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Article

Ecosystem Responses to Partial Harvesting in Eastern Boreal Mixedwood Stands

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Abstract: Partial harvesting has been proposed as a key aspect to implementing ecosystem management in the Canadian boreal forest. We report on a replicated experiment located in boreal mixedwoods of Northwestern Quebec. In the winter of 2000–2001, two partial harvesting treatments, one using a dispersed pattern, and a second, which created a (400 m^2) gap pattern, were applied to a 90-year-old aspen-dominated mixed stand. The design also included a clear cut and a control. Over the course of the following eight years, live tree, coarse woody debris, regeneration and ground beetles were inventoried at variable intervals. Our results indicate that all harvesting treatments created conditions favorable to balsam fir (*Abies balsamea*) sapling growth and trembling aspen (*Populus tremuloides*) sapling recruitment. However, balsam fir and trembling aspen regeneration and ground beetles response to gap cuts were closer to patterns observed in clear cuts than in dispersed harvesting. The underlying reasons for these differing patterns can be linked to factors associated with the contrasting light regimes created by the two partial harvesting treatments. The study confirms that partially harvesting is an ecologically sound approach in boreal mixedwoods and could contribute to maintaining the distribution of stand ages at the landscape level.

Keywords: forest ecosystem management; boreal mixedwoods; forest regeneration; coarse woody debris; ground beetles; succession; biodiversity

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1. Introduction

Mixedwood stands of the eastern North American boreal forest are generally associated with productive, mesic sites. They represent a transitional, post-fire stand development phase between break-up of an initial cohort of shade intolerant hardwoods and dominance by more tolerant, late-successional species [1,2]. The notion of natural dynamics-inspired silviculture or ecosystem management [3–5], notably for boreal mixedwoods [6,7], has progressively gained support in academic, governmental and forest industry communities and is now part of forest regulations in a number of jurisdictions.

Partial harvesting represents a key element to implementing ecosystem management in the Canadian boreal forest [4,7,8]. Partial cutting can be used to modify stand composition and structure similar to the processes of stem exclusion [9] and natural succession from even-aged intolerant hardwoods to multi-cohort mixedwoods or conifer-dominated stands [4,7]. Silvicultural objectives of partial harvesting may also include an increase in tree species and size diversity, establishment and growth of shade tolerant species and varying rotation lengths to generate more old growth stand attributes [10]. In contrast to clear-cutting, retaining forest structures should allow the maintenance of ecosystem functions within their historical range of variability [11].

Ground beetles (Coleoptera:Carabidae) are an abundant and diverse group of litter dwelling invertebrates and have been widely used to assess the impacts of a variety of intensities of forest harvesting [12,13], including clear cutting [14–16], salvage logging [17] and partial cutting with dispersed variable retention [18–20]. The intensity of overstory removal plays an important role mediating the composition of ground beetles. Reducing basal area generally results in a decrease in the abundance of common forest-associated species and increases in the number of open habitat-associated species. This pattern has proven to be consistent across a variety of silvicultural prescriptions and stand types and, thus, provides a comparable means by which to evaluate partial harvesting in relation to natural stands.

One of the first ecosystem-based silvicultural studies established in the boreal mixedwood of Quebec was the SAFE (*Sylviculture et aménagement forestier écosystémique*) Project [21–23]. Conducted within the Lake Duparquet Research and Teaching Forest (LDRTF) in Northwestern

Quebec [24], SAFE is a series of harvesting experiments set up to test the conceptual model of mixedwood dynamics and silviculture proposed by Bergeron and Harvey [4]. This research provides an experimental framework for (1) identifying the intensity and configuration of partial and selection cuts that will lead to the desired regeneration trajectories or conservation objectives; and (2) understanding the productivity implications of these new systems.

Conducted in aspen-dominated mixed stands, this study assesses the effect of partial harvesting on (1) stand dynamics and diameter distribution; (2) growth, density and composition of natural regeneration; (3) the recruitment and volume of deadwood (logs and snags); and (4) composition of ground beetles. Specifically, we hypothesized that partial harvesting of even-aged mixedwood stands would (1) drive stand composition and structure closer to those of older and more complex stands; and (2) promote assemblages of ground beetles associated with those of older stands.

2. Experimental Section

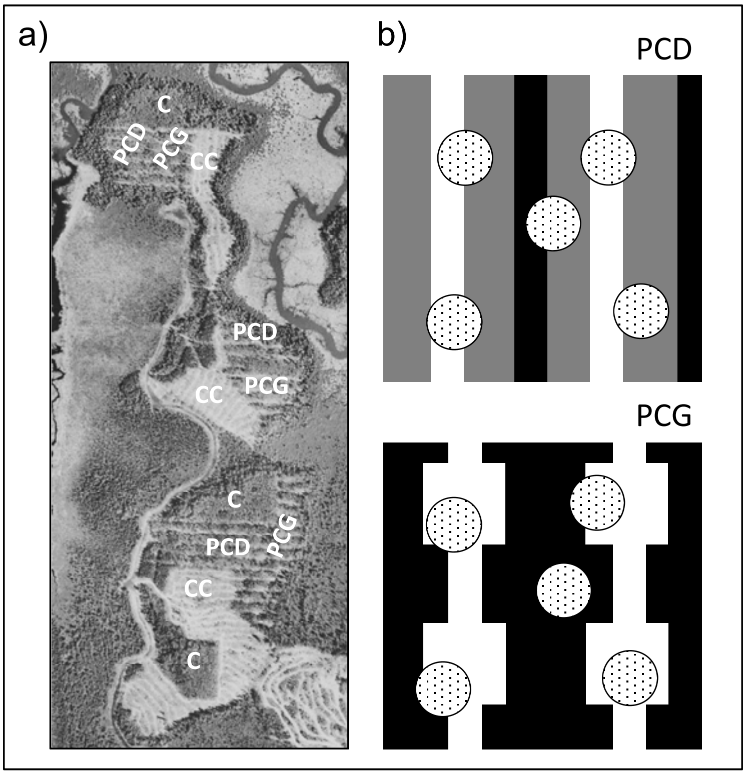
2.1. Study Area

The study area is situated in the Abitibi region of Northwestern Quebec (79°20' W, 48°30' N) within Rowe's (1972) Missinaibi-Cabonga forest region and the Abitibi Lowlands ecological region of Quebec [25]. It is centrally positioned in the large physiographic region known as the Great Clay Belt, characterized by the presence of extensive clay deposits that originated from the proglacial Lake Barlow-Ojibway [26]. The climate is continental with mean annual temperature of 0.7 °C and annual precipitation of 890 mm [27]. Studied stands are of fire origin (time since fire, ~90 years) and classified as mixed with 80% of the basal area in shade-intolerant hardwoods, primarily trembling aspen (*Populus tremuloides* Michx.), and 20% in softwoods, including white spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.).

