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Secondary disturbances of low and moderate severity drive the dynamics of eastern Canadian boreal old-growth forests

Maxence Martin[*1,2], **Hubert Morin**[2], **Nicole J. Fenton**[3]

[1] Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec G7H2B1, Canada

[2] Centre d'étude de la forêt, Université du Québec à Montréal, P.O. Box 8888, Centre-ville Station, Montréal (QC) H3C 3P8, Canada.

[3] Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada* Corresponding author: Tel.: +1 581 882 8651;

* Corresponding author: maxence.martin1@uqac.ca

Running head: Eastern Canadian boreal old-growth forests dynamics is driven both by low and moderate severity secondary disturbances. Each severity is defined by particular disturbance agents and temporal patterns. They have both specific influence on stand dynamics and structure, shaping therefore the diversity of boreal old-growth forests.

Keywords: Low severity, moderate severity, natural disturbance, succession, spruce budworm, windthrow

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Abstract

Context: A regular succession of low-severity disturbances are seen as determining the dynamics of the old-growth stage (gap dynamics); however, recent studies suggest that moderate-severity secondary disturbances also play an important role in the dynamics of eastern Canadian boreal forests.

Aim: This study aims to determine if eastern Canadian boreal old-growth forests are driven by a combination of low- and moderate-severity secondary disturbances.

Methods: We reconstructed the 200-year disturbance history of 20 boreal old-growth stands using dendrochronological analysis. We discriminated low- from moderate-severity disturbances based on their respective influence on mean stand growth (i.e. low-severity: no change in mean stand growth; moderate-severity: abrupt growth-release in the mean stand growth).

Results: The secondary disturbance regime of eastern Canadian boreal old-growth forests varies highly over time, reflected by disturbance peaks in the chronological record. Most peaks occurred during spruce budworm outbreaks related to both low- and moderate-severity disturbances. Between each peak, low-severity disturbances dominate. Each level of disturbance severity has specific consequences for stand dynamics.

Conclusion: Both low and moderate secondary disturbances are drivers of forest dynamics in eastern Canadian boreal old-growth stands and shape the structural diversity of these stands. The complexity of these dynamics should be recognized in management planning to ensure the efficiency of old-growth forest conservation policies.

Résumé

Contexte : On considère qu'une succession régulière de perturbations de faible sévérité détermine la dynamique des vieilles forêts (dynamique des trouées) ; cependant, des études récentes suggèrent que les perturbations secondaires de sévérité modérée jouent également un rôle important dans la dynamique des forêts boréales de l'Est du Canada.

Objectif : Cette étude vise à déterminer si les vieilles forêts boréales de l'Est du Canada sont dynamisées par une combinaison de perturbations secondaires de sévérités faibles et modérées.

Méthodes : Nous avons reconstitué l'historique de perturbation sur les 200 dernières années de 20 vieilles forêts boréales à l'aide d'analyses dendrochronologiques. Nous avons fait la distinction entre les perturbations sévérité faible et celles de sévérité modérée en fonction de leur influence respective sur la croissance moyenne des peuplements (c.-à-d. faible sévérité : aucun changement de la croissance moyenne des peuplements ; sévérité modérée : reprise de croissance abrupte de la croissance moyenne).

Résultats : Le régime de perturbations secondaires des vieilles forêts boréales de l'Est du Canada varie considérablement au fil du temps, comme en témoignent les pics de perturbations observés dans les données dendrochronologiques. La plupart des pics se sont produits pendant les épidémies de tordeuse des bourgeons de l'épinette, résultant aussi bien des perturbations de sévérités faibles ou modérées. Entre chaque pic, les perturbations de faible sévérité dominent. Chaque classe de sévérité a des conséquences spécifiques sur la dynamique du peuplement.

Conclusion : Les perturbations secondaires de sévérités faibles et modérées sont les moteurs de la dynamique forestière dans les vieilles forêts boréales de l'Est du Canada et façonnent la diversité structurelle de ces peuplements. La complexité de cette dynamique devrait être reconnue dans la planification de l'aménagement pour assurer l'efficacité des politiques de conservation des vieilles forêts.

Introduction

Recognition of the prominence of boreal old-growth stands, here defined as stands driven by secondary disturbances, represented a major paradigm shift in boreal forest ecology (Kneeshaw and Gauthier 2003; Kuuluvainen 2009). Prior to this shift, the assumptions held that old-growth forests were almost absent in boreal landscapes because of relatively frequent forest fires; and that some boreal forest stands did not remain stable in an old-growth phase, but they rather became open peatlands in the absence of fire (Bergeron and Harper 2009; Wirth and

Lichstein 2009). Nonetheless, old-growth forests are abundant in the boreal landscape, even in territories where the fire cycle is relatively short; this pattern reflects the random distribution of fires across all age classes (Bergeron et al. 2001). In addition, the distinctive structural attributes and ecological continuity of old-growth stands imply the presence of specific habitats that are absent from younger stands (Drapeau et al. 2002; Drapeau et al. 2003; Fenton and Bergeron 2008; Boudreault et al. 2018). For these reasons, boreal old-growth forests are now recognized as key components of boreal landscapes.

Since the mid-20th century, intensive industrial forest harvesting has expanded markedly across the boreal landscape. In territories that are characterized by severe crown fires, such as the boreal forests in Eastern Canada, the harvested surface area can approximate 75% of the burned surface area during the same period (Bouchard and Pothier 2011; Boucher et al. 2017). Furthermore, in landscapes driven by low-severity surface fires and where fire mitigation is very efficient, logging has almost become the only type of severe-intensity disturbance (Östlund et al. 1997). Clearcutting systems are by far the most common harvesting method in the boreal forest biome. This approach is most profitable for forest companies, and the effects of clearcutting are assumed to be equivalent to those from fire (Bergeron et al. 2001). However, fire burns trees of all age classes, while logging primarily affects mature and old forests, thereby rejuvenating the landscape (Östlund et al. 1997; Fall et al. 2004; Bergeron et al. 2006). In addition, the short-term rotation of clearcutting systems accelerates this rejuvenation by inhibiting the establishment of new mature or old stands (Bergeron et al. 2002; Kuuluvainen 2009). The result is a markedly diminished abundance of boreal old-growth forests in managed territories over the last century. The consequential environmental effects include a decline of floral, faunal, and fungal forest species associated with abundant dead wood of diverse decay stages (Siitonen 2001).

Alternative management models have emerged over the two last decades to counter the loss of old-growth stands in managed landscapes. These new approaches copy the natural disturbance regimes of the different managed regions (Bergeron and Harvey 1997; Harvey et al. 2002; Kuuluvainen 2002; Grandpré et al. 2009) or imitate stand-scale natural processes (Vanha-Majamaa et al. 2007;

Kuuluvainen 2009). The efficacy of these models, however, depends of an accurate understanding of disturbance regimes in a given area; however, each boreal region differs in terms of climatic factors, disturbance dynamics, and species' traits (Kneeshaw et al. 2011; Shorohova et al. 2011). As such, local-scale studies are necessary to assess whether a particular management strategy is or can be adapted to the local characteristics of a landscape.

The main drivers of secondary disturbance in eastern Canadian boreal forests are spruce budworm (SBW - Choristoneura fumiferana (Clem.)) outbreaks and windthrow events (Bouchard et al. 2006; Kerharo 2013; De Grandpré et al. 2018). Other disturbances that drive mortality in these forests include jack pine budworm (Choristoneura pinus pinus) and forest tent caterpillar (Malacosoma disstria) (Jan and Volney 1988; Bergeron and Charron 1994). However, as the main boreal hosts of these two defoliating insects are pioneer species (Nealis and Lomic 1994; Cooke and Lorenzetti 2006), their influence on old-growth dynamics are negligible.

