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Demographic disequilibrium caused by canopy gap expansion and recruitment failure triggers forest cover loss

Martin Barrette [a,b,*], Louis Bélanger [a,b], Louis De Grandpré [c], Alejandro A. Royo [d]

[a] Laboratoire d'aménagement intégré, Département des sciences du bois et de la forêt, 2405 de la Terrasse, Université Laval, QC G1V 0A6, Canada
[b] Chaire de recherche industrielle CRSNG-Produits forestiers Anticosti, Département de biologie, 1045 ave. de la Médecine, Université Laval, Québec, QC G1V 0A6, Canada
[c] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., Québec, QC G1V 4C7, Canada
[d] USDA Forest Service Northern Research Station, Irvine, PA 16329, United States

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ABSTRACT

In the absence of large-scale stand replacing disturbances, boreal forests can remain in the old-growth stage over time because of a dynamic equilibrium between small-scale mortality and regeneration processes. Although this gap paradigm has been a cornerstone of forest dynamics theory and practice for decades, evidence suggests that it could be disrupted, threatening the integrity and sustainability of continuous forest cover. The objective of this study was to evaluate the gap dynamics in old-growth boreal forests across a large landscape where deer populations currently exist at high abundance. We hypothesized that chronic deer browsing is limiting recruitment, particularly of palatable species, creating a demographic disequilibrium between canopy mortality and recruitment. We analysed understory regeneration density and distribution in relation to canopy gap size and condition on multiple sample areas within a 360 km^2 area of old-growth balsam fir (*Abies balsamea* [L.] Miller) forest on Anticosti Island, Canada. The combined effect of accelerating canopy gap expansion and recruitment failure created a demographic disequilibrium important enough to cause a loss of forest cover. The forest is now at risk of shifting to alternative successional pathways that seem to be dependent upon gaps size. Rather than sustaining historic balsam fir composition, sucession in 57% of gap area was more susceptible to following a pathway leading toward white spruce parklands, while sucession in the other 43% was more susceptible to following a pathway toward white spruce forests. The occurrence of these novel ecosystems represents a threat to biodiversity and ecosystem services that are provided by preindustrial forests. Climate change could exacerbate these threats by allowing deer to go into as yet unoccupied boreal forests that are driven by gap dynamics. Novel management issues will arise in these boreal ecosystems and challenge forest managers. When the traditional approaches of identifying gaps will not work because the forest itself is losing cover, the method we have developed will help forest managers recognize demographic disequilibrium threatening maintenance of forests.

1. Introduction

In the absence of large-scale stand replacing disturbances, boreal forests can remain in the old-growth stage over time because of a dynamic equilibrium between small-scale mortality and regeneration processes (Kuuluvainen, 1994; Kneeshaw and Bergeron, 1998; McCarthy, 2001; Caron et al., 2009). The mortality process is driven by the death of a single or of a small group of trees from insect, disease, or meteorological vectors creating a canopy gap (Kuuluvainen, 1994; McCarthy, 2001). The regeneration process in the gap is driven by the release of advance regeneration of shade tolerant species and to a lesser extent by the establishment of new regeneration of light demanding species from buried or dispersed seeds (Kneeshaw and Bergeron, 1998; McCarthy, 2001; Vepakomma et al., 2010). However, if canopy mortality is not offset by seedling establishment and growth, the disequilibrium between the two processes could increase gap turnover time, cause gap expansion, and even lead to multiple gaps coalescing as trees along the gap periphery experience elevated mortality rates (Worrall et al., 2005; Taylor and MacLean, 2007; Vepakomma et al., 2012). The increased light availability within these more persistent and

* Corresponding author at: Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs, 2700, rue Einstein, bureau C-1.105.2, Québec, QC G1P 3W8, Canada.
E-mail addresses: martin.barrette@mffp.gouv.qc.ca (M. Barrette), Louis.Belanger@sbf.ulaval.ca (L. Bélanger), louis.degrandpre@canada.ca (L. De Grandpré), aroyo@fs.fed.us (A.A. Royo).

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much larger gaps enhances establishment opportunities for light demanding species which could ultimately result in shifts in species dominance (Ban et al., 1998; Kneeshaw and Bergeron, 1998; Vepakomma et al., 2010).

