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# Gap dynamics of late successional sugar maple–yellow birch forests at their northern range limit

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## Abstract

**Questions:** We investigated whether the gap disturbance rate (percentage area disturbed by canopy gaps per year) differed at the northern range limit of sugar maple (*Acer saccharum*)–yellow birch (*Betula alleghaniensis*) forests compared to broad-leaf temperate deciduous forests located more to the south. As an ancillary question, we assessed the relationship between species composition and gap disturbance rate at the stand scale.

**Location:** Late successional sugar maple–yellow birch forests at their northern range limit in western Quebec, Canada.

**Methods:** To reconstruct past gap disturbances, we identified growth releases using the boundary line method applied to tree-ring chronologies obtained from 0.25-ha plots sampled within 11 late successional forest stands. We reconstructed past canopy gaps using release events, calculated historical gap disturbance rates and used redundancy analysis to evaluate the relationship between gap disturbance rate and species composition at the stand scale.

**Results:** The mean gap disturbance rate across the 11 late successional stands was $0.96 \pm 0.51\% \cdot yr^{-1}$. Mean gap size was $39 \pm 44$ m$^2$ and almost 85% of the gaps were <50 m$^2$. Stands with smaller gaps and lower gap disturbance rates had high importance values for balsam fir (*Abies balsamea*) and/or yellow birch.

**Conclusions:** The gap disturbance rate at the northern limit of sugar maple–yellow birch forest was similar to that reported in broad-leaf temperate deciduous forests located ca. 575–1300 km to the south. However, gaps were more numerous and smaller, which could be related to latitudinal differences in allometric traits of the dominant tree species and climate.

## Introduction

The natural disturbance regime of broad-leaf temperate deciduous forests is characterized by frequent canopy gaps created by the death of one or a few trees, resulting from senescence or low-severity disturbances (Lorimer & Frelich 1989; Fraver et al. 2009), with rarer more severe disturbances due to storms, insect outbreaks or forest dieback (Cohen et al. 2016). Increased light availability caused by canopy gaps affects important ecological processes such as species succession, establishment and competition (Runkle 1982; Frelich 2002). For example, larger gaps with more light promote shade-intolerant species, whereas smaller gaps promote shade-tolerant species (Bolton & D'Amato 2011; Leak et al. 2014; Kern et al. 2016).

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In broadleaf temperate deciduous forests, gap size can vary from <10 m$^2$ to more than 1 ha (Yamamoto 1992a; Tanaka & Nakashizuka 1997; Drobyshev 2001; Zeibig et al. 2005; Rugani et al. 2013; Hobi et al. 2015). Gap size distribution is usually skewed towards smaller sizes, with most gaps smaller than 100 m$^2$ (e.g. Zeibig et al. 2005; Petritan et al. 2013). The annual gap disturbance rate (percentage of stand area disturbed by gaps per year) has been estimated at 0.5–1.0% in late successional broad-leaf temperate deciduous forests in eastern USA (Runkle 1982; Dahir & Lorimer 1996; D'Amato & Orwig 2008; Fraver et al. 2009). Data are scarcer for sugar maple (*Acer saccharum* Marsh.)–yellow birch (*Betula alleghaniensis* Britton) forests typical of more northern broad-leaf temperate deciduous forests, but Payette et al. (1990) reported an annual gap disturbance rate of 2.2% in eastern Quebec.

We reconstructed the canopy gap dynamics of sugar maple–yellow birch forests at the northern limit of broad-leaf temperate deciduous forests for comparison with estimates for more southerly forests. A difference would have implications for ecosystem-based forest management, which seeks to emulate the spatiotemporal patterns created by natural disturbances. More specifically, we addressed three questions: (1) could shorter tree life spans due to less favourable climatic conditions in northern forests (Payette et al. 1990; Purves 2009) result in higher gap disturbance rates; (2) could smaller tree crowns in the north (Payette et al. 1990; Petritan et al. 2013; Rugani et al. 2013) result in a smaller mean gap size; (3a) could a higher proportion of conifers lead to a lower disturbance rate, due to their smaller crowns and lower average height, as compared to deciduous trees (Kneeshaw & Prévost 2007); and (3b) alternatively, as balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) have a shorter residence time in the canopy, could a higher proportion of conifers increase the disturbance rate (Kneeshaw & Prévost 2007)? To answer these questions, we characterized the canopy gap disturbance regimes of 11 late successional stands at the northern distribution limit of sugar maple–yellow birch forests in western Quebec, combining dendrochronological analysis and tree mapping to estimate gap size distributions and annual disturbance rates. We then compared our results with those from studies conducted in broad-leaf temperate deciduous forests located ca. 575–1300 km to the south.