2.2. Experimental Design and Treatment Description

In the winter of 2000, four levels of forest harvesting, including one no harvest (control, C) and one clear cut (careful logging, CC) treatment, were applied according to a randomized complete block (RCB) design, where independence of observations is guaranteed by random allocation of treatments to units. There were three replications of each treatment, for a total of 12 experimental units (EU = 2–3 ha). All harvesting treatments were applied using multifunctional (short-wood) harvesters and forwarders. The two partial cut treatments were designed to remove approximately 40% of the basal area (stems >9.1 cm dbh (diameter at breast height)). In the first treatment (partial cut, homogeneous or dispersed (PCD)), all trees were removed in 5 m-wide hauling trails, and approximately 25% of stems were harvested to a depth of 6 to 7 m in the adjacent strips (Figure 1). In the second treatment (partial cut, gap (PCG)), gaps were created by alternately harvesting stems in the trail only and enlarging the cutting area to a depth of 6 to 7 m on either side of trails (total width 16–18 m), done on lengths of 20 m. In both treatments, an unharvested band of 5–6 m was left between each sequence of trail—the partially harvested strip and the distance between adjacent to hauling trails was 15–17 m.

Figure 1. (**a**) Aerial photo of experiment showing treatment layout and (**b**) a schematic representation of partial harvesting treatments according to a dispersed pattern (top) and a gap pattern (bottom). Experimental units were 2–3 ha. The basal area removed was 100% in white areas (hauling trails and gaps), 25% in grey areas and 0% in black areas. Doted circles represent 400m^2 permanent sampling plots within experimental units. C: control stands; CC: clear cut; PCD: partial cut—dispersed; PCG: partial cut—gap.



2.3. Field Methods

Before harvesting and in all 12 EU, five circular (r = 11.28 m, 400 m^2) permanent sampling plots (PSP) were randomly located. All live trees and snags greater than 5.0 cm in dbh were identified to species and the dbh measured; snags were assigned to one of five decomposition classes [28]. In the northeast 100 m^2 quarter of each plot, all small saplings between 2.0 and 4.99 cm dbh were also identified to species, tagged and measured (dbh).

After harvesting in the spring of 2001, residual stems were tallied in all PSP in order to estimate the harvested and residual basal area. In each EU, the volume of downed logs was estimated using the line intercept method [29]. Accordingly, along each side (30 m) of an equilateral triangle, the frequency of logs was recorded by diameter (5 cm: 2.5–7.6 cm; 10 cm: 7.6–12.5 cm; 15 cm: 12.6–17.5 cm; and 17+ cm: 17.6 cm and greater) and decomposition class. Decomposition classes were based on visual criteria, such as the presence of branches, bark and mosses, and on the softness of the wood [30]. A five class system was used, with classes 1–3 representing fresh logs and classes 4 and 5 well-decayed wood.

In each PSP, regeneration was tallied in eight circular 2 m^2 sub-plots by seedling species and according to two size classes: small seedlings (0–1 m height) and large seedlings (from 1 m height to a 2 cm dbh). Subplots were positioned systematically two and four meters from the center of each PSP on the north, east, west and south radii of each PSP. A total of 480 regeneration sub-plots were surveyed in 2001, 2005 and 2008.

In 2007, height and radial growth response of balsam fir and trembling aspen saplings to harvesting was assessed. At the extremity of the north and east radii of each PSP, the nearest balsam fir sapling with a dbh between 2 and 5 cm was cut at ground level for measurements. The same procedure was followed for trembling aspen saplings at the extremity of the south and west radii. A total of 116 balsam fir and 79 trembling aspen saplings were sampled. Only height of collected aspen saplings was measured in the field, whereas for each sampled balsam fir, total height and annual height increment for the last eight years were measured in the field. For both species, a disc was collected at the base of each stem to estimate the minimum age of saplings and the annual basal radial growth from 2000 to 2006. In the laboratory, disks were sanded, the number of rings counted and the width of the last eight (8) rings measured along two (2) representative radii using a Velmex measuring system (Bloomfield, NY, USA).

Sampling of arthropods took place between 28 May and 8 September, 2005, and from 6 May to 23 September, 2006 (five and six years post-treatments). Two pitfall traps were placed in each of the five PSP within each EU. Traps consisted of two nested 200 mL disposable plastic cups with the outside cup acting as a sleeve and placeholder for the removable inside cup. Traps were filled with 20 mL of Prestone® low-toxicity propylene glycol preservative solution and sheltered by a square of corrugated plastic to keep out rainwater and debris. Traps were emptied at 2–3 weeks intervals throughout the sampling period. Traps were not baited; hence, the collected samples are unbiased estimators of the ground beetle species that occur within close proximity to the traps over the duration of the sampling period. Because of the small size of these traps, sampling has a negligible impact on local Carabid populations.

To evaluate whether partial harvesting created assemblages similar to those of older forest stands, we also collected ground beetles from three stands dating from a fire in 1760. These stands are located in the LDRTF, approximately 7 km from the partial harvesting experiments. They were affected by an eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak that occurred in 1970–1987 [31]. In the winter of 1999, a RCB experiment was established in these stands with clear cut and control (no harvest) treatments replicated three times for a total of six experimental units. All EU of this experiment were sampled over the same period and using an identical methodology, as previously described. A total of 180 traps were used for the two experiments combined, for a total of 41,263 trap days.