Although the gap paradigm has been a cornerstone of forest dynamics theory and practice for decades (Pickett and White, 1985; McCarthy, 2001), evidence suggests that a variety of biotic and abiotic forces could disrupt the dynamic equilibrium between small-scale mortality and regeneration processes in gap-driven forests by altering key germination, growth, and survival dynamics that underpin sucession. For example, it is now well-established that filtering of seedling recruitment by dense recalcitrant understory vegetation can alter, stall, or even arrest gap-phase succession (Zackrisson et al., 1997; Aubin et al., 2000; Royo and Carson, 2006). Similarly, trophic interactions can strongly suppress seedling regeneration and thereby contribute to the loss of forest cover and a concomitant shift towards more open woodlands containing large expanses of herbs, shrubs, or lichens (e.g., Dublin et al., 1990; Husheer et al., 2003; Ibáñez et al., 2015; Vézeau and Payette, 2016). Likewise, browsing by both native and introduced deer (Cervidae) can alter and inhibit tree seedling recruitment dynamic leading to regeneration failures, declines in forest cover, and shifts towards communities dominated by unpalatable non-tree species (e.g., ferns, graminoids) following canopy disturbance (Marquis, 1974; Husheer et al. 2003; Pedersen and Wallis, 2004; White, 2012; Nagel et al., 2015). Hence, where gap expansion and coalescence continue unabated and canopy mortality is not offset by seedling establishment and growth, the integrity and sustainability of continuous forest cover itself is at risk.

The objective of this study was to evaluate the gap dynamics in old-growth boreal forests across a large landscape where deer populations currently exist at high abundance. We hypothesized that chronic deer browsing is limiting recruitment, particularly of palatable species, creating a demographic disequilibrium between canopy mortality and recruitment. Thus, we predict seedling and sapling densities, particularly of palatable species, will be low. Moreover, we predict large proportion of the forest area will be in gaps and these individual gap size will be large as they expand and coalesce as recruitment fails to offset mortality. To test these predictions we analysed understory regeneration density and distribution in relation to canopy gap size and condition on multiple sample areas within a 360 km^2 area of old-growth balsam fir (*Abies balsamea* [L.] Miller) forest on Anticosti Island, Canada.

2. Materials and methods

2.1. Study area

Anticosti Island (7943 km^2) is located in the Gulf of St. Lawrence (49°28′N, 63°00′W; Fig. 1). The island forms part of the eastern balsam fir-paper birch (*Betula papyrifera* Marshall) bioclimatic subdomain of the Province of Quebec, Canada (Saucier et al., 2009). Forests on the island are managed using ecosystem management principles that seek to reduce differences between natural and managed forests (Provincial legislation: RLRQ, c. A-18.1, article 1). Mean annual temperature is 2 °C and mean annual precipitation is 907 mm (Environment Canada, 1982). Large-scale disturbances of the forest cover are rare events and partial canopy disturbances

