Moussaoui, Leduc, Fenton, Lafleur, & Bergeron, 2019). This implies that the forests observed in this study maintained an old-growth structure despite the presence of a stressful disturbance regime. Approximately 30 years separated the outbreaks, a period that corresponds to the dynamics of this insect in eastern Canada (Morin et al., 2009). Therefore, it suggests that boreal forests in this region are sufficiently resistant to recurrent, moderate-severity disturbances if these events are sufficiently spaced apart in time.

*Complex disturbance and growth processes produced simple vertical structures*

Codominant and dominant trees were generally the most common layers in the canopy of the study stands, although the density of saplings was often high. A vertical structure characterized by a majority of dominant and codominant trees is expected in even-aged

forests, whereas old-growth forests should normally be defined by a complex, multi-layered vertical structure (Franklin et al., 2002; Oliver & Larson, 1996). Our results showing a simpler vertical structure matched those of Martin, Fenton, & Morin (2020), which showed that the vertical structure of dense black spruce-dominated old-growth forests was often similar to that of even-aged stands.

A factor that may explain this counterintuitive result is the low height of boreal stands, which limits the development of complex, stratified vertical structures, such as those observed in temperate and tropical forests (Bergeron & Harper, 2009). In addition, the government of Québec established the height threshold between regeneration and canopy layers at 7 m for Québec (MRNF, 2008). The dominant height of the study stands varied, however, between 13 and 18 m, implying that suppressed trees had maximum heights ranging between 6.5 and 9 m. It is therefore likely that trees below this height threshold were generally too small to be considered as merchantable trees (i.e.  $DBH \geq 9$  cm) and were therefore classified as regeneration (saplings). Because of the low height and small diameter of boreal trees, the thresholds used to define the different layers may overrepresent codominant trees. In contrast, most suppressed trees are ignored because they do not attain a sufficient height and/or DBH.

Moreover, black spruce regenerates mainly through layering in old-growth forests (Harvey, Leduc, Gauthier, & Bergeron, 2002). Martin, Montoro Girona & Morin (accepted) hypothesized that these layers are under the hormonal control of the mother tree; the process of apical dominance can inhibit layers vertical growth because they are still partially connected to the mother tree as branches. Therefore, the death of the mother tree

478 is often required for layers to increase their vertical growth. Similarly to black spruce,  
479 balsam fir can regenerate by layers in old-growth forests (Bakuzis & Hansen, 1965;  
480 Krause, 2006; Sirois, 1997), suggesting, a priori, similar dynamics. Knowledge related to  
481 the importance of layering in balsam fir regeneration remains fragmentary and requires  
482 further research. Balsam fir also regenerates by seed under its own cover (Greene et al.,  
483 1999; Harvey et al., 2002; Rossi, Morin, Gionest, & Laprise, 2012). Balsam fir seedlings  
484 can remain suppressed for decades (McCarthy & Weetman, 2006; Morin & Gagnon, 1991;  
485 Parent, Morin, & Messier, 2000) with their growth rapidly increasing only once a gap is  
486 created in the canopy (Morin, 1994; Wilson & MacLean, 2015). Generally, the smallest  
487 black spruce and balsam fir seedlings present the greatest increases in growth (Martin et  
488 al., 2019; Parent & Ruel, 2002). As indicated by our results, the accession to the canopy is  
489 therefore often made in one major step rather than over several moderate ones. As a result,  
490 old-growth forests in this region are often defined by dense regeneration layers that  
491 increase minimally in height as long as the canopy is not disturbed (Martin et al., accepted).

