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Effects of post-windthrow salvage logging on microsites, plant composition and regeneration

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Black spruce–moss forest; Ecosystem management; Forest floor heterogeneity; Pit-and-mound microtopography; Post-disturbance key attributes; Understorey vegetation; Windthrow severity

Nomenclature
Marie-Victorin (1995)

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Abstract

Questions: How does windthrow influence plant diversity and composition as well as regeneration and microsite characteristics? What are the consequences of post-windthrow salvage logging on these key attributes?

Location: Eastern black spruce–moss forest, Quebec, Canada.

Methods: A total of 92 plots were sampled, each with a radius of 11.28 m; 49 of these plots were salvaged while 43 were unsalvaged. Regeneration density, plant diversity and seedbeds were characterized. We tested the effect of microtopography and windthrow severity on species richness and Shannon diversity index for salvaged and unsalvaged windthrows using a mixed model. Partial redundancy analysis (RDA) determined which environmental and stand characteristics were most important in explaining differences in plant species and forest floor types among the treatments. The effects of treatments (salvaged and unsalvaged windthrows), microtopography attributes, windthrow severity and regeneration species on seedling and sapling abundance were tested using a linear mixed model.

Results: Salvaged windthrow, with a large proportion of skid trails, dead mosses and *Sphagnum*, had a lower degree of seedbed heterogeneity. Also, some understorey species present in the unsalvaged ecosystem were absent from the salvaged windthrow. *Sphagnum* and other moss species were clearly associated with the unsalvaged treatment. White birches were positively associated with mound microtopography in the unsalvaged windthrow.

Conclusion: From an ecosystem-based forest management perspective, natural post-windthrow understorey conditions and microsite heterogeneity can be in part maintained in salvaged cut blocks by incorporating retention patches that include downed and standing dead wood and living trees of diverse sizes. These steps should favour plant regeneration and augment diversity for salvage logging after wind disturbance.

Introduction

In many parts of the world, major disturbance episodes often lead to salvage logging (often called sanitary logging in Europe; Lindenmayer et al. 2004, 2008). Functionally, salvage logging can be distinguished from other harvest operations in that, with salvaging after natural disturbance, the ecosystem is subjected to two sequential disturbances within a short period (Lindenmayer et al. 2008). Peterson & Leach (2008) suggest that multiple disturbance impacts need to be understood on the basis of cumulative severity. Indeed, recent conceptual advances (e.g. the cusp model of Frelich & Reich 1999; the three-axis model of Roberts 2004, 2007) have begun to address the potential for multiple disturbances to change the trajectory of community development, sometimes in undesirable directions (Paine et al. 1998). Because of the potential for the combined severity of natural disturbance followed by salvaging to yield unwanted 'ecological surprises' (Paine et al. 1998), guidelines are needed for the planning of

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post-windthrow salvage logging operations. Moreover, these guidelines should be focused on the main processes or forest attributes that are affected by the salvaging activity.

The ecological consequences of this type of forest intervention have been studied, but mostly following fire (Nappi et al. 2004; Purdon et al. 2004; Greene et al. 2006). The few studies that examined post-windthrow salvage logging highlighted the multiple ways that it may influence biological legacies (Elliott et al. 2002; Rumbaitis del Rio 2006; Peterson & Leach 2008; Jonášová et al. 2010). Peterson & Leach (2008) documented differences in relative abundances of microsite types in salvaged vs unsalvaged windthrow forests of Tennessee. Lang et al. (2009) pointed to the presence of tree-fall microtopography as a structural legacy, allowing establishment of species that would otherwise be rare or locally absent. Rumbaitis del Rio (2006) reported that salvaged areas had lower herbaceous abundance and diversity than unsalvaged areas, and that salvaged areas had widespread mortality of a pre-disturbance dominant shrub *Vaccinium* spp. Fischer et al. (2002), Rumbaitis del Rio (2006), Nelson et al. (2008), Lang et al. (2009) and Fischer & Fischer (2012) have all noted that salvaged areas have greater abundance of ruderal or pioneer species during the initial decades of regeneration.

Disturbance types differ in the legacy imprint they leave on boreal forest ecosystems. Windthrow legacies are characterized by deadwood, pit-and-mound microtopography, remnant trees of various sizes and diverse seedbed conditions (Vaillancourt 2008; Waldron et al. 2013). Such legacies are involved in tree regeneration processes and the maintenance of plant diversity. Soil turnover induced by tree uprooting has been shown to contribute to seedbed heterogeneity following windthrow (Peterson et al. 1990; Clinton & Baker 2000). Furthermore, the change in light and soil conditions following windthrow were shown to increase herbaceous and shrub species diversity (Peterson & Pickett 1990; Palmer et al. 2000; von Oheimb et al. 2006) and influence growth rate of tree regeneration (Ruel & Pineau 2002; Wohlgemuth et al. 2002; Kuuluvainen & Kalmari 2003). Most of these findings come from temperate forest ecosystems (exceptions are Ruel & Pineau 2002 and Kuuluvainen & Kalmari 2003), emphasizing the need to further document their role in boreal forests.

Post-windthrow heterogeneity in forest floor characteristics can favour bryophyte diversity, as many species are known to have specific habitat requirements (Jonsson & Esseen 1990). However, harvest operations negatively influence bryophyte diversity by changing the microclimatic conditions and through reducing suitable substrates (Fenton et al. 2003; Jonášová & Prach 2008). Pit-and-mound microtopography could also influence understorey plant composition and diversity (Peterson & Campbell 1993). However, the harvest of uprooted trees can make stumps return to their pre-windthrow position (Doyon & Bouffard 2008) and, thus, reduce the pit-and-mound microtopography (Waldron et al. 2013). As demonstrated in previous studies (Peterson & Pickett 1995; Kuuluvainen & Kalmari 2003), seedbed diversity in post-windthrow ecosystems positively affects plant regeneration.

This study characterizes understorey species composition, tree regeneration and forest floor heterogeneity, to see whether and how salvage logging affects these post-windthrow attributes. The aims of the study were to (1) characterize post-windthrow undergrowth vegetation, regeneration and seedbeds; and (2) compare those attributes with a post-windthrow salvage-logged area.