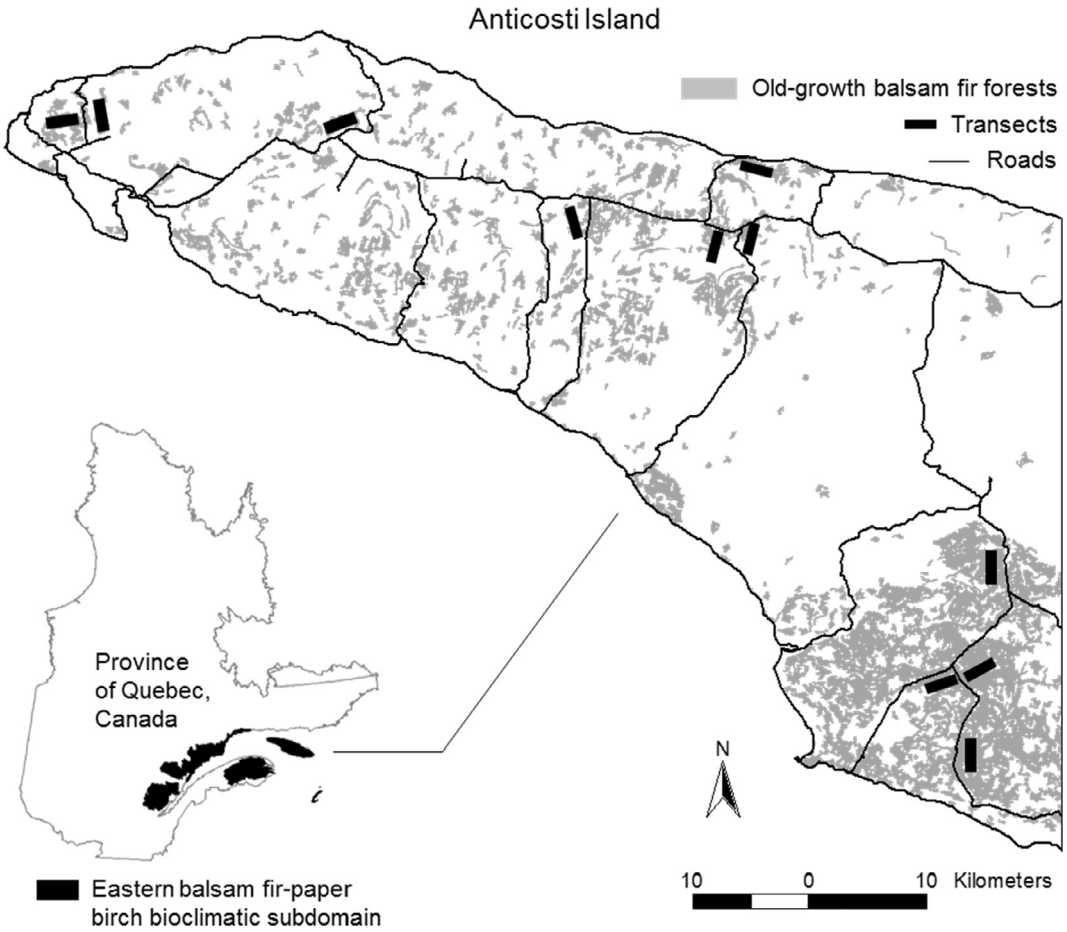

Fig. 1. Location of the 11 transects in the old-growth balsam fir forest.

are caused by tree senescence, pathogen, wind and insect defoliation (*Choristoneura fumiferana* [Clem.]; *Lambdina fiscellaria* [Guen.]; Barrette et al., 2010).

Historically, in the absence of large-scale disturbances, this boreal forest was largely driven by gap dynamics that assured the predominance and maintenance of old-growth balsam fir forests, which are mixed with white spruce (*Picea glauca* [Moench] Voss) and paper birch (Barrette et al., 2010). In such conditions, balsam fir typically creates dense and persistent understory seedling banks (i.e. >60,000 seedlings·ha^{-1}), which are highly shade-tolerant and that can promptly fill canopy gaps (Côté and Bélanger, 1991; McCarthy and Weetman, 2007). However, following the introduction of white-tailed deer (*Odocoileus virginianus*) at the end of the 19th century, and subsequent population explosion (>20 individuals/km^2; Potvin et al., 2003), the understory composition of balsam fir forests has shifted from regeneration that is dominated by balsam fir towards one that is dominated by white spruce, together with blue joint grass (*Calamagrostis canadensis* [Michaux] P. Beauv.), bracken fern (*Pteridium aquilinum* [L.] Kuhn), and thistle (*Cirsium* spp.), which are species that are not browsed by deer (Potvin et al., 2003; White, 2012; Hidding et al., 2013). The explosion of the deer population occurred in part because of the lack of predators. Moreover, the only other large ungulate (i.e. *Alces alces*) with which deer could have competed for food is rare (Potvin et al., 2003).

2.2. Field sampling

Sample site selection was based upon forest inventory maps that had been obtained from the Ministère des Forêts de la Faune et des Parcs du Québec (MFFPQ, 2015). To satisfy selection criteria, forest sites had to be composed of balsam fir (>75% of basal area), ≥90-year-old age-class, and forests ≥2 km^2. Only forest sites that were ≥90 years of age were considered because they correspond to the age class when canopy mortality, and therefore gap dynamics, begins to occur in balsam fir forests (McCarthy and Weetman, 2007). Due to our criteria, sampling was restricted to the western half of the island where old-growth balsam fir forests predominate (Fig. 1). The eastern part of the island is dominated by wetlands and unbrowsed, humid black spruce (*Picea mariana* [Miller] B.S. P.) forests. Eleven balsam fir forests were selected randomly from all available forest sites. In each of these sites, we placed a 4 metre-wide strip transect (Kuuluvainen et al., 2001), each with a length varying between 850 and 1000 m, depending upon site size, for a total length of 10,440 m and a total area of 4.18 ha (Fig. 1). Transect orientation followed the longest axis that defined the dimensions of each site.

We mapped all trees along transects enabling us to identify discontinuities in their spatial distribution that could be linked to gaps. To map trees efficiently, the 4 m-wide strip transect was divided into 5 m-long contiguous sections (Kuuluvainen et al., 2001). In each of these 20 m^2 sections, we counted live and dead trees (diameter at breast height [DBH] ≥9.1 cm), by species. Tree diameter (DBH) of trees was measured with calipers. Decay class (Table 1) and cause of mortality (unknown, e.g., snags or extensively decayed logs, stem breakage or uprooting) were assigned to all dead trees (Taylor and MacLean, 2007). To measure understory regeneration, live saplings (DBH: 1.1–9.0 cm) and seedlings (height: 61–130 cm) of each species were counted within each 20 m^2 section over the entire transect. Seedlings were measured in 9 of the 11 sites.

Table 1
Description of decay classes for snags and woody debris.