## Methods

### Study area

The study sites are located at the northernmost margin of the sugar maple yellow birch bioclimatic domain of western Quebec, Canada, in the Temiscamingue region (46°70′–47°22′ N, 78°49′–78°89′ W), a forest type typical of the broad-leaf temperate deciduous forests of northeastern North America (Westveld 1956; Fig. 1). The mean annual temperature is 4.4 °C and total annual precipitation is 963 mm, with an average of 23% falling as snow (Robitaille & Saucier 1998). Soils are humo-ferric podzols (Brown 1981).

Frequent canopy openings created by the death of one or a few trees constitute the main natural disturbance in the study area (Roy et al. 2010), creating a random pattern of tree ages, diameters and species (Després et al. 2014). Wildfires are rare in the study area and the fire cycle was estimated at several hundred years for the post-settlement period (Drever et al. 2006). Catastrophic blow-downs are also infrequent, with a cycle estimated to be between 1700 and 7000 yr (Roy et al. 2010; Bégin 2011).

### Field sampling

Late successional stands are rare in the study area, where industrial forest management has been active for more than 70 yr. Thus, sampled stands were located in protected areas (four in the Lake-Malakisis Ecological Reserve and four in Exceptional Forest Ecosystems; Villeneuve 1994; Villeneuve & Brisson 2003) or on islands (three stands). All sampled stands were at least 5 ha in size. We sampled 11 late successional stands in the summer of 2011, all of which were separated by >500 m (Fig. 1). As the study aimed at reconstructing the gap regime, stand selection was based on three criteria: (1) no trace of harvesting (i.e. every stem on the ground could be associated with its stump), (2) presence of dead trees at different size and decomposition stages (from recently dead to completely rotten; Tyrrell & Crow 1994) and (3) tree size classes reflecting an uneven-aged structure with diameters ranging from subcanopy (<10 cm DBH), to large trees (with at least 1% of trees with DBH >50 cm). This last criterion has been used previously to identify late successional temperate deciduous forests across Quebec (Villeneuve & Brisson 2003). The sampled stands were mainly composed of sugar maple and yellow birch. Balsam fir, red maple (*Acer rubrum* L.), white spruce and eastern hemlock (*Tsuga canadensis* (L.) Carr.) also occurred widely but were less common. Eastern white cedar (*Thuja occidentalis* L.), large-toothed aspen (*Populus grandidentata* Michx.) and eastern hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch) were present in one or two stands (Appendix S1). In each selected stand, we randomly located a 2500-m$^2$ (0.25 ha) circular sampling plot, separated from roads, water bodies, other non-forested areas and other plots by >100 m.

In each plot, we mapped and measured DBH of all dead and living trees ≥9.1 cm DBH. We also measured the

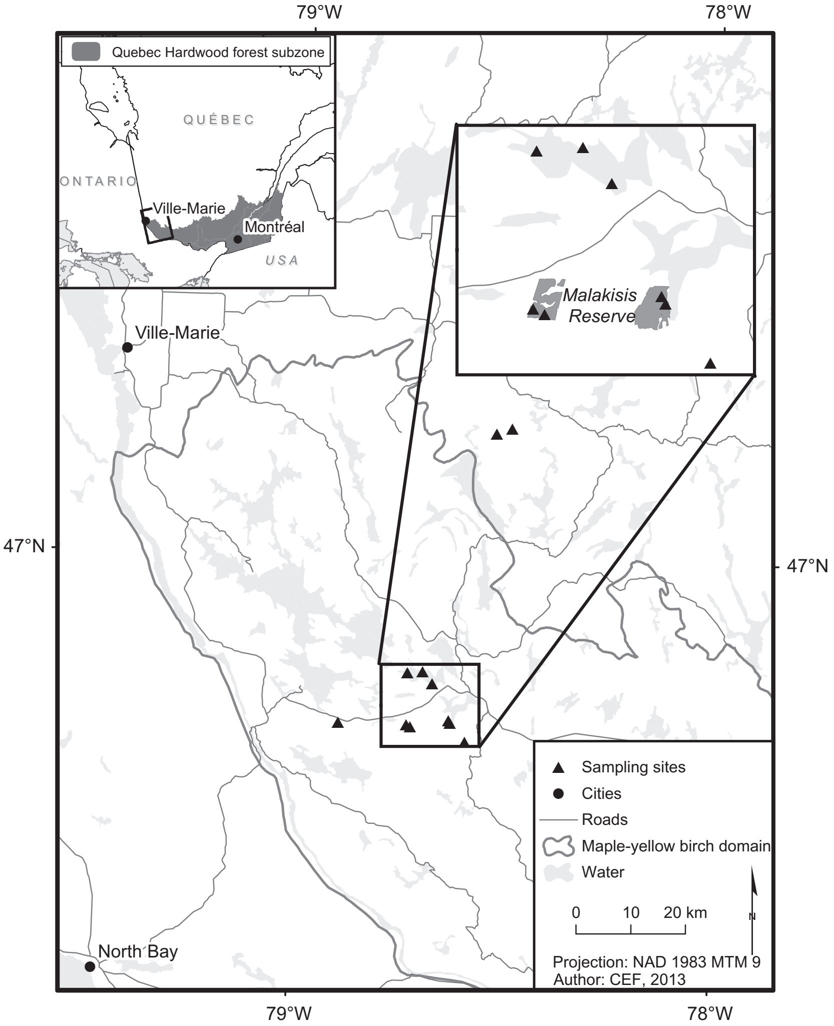

**Fig. 1.** Location of the sampling plots in western Quebec, close to the northern limit of temperate deciduous forests. The inset in the upper right corner is an enlargement of the zone surrounding the Lake Malakisis Ecological Reserve (shown in dark grey).