Carabids were sorted from trap contents and identified to species using Lindroth (1961–1969) and the "Ground Beetles of Canada" online resource from the Canadian biodiversity inventory. Voucher specimens were verified by comparisons with the Carabid collections at the Canadian Forest Service Laurentian Forestry Centre and the collection of André LaRochelle at the Université de Montréal.

Individual trap catch numbers were converted to daily trap catch rates per species. This conversion standardized catches by the number of days each trap was functioning and corrected for disturbed or missing traps.

2.4. Statistical Analyses

Data were treated according to a RCB design by means of general linear mixed models using the MIXED procedure of the SAS Institute [32]. Variance estimates were based on the restricted maximum likelihood and significance of fixed effects on the Type 1 test of hypothesis. Fixed factors were treatment, time since harvesting and their interaction. For regeneration density and growth response, time squared and its interaction with treatment were also included as fixed factors to take into account a quadratic relationship with time. Contrasts between (1) controls (C) and partial cuts (PC); (2) clear cuts (CC) and PC; and (3) dispersed partial cuts (PCD) and gap partial cuts (PCG) were also tested. The interactions and time squared were removed from models when found to be not significant ($p > 0.05$). Blocks, EU and PSP were treated as random factors; each one nested in the former. Repeated measure analyses, when appropriate, were conducted based on an autoregressive covariance structure [32].

For all models, the normality of conditional studentized residuals and their distribution in relation to predicted values were visually assessed. When residuals did not conform to a normal distribution or presented a funnel-shaped pattern when plotted against predicted values, variables were log-transformed. However, control (no cut) experimental units were removed from aspen regeneration models, because constant null values across time decreased the variance homoscedasticity beyond what is possible to correct by data transformation.

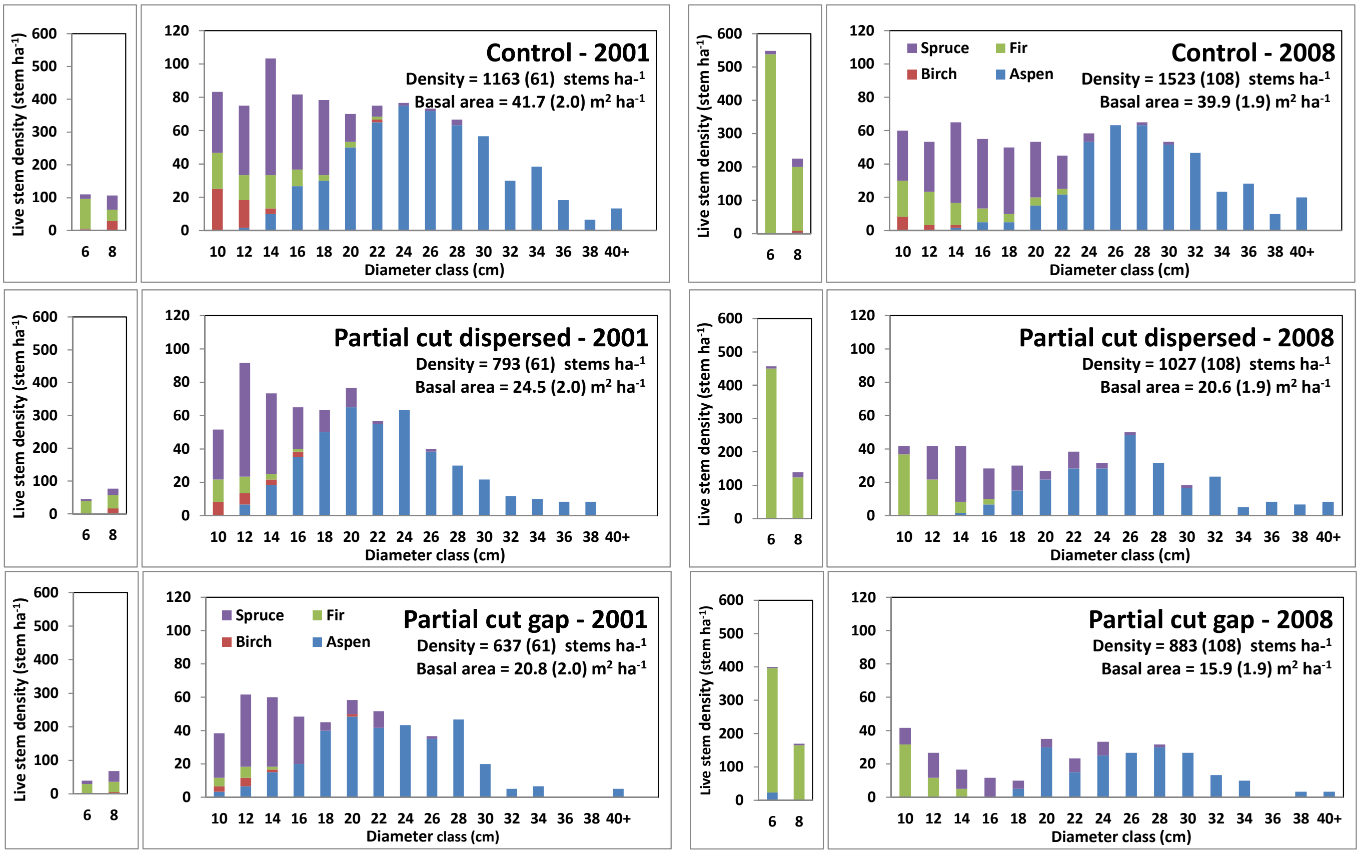
Ground beetle assemblages were analyzed using multivariate regression trees [33]. Multivariate regression trees are hierarchical models that successively split data into more homogeneous groupings based on a set of explanatory variables. This approach makes relatively few underlying assumptions about statistical distributions within the data and, thus, is widely applicable to assemblage data with many species. We used sum-of-squares multivariate regression trees (ssMRT) to characterize ground beetle assemblages as a function of stand type, harvesting treatment and sampling year. We selected the final tree size based on cross-validated errors. For a final tree, we selected the smallest tree whose cross validation error fell within one standard deviation of the minimum cross-validated relative error [33].