Methods

Study area

The study was conducted in the eastern black spruce–moss subdomain of the boreal forest in the North Shore administrative region of Quebec, Canada (MRN 2013; Fig. 1). The dominant tree species are black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) and balsam fir (*Abies balsamea* (L.) Mill.), but white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are also present. The main succession pattern in the area following fire is black spruce establishment, with a gradual increasing of balsam fir proportion with time since fire. This succession pattern can occur on all soil types. Other succession patterns may occur in the area, but are less frequent. Intolerant hardwoods can establish after fire and be gradually replaced by balsam fir 80–100 yrs after fire or by black spruce 100–140 yrs after fire (De Grandpré et al. 2009). Balsam fir is a shade-tolerant species and can remain for many years under the canopy, then rapidly start to grow when a canopy opening is created. Balsam fir regeneration can take place on a variety of seedbeds. Black spruce is also considered as relatively shade-tolerant, but less so than balsam fir. Black spruce produces small seeds that can establish on *Sphagnum*, but mineral soil is the preferred seedbed. Layering is also an important means of reproduction for black spruce, especially under existing canopies (Burns & Honkala 1990).

Balsam fir as a mean longevity of 60–100 yrs, and the mean longevity of black spruce is between 100 and 200 yrs (Burns & Honkala 1990). As the main species longevity is shorter than the fire cycle, more than 70% of the stands present an irregular size distribution and a large proportion are old-growth trees (Boucher et al. 2003; De Grandpré et al. 2009).

Regional topography is complex, including both high-elevation sites and deep valleys. Rocky outcrops are very frequent, and the main surface deposit is till. Across the

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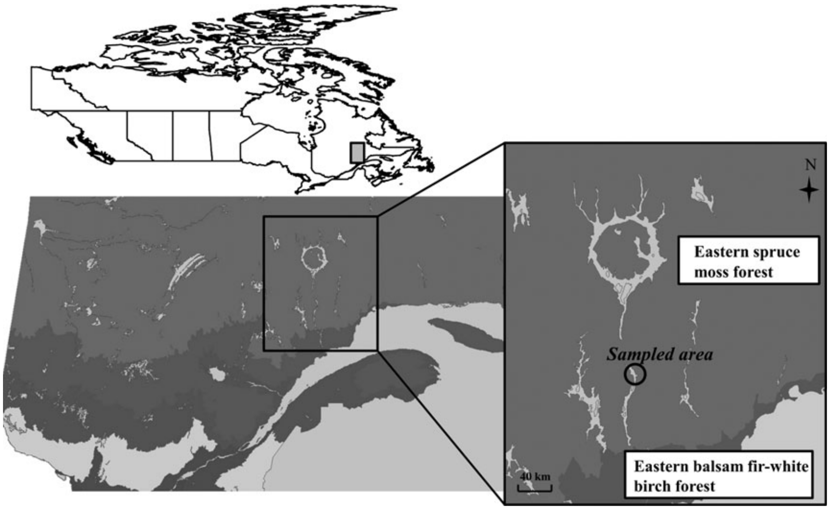

Fig. 1. Study area.

study area, mean slope is 14% and mean elevation is 442 m a.s.l. Annual precipitation averages about 1300 mm, while mean annual temperature ranges between −2.5 and 0 °C (Robitaille & Saucier 1998).

This area is characterized by a low frequency of forest fire because of the humid and cold climate (Bouchard et al. 2008). Windthrow and outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) are the main disturbances in this ecosystem (Pham et al. 2004; De Grandpré et al. 2009; Bouchard & Pothier 2010). A few recent windthrow episodes have severely affected the region. A partial windthrow occurred in 2003, which was followed by a major windthrow event in 2006. During this period, more than 88 000 ha were affected by windthrow. A salvage plan followed the 2006 windthrow and covered more than 20 000 ha (Ruel et al. 2010).

In Quebec, following a major natural disturbance, the Quebec Ministry of Natural Resources (MRNQ) allocates wood volume to forest industries that will salvage the affected stands in terms of priority. When executing salvage logging operations, industries can derogate from the RSFM (Regulation respecting standards of forest management for forests in the domain of the State), for the size and spatial repartition of the cut-blocks. Also, there is no specific recommendation about the amount of deadwood to be left on the cut-blocks during salvage logging operations (MRNF 2012). In the same area, a study on structural attributes after post-windthrow salvage logging showed a reduction of snag density and a homogenization of decay classes in comparison to unsalvaged windthrow. Also, mean downed deadwood volume after salvage logging was 43.8 $m^3 \cdot ha^{-1}$ in comparison with 80.3 $m^3 \cdot ha^{-1}$ after unsalvaged windthrow. Residual living trees were almost absent in salvaged windthrow (Waldron et al. 2013).

Data collection

Salvage logging plans that had been devised by the forestry company Resolute Forest Products (Baie-Comeau, QC, CA) were used to choose the salvaged sites. Salvaged sites had been harvested in the summer of 2007 or 2008, following the 2006 windthrow episode. We selected salvaged cut-blocks where no scarification and reforestation operations had been done. Also, cut-blocks chosen for this study were selected on the basis of similar initial stand characteristics and covering a wide range of windthrow severities. Stand composition prior to logging operations was determined with forest inventory maps provided by the MRNQ. These maps give information about stand and site characteristics, based on both photo-interpretation and field verification. High-resolution aerial photographs provided by MRNQ, together with ground truthing in the field, were used to determine windthrow severity. Severities were classified into four classes of stand mortality: (1) 0–24%, (2) 25–49%, (3) 50–74%, and (4) 75% or more. Six cut-blocks of approximately 25 ha were sampled. In each cut-block, sampling followed a systematic approach, with a plot established every 100 m along a transect, with a total of 43 plots.

Based on initial stand and soil characteristics from the MRNQ forest inventory maps, 49 unsalvaged plots, all affected by the 2006 windthrow episode and originating from primary forest, were established within 12 blocks. We selected the unsalvaged plot with the location of the plots from the forest inventory programme of the MRNQ, as we knew that those plots were relatively accessible. The number of blocks was higher for the unsalvaged treatment, as a systematic location of plots within the unsalvaged area was not possible because of safety and accessibility issues.

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A relatively wide range of windthrow severities was represented in the sampled plots, but most plots were restricted to severity classes 1 to 3 because of safety concerns (Table 1).