Decay class	Description of snags	Description of woody debris
1	Presence of needles and twigs	Presence of needles and twigs. Wood still solid
2	Needles absent, twigs may be present and bark still attached. Wood still solid	Needles absent, twigs may be present and bark still attached. Tree elevated on branches. Knife penetrates up to 1 cm
3	Main branches present only. Bark begins to loosen. Knife penetrates up to 1 cm	Knife penetrates between 1 and 3 cm. Presence of moss. More than 20% of bark has fallen
4	More than 20% of bark has fallen. Knife penetrates between 1 and 3 cm	Moss covers more than 20% of log. Knife penetrates between 3 and 5 cm
5	Knife penetrates between 3 and 5 cm. Broken top	Moss covers more than 50% of log. Knife penetrates all the way
6	More than 80% of bark has fallen. Knife penetrates all the way. Broken top	Moss covers most of log. Woody material crumbles between fingers
7		Flattened log incorporated into the humus layer and appears as red woody material without structure

2.3. Data analysis

We analysed basal area of live and dead trees in contiguous transect sections to identify discontinuities in their spatial distribution, which could be linked to canopy gaps. We used basal area because it is highly correlated with canopy cover density (Mitchell and Popovich, 1997; Bahamondez and Thompson, 2016). To be considered part of a gap, a section of transect had to have an openness index (i.e., dead tree basal area/live plus dead tree basal area) >50%. To include gaps with no or very few dead trees (St-Denis et al., 2010; Bahamondez and Thompson, 2016), any section with a basal area of live trees <0.05 m^2 was also considered as part of a gap. This threshold corresponds to the minimal basal area value of live trees found in sections with an openness index <50%. Gap size was determined from the number of contiguous sections that met gap criteria. Therefore, our estimates of gap size represent a linear evaluation.

Additionally, as old-growth boreal forests can have open canopies making it difficult to delineate one gap from another gap or from the natural openness of these forests (Kuuluvainen, 1994; McCarthy, 2001; St-Denis et al., 2010), we used a wavelet function to unambiguously detect discontinuities in the spatial distribution of trees and canopy gaps (Bradshaw and Spies, 1992; Dale and Mah, 1998; Camarero et al., 2006). A wavelet function is a scalable windowing function that can be used to characterize spatial patterns in canopy structure (Bradshaw and Spies, 1992; Rosenberg and Anderson, 2011). When the template of the wavelet function matches the original transect data, the associated wavelet variance at this position is high. Conversely, when the two do not match, the value of the wavelet variance is low (Rosenberg and Anderson, 2011). Hence, an abrupt change in tree basal area along the transect will result in a significant increase (i.e., peak) in wavelet variance at that position, indicating that the edge of a canopy gap has been encountered (Bradshaw and Spies, 1992; Camarero et al., 2006). To identify significant peaks in wavelet variance, we determined confidence intervals by generating wavelet analyses on 999 randomisations of the original data and considered the 90th highest value of variance for each position (Camarero et al., 2006). We used the software PASSAGE 2 (Rosenberg and Anderson, 2011) to perform the wavelet analysis with a Mexican hat template. The scalable windowing function of this particular template takes the two dimentional form of a Mexican hat which is particularly adequate to characterize spatial patterns in canopy structure when slid along transect data (Dale and Mah, 1998).

Finally, we analysed dead density and decay class to characterize canopy mortality patterns and seedlings and saplings densities to characterize recruitment patterns across a gradient in gap sizes.

We also analysed the distance of white spruce trees from gaps to characterize density and distance of potential seed trees. Differences between mean values of canopy mortality, decay class and recruitment were tested with the DIFF ADJUST (Tukey-Kramer) option of the LSMEANS statement, within a mixed linear model (PROC MIXED; SAS Institute, 2003), with gap size as a fixed effect and transects as a random effect. Since preliminary results revealed that gap size > 6 contiguous transect sections were rarer events, they were grouped in 3 classes (i.e. 7–8, 9–10 and 11–21).

3. Results

3.1. Canopy gaps

The forest canopy was composed of balsam fir (70% of live trees), white spruce (26%), paper birch (3%) and black spruce (1%; Table 2). We identified 446 canopy gaps, which represented 64% of the sampled area (Table 3). The occurrence of these gaps was largely confirmed by wavelet analysis: 84% percent of gaps were adjacent to a significant peak in wavelet variance (Fig. 2). Gaps with a linear size ≤ 4 contiguous sections (linear gap size $\leq 80\ m^2$) were the most numerous (81%), but they accounted for only half of the area in gaps. Gaps that spanned 5–21 contiguous sections (linear gap size 100–420 m^2) accounted for the other half of the area in gaps.

3.2. Dead trees in canopy gaps

The most abundant dead tree species in canopy gaps was balsam fir (60%), followed by white spruce (16%), unidentified coniferous species (16%), paper birch (4%) and black spruce (4%; Table 2). Seventy-two percent of dead trees were downed woody debris and 28% were snags (Fig. 3). Cause of snag mortality was unknown. The

Table 2
Species composition (X ± 1 SE) of live trees, of dead trees in canopy gaps and of advance regeneration in canopy gaps.