The disturbance regimes of Fennoscandian boreal forests are relatively well understood and involve a mix of low-, moderate-, and high-severity disturbances, i.e. disturbances causing a mortality gradient ranging from low (one tree or a few affected trees) to high (stand-replacing) (Kuuluvainen and Aakala 2011; Hart 2018). In contrast, the perception of dynamics within eastern Canadian boreal forests remains relatively simplistic, dividing the disturbance regime into low-severity secondary disturbances and high-severity stand-replacing disturbances (Bergeron and Harper 2009; Shorohova et al. 2011). Nonetheless, previous studies have highlighted that secondary disturbance dynamics in regional boreal old-growth forests vary in their severity, nature, and spatial distribution (Kneeshaw and Bergeron 1998; Pham et al. 2004; Aakala et al. 2007). It is likely that disturbances of moderate severity play an important role in the overall landscape disturbance regime, in particular because of the dynamics of the SBW (Kneeshaw et al. 2009; Shorohova et al. 2011).

Similarly, the structural diversity of eastern Canadian boreal forests suggests that these ecosystems are driven by both low- and moderate-severity disturbances (Martin et al. 2018). However, the transition toward an old-growth stage is a progressive process where late-successional species replace progressively the cohort that appeared following the last stand-replacing disturbance (Harper et al. 2005; Lecomte et al. 2006; Gauthier et al. 2010). It supposes that disturbances of moderate severity gain progressively in importance at the later stages of the old-growth succession process. Furthermore, differences in the severity of secondary disturbances also imply differences in the post-disturbance regeneration dynamics (Kneeshaw and Bergeron 1998; Montoro Girona et al. 2018). It is therefore likely that the secondary disturbance regime of eastern Canadian boreal forests is more complex than is currently portrayed.

Our study aims to determine if the secondary disturbance regime of eastern Canadian boreal stands is driven by various types of secondary disturbance. We hypothesized that (1) low- and moderate-severity disturbances present different temporal patterns and that (2) moderate-severity disturbances are more abundant in old-growth stands and favour different components of the regeneration layer. The innovative nature of our research lies in using dendrochronological data for analysing disturbances of low and moderate severity over the two last centuries in forests at different stages of the old-growth succession. Thus, our study is not restricted to the effects of the most recent secondary disturbances, but we will observe their long-term patterns of secondary disturbance and their influence on old-growth stand dynamics. Consequently, our research contributes to the increasing body of literature discussing the complexity of secondary disturbance regimes in boreal landscapes by reconstructing the disturbance history of a part of eastern Canadian boreal old-growth forests.

Methods

Study territory

The study was conducted in a 2200 km2 area of public lands, located south-east of Lake Mistassini, Quebec (72°52′36″W, 50°18′50″N) (**Figure 1**). This area lies within the black spruce (*Picea mariana* (Mill.))–feather moss bioclimatic domain, the dominant boreal forest domain in Eastern Canada. Regional topography is characterized by gentle hills having an altitude ranging from 350 to 750 m asl. Thick glacial till dominates the surficial deposits, and sand deposits or vast bogs often surround waterways. Mean annual temperature ranges from -2.5 to 0.0 °C, annual rainfall (rain and snow) is 900–1100 mm, and the growing season lasts 140–150 days (Robitaille and Saucier 1998). Black spruce and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species. We selected this study area as it encompasses the environmental diversity of the black spruce–feather moss bioclimatic domain, from poorly drained valley bottoms situated on organic deposits to well-drained till slopes. We also selected this area as timber exploitation began in 1991, initially at low levels until 2000 when harvest levels increased. Consequently, old-growth stands remain abundant and relatively accessible.

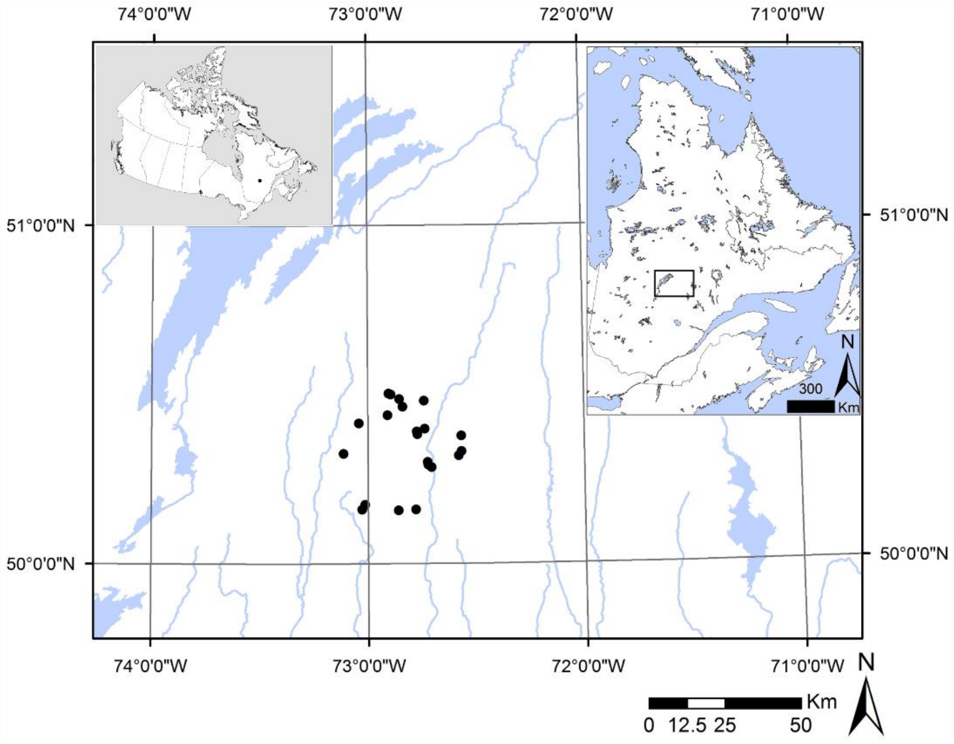

Figure 1 Map of the study area. Black dots represent the sample sites, blue lines and polygons represent rivers and standing waterbodies, respectively. The inset maps indicate the position of the study area map in Canada (left) and in the province of Quebec (right).

Sampling

Based on the nomenclature of the Quebec Ministry of Forests, Wildlife, and Parks (MFWP), the study area is divided into 19 environmental forest types. Six of these, however, cover 72% of the forest area. Given the environmental diversity of the study area, we focused our sampling within these six environmental forest types. Moreover, to encompass the complete old-growth successional sequence, we aimed to have an equal representation of sites belonging to mature, transition old-growth, and true old-growth phases. According to the literature for this ecosystem type (Uhlig et al. 2001; Bergeron and Harper 2009; Gauthier et al. 2010), the likely age classes associated with each phase are 80–100 years for even-aged mature stands, 100–200 years for transition old-growth, and >200 years for true old-growth.

We estimated the minimum age of 42 sites in a preliminary survey by sampling two cores at the base of five dominant and codominant trees at each site. Then, we performed a stratified random sampling to sample sites from each environmental type and age class. Twenty-one (21) sites were sampled during the summer and autumn of 2014 and 2015. We inventoried at least one site per environmental type and age class, except for the "Black spruce–feather moss on low slope, till deposit, and subhydric drainage" type, as we did not find a site within the 100–200 year age class (**Appendix A**).

We sampled coniferous basal discs in the same 20 × 20 m plots sampled by Martin et al. (2018), with the goal of obtaining 30 living and dead stems having a diameter at breast height (dbh) ≥9 cm (merchantable stems). We kept discs that showed stem decay if the rot was partial and the analysis of most of the tree rings remained possible. When it was impossible to sample a minimum of 30 stems per site, we sampled trees near the plot edge or saplings within the plot, depending on the site characteristics.