Data were collected during the summer of 2010. A total of 92 plots were sampled, each with a radius of 11.28 m (0.04 ha). Three transects of 19.54 m were positioned to form a triangle within each 0.04-ha plot. One of the corners was oriented northward from the plot centre. On each transect, two subplots of 1.13 m radius (4 m^2) were also established (Fig. 2). Transects without any treefall pit or mound were divided in three equivalent portions, and each of these portions was separated by the two subplots. When there were pits and/or mounds crossing the transect, subplots were placed equidistant between those pits and mounds. Thus, we had the same number of subplots on undisturbed forest floor in each plot, regardless of the presence of pit-and-mound microtopography. Pits and mounds are microtopographical features formed by tree uprooting and associated with an uprooted trunk.

In the main 11.28-m radius plot, all downed coarse woody debris (downed CWD) with diameters ≥9 cm and lengths ≥30 cm were measured. Wood volume was estimated with Smalian's formula, by taking the two end diameters (cm) plus the length (m) for each piece. We chose Smalian's formula because it is computationally straightforward and commonly used by the MRNFQ and Quebec forest industry (Lemieux 2011). When debris on the ground was a whole tree, the butt (large end) diameter was taken and the bole length measured until the diameter had decreased to 9 cm. When the log crossed a plot edge, only the portion within the plot was measured. Downed CWD was also classified using Hunter's decay classes (Hunter 1990; Hunter & Schmiegelow 2011). There are five classes for downed wood material. Class 1 is characterized by intact bark and wood texture with the presence of twigs. Class 2 also has intact bark but there are no twigs on the log. Classes 3 and 4 have lost almost all of their bark and sag near to the ground or totally on the ground. Finally, class 5 refers to a soft and powdery wood texture partially covered by bryophytes (Hunter & Schmiegelow 2011). CWD with Hunter classes 1 to 3 was considered as recent, while that in Hunter classes 4 or 5 was considered as old.

Table 1. Number of salvaged and unsalvaged plots in each windthrow severity class.

Severity class	Unsalvaged plots	Salvaged plots
1	15	2
2	12	29
3	14	14
4	2	4
Total	43	49

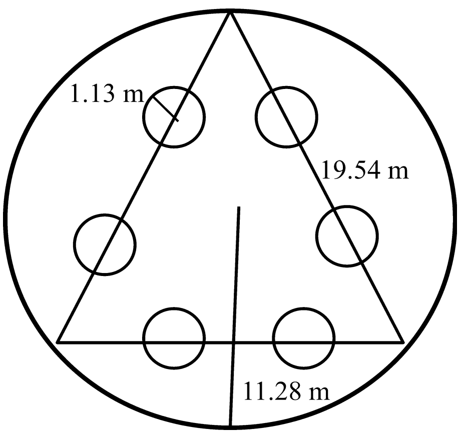

Fig. 2. Plot design. Deadwood volume and decay classes were measured in the 11.28-m radius plot; regeneration density, plant diversity and seedbeds on undisturbed forest floor were measured in each 1.13-m subplot; Regeneration density, plant diversity and seedbeds were measured on each pit and mound crossing the 19.54-m transects.

In each subplot (1.13-m radius) that had been established on undisturbed forest floor, ground vegetation was recorded. Except for mosses, *Sphagnum* and lichens, all taxa were recorded to species level and their cover was visually estimated in 5% classes. Seedbeds were characterized in each of the subplots by visually estimating cover of seedbed types in 5% classes. Seedbed categories were mosses, *Sphagnum*, dead mosses, dead *Sphagnum*, skid trail, rock, organic soil, mineral soil and water. Vegetation and seedbeds were also characterized on each pit and mound crossing a transect.

Regeneration of commercial tree species was counted in each subplot. Since both seedlings and saplings were considered, all stems taller than 5 cm and with a DBH < 9 cm were included. We used six height classes to characterize regeneration: (1) 5–30 cm, (2) 30–60 cm, (3) 60–100 cm, (4) 100–200 cm, (5) 200–300 cm and (6) >300 cm. We considered classes 2 to 6 to be advance regeneration, as the sampling was done 2–4 yrs after the disturbance. The tree species was also considered. Regeneration was also counted on pits and mounds.

Analysis

For the analysis, the sum of CWD volume of Hunter classes 1, 2 and 3 (recent CWD) and the sum of the volume of Hunter classes 4 and 5 (old CWD) were used for each plot of 11.28-m radius. For understorey vegetation and seedbed cover, the mean value of the six 4-m^2 subplots within each plot was used for the undisturbed forest floor. The mean value of understorey vegetation and seedbed cover on pits

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and on mounds within each plot was also calculated. Finally, for regeneration density, the mean value per subplot was used.

Vegetation biodiversity and seedbed characterization

We tested the effect of microtopography of both treatments (salvaged and unsalvaged windthrow) and windthrow severity on species richness (total number of species per subplot) and Shannon diversity index ($H' = -\sum c_i \ln c_i$, where c_i is the proportional cover of the i^{th} species in the subplot) using a mixed model. Blocks and plots were used as nested random factors. We included a different variance term for each treatment in the model to satisfy homoscedasticity (Pinheiro & Bates 2000), given a significant Leven's test. When a significant effect was detected, means comparisons were conducted using *post-hoc* Tukey tests. These statistical analyses were conducted using nlme v. 3.1-109 (http://cran.r-project.org/web/packages/nlme/nlme.pdf), car v. 2.10-18 (http://cran.r-project.org/web/packages/car/car.pdf) and multicomp v. 1.2-18 (http://cran.r-project.org/web/packages/multcomp/multcomp.pdf) packages of R, v. 3.0.1 (R Foundation for Statistical Computing, Vienna, AT).

Multivariate analyses determined which environmental and stand characteristics were the most important in explaining differences in plant species composition and seedbed types among the treatments. Plant species and seedbed data were first Hellinger-transformed with the vegan package v. 2.0-7 (http://cran.r-project.org/web/packages/vegan/vegan.pdf) in R to reduce the weight of high cover values and increase the weight of rare species (Legendre & Gallagher 2001; Borcard et al. 2011). Detrended correspondence analysis (DCA) was then used to estimate gradient length. As the gradients were <4, we considered that species and seedbeds were responding linearly to the environmental gradient (Borcard et al. 2011). Given these linear responses, we opted for partial redundancy analyses (partial RDA). Partial RDA was used to control for some site co-variables in the analysis. Thus, species and seedbed data could be displayed with other plot characteristics when the effects of the soil and stand factors were kept constant (Borcard et al. 2011). Variance inflation factors (VIF) were calculated prior to RDA using R vegan package, v. 2.0-7 to ensure that multicollinearity among the predictor variables was avoided (Zuur et al. 2010). We kept variables with VIF smaller than ten (Borcard et al. 2011). For forest floor characterization, one partial RDA was performed. The seedbed type proportions were included in the analysis, as dependent variable. The co-variables included in the analysis were stand composition, age, height, density and soil drainage, and were obtained from forest inventory maps provided by the Quebec Ministry of Natural Resources and Wildlife (MRNFQ). This information was originally acquired from photo-interpretation and field verification. The environmental or predictor variables used in this analysis were the treatment (represented by six categorical variables), forest floor, pits and mounds in unsalvaged windthrow, and forest floor, pits and mounds in salvaged windthrow. The other included environmental variable was windthrow severity.