3. Results and Discussion

3.1. Initial Stand Composition and Regeneration

The diameter distribution of control stands (Figure 2) reflects what is known of natural dynamics following fire on rich sites; that is, the dominance of a first cohort of fast growing intolerant species, with a gradual increase of slower growing, more shade-tolerant species into the canopy layers [1,34]. In 2001, the diameter distribution of trembling aspen followed a normal curve with a modal diameter of 24 cm and stems smaller than 14 cm dbh virtually absent. Shade tolerant species, balsam fir and white spruce and, to a lesser extent, white birch (*Betula papyrifera* Marsh.) dominated the smaller diameter classes. Live tree density (>5 cm dbh, all species) in control stands was 1163 stems ha^{-1} (Figure 2) and the basal area was 41.7 m^2 ha^{-1}.

Figure 2. Diameter distribution of live stems immediately (spring of 2001) and eight years (2008), following the partial harvesting of mixed boreal stands. Values in brackets are standard deviations. Total density and basal area values include stems 5 cm diameter at breast height (dbh) and larger.



Pre-harvest regeneration (Figure 3) was abundant and largely dominated by balsam fir despite the greater presence of white spruce in the canopy. The estimated minimal age of small balsam fir saplings (n = 111) ranged from 15 to 65 years. This is a clear indication that mature balsam fir stems were more abundant in the canopy prior to the last (1970–1987) spruce budworm outbreak [35]. Balsam fir is very shade-tolerant and seedlings can survive in the understory for years [36]. White spruce seedling establishment in these stands is hampered by the broadleaf forest litter and largely restricted to well-decayed logs. Moreover, being of intermediate shade tolerance, white spruce seedling survival may be constrained by insufficient light exposure in these stands [30].

3.2. Harvesting Effects on Stand Characteristics

Partial harvesting originally significantly reduced stand density by 32.8% and 45.2% and the basal area by 41.2% and 50.1% in dispersed cuts and gap cuts, respectively (Figure 2), without inducing noticeable immediate changes in the range of tree diameters. No significant differences in live stem density and the basal area were found between the two partial harvesting treatments (Table 1).

Figure 3. Balsam fir and trembling aspen regeneration densities in mixed boreal stands as a function of harvesting treatment and time since harvesting**.** Points are average observed values over experimental blocks. Lines are predicted values according to models (see Table 2 for model specifications). Control stand values were not included in statistical models for trembling aspen regeneration, but observed values are displayed in figures. C: control stands; CC: clear cut; PCD: partial cut—dispersed; PCG: partial cut—gap.

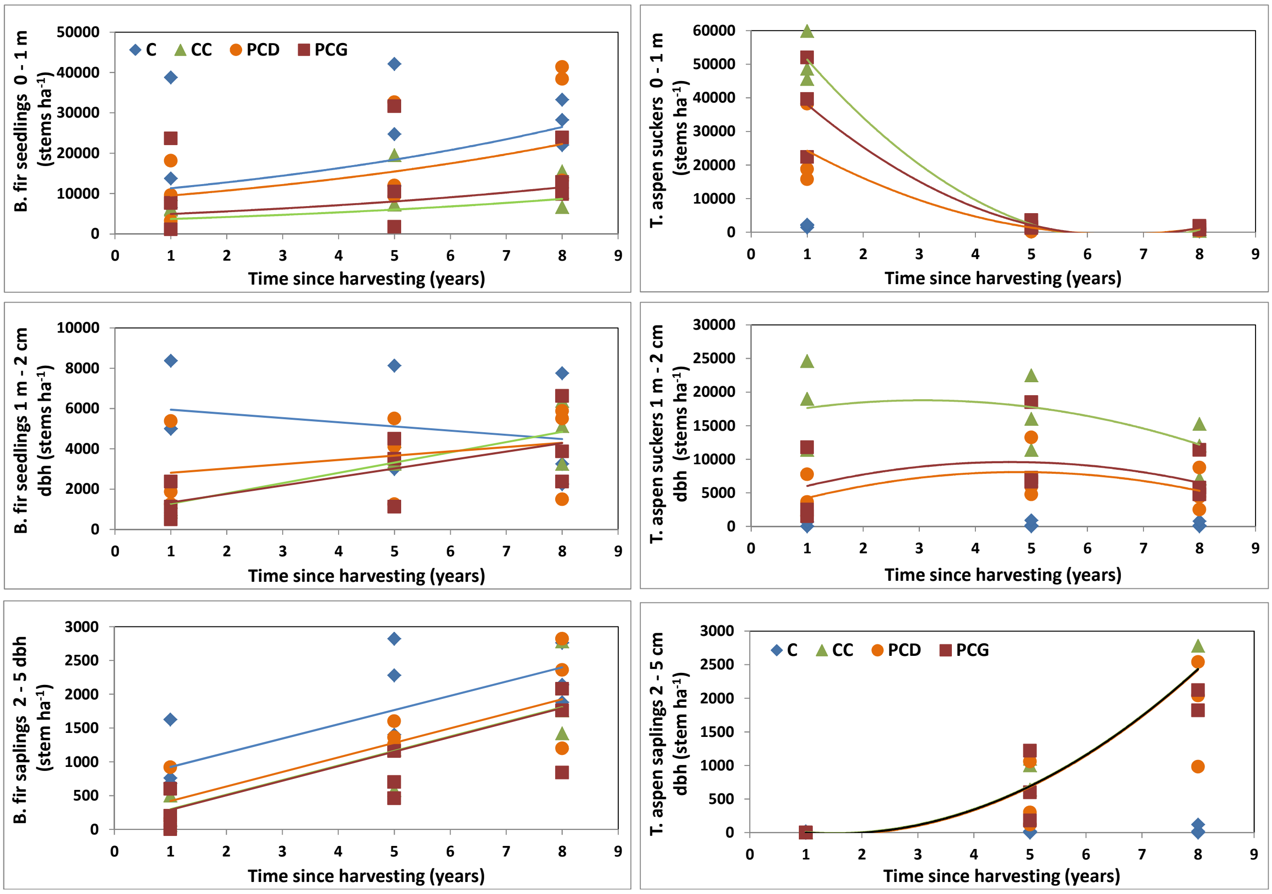


Table 1. Effects of complete and partial harvesting and time since harvesting on boreal mixed stands characteristics. Significance of fixed effects is based on the Type 1 test of hypothesis.