maximum crown radius of each living tree. We cored every living tree as close as possible to its base (usually within 20–30 cm above the ground surface), trying to reach the pith and making up to three trials. We dried, sanded and scanned all cores using Expression 10 000 XL scanner (Epson) and measured tree rings to the nearest 0.01 mm using CooRecorder (v 7.6; Cybis Elektronic & Data, Saltsjöbaden, SE). We cross-dated the cores using pointer years (Stokes & Smiley 1968) and used COFECHA to verify cross-dating accuracy (Holmes 1983). Shade-tolerant species are difficult to cross-date due to missing rings (Lorimer et al. 1999); hence cross-dating to yearly resolution was only possible for the last 80 yr.

To assess the effect of stand age on forest community patterns, we ranked stands according to the 90th percentile of the age distribution of successfully-aged trees, assuming the last stand-replacing disturbance is more ancient than the oldest-aged trees (see Keeton et al. (2007, 2011)).

### Estimation of gap disturbance regime parameters

We reconstructed gap formation by combining tree-ring data and tree locations (see Payette et al. (1990), Rankin & Tramer (2002), Fraver & White (2005a) and Khakimulina et al. (2016)). We used the boundary line criterion for growth releases detection (Black & Abrams 2003, 2004). We assumed that growth release were related to the death of a neighbouring tree or group of trees (Lorimer & Frelich 1989). To perform the boundary line method, we first computed percentage growth change for each ring using the method developed by Henry & Swan (1974) and popularized by Nowacki & Abrams (1997):

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$$\text{Percentage growth change} = \frac{M_2 - M_1}{M_1} \times 100 \qquad (1)$$

where $M_1$ and $M_2$ represent mean ring width over the preceding and following 10 yr, respectively (Leak 1987; Nowacki & Abrams 1997). The first and last 10 yr of each chronology cannot be analysed using this approach.

Growth releases identified with this method were assumed to indicate gap creation when the percentage growth change was beyond a given threshold. To obtain this threshold, we plotted the relationship between percentage growth change each year and average radial growth of the 10 previous years. Then, for every 0.5-mm increment of prior growth, the ten highest percentage growth changes were averaged. Those averages were fitted with different functions (exponential, logarithmic, linear or power functions). The function with the highest $R^2$ was retained as the 100% threshold of the boundary line. For further analyses, only peaks of growth change ≥10% between two consecutive years were selected to avoid identifying consecutive years as release years (Black & Abrams 2003). Growth changes >50% of the boundary line were interpreted as major releases, whereas growth changes between 20.0% and 49.9% of the boundary line were regarded as moderate releases.

We used data from our study plots to compute sugar maple and yellow birch boundary lines. Sample size was inadequate to compute boundary lines for balsam fir, red maple and white spruce, so we enlarged our data set by adding trees from other late successional sites: 168 red maples from sites on till deposits located <50 km from the study area (Zhang et al. 2014), and 598 balsam fir and 123 white spruce trees from sites 270 km north of the study area on mesic clay deposits (Bergeron 2000). For balsam fir and white spruce, surface deposits were different from those of the study area, which could have introduced statistical noise in the estimation procedure. However, the effect of substrate type was probably limited, as both species are able to grow on a wide variety of mesic substrates (Frank 1990; Nienstaedt & Zasada 1990).

To verify the robustness of the boundary line technique, we re-ran the gap reconstruction protocol using the methods suggested by Nowacki & Abrams (1997), Splechtna et al. (2005), and Fraver & White (2005b) using the *TRADER* package in R (Altman et al. 2014; Appendix S2; R Foundation for Statistical Computing, Vienna, AT).