Species	Tree basal area[a] ($m^2 \cdot ha^{-1}$)				Advance regeneration density ($stems \cdot ha^{-1}$)			
	Live trees		Dead trees in gaps		Saplings in gaps[b]		Seedlings in gaps[c]	
Balsam fir	19	±1	15	±2	17	±8	129	±124
White spruce	7	±2	4	±1	228	±75	1683	±387
Black spruce	0.2	±0.1	1	±1	12	±3	95	±43
Unidentified coniferous			4	±1				
Paper birch	1	±0.2	1	±0.3			8	±3

[a] Diameter at breast height (DBH) ≥ 9.0 cm.
[b] DBH 1–9.0 cm.
[c] Height 61–130 cm.

Table 3
Characteristics of gaps and of dead trees in canopy gaps for each linear size of gap, i.e., number of contiguous 20 m^2 transect sections.

Linear gap size (sections of transect)	Gap (sum)		Number of dead trees in gaps (mean (±1 SE))				Number of decay classes of dead trees in gaps (mean (±1 SE))			
	Number	Area (m^2)	Snag		Woody debris		Snag		Woody debris	
1	176	3520	1	±0.2	2	±0.3	1	±0.1	2	±0.1
2	90	3600	2	±0.3	3	±0.4	2	±0.1	2	±0.1
3	61	3660	3	±0.4	4	±1	2	±0.1	2	±0.2
4	34	2720	3	±0.4	5	±1	2	±0.2	3	±0.2
5	28	2800	3	±1	7	±1	2	±0.2	4	±0.2
6	17	2040	3	±1	8	±1	2	±0.2	4	±0.3
7–8	14	2100	4	±1	14	±1	2	±0.2	4	±0.3
9–10	13	2420	5	±1	16	±1	2	±0.2	4	±0.3
11–21	13	3740	6	±1	26	±1	3	±0.3	6	±0.4

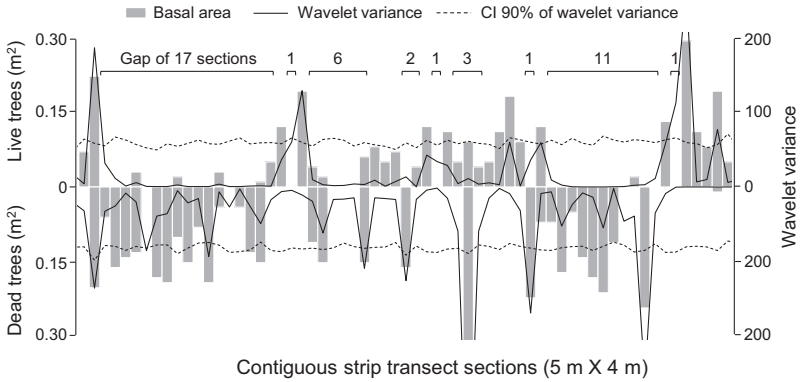

Fig. 2. Illustrating the identification of 9 canopy gaps covering 43 out of 64 sections of a strip transect. A section was part of a gap if it had an openness index (i.e., dead tree basal area/live plus dead tree basal area) >50%. To include gaps with no or very few dead trees, a section with a basal area of live trees <0.05 m^2 was also considered as part of a gap. This threshold corresponds to the minimal basal area value of live trees found in sections with an openness index < 50%. Numbers above brackets indicate the linear size of gaps, determined from the number of contiguous transect sections meeting gap criteria. The occurrence of canopy gaps was confirmed using a wavelet function. A significant peak in wavelet variance (i.e., solid line above dotted line) indicated that the edge of a canopy gap was encountered.

cause of mortality of woody debris was stem breakage (59%), uprooting (31%), and unknown (9%). Dead trees were mostly in decay classes 1–4 (79%), which were followed by dead trees in classes 5, 6 and 7 (21%).

Both the dead density and decay status range increased with gap size ($t_{268} = -7.1$, $P < 0.001$ and $t_{266} = 9.8$ $P < 0.001$ for density and decay class, respectively; Table 3). The smallest gaps had three dead trees in two decay classes, while the largest gaps had 32 dead trees spanning six decay classes (Table 3). The mean DBH of dead trees in canopy gaps was 256 mm (±6).