Fixed Factors	Time	C *vs.* PC	CC *vs.* PC	PCD *vs.* PCG	Time × Treatment
		Live stems (trees >5 cm dbh)			
Density	***	***	NA	NS	NS
Basal area	***	***	NA	NS	NS
		Snag density (snags >5 cm dbh)			
Aspen snags	*	NS	***	*	***
Softwood snags	***	NS	*	NS	*
Snags >20 cm	***	NS	***	NS	*
		Downed log volume			
Fresh logs	NS	NS	NS	NS	***
Well decayed logs	*	NS	*	NS	NS
Logs >20 cm	NS	NS	NS	NS	NS

***: $p < 0.001$, **: $0.001 < p < 0.010$, *: $0.010 < p < 0.050$, NS: $p > 0.051$, NA: not applicable.

3.3. Balsam Fir Regeneration Response to Harvesting

Clear cut and partial harvesting initially reduced balsam fir regeneration abundance (Figure 3, Table 2) in relation to controls for all regeneration size classes, with larger differences observed for small saplings (stems from 1 m height to 2 cm dbh). Significant differences among the three harvesting treatments were only found for balsam fir seedlings <1 m height. Snow cover may have offered some protection for small seedlings, but this protection was clearly not effective in hauling trails and the reduced abundance of small seedlings reflects the extent of site disturbance induced by treatments (Figure 3). Sudden sun exposure and water stress could also have induced some mortality in the larger seedlings immediately following canopy opening [37].

With time, balsam fir regeneration abundance increased for all size classes and in all treatments. The only exception was in the 1 m to 2 cm dbh class in control stands, which decreased over the eight year period to a level similar to those observed in harvesting treatments (Figure 3, Table 2). We suspect light conditions in the understory of control stands were insufficient [38] to promote the growth of the smaller seedlings [39] and their recruitment in the 1 m to 2 cm dbh class. However, because taller balsam fir seedlings are less penalized by low light availability than smaller ones [39], the 1 m to 2 cm dbh seedlings were able to move into the small sapling class (2 to 5 cm dbh) at similar rates for all treatments.

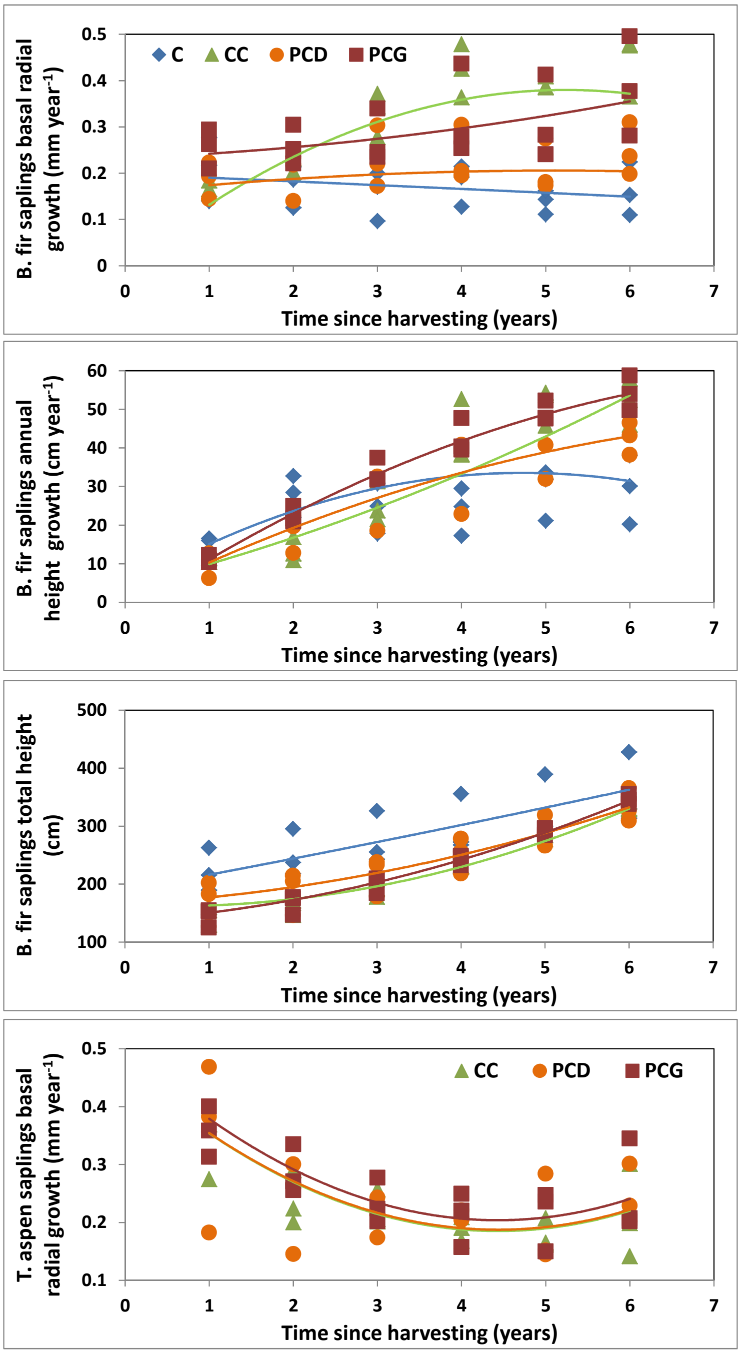
Table 2. Effects of harvesting and time since harvesting on balsam fir and trembling aspen regeneration density and growth in mixed boreal. Significance of fixed effects is based on the Type 1 test of hypothesis.