We drew maps of tree locations using the *spatstat* R package (Baddeley & Turner 2005) and added growth release data to reconstruct gap formation between 1942 and 2001 (the last possible year to detect growth change according to equation [1]). To delineate gaps, we: (1) mapped every living tree for three 20-yr periods: 1942–1961, 1962–1981, 1982–2001; and (2) assumed that major growth releases indicated gap formation and subsequent filling at the focal tree location, whereas moderate releases indicated formation and subsequent filling of a nearby gap through lateral branch expansion (Runkle 2013; Blackburn et al. 2014). Hence, gap boundaries were drawn to include trees showing major growth releases, whereas trees with moderate or without releases were used to delineate the margins of the extended gaps (Appendix S3). We measured the areas of extended gaps (area of the canopy gap together with adjacent area extending to bases of surrounding canopy trees; *sensu* Runkle 1981)). Extended gaps better account for the area affected by increased light intensity (Runkle 1981). The size difference between canopy gaps (smaller) and extended gaps (larger) is ca. 8–13% across different boreal forest types (hardwood, mixed and conifer; Kneeshaw & Bergeron 1998), but mostly depends on crown size of the dominant species. (3) For isolated trees showing a moderate or major release, a circle of 2.93-m radius was used to approximate minimum gap size (equal to 27 $m^2$). This radius – the mean distance between the stems of neighbouring trees for all trees measured within all sampling plots – defines a 'single tree extended gap'. Incomplete gaps identified from releases of isolated trees <5.8 m from the edge of a plot (56 trees, or 14% of all gaps) were assigned a size equal to half the gap size for isolated trees within a plot (i.e. 14 $m^2$ instead of 27 $m^2$; Appendix S3). (4) When two trees with a moderate release were separated by <8 m (diameter of a circle with an area equal to twice the area used as gap size for isolated trees: 54 $m^2$), the gap was delimited as a single circle with a diameter equal to the distance between the trees (Appendix S3). For three adjacent trees showing moderate release with a distance of <10 m between the two furthest trees (i.e. diameter of a circle with an area equal to three times the area used as gap size for isolated trees: 78 $m^2$), the gap was delimited as a single circle with a diameter equal to the distance between the two furthest trees (Appendix S3).

Applying these rules sometimes resulted in two gap polygons sharing a common segment (i.e. the two polygons were contiguous). We compared outcomes for two different procedures for treatment of contiguous gaps: (1) gap number maximization (GNM), where contiguous gaps were considered separately; and (2) gap size maximization (GSM), where contiguous gaps were combined. For both procedures, we computed the gap size distribution for each sampling plot and for three consecutive 20-yr periods. We then computed annual disturbance rates as percentage area disturbed by gaps (in $m^2$) per year for each sampling plot and for each 20-yr period by summing all gap sizes before dividing by the sampling plot area (0.25 ha) and by 20 yr.

We used bootstrap Kolmogorov-Smirnov tests conducted with the *Matching* R package (Sekhon 2011) to compare gap size distributions between gap delineation procedures and among different time periods. We adjusted the $\alpha = 0.05$ threshold value to account for multiple (six) comparisons (Bonferonni adjustment: $\alpha = 8.33 \times 10^{-3}$). We performed an ANOVA to compare disturbance rates between time periods.

We compared tree release records from the sampled stands (percentage trees showing releases per unit time) to historical records of natural disturbances (i.e. blow-downs, wildfires, insect outbreaks, etc.). However, growth release peaks detected with the boundary line method can occur several years after disturbance (Copenheaver et al. 2014).

We used the *vegan* R package (v 2.0-10) to conduct a RDA to explore the link between annual gap disturbance rate (dependent variable) and a matrix of response variables, which included tree composition, stand age and mean gap size (computed for each of the 11 plots for all three time periods combined). We used species importance values (average of relative density – % number of trees, relative dominance – % basal area; Curtis & McIntosh 1951), in the community data matrix (Appendix S1). Tree basal area and density data for the 11 plots are published elsewhere (Table 2 in Després et al. 2014). We performed a Hellinger transformation on importance values to reduce the weight of rare species (Legendre & Gallagher 2001; Borcard et al. 2011). Preliminary analysis showed no evidence that the relationship between species' importance values and the constraining matrix of environmental variables was not linear, thus justifying the use of RDA. We used permutations to test the significance of the RDA canonical axes (Borcard et al. 2011).

## Results

### Disturbance rate

Total chronology length varied among plots from 125 yr (SP6) to 269 yr (SP2) (Fig. 2). The mean annual disturbance rate (percentage area affected by gaps per year) for the entire studied period (1942–2001) and for all plots combined was 0.96 ± 0.51% (minimum = 0.59%, maximum = 1.56%; Table 1). Considering all plots and time periods separately, 67% of the annual disturbance rates were between 0.5% and 1.0%, and only 15% were >1.5% (Table 1). The mean annual disturbance rate over all plots combined did not significantly differ between time periods ($F = 0.35$, $P = 0.71$). Furthermore, mean disturbance rates on island (SP3, 4 and 5) and mainland (all other) plots were not significantly different ($F = 2.0$, $P = 0.17$).