492 Finally, spruce budworm outbreaks were periodic disturbances that caused phases of  
493 regular and significant mortality in the study stands. This secondary disturbance regime is  
494 therefore different to that regularly observed in old-growth forests, generally defined by a  
495 background noise of small-scale mortality punctuated at random by more severe  
496 disturbances (Hart & Kleinman, 2018; Kuuluvainen et al., 2014; Trotsiuk et al., 2014). For  
497 this reason, Shorohova et al. (2011) hypothesized that many boreal old-growth forests of  
498 eastern Canada may be defined by cohort dynamics, i.e. regeneration of new cohorts under  
499 the cover of old cohorts due to moderate-severity disturbances (Angelstam and  
500 Kuuluvainen, 2004), similar to Scots pine (*Pinus sylvestris* L.) stands in Fennoscandia or

Russia (Angelstam & Kuuluvainen, 2004; Shorohova, Kuuluvainen, Kangur, & Jõgiste, 2009). Most studied trees presented evidence of juvenile suppression, implying that most seeds or layers appeared before the disturbances. Spruce budworm outbreaks are “top-to-down” disturbances, which kill trees in the canopy but preserve some regeneration (De Grandpré, Waldron, et al., 2018; Lavoie, Giron, & Morin, 2019). Therefore, in coniferous forests recently disturbed by spruce budworm outbreaks, most of the observed regeneration germinated decades before the disturbance and not immediately after (Martin et al., 2019; Parent, Simard, Morin, & Messier, 2003; Rossi & Morin, 2011). We therefore consider that the dynamics observed in the study stands likely do not correspond to cohort dynamics. We suggest rather that the dynamics of these forests result from the combination of several interdependent processes: (i) a slow vertical growth of the understorey as long as the canopy is not disturbed; (ii) a disturbance regime driven by periodic and moderate-severity disturbances that preserve the regeneration layer; (iii) after a disturbance, understorey trees reaching the canopy in one major increase in height and diameter; and (iv) once the canopy is attained, the trees changing minimally in height.

## **Conclusion**

The studied old-growth stands were driven mainly by periodic and moderate-severity secondary disturbances caused by spruce budworm outbreaks. Trees from the understorey rapidly filled the created gaps, thereby maintaining the integrity of the stand structure. Understorey trees tended to reach the canopy in one major growth release, regardless of the species (black spruce or balsam fir). Trees that were unable to reach the upper layers of the canopy at that time, however, could generally not attain the canopy afterward. Access



to the dominant or codominant layers therefore represents a once-in-a-lifetime opportunity for suppressed trees in the lower strata of eastern Canadian boreal old-growth forests driven by recurrent and moderate-severity spruce budworm outbreaks.

Our results highlight the resistance of boreal old-growth forests in eastern Canada in relation to recurrent disturbances that kill a significant portion of the overstorey. Close-to-nature silvicultural practices (e.g. partial and stem-selection cuts) are viewed increasingly as plausible alternatives to clearcutting. The natural dynamics observed in this study may therefore serve as guidelines for evaluating the efficacy of these novel silvicultural treatments. Moreover, the combination of low stand height, periodic disturbances, and rapid canopy closure in old-growth forests can produce vertical structures that are similar to those observed in even-aged forests in this region. In remnant natural landscapes, aerial forest surveys may erroneously classify a significant portion of old-growth forests as even-aged stands. Further research is therefore necessary to ensure that boreal old-growth forests are accurately identified as such in eastern Canada.

#### **Authors contribution**

MM and HM conceived the ideas and designed methodology; HM organized and supervised the data collection; MM prepared and analysed the data; CK and HM supervised the analysis and interpretation of the results; MM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### **Data availability**

In the case that the article is accepted for publication, the data used for this article will be archived in the institutional repository of the Université du Québec à Chicoutimi. If the institutional repository is not considered acceptable according to the Journal of Ecology policy, we could otherwise use a public repository (e.g. Figshare or Dryad).

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### 883 Tables and figures

884 **Table 1:** Structural attributes of the sampled stands. The asterisks indicate that the value is  
885 based on the proportion of the tree species in the tree basal area.