Factors	Time	Time^2	C *vs.* PC	CC *vs.* PC	PCD *vs.* PCG	Time × Treatment	Time^2 × Treatment
Balsam fir regeneration density							
Seedlings <1 m (log)	**	NS	*	**	*	NS	NS
Seedlings 1 m–2 cm dbh	***	NS	***	NS	NS	***	NS
Saplings 2–5 cm dbh	***	NS	**	NS	NS	NS	NS
Balsam fir small sapling growth							
Annual basal radial growth	***	***	NS	***	NS	***	***
Annual height growth	***	**	NS	NS	NS	***	*
Total height	***	***	*	NS	NS	**	***
Trembling aspen regeneration density							
Seedlings <1 m	***	***	NA	**	*	***	**
Seedlings 1 m–2 cm dbh	NS	***	NA	***	NS	*	NS
Saplings 2–5 cm dbh	***	***	NA	NS	NS	NS	NS
Trembling aspen small sapling growth							
Annual basal radial growth	***	***	NA	NS	NS	NS	NS

Time^2: time × time; ***: $p < 0.001$, **: $0.001 < p < 0.010$, *: $0.010 < p < 0.050$, NS: $p > 0.051$, NA: not applicable.

Balsam fir saplings sampled for growth analyses six years following harvesting were between 2.5 and 4.5 m high (Figure 4) with no differences between treatments at sampling time. However, growth analyses revealed that saplings from uncut control stands were originally taller than saplings from harvest treatments, but experienced decreasing height and radial growth rates with time (Figure 4, Table 2). In contrast, radial and height growth of saplings in clear cut and gap cut treatments increased with time up to six years following harvesting. Radial growth of saplings in the dispersed cuts did not improve following harvesting, but their height growth increased with time, although at a slower rate than what was observed in the gap cut treatment.

Figure 4. Balsam fir and trembling aspen small saplings growth in mixed boreal stands as a function of treatment and time since harvesting. Points are average observed values over experimental blocks. Lines are predicted values according to models (see Table 2 for model specifications). Control stands observed values for trembling aspen are not presented. C: control stands; CC: clear cut; PCD: partial cut—dispersed; PCG: partial cut—gap.



Balsam fir growth response to treatments was conditioned by its high morphological plasticity and mostly its capacity to increase height growth in response to canopy opening [39,40]. Despite having similar residual basal area (Figure 2, Table 1), partial cut treatments differed by the spatial distribution of residual stems, leading to large differences in understory light availability. Modeling light conditions in mixedwood boreal stands following removal of 45% of basal area according to dispersed and gap patterns, Beaudet *et al*. [38] found that gap cuts received almost twice the direct and diffuse light transmission than dispersed cuts.

Clear cutting did not provide short term advantages for balsam fir growth. The sudden exposure to sunlight and wind following clear cutting may have caused balsam saplings to initially experience a reduced growth rate (Figure 4). Moreover, above 25% of light transmission, the increase in height growth with increasing light of balsam fir saplings tends to attenuate [39]. This would explain why patterns observed in the clear cut remained close to those observed in gap cuts (Figure 4, Table 2). However, while height growth was still increasing six years after harvesting in the clear cuts, the growth rate had started to slow down in the gap cuts.

3.4. Trembling Aspen Regeneration Response to Harvesting

Trembling aspen is a clonal species with the ability to produce large numbers of root suckers following disturbance [41]. Up to 60,000 trembling aspen suckers <1 m, and 25,000 suckers between 1 m and 2 cm dbh were present in clear cuts at the end of the first growing season following harvesting (Figure 4). Trembling aspen suckers were initially less abundant in partial cuts than in clear cuts and less abundant in dispersed than in gap cuts (Table 2, Figure 3). These results are similar to those of other studies on partial harvesting of trembling aspen-dominated stands in the boreal mixedwood forest [21,42].

However, it is not the initial sucker density, but the ability of these stems to recruit into the sapling layer that will count over the longer term. Despite mortality rates of the initial sucker cohort ranging from 69% to 77%, sucker recruitment into the 2 to 5 cm dbh class reached 2400 stem ha^{-1} eight years after harvesting and was identical in all harvesting treatments (Table 2, Figure 3). Saplings sampled for growth analyses six years following harvesting (n = 79) measured between 2.6 and 5.9 m (average 3.8 m, SD = 0.7) across treatments. Radial growth was similar among harvesting treatment (Table 2, Figure 4), decreasing from year 1 to year 4 after harvesting and increasing thereafter. Aspen, a highly shade-intolerant species, shows little plasticity in relation to light environment and virtually all collected basal disks indicated that establishment occurred immediately following clear cut and partial harvesting treatments [36].

Our results indicate that the dispersed partial cuts provided the minimal conditions beyond which no increase in survival or growth rates of aspen were observed. These results are consistent with those of Paré *et al*. [43] on aspen growth in natural gaps and confirm the feasibility of converting even-aged aspen stands into multi-cohort structured stands. The pattern is comparable to patterns observed regionally in natural stands [1] and linked to severe forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) outbreaks [44]. Whether the spatial distribution of saplings is comparable to that of natural stands remains to be investigated.