Discs were air-dried and mechanically sanded for tree-ring measurements. Then, we measured tree rings along two radii to the nearest 0.01 mm. These ring-width series were corrected by a combination of visual cross-dating and the use of the COFECHA computer program (Holmes 1983). We rejected accurately dated series having a poor statistical fit with the average curve of the disc due to growth anomalies. Similarly, we removed a disc from the final dataset when one of the two series measured on the basal disc correlated poorly with the mean stand chronology. We obtained 1550 accurately dated dendrochronological series, belonging to 775 trees.

Data preparation

We determined the diameter distribution of merchantable stems (dbh >9 cm) and saplings (height ≥1.3 m and a dbh <9 cm) in each plot following Martin et al. (2018) and using Weibull's equation (Bailey and Dell 1973). A Weibull's shape parameter (WSP) ≥1.5 indicates a normal diameter distribution, and a WSP <1.5 indicates an irregular diameter distribution. We also calculated the cohort basal area proportion (CBAP) for each site using the formula of Kneeshaw and Gauthier (2003):

$$CBAP = \frac{(BA_{N+1\ trees} + 0.1)}{(BA_{N+1\ trees} + BA_{First\ cohort\ trees} + 0.1)}$$

where BA is the basal area. We identified first cohort trees, N+1 trees, and the old-growth stage of each plot following Martin et al. (2018). Stands were defined as even-aged if WSP ≥1.5 and CBAP <0.3, true old-growth when WSP <1.5 and CBAP >0.6, and transition old-growth for all other conditions. We selected this methodology due to the increasing acknowledgement of the complexity of forest succession, including that of boreal forests (Cumming et al. 2000; McCarthy and Weetman 2006; Smirnova et al. 2008). Therefore, combining the CBAP and the WSP improves the discrimination of the different stages of old-growth succession while recognizing both the intrinsic progressive nature of the transition toward the old-growth stage and alternative successional pathways. Among the 21 sites sampled, 1 was identified as even-aged, 10 as transition old-growth, and 10 as true old-growth (**Appendix B**). We therefore removed the even-aged site from further analysis. In addition, the number of trees sampled was almost equivalent between the two old-growth stages for CE 1800–2000 period; however, the number was very low for both old-growth stages prior to CE 1800. For this reason, analyses focused on the CE 1800–2000 period (**Appendix C**).

Abrupt and persistent growth changes (%GC) are an effective proxy for indicating the occurrence of a secondary disturbance and thus override short- and long-term growth patterns associated with climate (Nowacki and Abrams 1997; Fraver and White 2005). We identified these growth changes by comparing sequential 10-yr ring widths via the formula of Nowacki and Abrams (1997):

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

where M1 is the mean ring width for the first 10-year period, and M2 is the mean ring width for the subsequent 10-year period. We classified growth changes by intensity based on the classes defined by Nowacki and Abrams (1997): major (%GC ≥50%) and minor (%GC = 25%–50%). These thresholds are well adapted to boreal forests, where tree growth is generally low (Tremblay et al. 2011). We calculated %GC for each tree, using the mean value of the two raw ring-width series measured for each tree (tree chronology), and for each species per stand, using the mean value of all raw ring-width series measured for each species in the plot (mean plot chronology). We chose to separate tree species due to the different dynamics and strategies vis-à-vis disturbances for black spruce and balsam fir. Relative to black spruce, balsam fir is more sensitive to SBW outbreaks, windthrow events, and root rot (Basham 1991; Ruel 2000; Morin et al. 2009); however, balsam fir regeneration is more competitive than that of black spruce when a canopy opening occurs following a disturbance (Doucet and Boily 1995; Messier et al. 1999). As a result, the abundance of balsam fir in an eastern Canadian old-growth stand may vary markedly over time (Pham et al. 2004; De Grandpré et al. 2009). Therefore, merging the results of both species in mixed stands could have biased the results. We determined growth releases from mean plot chronologies only when ≥10 trees constituted the chronology to ensure that the chronologies were representative of the stand's dynamics.

Discriminating low- from moderate-severity disturbances is challenging, as the threshold between the levels of low and moderate is often unclear (Hart and Kleinman 2018). The most common solution is to use size thresholds, either defined arbitrarily or related to stand characteristics (McCarthy 2001; Reyes and Kneeshaw 2008; Hart and Kleinman 2018). However, such methods cannot be used with dendrochronological data, as information related to the disturbances themselves is generally missing. Yet, tree growth releases are reliable indicators of disturbance dynamics and thus for canopy and tree population turnover (Nowacki and Abrams 1997; Szewczyk et al. 2011; Khakimulina et al. 2016); this makes them a relevant proxy for the disturbance regime. To determine the severity of a secondary disturbance, we considered that a low-severity disturbance would induce individual tree growth release but would not influence mean plot growth, i.e., no growth release in the mean plot chronology, as only a small fraction of the trees is disturbed. This scenario implies few changes in the stand canopy and age structure. In contrast, a disturbance of moderate severity will disturb a larger proportion of trees, leading to important changes in stand structure. In turn, this provokes a greater number of growth releases that will influence mean plot growth. As such, we defined low-severity disturbances as disturbances lacking a significant influence on post-disturbance stand growth because of low overstorey mortality. Moderate-severity disturbances are disturbances that significantly and positively influence post-disturbance stand growth because of moderate overstorey mortality.

To link the two scales (tree and plot) and determine if each release observed between CE 1800 and 2000 on an individual tree was part of a secondary disturbance of low or moderate severity, we compared the occurrence of tree growth releases to releases of the corresponding stand and species. We used stand growth release—identified on the mean plot chronologies—to define windows within which individual tree growth release could be considered as resulting from a moderate-severity disturbance. For a given stand, all individual tree growth releases that occurred in the nine years before or the nine years after an observed stand growth release were classified as moderate-severity secondary disturbance releases, i.e., the individual tree releases contributed to growth release at the plot scale. If not, they were classified as low-severity secondary disturbance releases, i.e., the individual tree releases did not contribute to any growth change at the plot scale. We selected a nine-year threshold as Nowacki and Abrams (1997) applied a ten-year window to identify growth releases. Hence, all individual tree growth releases that occurred nine years before or after a stand growth release may have contributed to this release. As such, our methodology accounts for potential lags that can be observed between disturbance and growth releases, as well as lags between disturbance and tree mortality (Worrall et al. 2005; De Grandpré et al. 2018). To distinguish between strong juvenile growth after a stand-replacing disturbance and growth release due to low- or moderate-severity secondary disturbance, we only considered growth releases that occurred 40 years after the minimal year of stand establishment. This 40-year threshold corresponds to the end of the marked juvenile post-fire recruitment period in even-aged stands (Rossi et al. 2009) as well as the beginning of gap dynamics under particular conditions (Cumming et al. 2000). Finally, we only retained growth releases for each site and year when the number of trees sampled was ≥10, i.e., we did not determine stand growth release when this condition was not fulfilled.

Statistical analysis

To test our first hypothesis—that low- and moderate-severity secondary disturbances differ in their temporal patterns—we identified for each site and each year the percentage of trees being in a state of growth release and the severity of the secondary disturbance (low or moderate). This method provides an improved description of the stand dynamics to using only the absolute number of trees. Tree and sapling density in eastern Canadian old-growth boreal forests may vary markedly between stands, independent of old-growth stage (Martin et al. 2018). In contrast, the frequency of trees in growth release puts into perspective results extracted from the dendrochronological series at the stand scale, and it is therefore a more suitable descriptor. We then applied a locally weighted regression scatterplot (loess) smoothing with a 10% span (Trexler and Travis 1993) for various classes of secondary disturbance severity—low and moderate severity combined, low severity only, and moderate severity only—to observe the presence of release peaks and their co-occurrence between stands. By smoothing the annually observed growth releases for all stands, we expect that this methodology will neutralize potential lags in growth releases that can be observed from one stand to another following a single disturbance event. In addition, we compared the occurrence of these peaks with the chronologies of Morin and Laprise (1990) and Krause (1997), who identified the SBW outbreaks over the last three centuries at sites near our study area. We considered that the occurrence of a release peak during a SBW outbreak period implied that this insect was the main disturbance agent explaining this peak.