Another partial RDA was used to visualize plant species assemblages on forest floor, pits and mounds for both treatments. Dependent variables were the transformed species cover; the co-variables were, as in the seedbed description, stand composition, age, height, density and soil drainage. Environmental variables that were used were treatment, represented by the same six categorical variables as used for seedbed description. Windthrow severity, total volume ($m^3 \cdot ha^{-1}$) of recent CWD, total volume ($m^3 \cdot ha^{-1}$) of old CWD, mineral soil cover and organic soil cover were also used as environmental variables.

Regeneration

The effects of the treatments, microtopography attributes, windthrow severity and regeneration species on seedlings and saplings were tested using a linear mixed model. At first, regeneration height classes were included in the model; however, as most of the regeneration was advanced, height classes had no statistical effect. Thus, the data were pooled without considering height classes. The same random factors selected for diversity analysis were used, with the same packages of R software. We conducted *post-hoc* Tukey tests to characterize the effect of treatment and microtopography attributes on the numbers of seedlings and saplings. We compared numbers of seedlings and saplings distributions for the three tree species (black spruce, balsam fir and white birch) among windthrow severity classes using contingency tables and χ^2 tests.

Results

Seedbed characterization

In order to characterize seedbed heterogeneity, we analysed a matrix with the different seedbed covers: mosses, *Sphagnum*, dead mosses, dead *Sphagnum*, skid trail, rock, organic soil, mineral soil and water as dependent variables. Treatments (forest floor, pits and mounds for salvaged and unsalvaged windthrow) and windthrow severity were used as environmental variables. Co-variables were stand composition, age, height, density and soil drainage. The first two axes of the partial RDA explained 16.1% of the variation in forest floor variables (axis 1, 12.0%; axis 2, 4.1%). The first axis contrasted moss and *Sphagnum* to dead moss and dead *Sphagnum*. The first axis was constrained by windthrow severity, and desiccation stress became increasingly more important as windthrow severity increased, as shown by the association between dead moss and dead *Sphagnum* and windthrow severity vectors. Also, salvaged logging treatment was associated with dead moss and *Sphagnum*. Mineral and organic soil vectors were positively associated with pits and mounds of unsalvaged treatments. Rock was related to pits and mounds in the salvaged treatment. Skid trails and dead lichen seedbeds were highly associated with forest floor after salvage logging, and woody debris and *Sphagnum* were positively associated with forest floor of unsalvaged windthrow (Fig. 3).

Understorey species diversity and composition

Microtopography types had a significant effect on the number of species per subplot ($F = 20.15$, $df = 5$, $P < 0.0001$), but windthrow severity did not. Number of species on each microsite type (undisturbed forest floor, pits and mounds) did not differ between salvaged and unsalvaged treatments. For unsalvaged windthrow, mean species number per subplot was significantly higher on the forest floor (8.37 ± 0.21) than on mounds (6.56 ± 0.52), which were both significantly higher than on pits (5.26 ± 0.56; Fig. 4). After salvage logging, species richness followed the same trend among microsite types, but the types did not significantly differ from unsalvaged windthrows. Shannon diversity results are not presented as they follow exactly the same pattern as richness values.

In order to characterize species composition, we analysed a matrix with the different plant cover as dependent variables, while controlling for stand composition, age, height, density and soil drainage. The first two axes explained 17.3% of the variation in plant composition (axis 1, 11.9%; axis 2, 5.4%; Fig. 5). The first axis was constrained by the mineral soil vector; the second axis was constrained by old CWD, recent CWD, and windthrow severity, although the relationship between axes and the latter two categories was weak. In the windthrow treatment (W), forest floor, windthrow pits and windthrow mounds were widely separated from one another. The forest floor of the windthrow treatment is separate on the left side of the first axis. Further, the centroids of the salvaged treatment (S) are closely clustered together (Fig. 5).

Understorey species tended to cluster with different attributes. Together with *P. mariana*, the ericaceous species *Vaccinium myrtilloides* Michaux, *V. vitis-idaea* L., *Gaultheria hispidula* (L.) Mühl. ex Bigelow, *Kalmia angustifolia* L. and *Ledum groenlandicum* (Oeder) Kronn & Judd clustered

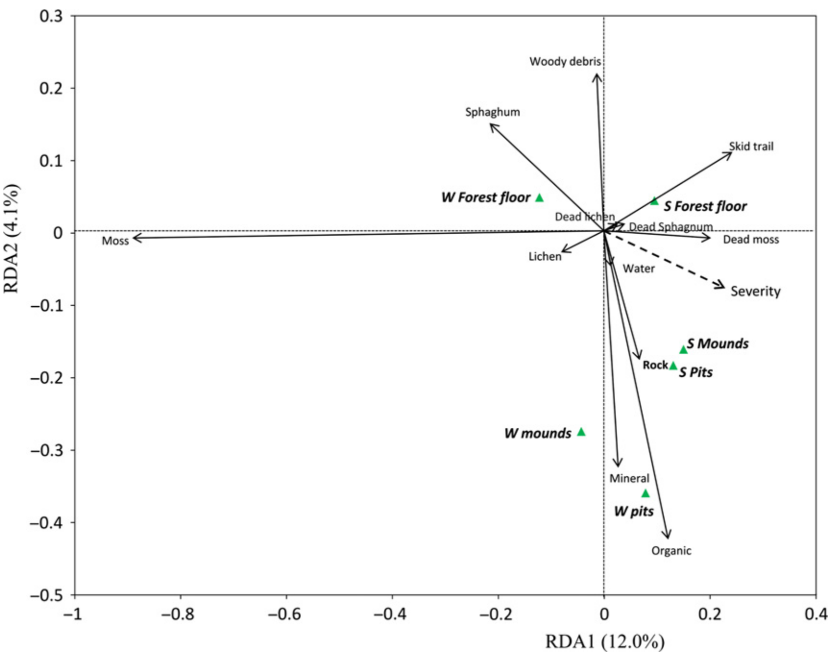

Fig. 3. Partial RDA ordination of seedbed characterization**.** The seedbed proportion (dependent variable) is represented with a full arrow. The environmental variables were treatment and windthrow severity. The centroids of the treatment represented by six categorical variables, which were forest floor, pits and mounds in unsalvaged windthrow (W), and forest floor, pits and mounds in salvaged windthrow (S), are represented by triangles. The windthrow severity is represented with a dotted arrow. The co-variables included in the analysis were stand composition, age, height, density and soil drainage.