3.3. Regeneration in canopy gaps

Seedling and sapling advance regeneration was depauperate across our survey areas. A majority of our gaps (72% of gaps, 57% of gap area) had combined seedling and sapling densities of ≤1500 stems per hectare (Fig. 4). In fact, 44% of the gaps (25% of gap area) was completely devoid of advance regeneration (Fig. 4). Even where advance regeneration occurred, it was species-poor. White spruce was, by far, the dominant species in the seedling and sapling layer (Table 2 and Fig. 5). All other species were rare or absent. Advance regeneration density increased with the size of gaps (Fig. 6; $t_{336} = 4.0$, $P < 0.001$), from 1372 seedlings and saplings per hectare in the smallest gap size to 4392 seedlings and saplings per hectare in the largest gap size ($t_{337} = -3.29$, $P = 0.001$). Potential seed trees (i.e., white spruce trees) in the forest matrix, were at a mean distance of 37 m (±3) from gap

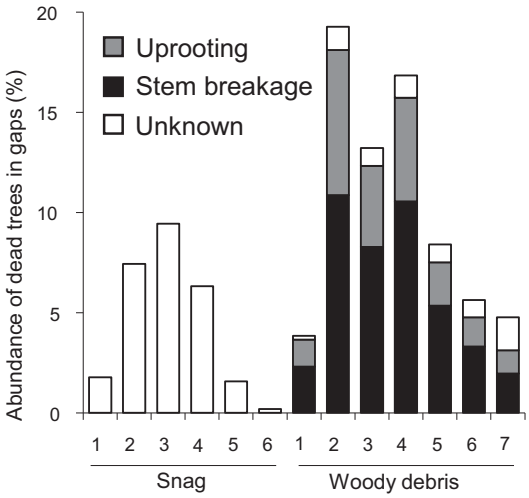

Fig. 3. Cause of mortality and decay classes of dead trees in canopy gaps.

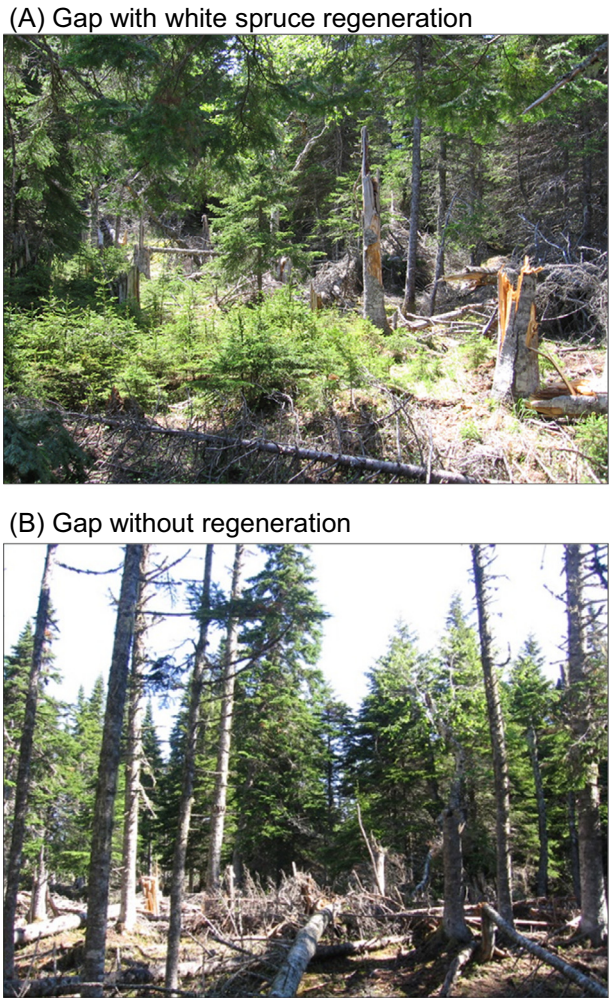

Fig. 5. Photographs showing gaps in balsam fir forests with (A) and without (B) advance regeneration.

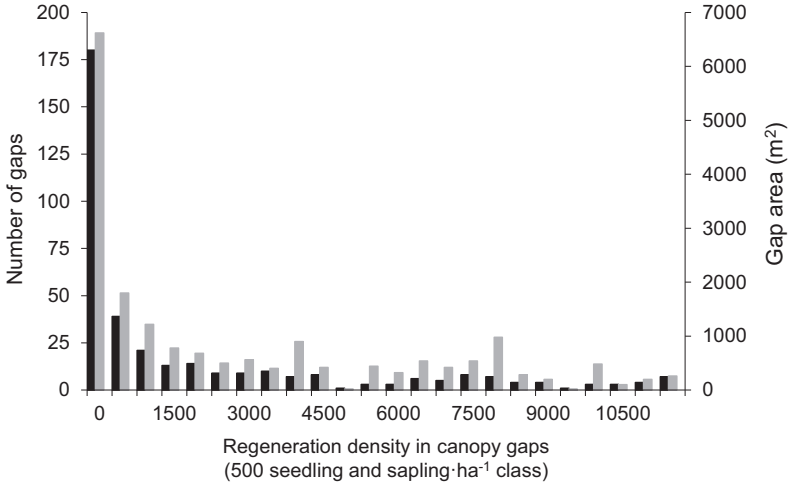

Fig. 4. Distribution of the number of gaps (black bars) and gap area (grey bars) according to advance regeneration density in canopy gaps.