We detected an average of 1.51 major growth release per tree per century (SD = 1.07) and 7.20 moderate releases per tree per century (SD = 3.06) in all plots combined. Over the last ca. 250 yr, periods of simultaneous

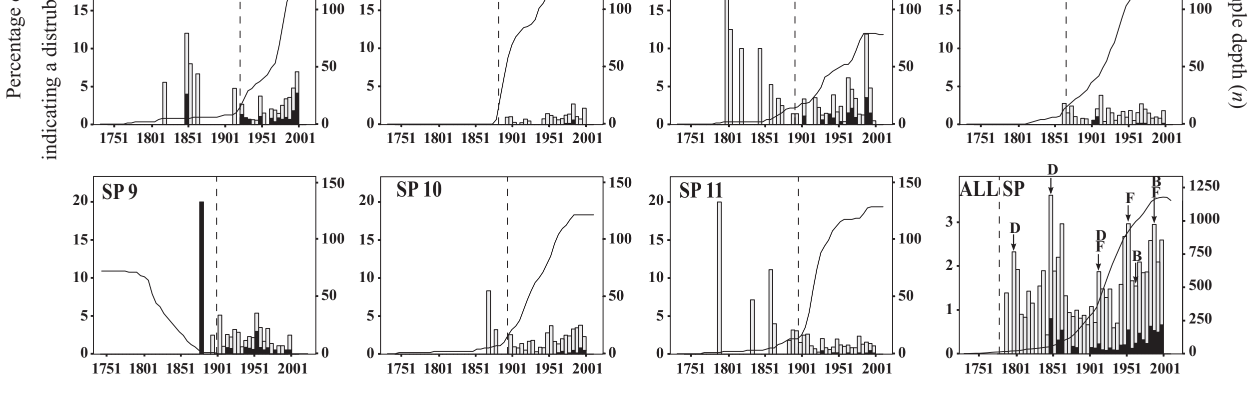

**Fig. 2.** Percentage of trees, per 5-yr interval, having recorded a major (black) or a moderate (grey) release for each of the 11 sampling plots and for all plots combined. Sample depth is indicated on the right-hand *y*-axis. Vertical dashed lines indicate the threshold below which results were not interpreted (set at 15 individuals after Fraver & White 2005a; Firm et al. 2009). Arrows indicate decades of known moderate disturbance events having occurred in the study area, as recorded in the literature (F = forest tent caterpillar; B = blow-down; D = drought).

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**Table 1.** Annual disturbance rates (percentage area disturbed by gaps per year) for three consecutive 20-yr periods in each sampling plot (SP). Total disturbance rate is for the 60 yr combined (1942–2001). Mean (± SD) disturbance rate for all SPs is also provided for each time period. Notes: SD of the total mean disturbance rate was computed from all disturbance rates from all time periods. The disturbance rate is the same regardless of delimitation procedure used (gap number maximization (GNM) or gap size maximization (GSM)).

| | 1942–1961 | 1962–1981 | 1982–2001 | Total Disturbance Rate |
|---|---|---|---|---|
| SP1 | 0.78 | 2.07 | 0.87 | 1.24 |
| SP2 | 1.20 | 0.98 | 1.91 | 1.36 |
| SP3 | 0.99 | 0.56 | 0.51 | 0.69 |
| SP4 | 1.08 | 0.56 | 0.70 | 0.78 |
| SP5 | 0.36 | 0.57 | 1.49 | 0.81 |
| SP6 | 0.54 | 0.50 | 0.73 | 0.59 |
| SP7 | 0.66 | 1.74 | 2.27 | 1.56 |
| SP8 | 0.88 | 0.99 | 0.69 | 0.85 |
| SP9 | 1.86 | 0.71 | 0.51 | 1.03 |
| SP10 | 0.60 | 0.99 | 1.45 | 1.01 |
| SP11 | 0.66 | 0.76 | 0.52 | 0.65 |
| Mean ± SD | 0.87 ± 0.41 | 0.95 ± 0.51 | 1.06 ± 0.62 | 0.96 ± 0.51 |

gap formation across study plots, indicated by increased frequency of growth releases, were recognized qualitatively in the 1790s, 1850s, 1910s, 1950s and 1980s (Fig. 2). Moderate growth releases were recorded continuously over the whole studied period, whereas major releases were mostly recorded in the 20th century (Fig. 2).

The four different methodologies used to detect growth releases showed some differences. The ratio minor/major growth releases changed from one method to another (Appendix S2). However, most of the peaks were consistently detected regardless of the growth release method used. Only the 1796 peak (associated with drought) was not recorded using the Absolute Increase method (Appendix S2).

### Gap size

Mean gap size was 39 ± 44 $m^2$ with the GNM protocol and 42 ± 67 $m^2$ with the GSM protocol. Maximum gap size was higher with the GSM protocol than with the GNM protocol (750 $m^2$ vs 444 $m^2$, respectively; Appendices S4 and S5). The total gap size distribution (all three periods pooled) followed a power distribution (GNM: $y = 257.06\ x^{-2.747}$, $R^2 = 0.95$; GSM: $y = 122.96\ x^{-2.015}$, $R^2 = 0.87$), with about 85% of the gaps <50 $m^2$ (Fig. 3). The use of two gap delineation procedures did not produce statistically different distributions (bootstrapped Kolmogorov-Smirnov between GNM and GSM: $D = 0.02$, $P = 0.99$). Gap size distributions also did not differ between time periods (Appendix S6).