For testing our second hypothesis—that low- and moderate-severity secondary disturbances have different effects on the subsequent stand dynamics—we first used logistic regression to compare stand, tree, and release characteristics related to each identified tree growth release for the transition and true old-growth stands. Secondary disturbance severity (low/moderate) was the binary dependent variable, and the following parameters were the independent variables: release intensity (minor/major), old-growth stage (transition/true old-growth), species, and diameter class at release. We applied a likelihood ratio test and residual equidispersion to assess model validity. In addition, we checked model predictive ability using the area under the receiver operating characteristic curve (AUC) method (Zweig and Campbell 1993) and Tjur's coefficient of discrimination (COD; Tjur (2009)). An AUC value >0.7 and a COD >0.2 represents an excellent predictive ability. In addition, we determined for each disturbance severity the mean percentage of trees presenting growth releases per decade and per site to observe the variation in disturbance history and severity between the study sites. We compared these values by combining old-growth stage and release type using a Kruskall-Wallis test followed by a pairwise Wilcoxon test.

We used R-software, version 3.3.1 (R Core Team 2016) for all statistical analyses, running the *ROCR* (Sing et al. 2005), *DescTools* (Signorell 2017), and *ggplot2* (Wickham 2016) packages. We selected a threshold of $p < 0.05$ to establish significance.

Results

Temporal pattern of low- and moderate- severity secondary disturbances

Considering low- and moderate-severity disturbances together during the CE 1800–2000 period, the proportion of trees having growth releases in the studied stands varies greatly from year to year; nonetheless, eight peaks emerge (**Figure 2**). Six of these peaks occurred during SBW epidemics. In addition, there is no period where tree growth releases are absent, except in the oldest portion of the chronology; therefore, secondary disturbances of variable severity represent a continuous element in the studied old-growth stands over the two last centuries.

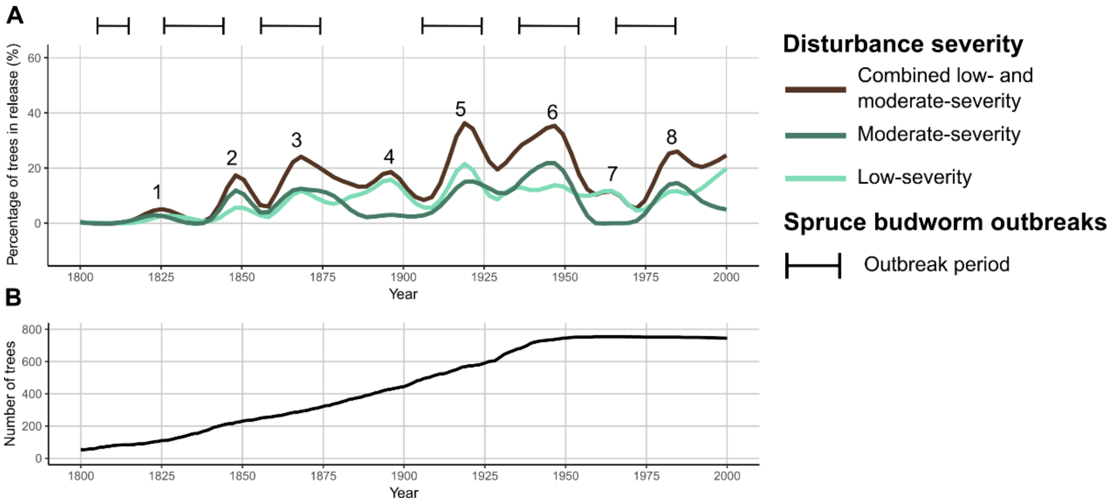

Figure 2 (A) Loess smoothing of the percentage of trees having growth release events per decade grouped by secondary disturbance severity: combined low and moderate severity (brown curve), moderate severity (dark green curve), and low severity (light green curve). Numbers identify the eight peaks, and hooks indicate spruce budworm outbreaks. Spruce budworm outbreaks are based on Morin and Laprise (1990) and Krause (1997). (B) Number of trees that make up the developed tree-ring chronology for the period CE 1800–2000.

Relative to the moderate-severity disturbances, the frequency of tree growth releases linked to low-severity disturbances vary much less from year to year. Nevertheless, we still observe the eight previously identified peaks, although they tend to be less pronounced. In contrast, the percentage of trees having growth release related to disturbances of moderate severity varies widely over time; this relative abundance alternates between periods where this proportion is equal or greater to the proportion of trees with growth release resulting from low-severity disturbance and periods where the proportion is near zero.

The relative contribution of secondary disturbances of low and moderate severity to the disturbance peaks varies between peaks. Moderate-severity disturbances contributed to six of the eight identified peaks (peaks 1, 2, 3, 5, 6, 8); five occur during SBW outbreaks. The contribution from moderate-severity disturbances is generally equal to that of low-severity disturbances, except for peaks 2 and 6, where moderate-severity disturbances contribute much more. In contrast, peaks 4 and 7 are due solely to low-severity disturbances and occur outside periods of SBW outbreaks. Therefore, both low- and moderate-severity disturbances drive the secondary disturbance regime of boreal old-growth forests; however, given as they often overlap, the implication is that both can result from the same disturbance agents.

Dynamics of old-growth stages

Table 1 Results of the logistic regression model comparing the characteristics of the growth releases according to the disturbance severity. AIC: Akaike information criterion; AUC: area under the receiver operating characteristics curve; COD: Tjur's coefficient of discrimination.

Resid. Df	Resid. Dev.	Df	Deviance	Pr(>Chi)	AIC	AUC	COD	Parameter	Df	Deviance	Resid. Df	Resid. Dev.	Pr(>Chisq)
1612	2110.6	-6	-340.69	<0.001	1783.9	0.76	0.2	Old-growth stage	1	233.232	1611	1877.3	<0.001
								Release intensity	1	69.162	1609	1797.5	<0.001
								Diameter class at the release	3	27.627	1606	1769.9	<0.001
								Species	1	10.666	1610	1866.7	<0.01

The four parameters analysed via logistic regression—old-growth stage, release intensity, tree species, and diameter class at release—differed significantly between the levels of disturbance severity (**Table 1**). The logistic regression model presents an excellent predictive value, as evidenced by the significant log-likelihood test ($p < 0.001$), the strong AUC value (0.76), and the high COD (0.2).