Category	Attribute	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Living trees	Tree density (n/ha)	1,125.00	1,625.00	900.00	1,025.00	1,700.00	1,250.00	1,475.00	616.67
	Sapling density (n/ha)	4,000.00	4,800.00	5,200.00	6,000.00	3,000.00	5,000.00	6,200.00	4,600.00
Snags	Tree basal area (m <sup>2</sup> /ha)	16.52	27.50	17.59	20.13	34.19	25.23	24.06	9.98
	Snag density (n/ha)	75.00	25.00	125.00	175.00	300.00	250.00	125.00	275.00

	Snag basal area (m <sup>2</sup> /ha)	1.53	0.21	5.44	4.40	5.63	4.00	3.10	5.43
<b>Composition</b>	Black spruce proportion (%)*	94.12	93.87	95.43	93.80	30.76	83.93	93.93	48.37
	Balsam fir proportion (%)*	5.88	6.13	4.57	6.19	69.24	16.07	6.07	49.96
<b>Height</b>	Maximum height (m)	13.64	14.78	15.08	17.60	16.40	17.33	15.54	14.27
	Dominant height (m)	13.64	17.77	15.62	18.00	16.40	16.93	15.53	14.55
	Mean height (m)	9.69	10.20	9.47	12.70	11.20	11.50	11.30	9.36
	Height standard deviation (m)	2.47	2.77	3.01	2.98	3.31	3.26	2.06	2.90
<b>Age structure</b>	Oldest tree age (years)	221.00	246.00	251.00	267.00	177.00	205.00	179.00	206.00
	Mean tree age (years)	159.00	131.00	133.00	207.00	132.00	139.00	133.00	122.00
	Tree age standard deviation (years)	28.20	28.00	40.60	43.20	22.60	31.70	22.60	35.70

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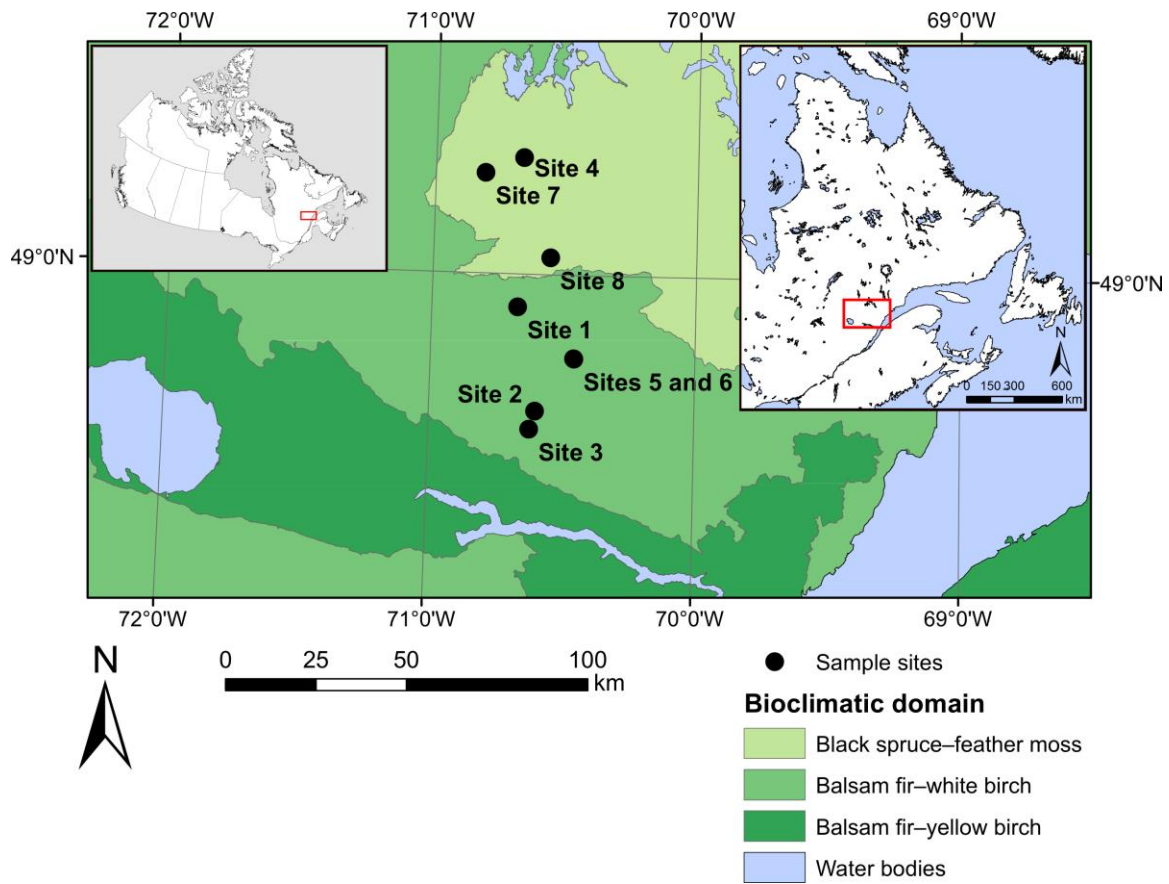
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888 **Table 2:** Distribution (%) of canopy layers within the study sites.