Maximum crown radius was larger in deciduous species (mean = 5.1, 5.5 and 5.9 m for yellow birch, sugar maple and red maple trees of 20–40 cm DBH, respectively) than in coniferous species (mean = 2.5 and 2.6 m for balsam fir and white spruce trees of 20–40 cm DBH, respectively).

### Relationships between species composition and gap dynamics, mean DBH and stand age

The first RDA axis, linked to mean gap size, disturbance rate and stand age, explained 40% of the variability in species composition ($F = 5.1$, $P = 0.03$; Fig. 4). Plots dominated by sugar maple (SP1, SP2, SP7 and SP9) tended to have larger gaps and higher disturbance rates than plots dominated by yellow birch and balsam fir (SP4, SP5 and SP6; Appendix S1, Fig. 4). Plots dominated by sugar maple were also slightly older (Fig. 4). The second RDA axis, with eastern hemlock and eastern white cedar at one end, and red oak and white spruce at the other end, was related to mean DBH of the dominant trees and mean gap size, but only explained 7% of the variability in species composition and was not significant ($F = 0.9$, $P = 0.44$).

## Discussion

### Disturbance rate

The mean annual gap disturbance rate at the northern limit of the sugar maple–yellow birch bioclimatic domain (0.96% annually) was identical to that reported ca. 755 km to the east in Maine, using dendrochronological methods (0.96%; Fraver et al. 2009), and similar to that reported, based on field measurement of gaps in other broad-leaf temperate deciduous forests ca. 575–1300 km to the south in eastern USA (1%; Runkle 1982). The gap disturbance rate we measured was <50% of the 2.2% reported in Payette et al. (1990), the only other estimate at the northern limit of sugar maple–yellow birch forests, but ca. 560 km to the east. Their study site was located on a hill-top, potentially more prone to wind disturbance than our sites, which were all located in a flat landscape. Nevertheless, variability in the mean annual gap disturbance rate between our 11 plots (0.66–2.27%) encompassed the value reported in Payette et al. (1990).

Decadal peaks in gap formation were qualitatively identified in the 1790s, 1850s, 1910s, 1950s and 1980s (Fig. 2), pointing towards synchronous tree mortality likely caused by large-scale biotic (e.g. insect outbreaks) or abiotic (e.g. intermediate blow-down or drought) disturbances. Reported forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks could be associated with peaks recorded in our study area in the 1910s, 1950s and 1980s (Cooke & Lorenzetti 2006). We also observed a correspondence between gap-prone periods and independent