3.5. Changes in Stand Diameter Distribution in Response to Harvesting

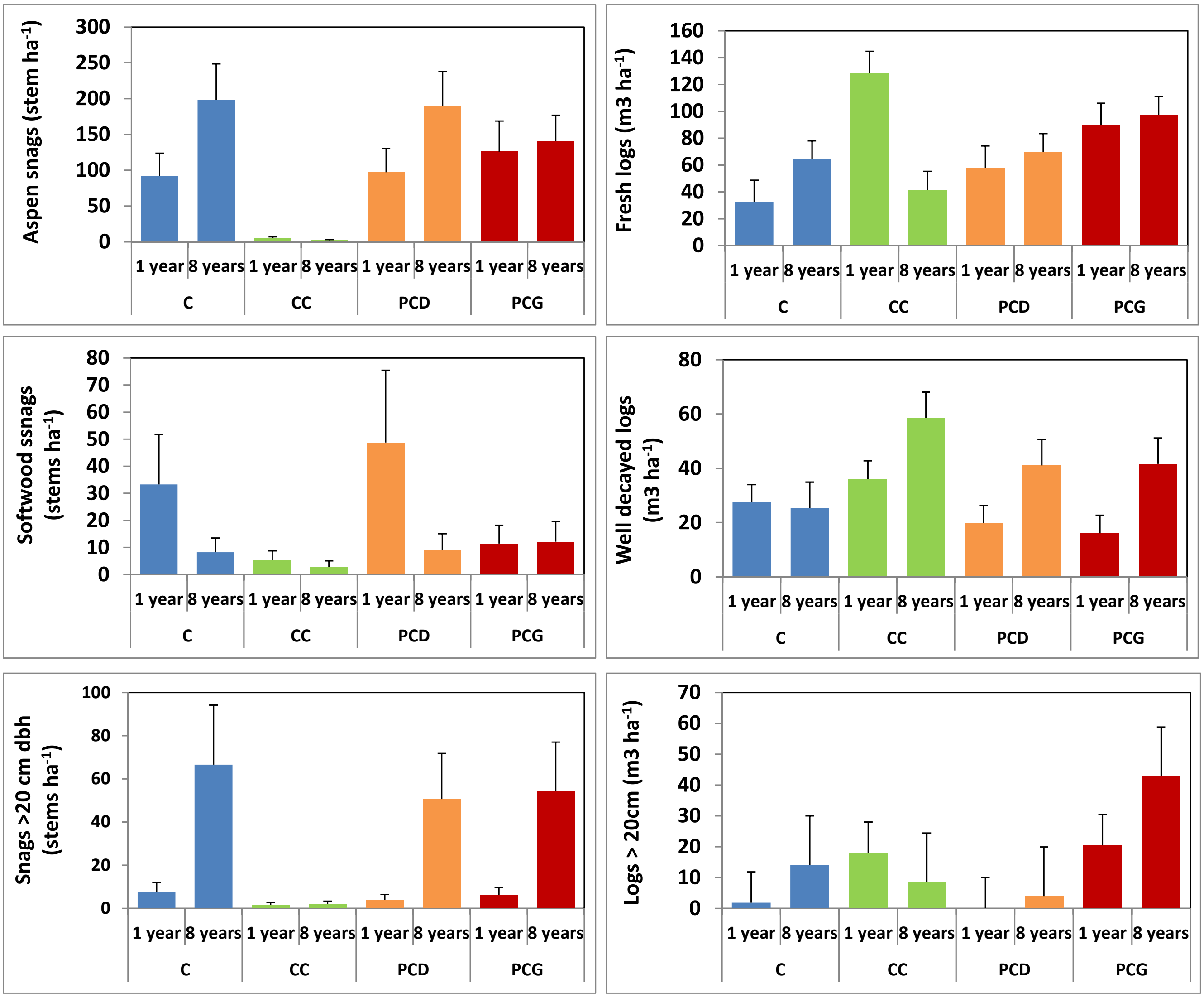
Between 2001 and 2008, stem recruitment in the large sapling class (5–9.9 cm dbh) (Figure 2) was almost exclusively in balsam fir, ranging from 538 stems ha^{-1} in gap cuts to 728 stems ha^{-1} (SD = 225) in controls (Figure 2). Little recruitment took place in the 10–19.9 cm dbh class for any of the species and treatments. No differences were observed between treatments for either 5–9.9 or the 10–19.9 cm dbh diameter classes. Significantly higher recruitment was observed in controls compared with both partial cuts for trembling aspen ($p < 0.001$) and white spruce ($p = 0.043$) stems >20 cm. Hence, 395, 227 and 183 aspen stems ha^{-1} (SD = 31) moved into the >20 cm dbh class for controls, dispersed partial cuts and gap cuts, respectively. Respective numbers for white spruce were 60 stems ha^{-1} (SD = 12) in controls and 23 stems ha^{-1} for both partial cut treatments. The differences between controls and partial cuts reflect the reduced density of stems in the <20 cm dbh classes following partial harvesting.

During the same period, no significant differences were observed among treatments for absolute mortality of any of the species-dbh class combination. Little mortality was observed for balsam fir in the 5–9.9 and 10–19.9 cm dbh classes (less than 25 stems ha^{-1}) and for white spruce in the 10–19.9 cm dbh class (30–85 stems ha^{-1}). The low mortality rate of small diameter balsam fir stems may be a reflection of the gradual canopy opening and increased light conditions created by aspen mortality in the canopy.

Trembling aspen incurred most of the mortality, 50–65 stems ha^{-1} in the 10–19.9 cm dbh class and 80–95 stems ha^{-1} in the >20 cm dbh class over the eight year period. Similar absolute mortality rate between partial cuts and control stands implies a larger proportion of aspen dyed in partial cuts than in control stands. Damage caused by harvesting equipment [45] may accentuate mortality in partially harvested stands. Most of the dead stems were found standing up (snags, Figure 5), precluding windthrow as the dominant cause of mortality. However, the proportion of aspen in terms of total stand density followed a similar trend with time in the two partial cut and control treatments, decreasing from 48%–53% in 2001 to 24%–27% in 2008. Stand total basal decreased similarly in all treatments (Figure 2, Table 1), and no significant interaction was found between time and treatment for basal area (Table 1).

Stands in all treatments, except clear cuts, included four distinct layers: (1) an aging cohort of aspen mixed with white spruce of comparable age, but smaller stem size; (2) an intermediary layer of balsam fir (5–9.9 cm dbh); (3) a vigorous small saplings layer (2–4.99 dbh); and (4) the layer of seedling to low shrub-sized balsam fir regeneration. The main differences between the control (undisturbed) stands and partial cuts were the lower basal area of first cohort aspen and white spruce and the mixed composition of the sapling layer in partial cuts (Figure 3). These attributes are consistent with recent observations from aspen or mixed aspen stands affected by prolonged forest tent caterpillar outbreaks [44,46]. While in the absence of further disturbance, control stands will evolve towards softwood dominance [1], partially harvested stands could maintain a mixed composition for a much longer period.

Figure 5. Snag density and downed log volume immediately and eight years following partial and clear cut harvesting of mixed boreal stands. C: control stands; CC: clear cut; PCD: partial cut—dispersed; PCG: partial cut—gap.