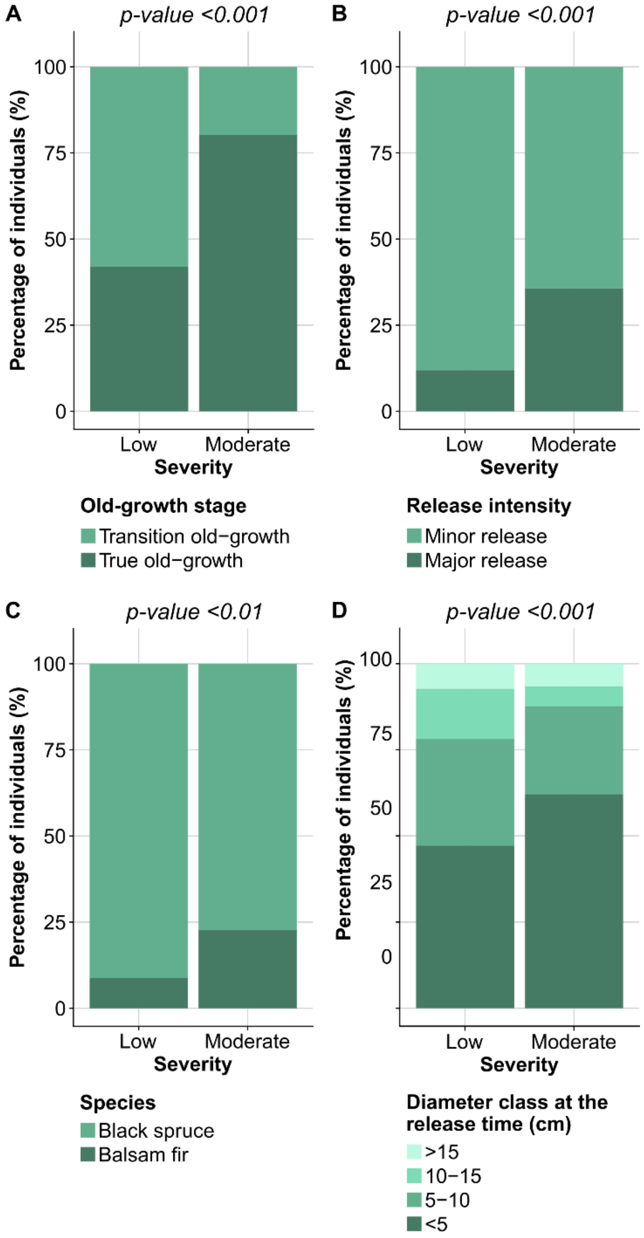

Figure 3 Class distribution and *p*-values of the four parameters analysed in the logistic regression as a function of the severity of secondary disturbance (low or moderate); (A) old-growth stage, (B) release intensity, (C) species, and (D) diameter class at release. The *p*-values above each bar represent the significance of the specific parameter based on the logistic regression model (see **Table 1**).

For both levels of disturbance severity, trees that show growth releases are mainly small (tree diameter at the moment of release <10 cm) (**Figure 3**). Despite their small size, most trees having a diameter at release of <10 cm are old (>50 years, **Appendix D**). Thus, most observed releases are due to suppressed trees that benefit from an opening of the canopy. Yet, these trees were generally smaller and younger in moderate-severity disturbances than in low-severity disturbances. Furthermore, the frequency of release observed for balsam fir is higher in moderate than in low-severity disturbances, even if black spruce is the dominant species for both disturbance severity. Similarly, the frequency of major growth release is higher in moderate than in low-severity disturbances; however, minor releases are the dominant release type for both types of disturbance. Therefore, the characteristics of the gap fillers differ depending on disturbance severity. The distribution of growth releases resulting from low- and moderate-severity disturbances also varies between the different old-growth stages.

The mean decadal percentage of trees having growth releases due to low-severity disturbances did not differ between old-growth stages, but there were fewer trees showing a growth release from moderate-severity disturbances in the transition old-growth than in true old-growth (**Figure 4**). Interestingly, in true old-growth, the mean decadal percentage of trees having low-severity disturbance–induced growth release was similar to that of trees having moderate severity disturbance–induced growth release. Therefore, the dynamics due to disturbances low severity are similar between the transition and true old-growth forests. Furthermore, stand dynamics related to disturbances of moderate severity are at a similar level to that of low-severity disturbances in true old-growth forests. Consequently, the balance between low- and moderate-severity disturbances changed with the disappearance of the first cohort.

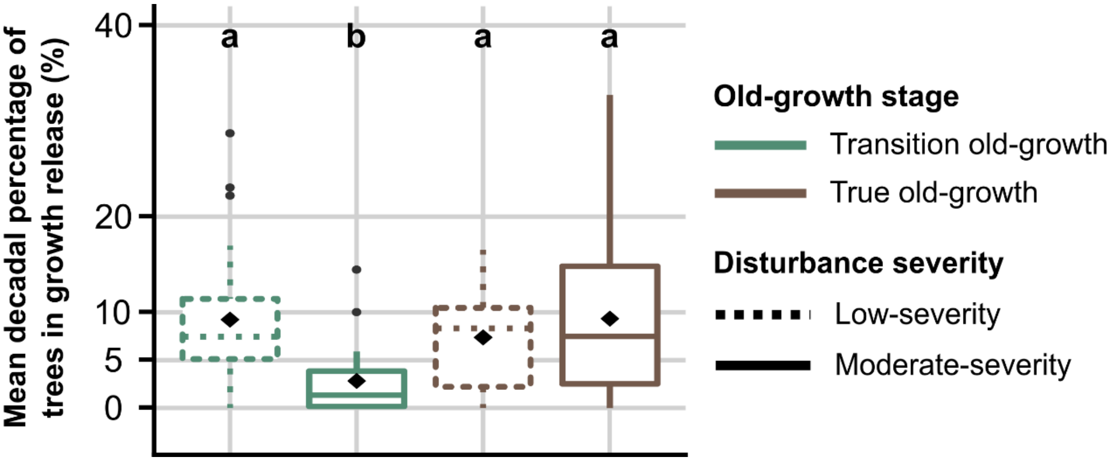

Figure 4 Box plot of the stand mean decadal percentage of trees experiencing growth release based on old-growth stage and disturbance severity. Diamonds represent mean values and letters identify significant differences.

Discussion

In Eastern Canada, both low- and moderate-severity secondary disturbances drive the dynamics within boreal old-growth forests; however, the disturbances occur in both analogous and non-analogous temporal patterns. Secondary disturbances occur continuously across the landscape. Their severity, however, is not constant over time; severity increased during eight distinct peaks over the last 200 years. Six of these eight peaks coincided with SBW outbreaks. Low- and moderate-severity disturbances also influence gap-filler characteristics, e.g., species and age, and vary between the different old-growth stages.

Mixed severity secondary disturbances drive the dynamics of boreal old-growth forests

We found that in addition to low-severity disturbances, moderate-severity disturbances are a distinct component of boreal old-growth forests dynamics in Eastern Canada, as hypothesized by Shorohova et al. (2011) and Martin et al. (2018). Our results add to the literature highlighting the dynamism of boreal old-growth forests in this region (Kneeshaw and Bergeron 1998; Pham et al. 2004;

Aakala et al. 2007) and underline that boreal old-growth forests are not declining ecosystems but rather remain productive and dynamic over centuries in the absence of stand-replacing disturbance (Garet et al. 2009; Pollock and Payette 2010; Ward et al. 2014). This dynamism is driven by recurrent mortality events. Our study therefore underlines the long-term resistance and resilience of these ecosystems (*sensu.* Perry and Amaranthus (1997) given that most of the studied stands experienced secondary disturbances of varying severity over the past two centuries. The percentage of trees that experienced growth release was, however, lower in the 19th century relative to the 20th century. Black spruce and balsam fir longevity is relatively low (often <200 years), and slow-growing trees tend to live longer than fast-growing ones (Laberge et al. 2000; Larson 2001). It is therefore likely that only a small fraction of the trees that benefited from 19th-century disturbances survived until the present. Nevertheless, the release patterns for both disturbance types were similar throughout both centuries. This similarity implies that the studied stands were driven by comparable disturbance dynamics during the CE 1800–2000 period, although these dynamics were less obvious in the 19th century.