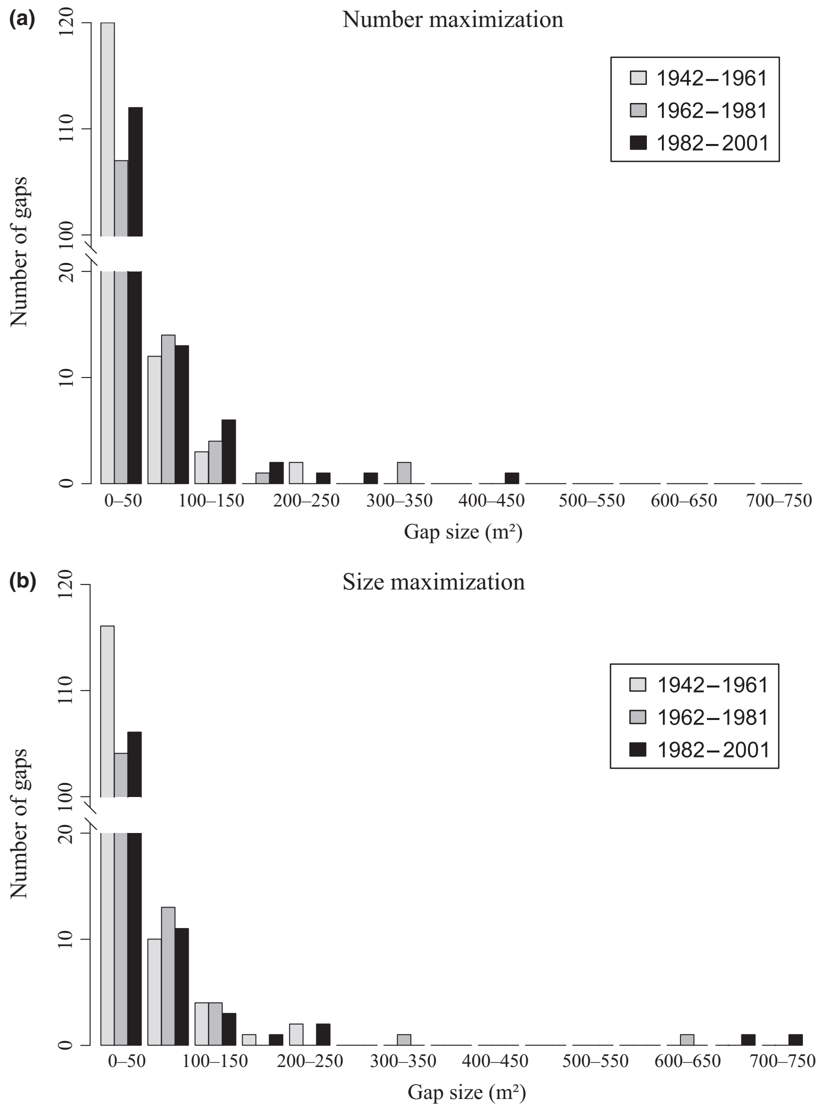

**Fig. 3.** Number of gaps per 50-m$^2$ size class and time periods: 1942–1961 (light grey), 1962–1981 (dark grey), 1982–2001 (black) for the combined 11 sampling plots with the gap number maximization (**a**) and gap size maximization (**b**) procedures.

reconstructions of drought and blow-down events. Dendrochronological reconstruction indicated severe droughts in eastern Canada in 1794, 1849 and 1916 (Girardin et al. 2004). Intermediate blow-downs were recorded in the study area in 1962, 1983 and 2006 (Roy et al. 2010). The 1962 blow-down did not correspond to a peak in gap formation, perhaps because it was less severe than the 1983 blow-down (557 ha in 1962 vs 3276 ha in 1983; Roy et al. 2010). Our sample sites were outside of the affected zone for the 2006 blow-down.

## Gap size

Mean size of extended gaps was smaller in our study area (39–42 m$^2$) than in other broad-leaf temperate deciduous forests, e.g. North American sugar maple forests (115.1 m$^2$ extended gaps; Dahir & Lorimer 1996), European beech forests (141–297 m$^2$ canopy gaps; Rugani et al. 2013; Hobi et al. 2015) and Japanese temperate forests dominated by *Quercus serrata* and *Fagus japonica* (70–190 m$^2$ canopy gaps; Yamamoto 1992a; Abe et al. 1995; Tanaka & Nakashizuka 1997). Dendrochronological reconstruction may overestimate gap size compared to direct gap measurements, but to our knowledge, no study has assessed this possibility. Furthermore 94% of the gaps were <100 m$^2$ in the stands we studied, whereas this size class only represented 60–70% of the gaps reported in North American and European broad-leaf temperate deciduous forests (Runkle 1982; Petritan et al. 2013; Rugani et al. 2013; Hobi et al. 2015). Moreover, we reconstructed extended gaps,

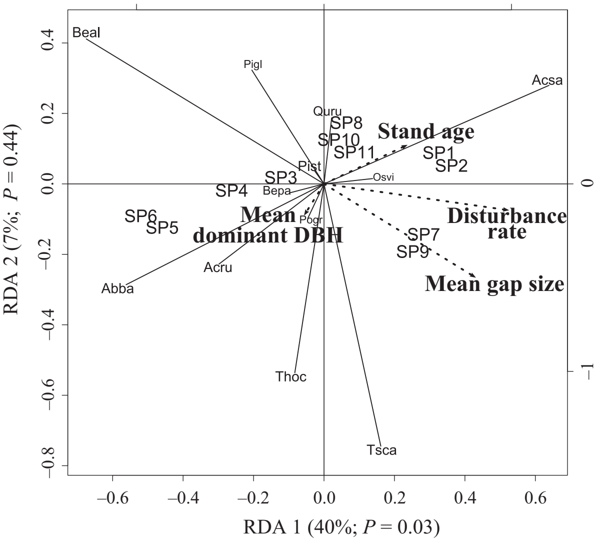

**Fig. 4.** RDA relating species to disturbance rate using the gap number maximization procedure, mean gap size, mean DBH of dominant trees and plot age (stand age) for all sampling plots (SP). Acsa: *Acer saccharum* Marsh.; Beal: *Betula alleghaniensis* Britton; Abba: *Abies balsamea* (L.) Mill.; Tsca: *Tsuga canadensis* (L.) Carr.; Acru: *Acer rubrum* L.; Pigl: *Picea glauca* (Moench) Voss; Thoc: *Thuja occidentalis* L.; Bepa: *Betula papyrifera* Marsh.; Osvi: *Ostrya virginiana* (Mill.) K. Koch; Quru: *Quercus rubra* L.; Pogr: *Populus grandidentata* Michx.; Pist: *Pinus strobus* L.

whereas all of the aforementioned studies except Dahir & Lorimer (1996) measured canopy gaps (i.e. areas under the open sky, not extending to the surrounding tree bases). While mean gap sizes <40 m$^2$ are not common in late successional broad-leaf temperate deciduous forests, they were recorded in sugar maple–American beech (*Fagus grandifolia* Ehrh) forests that had not yet reached the late successional stage (28.1 ± 59.1 m$^2$ extended gaps; Cho & Boerner 1991). Hence, gaps are usually large and occur at low frequencies in late successional broad-leaf temperate deciduous forests of the eastern US (Lorimer 1989; Hart 2016). Differences in species composition between the sites studied here and sites sampled in previous studies could partially explain the observed differences in mean gap size. Sugar maple and yellow birch have smaller crown sizes than American beech, which is well represented in several other studies (Burns et al. 1990). Gap size distribution was not affected by use of either the gap number or gap size maximizing procedure, thus indicating the robustness of our result.