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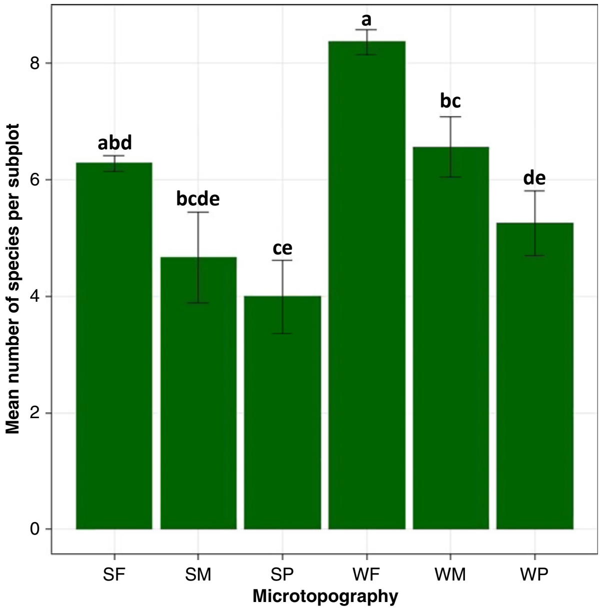

Fig. 4. Mean number of species by subplot according to the microtopography. SF, salvaged forest floor; SM, salvaged mound; SP, salvaged pit; WF, unsalvaged windthrow forest floor; WM, unsalvaged windthrow mound; and WP, unsalvaged windthrow pit. Means with the same letter do not significantly differ at $P = 0.05$, according to *post-hoc* Tukey's tests.

along the left end of axis 1, which is associated with increasing forest floor cover of the unsalvaged treatment. *Cornus canadensis* L. was strongly associated with recent CWD. *Betula papyrifera* Marsh., *Oxalis montana* Raf. and *Maianthemum canadense* Desf. were closely associated with unsalvaged windthrow mounds, with windthrow severity and old CWD. No species were clearly associated with the salvage logging treatment and with unsalvaged pits (Fig. 5).

Commercial species regeneration

As the main commercial species (i.e. balsam fir and black spruce) were not related specifically to pits or mounds (see Fig. 5), the seedling and sapling analysis excluded microtopographic features. When mean densities of saplings and seedlings per subplot were compared, we observed significant interactions between treatments and seedling and sapling species, and between severity and tree species. There was no significant interaction between treatment and severity class (Table 2). In other words, the effect of treatment on the density of saplings and seedlings varied between tree species ($F = 7.95$, $df = 2$, $P = 0.0004$) but not between severity classes ($F = 0.59$, $df = 3$, $P = 6.2$). Unsalvaged windthrow contained the highest amount of regeneration. Moreover, balsam fir was significantly more abundant (5.0 ± 0.42 stems·plot^{-1}) in the unsalvaged plots (Fig. 6a). Salvage logging reduced balsam fir density (3.17 ± 0.55 stems·plot^{-1}) to a level comparable to that of spruce (salvaged treatment, 2.44 ± 0.28 stems·plot^{-1}; unsalvaged treatment, 3.33 ± 0.34 stems·plot^{-1}). White birch had the lowest amount of regeneration among tree species, with no difference between salvaged (0.15 ± 0.04 stems·plot^{-1}) and unsalvaged (0.53 ± 0.11 stems·plot^{-1}) treatments.

Distribution of seedling and sapling abundances among windthrow severity classes differed between species ($\chi^2 = 335.27$, $df = 6$, $P < 0.001$). Partial χ^2 tests between species showed significant differences for all severity classes ($P < 0.001$). Windthrow severity classes positively influenced seedling and sapling abundance, at least for balsam fir and white birch regeneration. Indeed, balsam fir seedlings were most abundant for severity classes 2 to 4. However, the effect of increasing severity on black spruce was not clear, as spruce density was similar in classes 1 to 3, but was lowest in severity class 4 (Fig. 6b).

Discussion

Although the forest industry did select salvage sites randomly, as the decision to salvage was based mainly on accessibility issues, the differences reported here do not appear to be biased. A comparison of initial forest composition revealed that both treatments had the same pre-disturbance species composition. Also, we used plots in all severity classes and integrated a block factor in our analysis to control for the effect of differences in site and stand types. Therefore, we are confident that the reported results represent differences between the treatments.

Seedbed characterization

The partial RDA analysis allowed us to measure the variation in seedbed type cover attributable to treatment and gradient of windthrow severity. Our results show that *Sphagnum* and moss species were clearly associated with the unsalvaged treatment. Lichen seedbeds were also associated with unsalvaged windthrow forest floor. The first axis was constrained by windthrow severity. Bryophyte cover was the most marked response to windthrow severity. Harvesting operations are known to affect bryophyte populations, as they influence microclimatic conditions and substrates (Fenton et al. 2003; Jonášová & Prach 2008). Environmental factors that affect bryophyte and lichen growth are humidity, light and the quantity of downed CWD and snags (Andersson & Hytteborn 1991). The higher density of standing trees in unsalvaged windthrow in comparison to the salvaged areas (Waldron et al. 2013) might affect environmental conditions. Overstorey trees can protect the forest understorey from direct