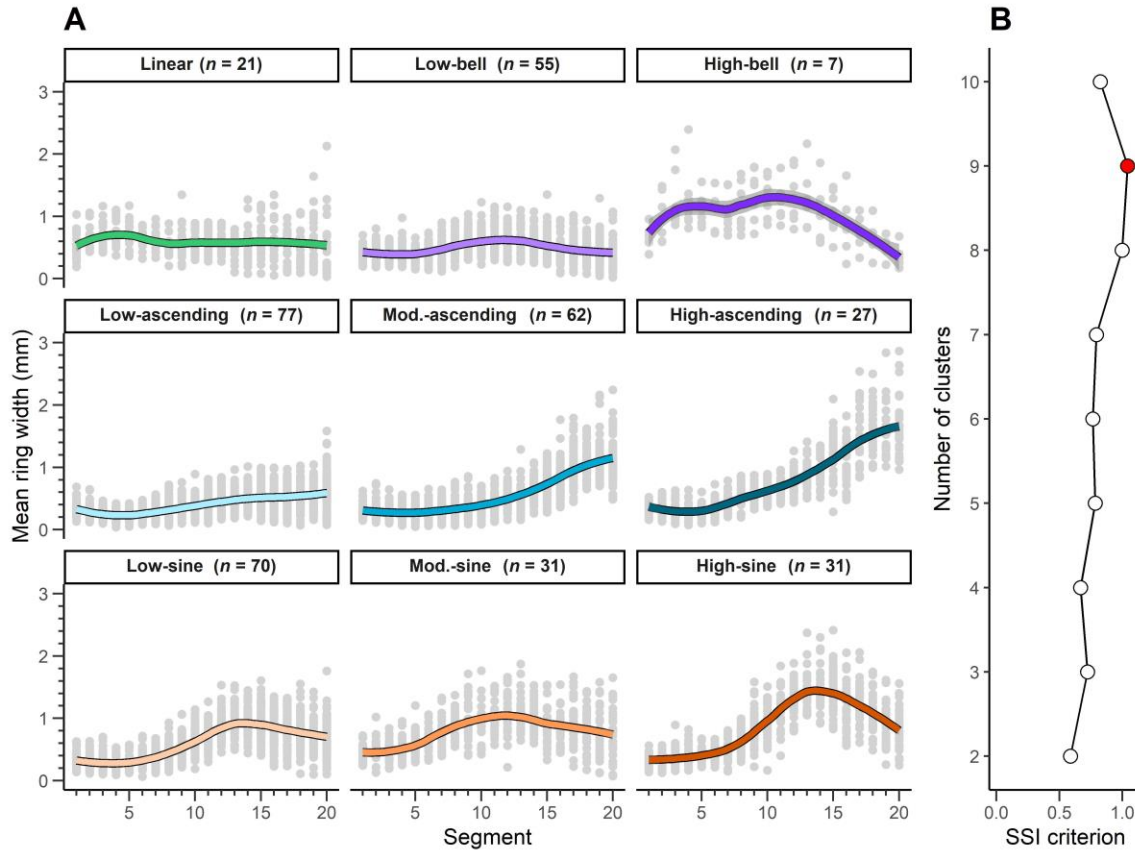
<i>Canopy layer</i>	<i>Site</i>							
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Dominant	2.3	3.1	2.3	5.1	3.9	4.1	1.8	3.1
Codominant	59.1	57.8	31.8	66.7	56.9	42.9	69.6	37.5
Intermediary	27.3	20.3	27.3	17.9	19.6	26.5	25.0	31.2
Suppressed	11.4	18.8	38.6	10.3	19.6	26.5	3.6	28.1