Maximum gap size seemed smaller in our study area (444–750 m$^2$) than in other studies (800–1000 m$^2$; Yamamoto 1992b; Rugani et al. 2013; Hobi et al. 2015). A border effect or different methods (dendrochronology in our study vs field measurements in the others) could have led us to underestimate gap sizes. Moreover, using moderate releases to delimit gap periphery could have led us to underestimate mean gap size. For example, the largest gap we recorded (750 m$^2$) was located at the edge of a plot and could have actually been larger (Appendix S4). Nevertheless, the size of our sampling plots was comparable to or larger than those reported in most other studies, thus warranting the comparison.

Gaps >100 m$^2$ are rare in our study area (6% of total area), whereas recruitment of yellow birch, a mid-tolerant species, requires openings between 100 and 250 m$^2$ (Webster & Lorimer 2005). Thus, persistence of yellow birch in the landscape apparently requires additional large canopy openings that can be created by intermediate disturbances (Woods 2004). Indeed, almost no yellow birch sapling recruitment was observed in the sample plots (Després et al. 2014).

Mean crown size of the main deciduous species was similar between our study area and sugar maple–yellow birch forests located to the south. Crown radii for 20–40 cm DBH yellow birch, sugar maple and red maple trees sampled in Wisconsin varied between 3.8 and 6.0 m (Webster & Lorimer 2005), whereas we measured mean radii of 5.1, 5.5 and 5.9 cm for the same species and DBHs. However, where American beech is present (Runkle 1982), its larger crown size (Burns et al. 1990) could explain larger gap size. Thus, it is impossible to determine if smaller gap size in the north can be explained by smaller crown size.

Plots with high proportions of balsam fir tended to be younger and have lower disturbance rates and smaller mean gap sizes as compared to plots dominated by sugar maple (Fig. 4). Balsam fir is a short-lived tree compared to sugar maple, and it also has a smaller crown as compared to deciduous species (Kneeshaw & Bergeron 1998; Kneeshaw & Prévost 2007). Moreover, balsam fir generally occupies a sub-canopy position in the sugar maple yellow birch bioclimatic domain. Thus, a higher mortality rate of balsam fir trees does not result in a higher rate of canopy gap formation. Our plots with balsam fir were dominated by yellow birch, and this could further explain their smaller average gap size and lower disturbance rate. For trees with a DBH >15 cm, yellow birch is more wind-firm than sugar maple (Canham et al. 2001; Nolet et al. 2012). Strong wind episodes likely result in partial branch-by-branch dieback of yellow birch trees and rarely in complete tree blow-downs, a phenomenon noted during our fieldwork. This pattern suggested that old and large yellow birch trees do not create large canopy openings, but rather multiple small gaps caused by branch shedding.

## Conclusion

Sugar maple–yellow birch forests at their northern distribution limit exhibited smaller and more numerous canopy gaps, but the same annual gap disturbance rate by area as in broad-leaf temperate deciduous forests located ca. 575–1300 km to the south in eastern US. This difference is important to consider in ecosystem-based forest management plans aiming to emulate natural gap disturbance regimes. In northern sugar maple–yellow birch forests, management plans should rely on selection cuts mimicking frequent small-scale canopy gaps (i.e. 10–70 $m^2$ for a global disturbance rate of $0.96\%\cdot yr^{-1}$), in contrast to other broad-leaf temperate deciduous forests located further south, where larger cuts can be used to emulate larger gaps (i.e. 100–200 $m^2$ (Dahir & Lorimer 1996) for a global disturbance rate near 1% (Runkle 1982; Dahir & Lorimer 1996; Fraver et al. 2009)). Nevertheless, occasional larger-scale cuts (>100 $m^2$) will still be necessary to reproduce the effects of episodic blow-downs and to help maintain intermediate shade-tolerant species like yellow birch. Further work will be needed to document gap dynamics across different substrate types and stand ages. Finally, a methodological comparison between dendrochronology and field measurements would be needed to evaluate the precision of dendrochronological reconstructions of gap dynamics.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Species importance values for each sampling plot.

**Appendix S2.** Reconstruction of past disturbances using different release detection methods for all sample plots combined.

**Appendix S3**. Examples of gap delineation.

**Appendix S4**. Gap reconstructions using the gap size maximization procedure for three 20-yr periods and for the 11 sampling plots.

**Appendix S5**. Gap reconstructions using the gap number maximization procedure for three 20-yr periods and for the 11 sampling plots.

**Appendix S6**. Bootstrap Kolmogorov-Smirnov test comparing gap size distributions obtained from the gap size maximization and the gap number maximization delineation procedures for each time period.