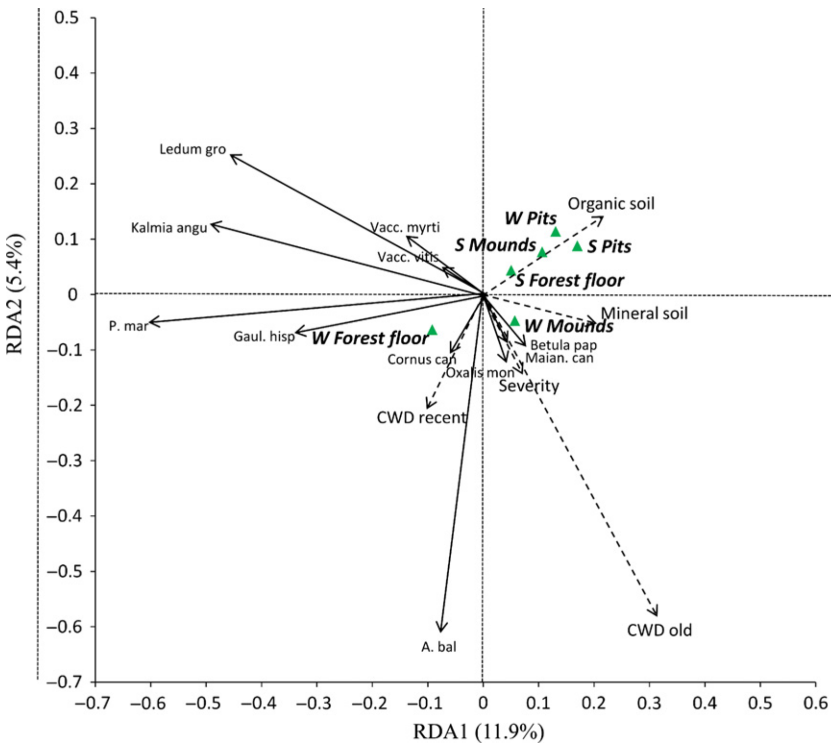

Fig. 5. Partial RDA ordination of understorey plant cover. The plant cover (dependent variable) is represented with a full arrow. The environmental variables were treatment, windthrow severity, old and recent CWD, mineral and organic soil. The centroids of the treatment are represented by six categorical variables (triangles): forest floor, pits and mounds in unsalvaged windthrow (W), and forest floor, pits and mounds in salvaged windthrow (S). The other environmental variables are represented with a dotted arrow. The co-variables included in the analysis were stand composition, age, height, density and soil drainage.

Table 2. ANOVA summary of the linear mixed effect model of sapling and seedling quantity.

Effect	*df*	Sapling and Seedling Number	
		F	*P*
Treatments	1	7.87	0.0149
Species	2	73.28	<0.0001
Severity	3	1.70	0.1743
Treat*Species	2	7.95	0.0004
Treat*Severity	3	0.59	0.6222
Severity*Species	6	7.78	<0.0001

Significant factors ($P < 0.05$) are shaded.

sunlight and desiccation. In the salvaged plots, moss and *Sphagnum* were found predominantly in a desiccated state. Also, the low volume of downed CWD and low number of snags in the salvaged treatment (Waldron et al. 2013) might affect the presence of bryophytes and lichens. Some studies have shown that non-vascular plants are particularly affected by silvicultural practices that do not allow persistence of large dead wood and snag recruitment (Haeussler et al. 2002). Cryptograms are conspicuous in *P. mariana* stands of the eastern boreal forests of Quebec, and have a strong influence on understorey plant regeneration and growth (De Grandpré et al. 2003). Forest floor disturbance due to salvage logging can reduce moss and *Sphagnum* cover, which may explain the trend of diminishing species number and the absence of specific vegetation after salvage logging when compared to unsalvaged windthrow. One way this might happen is the presence of machinery tracks or skid trails. Skid trails were directly related to salvage logging operations, and were found in every salvaged plot and in some subplots. In many cases, skid trails were very deep and soil was severely compacted, which could partly explain the absence of vegetation on this type of substrate and also the tendency for a lower mean number of species per subplot.

Tree uprooting in unsalvaged windthrow contributes to the formation of pit-and-mound microtopography and the exposure of mineral and organic soil. However, after salvage logging, many stumps are returned, either partially or completely, to their pre-windthrow position (Doyon & Bouffard 2008), so that organic or mineral soil seedbeds are mostly absent. This phenomenon was observed in our salvaged plots.

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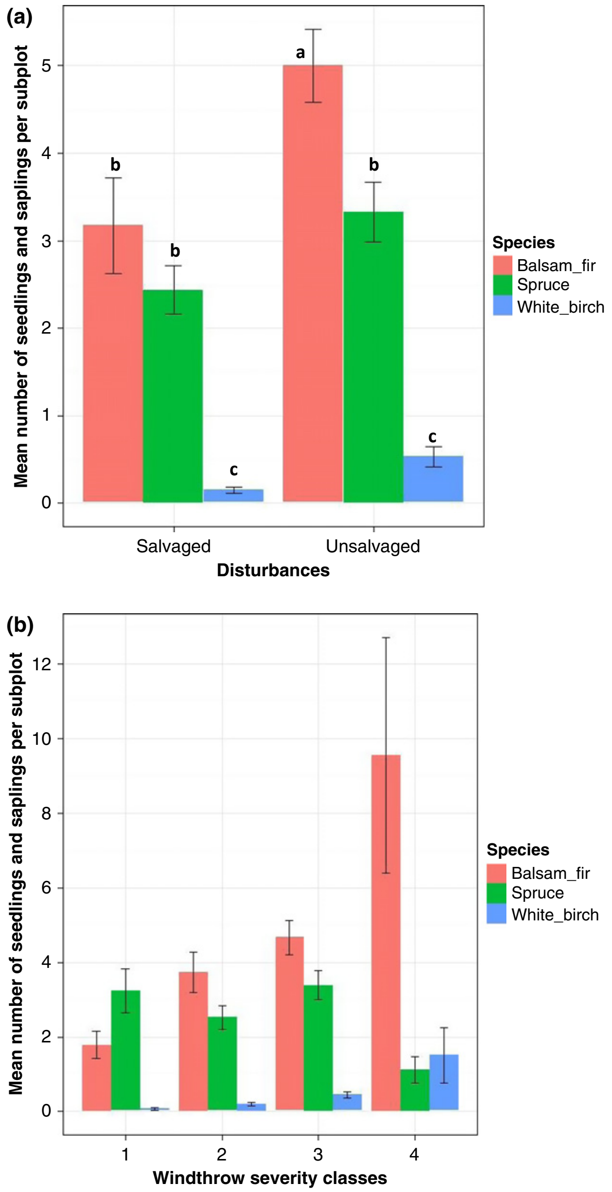

Fig. 6. Mean number of seedlings and saplings per subplot for the three main tree species (black spruce, balsam fir and white birch) according to (**a**) disturbance and (**b**) windthrow severity class. Means with the same letter do not significantly differ at $P = 0.05$, according to *post-hoc* Tukey tests.