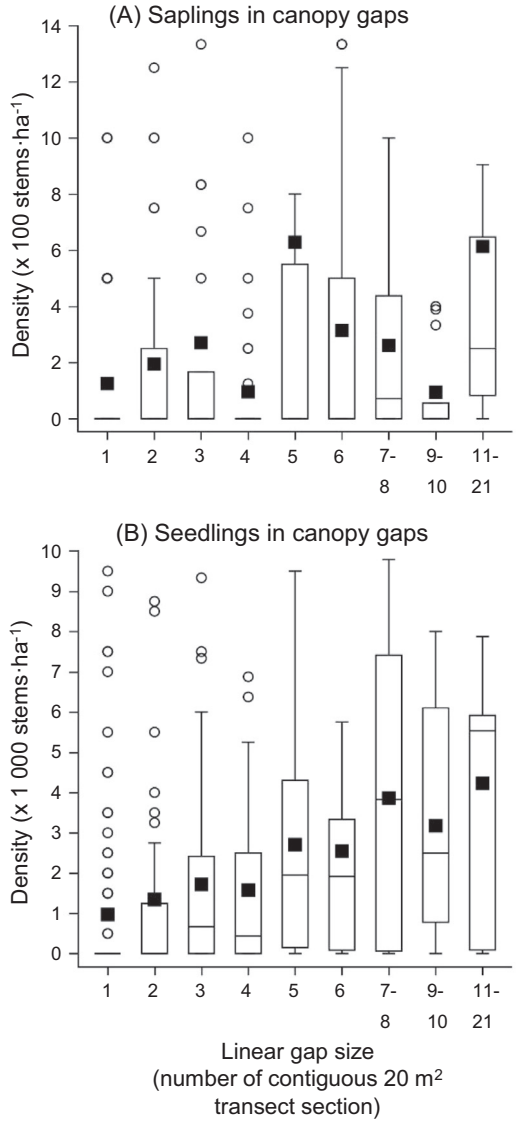

Fig. 6. Boxplots showing mean advance regeneration density for each linear size of gap. The black square and the horizontal line in each box are the mean and median, respectively. Boxes enclose the 75th and 25th percentiles, and whiskers enclose minimum to maximum value excluding outliers. The white circles are outliers (>1.5 x interquartile distance).

periphery; there were 1925 (±153) such trees per hectare, within 25 m before and after each gap periphery.

4. Discussion

4.1. Disruption of gap dynamics

The dynamic equilibrium between the tree mortality and regeneration processes was disrupted. As predicted seedling and sapling densities, particularly of palatable species, was startlingly low. Balsam fir, the dominant tree species, and paper birch were generally absent from the understory. This is a particularly concerning result considering that balsam fir forests usually feature an understory that is dominated by balsam fir (i.e. >60,000 seedlings·ha^{-1}; Côté and Bélanger, 1991). Moreover, as basically the sole remaining tree species in the regeneration layer, white spruce was absent or at low abundance in a large proportion of sampled sites.

As a consequence, and as predicted, a large proportion of the forest area was in gaps as recruitment failed to offset mortality. Canopy gaps covered close to two-thirds of the forest. Gap fractions in similar gap driven boreal ecosystems usually plateaus at lower levels than what we observed (Kuuluvainen, 1994; McCarthy, 2001). For example, on average, gaps covered 31%–43% of *Picea abies* ([L.] Karst.) forests (Liu and Hytteborn, 1991; Hytteborn et al., 1991; Caron et al., 2009), 26%–37% of balsam fir - yellow birch (*Betula alleghaniensis* Britt.) forests (Messier et al., 2005), 38%–40% of balsam fir forests (Kneeshaw and Bergeron, 1998; Vepakomma et al., 2008), or 54% of balsam fir - black spruce forests (Pham et al., 2004). Interestingly, higher gap fractions (i.e. up to 77%) was found in black spruce forests, but it was due to canopy disturbances not being offset by seedling growth (St-Denis et al., 2010).