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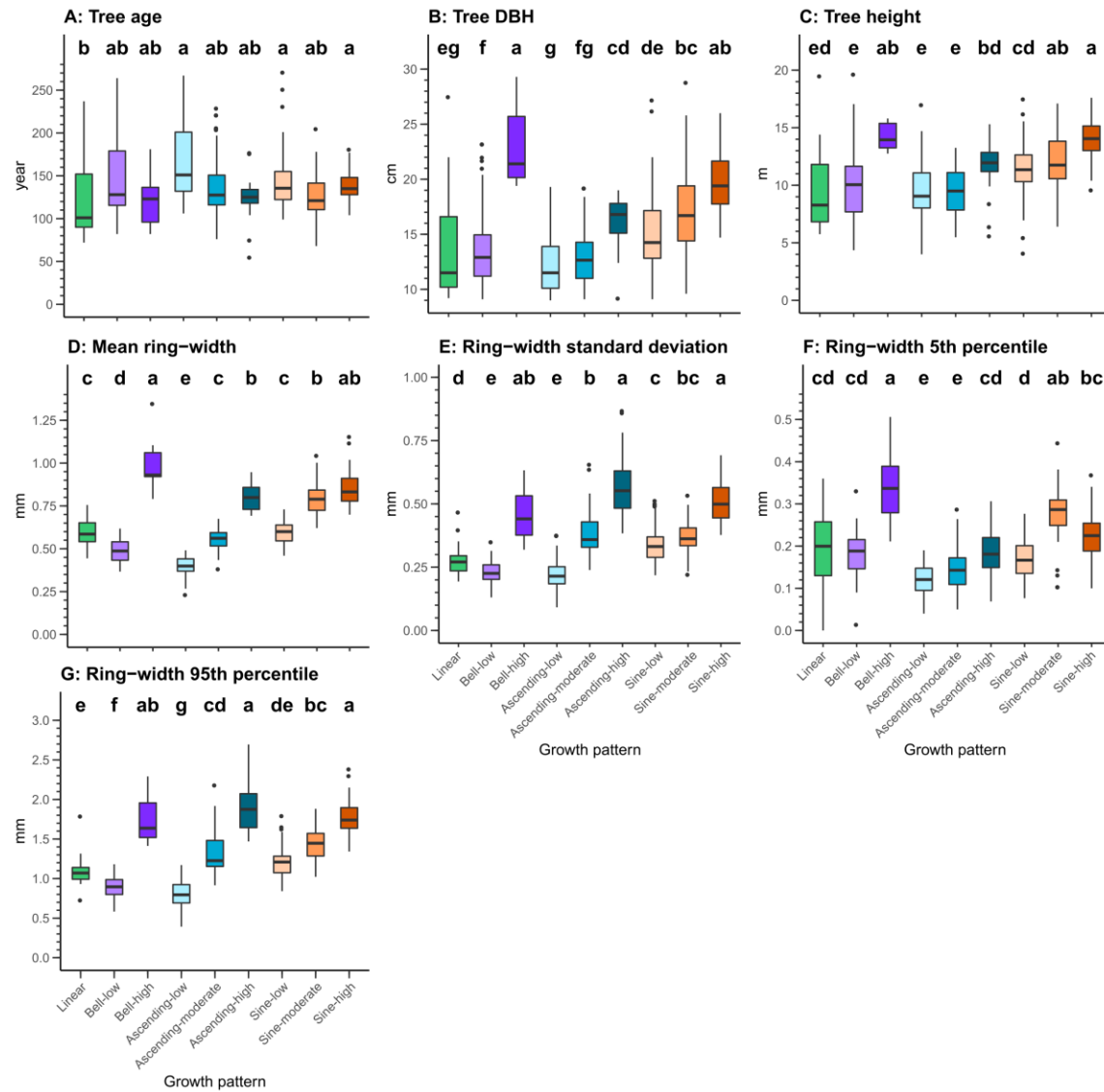
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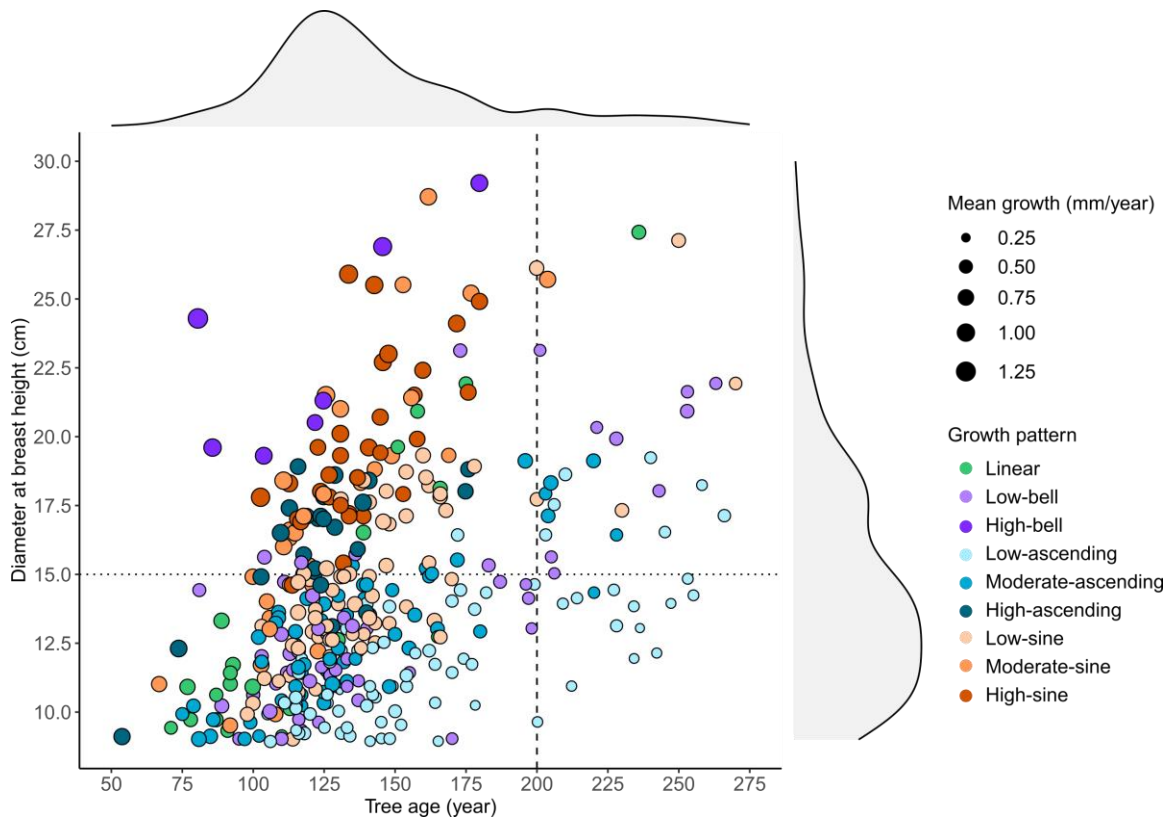
**Figure 1** Location of the study sites on the study territory. The inset maps indicate the location of the study territory in Canada (left) and in Québec (right).