Our results confirmed that windthrow creates a high diversity of microsites (Peterson & Campbell 1993; Ulanova 2000), which contribute to the heterogeneity of post-windthrow ecosystems. Forest floor heterogeneity may thus explain the presence of some plant species that were specific to unsalvaged windthrows. Salvaged windthrow, with the large proportion of skid trails and dead moss or *Sphagnum*, had lower seedbed heterogeneity, as also observed by Peterson & Leach (2008).

Understorey diversity and composition

The partial RDA analysis allowed us to measure the variation in plant species cover attributable to treatment and gradient of windthrow severity, old and recent CWD, as well as mineral and organic soil. Our results show that, in unsalvaged windthrow, diversity index and number of species are higher on undisturbed forest floor than on pits or mounds. The importance of pits and mounds in post-windthrow vegetation biodiversity has been demonstrated mostly in hardwood or mixed hardwood forests (Peterson & Pickett 1990; Peterson & Campbell 1993; Ulanova 2000). Plant diversity is higher in these forest ecosystems than in black spruce boreal forests, where the number of species is limited. Moreover, pits and mounds in boreal forest do not have the same properties and size as in more temperate hardwood forests, perhaps due to the superficial root systems produced by black spruce and balsam fir and because of the relatively small size of the trees in the former compared to the latter forests (Clinton & Baker 2000; Doyon & Bouffard 2008; Waldron et al. 2013). This could be part of the explanation for the absence of specific vegetation and low diversity on pits and mounds. Many studies have shown that pits are not good sites for vegetation establishment (Beatty & Stone 1986; Schaetzl et al. 1989; Peterson et al. 1990; Harrington & Bluhm 2001). Pits generally have lower temperature and light levels than mounds (Clinton & Baker 2000), and seedlings can become buried by soil eroding from the root plate. This could explain why, in the unsalvaged treatment, mounds have higher species richness and diversity than pits. Moreover, mounds likely supported existing pre-disturbance vegetation, while pits were new sites for colonization. Mounds, therefore, might have some diversity immediately after disturbance, while diversity would necessarily have to accumulate from zero in pits.

The only species that was clearly related to microtopography attributes in unsalvaged windthrow was white birch. Our results (Fig. 5) showed that birches were positively associated with mound microtopography. Birch species are known to establish and grow on exposed mineral soil or decomposed coarse woody debris (Perala & Alm 1990). This result is consistent with other studies that showed that pioneer species are likely to be found on mounds (Carlton & Bazzaz 1998; de Chantal et al. 2009). However, this result is a tendency, given that the first two axis of our partial RDA analysis explained only 14.0% of the variance.

Our study was performed between 2 and 4 yrs after windthrow and salvage logging. Most pits and mounds had been created by the most recent windthrow episodes so that most microtopographic features were relatively recent. Pits and mounds are not stable in the initial years following disturbance, and their characteristics change over time (Ulanova 2000). Many authors have shown that plant diversity associated with microtopographic features is highest in the first years after disturbance (Palmer et al. 2000; von Oheimb et al. 2006). Although these studies were done in hardwood forests, they suggest the importance of time since pit-and-mound formation in the development of plant communities. Thus, it would be interesting to see the effects of pit-and-mound microtopography on plant diversity in subsequent years, when both pits and mounds have become more stable.

Our study did not take into consideration the diversity of bryophytes, although our results showed that mosses and *Sphagnum* cover are associated with unsalvaged windthrow. Jonsson & Esseen (1990) showed that in Scandinavian spruce forests, bryophyte diversity was high in forests that had been affected by windthrow, with the high number of species being explained by the microsite diversity caused by tree uprooting. In Quebec boreal forest, Desponts et al. (2004) demonstrated that high bryophyte diversity of old-growth stands was explained by the structural heterogeneity of this type of ecosystem. Since our results showed that salvage logging affected microsite and forest floor characteristics, it would be useful to characterize moss and *Sphagnum* species diversity.

The presence of several plant species was positively associated with the post-windthrow forest floor rather than with pits and mounds. Most of these plants were ericaceous species. For example, *L. groenlandicum* and *K. angustifolia* are known to spread rapidly after disturbance (Mallik 1994; Jobidon 1995). Given that *L. groenlandicum* grows on humid soil, particularly on *Sphagnum* sites (Jobidon 1995), and that *Sphagnum* is associated with unsalvaged windthrow forest floor, a positive relationship between *L. groenlandicum* and the forest floor in unsalvaged windthrow was not surprising. Further, aggressive competition between black spruce and *K. angustifolia* and *L. groenlandicum* is well documented (Mallik 1987; Inderjit & Mallik 1996a,b), but our results showed that black spruce cover was higher on the forest floor. Most spruces present on our unsalvaged site were advanced saplings, which could explain the high cover of spruce, despite the presence of *K. angustifolia* and *L. groenlandicum* on unsalvaged forest floor. Most of these ericaceous species grow in the old-growth boreal forests of eastern Canada. The heterogeneity in forest floor composition after windthrow, even if it did not change species composition, may have changed species abundance.

In salvaged windthrow, the mean number of species was not higher on the forest floor than on pit-and-mound microtopography, unlike the unsalvaged treatment. After salvage logging, light conditions are more homogeneous and there is marked soil disturbance because of the use of machinery. This homogenization could explain the lack of differences in the number of species among microtopographic features in salvaged plots. However, diversity was higher on salvaged forest floor than on microtopographic features. Pits and mounds are very small after salvage logging, and many are affected by forestry operations (Waldron et al. 2013), which could explain the low biodiversity on microtopographic features after salvage logging. Overall, however, we did not find a significant reduction in species diversity after salvage logging in comparison to unsalvaged plots. In comparison with other studies of salvage logging following windthrow (Elliott et al. 2002; Ilisson et al. 2006; Rumbaitis del Rio 2006), our study area was characterized by a low number of species. This could explain our difficulties in finding differences in species number between treatments. The main effect of salvage logging seems to be related to a reduction in structural heterogeneity rather than to a reduction of plant diversity and richness.