Moderate-severity disturbances occurred mainly during previously identified SBW outbreaks in the southern portion of the region (Morin and Laprise 1990; Krause 1997). In the eastern Canadian boreal forest, SBW is the main agent of large secondary disturbance (Morin et al. 2009; Shorohova et al. 2011). Previous studies have demonstrated the importance of SBW outbreaks for the dynamics of boreal old-growth forests situated in the main SBW distribution range (Kneeshaw and Bergeron 1998; Pham et al. 2004; Aakala et al. 2007). However, our study sites are currently at the northern edge of SBW distribution; thus, SBW outbreaks should have a limited influence on the disturbance regime of our study stands (Gray 2008). Recent reconstructions of the spatial patterns of SBW outbreaks in Quebec over the 20th century (Navarro et al. 2018) also indicate that our study stands lie outside of SBW hotspots. Nonetheless, we observed a strong influence of this disturbance agent over the two last centuries within our study area; this observation highlights the importance of SBW in landscape dynamics, even at the northern limit of its normal range. SBW outbreaks are cyclical events having a 30-year periodicity (Morin et al. 2009). Moderate-severity disturbances from SBW outbreaks follow the same temporal cycle. Furthermore, mortality caused by SBW is highly variable between stands during an outbreak; the effects vary from a moderate thinning of suppressed trees to a significant mortality of canopy trees (Lesieur et al. 2002; Kneeshaw et al. 2009; Morin et al. 2009). 2009). Similarly, the identified SBW outbreak peaks in our study provoked disturbances of both low and moderate severity, indicating differences in mortality between stands during a single outbreak. This complex pattern of disturbance may also be explained by our study stands being at the northern range of SBW distribution, thereby resulting in SBW-related damage to be more limited relative to areas further south (Bergeron et al. 1995; MacLean and Andersen 2008; Kneeshaw et al. 2009). Thus, SBW is an important driver of the secondary disturbance regime in our study area; its influence is cyclical and varies in severity between stands and during a SBW outbreak.

Secondary disturbances of low severity occurred almost continuously throughout our 200-year chronology. This pattern contrasts with that of secondary disturbances of moderate severity that occurred more sporadically. This continuous low-severity disturbance implies a background mortality throughout the study area. The causes of this background mortality include windthrow, fungal rot and tree senescence, but these events occur more randomly and cause a lower degree of mortality at the landscape scale than do SBW outbreaks (Kerharo 2013; Waldron et al. 2013; Girard et al. 2014). However, two of the eight identified peaks occurred outside SBW outbreaks and were dominated by low-severity disturbances. It is possible that these two peaks resulted from particular climatic events that caused simultaneous low-severity windthrow events across the landscape. In eastern Canadian boreal forests, the secondary disturbance regime is a complex process that comprises a constant background mortality punctuated by moderate-severity disturbances.

Influence of the mixed severity secondary disturbance regime on forest structure and succession

We observed moderate-severity disturbances mainly in true old-growth stands, and these disturbances favoured smaller trees in the regeneration layer. The difference in disturbance severity between the transition (low severity) and the true old-growth stages (moderate severity) may be partially due to the divergence in the structural attributes of old-growth stands. Older and taller black spruce and balsam fir are more prone to windthrow than younger and smaller trees (Viereck and Johnson 1990; Robichaud and Methven 1993; Girard et al. 2014). Similarly, balsam fir is very sensitive to SBW-induced defoliation, thereby resulting in important peaks of balsam fir mortality (Kneeshaw et al. 2009; Morin et al. 2009; Garet et al. 2012). In contrast, SBW outbreak–induced mortality is generally low for black spruce (Lesieur et al. 2002; Garet et al. 2012). As such, the abundance of balsam fir often fluctuates within old-growth stands (Pham et al. 2004; Grandpré et al. 2009). However, old-growth stands are characterized by a greater abundance of balsam fir and taller and older individual trees (Martin et al. 2018); these characteristics render them potentially more sensitive to secondary disturbances than younger stands.

The characteristics of the trees that fill the canopy openings differ based on the severity of the secondary disturbance. For both low- and moderate-severity disturbances, growth release intensity is generally minor; this pattern confirms that what we identified as disturbances of moderate severity are real and not artefacts created by a small number of major releases. Rather, the large and abrupt canopy openings favoured the growth of a significant fraction of the understorey. In contrast, low-severity secondary disturbances likely created only small canopy openings, favouring the growth of a small number of understorey trees. In a context of a limited opening of the canopy, i.e., low-severity disturbance, the older and taller trees in the regeneration layer are more competitive than the smallest and youngest trees. In contrast, as moderate-severity disturbances affect a greater proportion of the canopy, even the smaller trees in the regeneration layer benefit from this important increase in light availability. Furthermore, the tallest trees of the regeneration layer are more likely to be killed by a moderate-severity disturbance as SBW outbreaks or windthrow events are often “top-to-down” disturbances, first killing the tallest trees and then affecting the smaller trees as disturbance severity increases (De Grandpré et al. 2018). This mortality pattern therefore favours the smallest trees. As such, the differences in disturbance severity have specific impacts on the horizontal and vertical structure of a stand as well as the subsequent stand dynamics; low-severity disturbances lead to a progressive and small-scale replacement of the killed trees by the oldest and tallest suppressed trees. In contrast, moderate-severity disturbances lead to a quick and larger-scale replacement of the killed trees, mainly by the youngest and smallest suppressed trees.

The disturbance regime within this study territory is similar to that observed by Kuuluvainen et al. (2014) and Khakimulina et al. (2016) in northern European Russia; they observed low-severity disturbances and punctual moderate-severity disturbances as a result of insect outbreaks. In both studies, low-severity disturbances created gaps, i.e., canopy openings of <200 m2 based on McCarthy's definition (2001), while moderate-severity disturbances created patches, i.e., canopy openings of >200 m2 (McCarthy 2001). This combination of gap and patch dynamics are likely a common secondary disturbance regime in Fennoscandian boreal forests (McCarthy 2001; Kuuluvainen and Aakala 2011).

In our study, the size of the canopy opening resulting from each identified disturbance cannot be estimated precisely because of our methodology; it is therefore impossible to assess whether the moderate-severity disturbances effectively correspond to the creation of patches and low-severity disturbances correspond to the creation of gaps in our study stands. However, Kneeshaw and Bergeron (1998) observed a large diversity in the size of canopy openings in Quebec’s boreal forests, corresponding both to gaps and patches. SBW can also create large (>200 m2), yet continuous, mortality areas; this creates a patchy distribution of dead and live trees in a landscape disturbed by this insect (Kneeshaw et al. 2009). Therefore, a combination of gap and patch dynamics may be a common disturbance regime in eastern Canadian boreal old-growth forests.

Our results also fall within the paradigm of a complex forest succession and disturbance regime within boreal forests. Forest succession should not be viewed as a linear pathway from structurally simple, post– stand-replacing disturbance, even-aged stands to structurally complex old stands driven by low-severity disturbances, but rather as several imbricated pathways (Kuuluvainen 2009; Reilly et al. 2015; Halpin and Lorimer 2016). Admittedly, the model describing old-growth dynamics driven solely by small-scale and low-severity disturbance remains partially valid, as some of our stands showed evidence of only low-severity disturbances over the centuries. Yet, the recurrence of moderate-severity disturbances and, more particularly, the fact that they were mainly found in true old-growth stands suggest the existence of other dynamics and succession patterns. First, the occurrence of disturbances of moderate severity in transition old-growth forests may accelerate the shift to the true old-growth stage, as a large part of the post– stand-replacing disturbance cohort is quickly killed and replaced. This may explain why moderate-severity disturbances are almost absent in the studied transition old-growth forests. Thus, the duration of the replacement of the post– stand-replacing disturbance cohort in a boreal old-growth stand may vary significantly from one stand to another. Second, once the true old-growth stage is reached, each stand may be driven by a particular secondary disturbance regime, mixing low- and moderate-severity disturbances at different proportions, and producing the structural diversity observed by Martin et al. (2018). Third, disturbances of moderate severity can create young forest structures that are neither even-aged nor old-growth (Donato et al. 2012; Meigs et al. 2017; Hart and Kleinman 2018). Donato et al. (2012) qualified these stands as “born-complex” forests, i.e., young stands exhibiting a structural complexity usually attributed to old-growth forests. Considering the importance of moderate-severity disturbances in the secondary disturbance regime, it is thus possible that the creation of born-complex forests is relatively common. In this context, structural differences between born-complex and old-growth forests are probably minimal, making it difficult to distinguish between these two ecosystems and thus question the "young forest/old forest" dichotomy. Therefore in Eastern Canada, recent findings regarding the complexity of the secondary disturbance regime should encourage forest ecologists and managers to re-evaluate the dynamics and the succession of boreal forests (**Figure 5**).