**Figure 2** (A) Scatterplots of the growth patterns identified using a k-means cluster algorithm. Grey dots represent the values of each segment of the 20-segment series of the trees constituting the clusters. We obtained coloured lines using loess smoothing of the data with a 50% span. (B) Values of the SSI criterion according to the number of clusters. The red dot indicates the maximum SSI criterion value. Mod.: moderate,  $n$ : number of sampled trees per cluster.

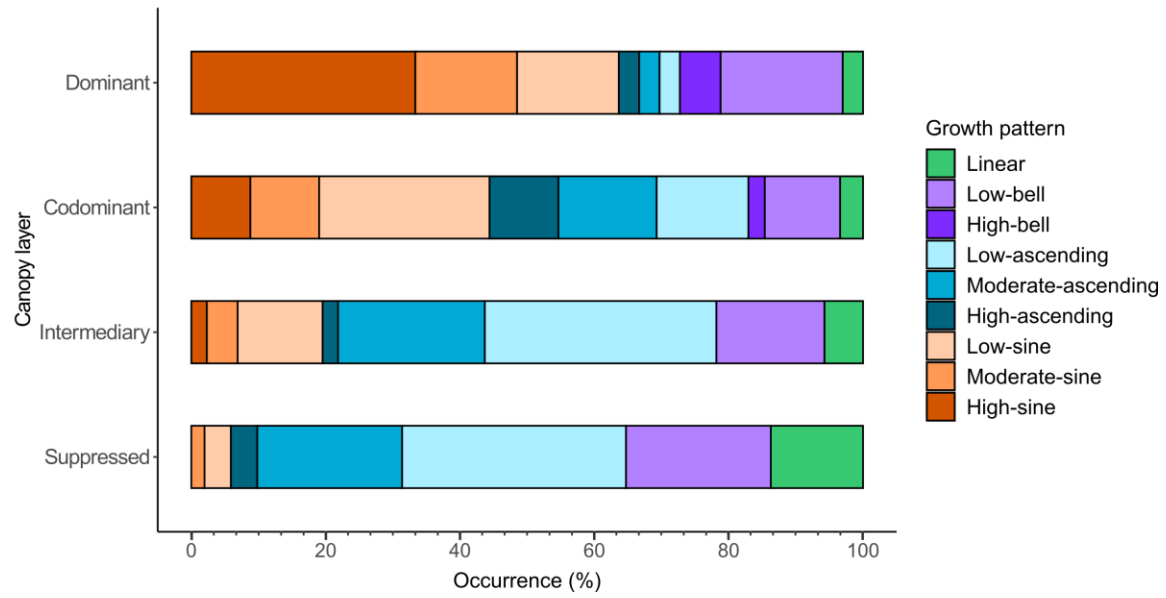


**Figure 3** Boxplots of tree and growth attributes per growth pattern. Letters indicate significant differences, with  $a > b > c > d > e > f > g$ . Details of the model results are presented in **Appendix A**.