Despite the absence of significant differences between treatments in terms of Shannon diversity and species richness per subplot, RDA analysis showed different species assemblages between the treatments. Most species were related to unsalvaged windthrow, while salvage logging treatment was not associated with any specific vegetation, which could be attributed once again to homogenization of the salvaged area. This could be partially explained by the relationship between the volume of recent and old downed CWD and many plant species. Salvaged logging removes wood, so both the volume and structure of CWD are modified by this treatment. Even old CWD is reduced after salvage logging, probably because of the machinery impacts (Waldron et al. 2013). The presence of CWD could be suitable for some species establishment and growth, e.g. *O. montana* (Perala & Alm 1990; Ringius et al. 1997). After unsalvaged windthrow, structural attributes such as living trees and snags are more abundant than after salvage logging (Waldron et al. 2013). These attributes may play a role in the establishment and growth of some species. Also, the high density of logging trails and the relative structural homogeneity after salvage logging operations may reduce the capacity for plants to establish and germinate. Salvage logging certainly modified light and humidity conditions, which are the dominant factors influencing composition and structure of understorey vegetation (De Grandpré et al. 2003). Species like *G. hispidula* and *O. montana* were related to the unsalvaged treatment. These species are known to be associated with old forest environmental conditions, e.g. lower light levels, humid soil conditions and cool soil temperatures. They persist when soil disturbance is relatively low (De Grandpré et al. 2003), which is not the case in salvaged windthrow. Even if *Vaccinium* spp. tolerate harvest operations, Atlegrim & Sjöberg (1996)

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showed that *V. myrtillus* decreased after clear-cutting in *Picea abies* forest. Our results trended in the same direction, and showed that *Vaccinium* spp. are related to *Sphagnum* cover and, therefore, to the unsalvaged environment.

Regardless of whether the number of species and the Shannon index were affected by salvage logging or not, a specific vegetation pattern could be associated with post-windthrow plots, which was not the case with the salvaged plots. Again, it is important to mention that these results should be considered as tendencies, given the relatively low percentage of variance explained by the first two ordination axes.

Regeneration

In the unsalvaged treatment, balsam fir had the highest number of saplings and seedlings, followed by black spruce, and finally white birch. RDA revealed that black spruce and balsam fir were related to unsalvaged forest floor, but this analysis also used species cover percentage. Even though spruce and fir had high cover after windthrow, the number of saplings and seedlings was relatively low. Thus, most black spruce and balsam fir in the unsalvaged plots were advance regeneration, which had higher cover than new seedlings. These results are consistent with other studies where advanced regeneration in a post-windthrow ecosystem predominated (Wohlgemuth et al. 2002; Jonášová et al. 2010). The low proportion of birch in the original stand probably explains the low number of its seedlings and saplings after windthrow. An additional explanation would be the low pit-and-mound cover, leading to a lack of adequate seedbeds (Waldron et al. 2013).

For both treatments, our results showed no link between regeneration quantity and microtopographic features, which may be explained by the lack of specialist species in our study area; thus, it is hard to see a relationship between these species and microtopographic attributes. Overall, the mean number of seedlings and saplings after salvaged windthrow is lower than for unsalvaged windthrow. This could be explained by high soil disturbance during logging operations and a high density of skid trails, which negatively affect advance regeneration (Jonášová et al. 2010; Fischer & Fischer 2012), together with the new recruits. In unsalvaged windthrow, soil disturbance was less severe and, therefore, advance regeneration was not as severely affected as after salvage logging. Our results also show that balsam fir densities were not significantly higher than those of spruce in salvaged windthrows. These results are interesting, particularly in a context where there are concerns regarding balsam fir overstocking following logging operations (Haeussler & Kneeshaw 2003; Côté 2006).

Windthrow severity affected regeneration in both treatments in the same manner. Yet, the higher number of firs with increasing windthrow severity was hard to explain. Since balsam fir are known to be more susceptible to windthrow than black spruce (Ruel & Benoit 1999; Ruel 2000), the most logical explanation for this result would be that in plots affected by severe windthrow, balsam fir was locally more abundant prior to the episodes of windthrow. The increased importance of fir in the canopy could then favour a higher presence of this species in regeneration of these plots.

Management implications and conclusion

Forest floor composition was affected by salvage logging operations, particularly mosses and *Sphagnum* cover, which are sensitive to soil disturbance (De Grandpré et al. 2003). This diminution of forest floor heterogeneity, together with the reduction in downed and standing dead wood (Waldron et al. 2013), influenced understorey plant composition. However, the volume of down deadwood on the salvaged cut-blocks remained relatively high (see Waldron et al. 2013) and the impact of salvage logging on regeneration was low. Thus, we can assume that the salvaged and unsalvaged windthrows will tend to converge over time. Long-term studies on the effects of salvage logging on key ecosystem attributes should be executed in order to verify this assumption.

To maintain post-windthrow forest floor characteristics and thereby reduce the short-term impacts of salvage logging on vegetation, retention patches should be kept within the harvested area. These retention patches should include not only downed and standing deadwood, but also living trees of various sizes, which will maintain a certain degree of structural heterogeneity on the cut-blocks (Kuuluvainen 2002). Indeed, the reduction of structural heterogeneity (living trees, down and standing deadwood) after salvage logging may also affect bird species (Lain et al. 2008; Żmihorski 2010), invertebrates (Bouget & Duelli 2004; Żmihorski & Durska 2010) and small mammal populations and species assemblage (Loeb 1999). Our results also showed that salvaged logging operations reduce advance regeneration cover compared to unsalvaged windthrows. Retention patches would also improve the preservation of a certain quantity of advance regeneration on the cut-blocks.

Thresholds on the size and number of patches that should be preserved on cut-blocks in order to maintain key post-windthrow attributes and mitigate the impacts of salvage logging are hard to establish because of the paucity of studies regarding these attributes and their specific effects on other values, such as wildlife (Vaillancourt 2008). However, in Quebec, retention patch sizes are currently between 150 and 300 m^2 (Leblanc & Pouliot 2011), which is probably too small to maintain natural understorey conditions (Bradbury 2004; Jönsson et al. 2007). Studies on patch size and post-windthrow structural attributes should be performed to provide indicators of the minimum acceptable size of patches in the eastern boreal forest of Quebec. Monitoring of biological legacies in retention patches must also be performed and thresholds must be altered where necessary (Drapeau et al. 2009; Gauthier et al. 2009). At the stand and landscape levels, it is important to ensure that a proportion of windthrow areas is retained intact. In Quebec, Nappi et al. (2011) suggested that for salvage logging after fire, at least 30% of fire-affected forest should be left unsalvaged at the management unit scale. This threshold could also be applied to windthrow, but should be refined through monitoring, which is a key requirement in ecosystem management (Drapeau et al. 2009; Gauthier et al. 2009).

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