Discriminating low- from moderate-severity secondary disturbances by comparing tree and stand growth releases is an uncommon methodological approach. Observing the spatial patterns of tree mortality or canopy opening are preferred methods (e.g., Aakala et al. 2007; Janda et al. 2014; Khakimulina et al. 2016). In particular, it is easier to identify multiple and clustered growth releases that result, for example, from the death of a single large tree using spatialized data. This type of disturbance may challenge our definition of moderate-severity disturbances, as it could significantly change the mean stand growth. However, tree size is relatively limited in eastern Canadian boreal forests and broad-leaved species, i.e., species having the largest canopy disappear quickly during the old-growth transition (Bergeron and Harper 2009). Moderate-severity disturbances were infrequent in transition old-growth stands, i.e., stands that were the most likely to record the death of an old and large broad-leaved tree. This implies that the misclassification of disturbance severity caused by highly clustered growth releases was very unlikely. In contrast, the observed moderate-severity disturbance patterns resulted from multiple and coordinated minor understorey-tree growth releases in a number of stands. Our results therefore support the hypothesis of a mixed low- and moderate-severity secondary disturbance regime in eastern Canadian boreal old-growth forests over the last centuries. Finally, a 400-m2 plot surface is considered to be representative of the sampled boreal stand (MFFP 2016). Hence, we assume that disturbance dynamics observed within our plots are representative of the overall stand dynamics. Admittedly, complementary research analysing the spatial patterns of canopy gaps and their influence on tree growth releases in the studied stands would improve our understanding of secondary disturbance dynamics in boreal old-growth forests. The use of large-scale aerial or satellite images, e.g., Kuuluvainen et al. (2014) or light detection and ranging (LiDAR) data, e.g., Vepakomma et al. (2010), offer methods to overcome the intrinsic limits of plot-scale dendrochronological analysis.

Conclusion and management implication

Boreal old-growth stand dynamics generated by secondary disturbances are characterized by spatial and temporal complexity. Our study demonstrates that a given secondary disturbance regime will produce disparate severities across the landscape. This disparate pattern occurs because of a regime’s inherent spatial heterogeneity and the diversity of structural characteristics of the stand subjected to the disturbance. Furthermore, two disturbances are rarely comparable, even if they share a similar nature; for example in Eastern Canada, SBW outbreaks are cyclical but differ from each other in terms of spatial distribution and severity (Morin et al. 2009; Navarro et

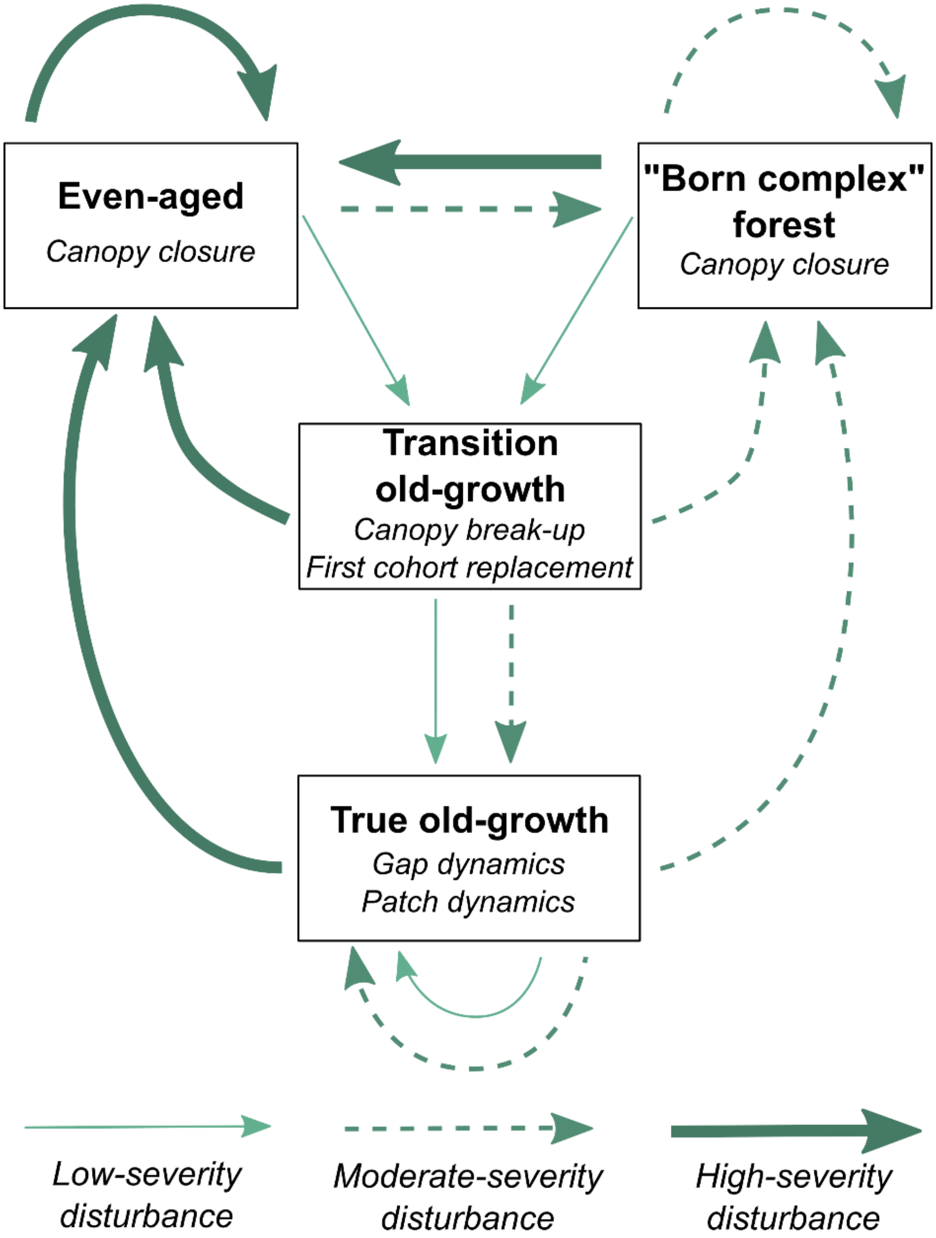

Figure 5 Conceptual model of the theoretical dynamics of boreal old-growth forests under a disturbance regime that combines low-, moderate-, and high-severity disturbances. Boxes represent the different successional stages. The "born-complex" forest stage refers to the theoretical and alternative stage described by Donato et al. (2012). Sentences in italics inside the boxes indicate the main processes driving that successional stage.

al. 2018). Our results underline this important “complexity challenge” faced by natural disturbance–based management (Kuuluvainen 2009), as the secondary disturbance regime is a very heterogeneous process.

Martin et al. (2018) hypothesized that boreal old-growth forest structural diversity results from a combination of low- and moderate-severity disturbances. Our results support this hypothesis, highlighting the importance of disturbance heterogeneity in the creation of old-growth structural richness. In addition, such complex disturbance histories are evidence of both the strong resistance and resilience of boreal old-growth forests. Yet, recent studies have emphasized how moderate-severity disturbances can, in some cases, rejuvenate mature and old-growth stands (Donato et al. 2012; Meigs et al. 2017). Similarly, our results illustrate that moderate severity disturbances, due to their abundance and regularity in the boreal forests of Eastern Canada, can probably lead to similar rejuvenation patterns. Therefore, managing old-growth boreal forests requires caution and a thorough knowledge of stand characteristics to ensure their sustainable management.