The high gap fraction we have reported coupled with substantial wind-related mortality (i.e., stem breakage and uprooting; 65%) indicates that canopy loss has possibly passed a critical threshold instead of plateauing, having entered an accelerated phase of canopy opening. This idea of a recent phase of accelerated mortality was also supported by the fact that most dead trees in gaps (i.e. gap makers) were found to be in low decay classes (classes 1–4; 79%), which can be associated with recent mortality events (Kuuluvainen et al., 2001). Usually, gap makers in balsam fir dominated forests are mostly found in the more advanced decay classes (Pham et al., 2004; St-Denis et al., 2010). Taylor and MacLean (2007) also proposed that when a critical state of decline is reached (<40% crown closure), the probability of mortality for remaining trees is dramatically increased because protection from neighbouring trees is decreased which increases wind exposure and incurs rapid stand break-up. Consequently, many gaps likely recently expanded into larger gaps because of elevating mortality rates along the gap periphery and coalescence of adjacent gaps. Coalescence of multiple smaller gaps is made evident by the fact that large gaps contained around 7 times more gap makers than in other gap studies (Pham et al., 2004; St-Denis et al., 2010) and had gap makers in as many as six different decay classes which can represent multiple mortality events (Kuuluvainen et al., 2001). Hence, the combined effect of accelerating canopy gap expansion and recruitment failure created a demographic disequilibrium important enough to cause a loss of forest cover. The profound and widespread impact of deer browsing on understory regeneration of Anticosti Island's forests was demonstrated experimentally with the use of exclosures in other studies (Potvin et al., 2003; Hidding et al., 2013). Hence, as hypothesized, chronic deer browsing was the initial cause of the demographic disequilibrium.

4.2. Alternative successional pathways

The current balsam fir forest canopy of Anticosti Island is losing cover and is now at risk of shifting to alternative successional pathways. These successional trajectories seem to be dependent upon gaps size. Small gaps (i.e., $\leq$4 transect sections 80 m^2) generally had a density of white spruce advance regeneration inferior to 1500 stems per hectare which is the density necessary to reach 50% stocking (i.e., proportion of area occupied by trees) according to Greene et al. (2002). It is highly improbable that forests with lower stocking levels will have more than half of their area covered by trees, especially considering the mortality risks to regeneration (Raymond et al., 2000). We consider such semi-treeless ecosystems would correspond more to parklands than to forests. White spruce seed availability was not a factor which could explain the low advance regeneration density. Seed tree density was high within a distance of gaps that was considered as optimal for seedling establishment (Burns and Honkala, 1990). Furthermore, Barrette et al. (2014) reported high seed density and the availability of suitable substrates for establishment of white spruce seedlings in old-growth balsam fir forests of Anticosti Island. However,

mid-tolerance of white spruce to shade (Burns and Honkala, 1990) could explain why advance regeneration density was generally low in small gaps where the environment is generally shady (McCarthy, 2001). White spruce seedlings usually do not survive more than 2–4 years in such an environment (Raymond et al., 2000). Hence, white spruce seedlings in small gaps that are not expanding rapidly to larger size gaps may not survive long enough to benefit from eventual increased sunlight.

In larger gaps (i.e., >4 transect sections), white spruce advance regeneration density was generally above the density necessary to reach 50% stocking (i.e., 1500 stem per hectare; Greene et al., 2002). However, even in such cases, white spruce seedlings and saplings obviously did not close gaps promptly enough to offset canopy mortality. White spruce seedlings are vulnerable to overtopping by a recalcitrant understory layer, which impairs their establishment (Lieffers et al., 1993; Cole et al., 2013). Recalcitrant understory layers are dense and persistent mono-dominant strata that can impede regeneration processes, by altering the rate and shifting the direction of forest succession (Royo and Carson, 2006). Barrette et al. (2014) showed that bluejoint, bracken fern and thistle form such layers on Anticosti Island following clear-cutting, thereby shifting succession toward white spruce parklands. Hence, competitive interactions with the recalcitrant understory layer may contribute to the poor performance of white spruce to fill larger gaps promptly. Other authors have also recognised that white spruce is usually not apt to fill gaps (Brassard and Chen, 2006). Overall, rather than sustaining historic balsam fir composition, sucession in 57% of gap area was more susceptible to following a pathway leading toward white spruce parklands, while sucession in the other 43% was more susceptible to following a pathway toward white spruce forests.

4.3. Implications for management of gap driven boreal forests

White spruce forests and parklands would be assemblages of species that have not co-occurred historically (Barrette et al., 2014). The occurrence of these novel ecosystems would represent a threat to biodiversity (e.g., shifts in ecosystem composition, structure and function) and ecosystem services (e.g., lower carbon sequestration and wood fibre production) that are provided by preindustrial forests (Hobbs et al., 2014). Climate change could exacerbate these threats by allowing deer to go into as yet unoccupied boreal forests that are driven by gap dynamics (Parmesan and Yohe, 2003; Côté et al., 2004; Frelich and Reich, 2010). Novel management issues will arise in these boreal ecosystems and challenge forest managers. When the traditional approaches of identifying gaps (e.g., Runkle, 1992) will not work because the forest itself is losing cover, the method we have developed will help forest managers recognize demographic disequilibrium threatening maintenance of forests. Protecting advance regeneration with exclosures or hunting to reduce deer density in combination with planting species that are capable of filling gaps promptly could be investigated to maintain or restore regeneration process of boreal forests that are driven by gap dynamics.

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