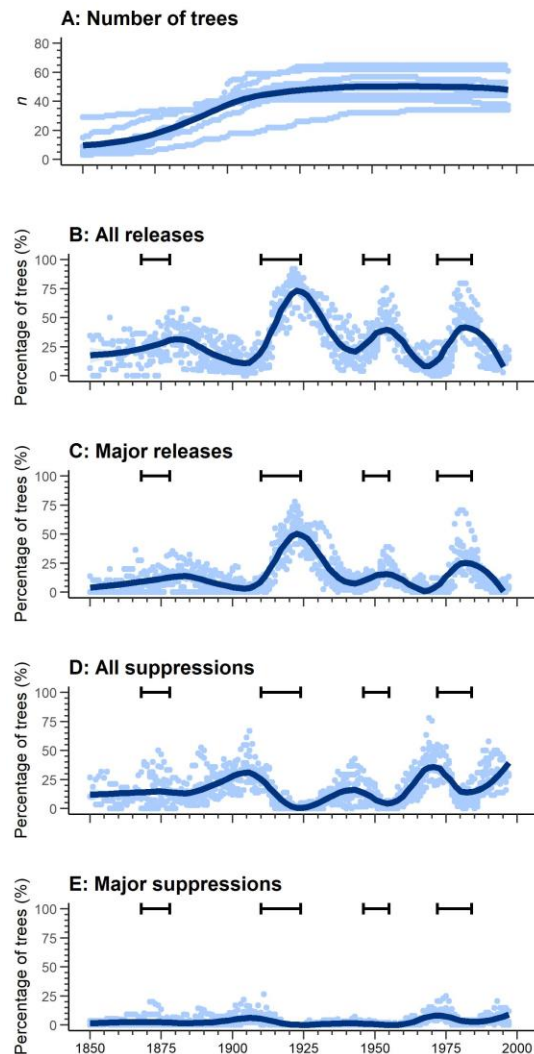


**Figure 4** Scatterplot of the studied trees based on their age, DBH, growth pattern, and mean tree-ring width. Shaded grey areas above and to the right of the scatterplot indicate point density along the x and y axes, respectively. The dashed line separates trees younger or older than 200 years old; the dotted line separates trees having a DBH greater or less than 15 cm.





**Figure 5** Occurrence of the growth patterns in the different layers of the canopy.



**Figure 6** Number of trees sampled and growth changes in the period 1850–2000 for the studied stands (pale blue points). “All releases” includes both minor and major releases; “all suppressions” indicates both minor and major suppressions. We obtained dark blue lines using loess smoothing of the data with a 50% span. Brackets indicate periods of spruce budworm outbreaks in this region based on Morin & Laprise (1990) and Krause (1997).

# Appendix

**Appendix A:** Details of the linear mixed-effects models. DF: numerator degrees of freedom, DenDF: denominator degrees of freedom, Log: logarithmic, DBH: diameter at breast height, RW: ring width

Attribute	DF	DenDF	<i>F</i> -value	<i>p</i> -value	Transformation
Tree age	8	365	4.18	<0.0001	Log
Mean RW	8	365	163.342	<0.0001	Log
Tree DBH	8	365	32.375	<0.0001	Log
Tree height	8	357	19.897	<0.0001	
RW standard deviation	8	365	86.182	<0.0001	Log
RW 5th percentile	8	361	30.188	<0.0001	Log + outlier removal
RW 95th percentile	8	365	108.065	<0.0001	Log

**Appendix B** Absolute and relative frequency of the different growth patterns by species.  
 $\chi^2$ : chi-square, df: degrees of freedom.

<i>Growth pattern</i>	<i>Species</i>		<i>Total</i>
	<i>Black spruce</i>	<i>Balsam fir</i>	
Linear	13	8	21
	4.5%	8.8%	5.5%
Low-bell	42	13	55
	14.5%	14.3%	14.4%
High-bell	4	3	7
	1.4%	3.3%	1.8%
Low-ascending	54	23	77
	18.6%	25.3%	20.2%
Moderate-ascending	47	15	62
	16.2%	16.5%	16.3%
High-ascending	18	9	27
	6.2%	9.9%	7.1%
Low-sine	60	10	70
	20.7%	11%	18.4%
Moderate-sine	26	5	31
	9%	5.5%	8.1%
High-sine	26	5	31
	9%	5.5%	8.1%
<b>Total</b>	290	91	381
	100%	100%	100%

$$\chi^2 = 12.166 \cdot \text{df} = 8 \cdot \text{Cramer's } V = 0.179 \cdot \text{Fisher's } p = 0.132$$