To emulate low- and moderate-severity secondary disturbance requires the use of partial-cut and stem-selection harvesting. Favouring harvest practices that have varying retention levels could imitate the heterogeneity in the severity of disturbances (Hart and Kleinman 2018). By identifying temporal and severity disturbance patterns, our results can therefore serve as a basis for old-growth forest management. These proposed treatments may, however, cause post-harvest mortality and should be reserved for the most resilient old-growth structures (Girard et al. 2014; Bose et al. 2015). However, in the context of this study, it is impossible to clearly discriminate between stand structures in terms of resilience. Further research should be undertaken to better understand how the structural attributes of old-growth stands identify those stands more suitable for partial-cut or stem-selection harvests. Salvage logging in recently disturbed stands, especially after moderate-severity disturbances, can offer another solution. Exploiting naturally disturbed trees ensures that changes in the canopy structure result from natural processes. However, this type of forest intervention may have negative effects on the biodiversity, especially on saproxylic species, and thus should be used with caution (Nappi et al. 2004, 2015, Lindenmayer et al. 2004;

Nappi and Drapeau 2009, St-Germain et al. 2008; Thorn et al. 2018). Furthermore, natural secondary disturbances still occur in managed territories, and their occurrence and severity vary over time. Consequently, during periods of high natural mortality, such as during SBW outbreaks, living-tree harvesting levels should be reduced to limit pressure on the landscape.

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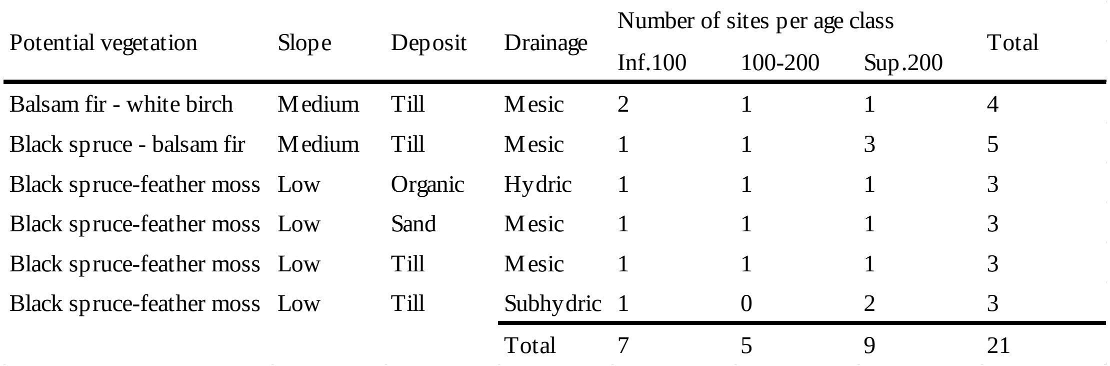
Supplementary materials



Potential vegetation	Slope	Deposit	Drainage	Number of sites per age class Inf.100	 100-200	 Sup.200	Total
Balsam fir - white birch	Medium	Till	Mesic	2	1	1	4
Black spruce - balsam fir	Medium	Till	Mesic	1	1	3	5
Black spruce-feather moss	Low	Organic	Hydric	1	1	1	3
Black spruce-feather moss	Low	Sand	Mesic	1	1	1	3
Black spruce-feather moss	Low	Till	Mesic	1	1	1	3
Black spruce-feather moss	Low	Till	Subhydric	1	0	2	3
			Total	7	5	9	21

Appendix A Distribution of the sample sites per environmental type and age class

A

Site	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**	**Site 10**
Cohort basal area proportion	0	0.54	0.98	0	0.12	0.12	0	0	0.15	0.83
Weibull's shape parameter	1.26	1.44	2.75	1.38	0.74	1.19	0.69	1.29	1.05	2.67
Min. time since the last fire (years)	86	219	206	195	184	193	89	89	218	286
Tree density (n.ha^{-1})	1100	1250	1275	1875	950	1025	1575	50	450	1325
Sapling density (n.ha^{-1})	1100	1050	275	2400	1125	1200	3200	4050	1225	650
Basal area (m^2.ha^{-1})	30.63	25.19	35.45	21.75	20.13	14.52	29.73	0.36	5.52	20.57
Maximum height (m)	13.4	20.3	19.4	14.4	19.1	16.2	16.7	7.9	13.9	17.5
Slope (%)	35	8	3	0	10	7	5	0	0	27
Depth of the organ. Horizon (cm)	12	39	40	16	40	45	13	65	38	25

B

Site	**Site 11**	**Site 12**	**Site 13**	**Site 14**	**Site 15**	**Site 16**	**Site 17**	**Site 18**	**Site 19**	**Site 20**
Cohort basal area proportion	0.92	1	0.86	0.75	0.83	0.85	0.92	0.93	0.63	0.65
Weibull's shape parameter	0.97	0.72	1.14	0.89	0.69	0.76	0.97	0.89	0.9	0.73
Min. time since the last fire (years)	189	263	281	256	277	279	283	266	193	238
Tree density (n.ha^{-1})	975	675	675	500	1125	950	850	700	850	600
Sapling density (n.ha^{-1})	8550	1750	2150	1800	2525	3650	2800	1175	2250	2750
Basal area (m^2.ha^{-1})	15.18	18.48	6.84	7.1	28.29	12.67	17.68	14.27	16.09	20.7
Maximum height (m)	17.7	22.6	16.9	15.8	21.2	17.8	23.4	19.4	21.5	21.6
Slope (%)	18	19	0	0	18	2	26	5	7	22
Depth of the organ. Horizon (cm)	45	17	34	20	31	50	43	15	20	14

Appendix B: Structural and environmental characteristics of the studied (A) transition old-growth and (B) true old-growth stands

A

Succession stage		**Transition old-growth**									
Parameter	**Species**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**	**Site 10**
Number of trees	Black spruce	15	33	50	40	37	37	44	43	18	20
sampled	Balsam fir	3	0	12	0	0	0	0	0	0	3
Year on which n.	Black spruce	1939	1820	1938	1899	1854	1910	1840	1875	1811	1832
trees≥10	Balsam fir	-	-	1907	-	-	-	-	-	-	-

B

Succession stage		**Transition old-growth**									
Parameter	**Species**	**Site 11**	**Site 12**	**Site 13**	**Site 14**	**Site 15**	**Site 16**	**Site 17**	**Site 18**	**Site 19**	**Site 20**
Number of trees	Black spruce	24	26	30	15	23	34	37	37	36	10
sampled	Balsam fir	16	15	0	0	29	0	8	2	13	13
Year on which n.	Black spruce	1929	1872	1935	1808	1824	1876	1806	1894	1825	1837
trees≥10	Balsam fir	1939	1920	-	-	1869	-	-	-	1925	1892

Appendix C: Number of trees sampled and year (CE) by which at least ten trees were sampled by species in the studied (A) transition old-growth and (B) true old-growth stands

Diameter at the release (cm)	**Age at the release (year)**				**Total**
	<50	50-100	100-150	>150	
<10	473 *36 %*	552 *42 %*	239 *18.2 %*	51 *3.9 %*	1315 *100 %*
≥10	4 *1.3 %*	84 *28.2 %*	121 *40.6 %*	89 *29.9 %*	298 *100 %*
Total	477 *29.6 %*	636 *39.4 %*	360 *22.3 %*	140 *8.7 %*	1613 *100 %*

χ^2 *=354.016 · df=3 · Cramer's V=0.468 · p<0.001*

Appendix D: Contingency table of the age and diameter of trees at the release times within the studied chronologies