3.6. Recruitment and Volume of Deadwood Following Partial and Clear Cut Harvesting

Coarse woody debris (CWD), snags and downed logs, is a key attribute of forest ecosystems, sustaining a myriad of species [47,48] and structural diversity [49], as well as contributing to seedling establishment [30]. One underlying objective of partial harvesting in the context of ecosystem management is to increase the recovery time of CWD dynamics following harvesting [50]. In control stands, trembling aspen snag density doubled between 2001 and 2008 from 92 to 198 stems ha^{-1} (Figure 5, Table 1). A similar increase in snag density was observed in the dispersed partial cut treatments. However, trembling aspen snag density in the gap cuts increased by merely 25 stems ha^{-1} (Figure 2, Table 1) during the eight year period. The most significant differences among treatments (Table 1) were caused by the large differences between the clear cuts and partial cuts and the lack of aspen snag recruitment in the clear cuts. Densities of large snags (>20 cm dbh), a forest attribute associated with old-growth forests [50], increased in the control and partial cut treatments. These stands appear to be entering a canopy transition phase characterized by death of dominant and codominant stems [9], a phase usually associated with increasing volumes of CWD [51]. Due to the low mortality rate of balsam fir, softwood snag density decreased in all treatment between 2001 and 2008.

In 2001, total downed wood volumes ranged from 60 m^3 ha^{-1} in control stands to 165 m^3 ha^{-1} in clear cuts. Partial cuts had intermediary values. The high volume of fresh logs observed in clear cuts (Figure 3) resulted from stem only harvesting: trees were delimbed on site, creating a large amount of fresh small-sized woody debris. Contrary to another experiment in the SAFE Project [21], clear cuts were also characterized by higher volumes of well decomposed logs than partial cuts. No significant differences were found between control and partial cuts or between partial cut treatments for fresh or well decomposed logs or for large diameter logs (Table 1).

Between 2001 and 2008, fresh log volumes significantly increased in control stands and partial cuts (Figure 3, Table 1). Well decomposed log volume increased in partial cut treatments, but remained stable in controls. In clear cuts, where there is little possibility of log recruitment, fresh log volume decreased, while well decayed log volumes increased and remained higher than in any of the other treatments throughout the study period. However, total downed wood volume in clear cuts decreased by 39% over the period. The volume of large logs (>20 cm) remained low in all treatments, except in the gap cuts where they reached an average of 42 m^3 ha^{-1} in 2008. However, the differences between treatments were not found to be significant, because of large variations around means.

In the short term, partial harvesting maintained CWD dynamics comparable to those of control stands and significantly different from those of clear cuts. In the longer term, continuous recruitment of CWD, including large sized snags and logs, should be maintained in partial cuts albeit in smaller volumes.

3.7. Response of Ground Beetles to Harvesting

Neither dispersed partial cutting nor gap cuts created assemblages consistent with uncut or clear cut sites in the later successional balsam fir stands (Figure 6). Differences in assemblages between mixedwood and balsam fir stands accounted for 20.95% of the total variance explained in the ssMRT These differences were defined primarily by nine species, each of which contributed more than 0.5% to the total variance explained and together accounted for 19.11% of the total variance explained (Table 3).

The first split was driven in large part by the relatively large abundance of *Sphaerodeus stenostomus* restricted to mixedwood stands (Figure 7). This species accounted for 11.58%, more than half, of the variance attributable to the initial split in the ssMRT. Mixedwood stands had higher relative abundance of *Pterostichus pensylvanicus* LeConte (1.56%), *Pterostichus coracinus* (Newman) (0.68%), *Synuchus impunctatus* (Say) (0.72%) and *Calathus ingratus* Dejean (0.64%), whereas balsam-fir stands had higher relative abundances of *Pterostichus adstrictus* Eschscholtz (1.9%). Balsam fir stands were further characterized by *Scaphinotus bilobus* (Say) (0.87%) and *Pseudoamara arenia* (Leconte) (0.62%), which were found exclusively in either managed or unmanaged stands. This suggests partial harvesting induced only minor changes in species assemblages when compared to longer-term successional changes in stand composition and structure. It may be argued that these differences were caused by geographical distance between experimental sites (7 km). However, *Pterostichus pensylvanicus*, *Synuchus impunctatus* and *Calathus ingratus*, found to be more abundant in mixedwood stands, were also found in a 86-year-old jack pine stand located within 2 km of the balsam fir stands [52].

Figure 6. Multivariate regression tree of ground beetles assemblages following clear cut and partial harvesting of boreal mixedwood stands. Balsam fir data were collected in older forest stands dating from a fire in 1760 that were later affected by a spruce budworm outbreak that occurred in 1970–1987.

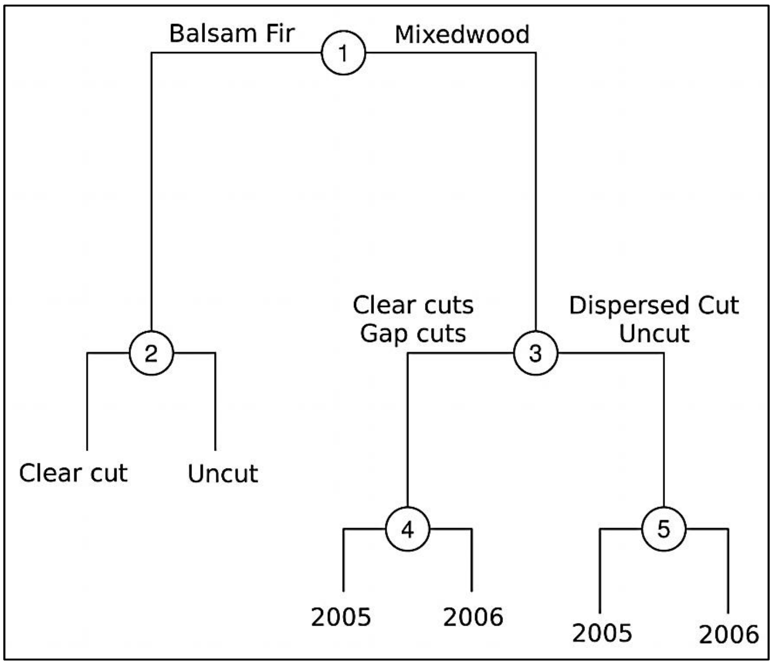


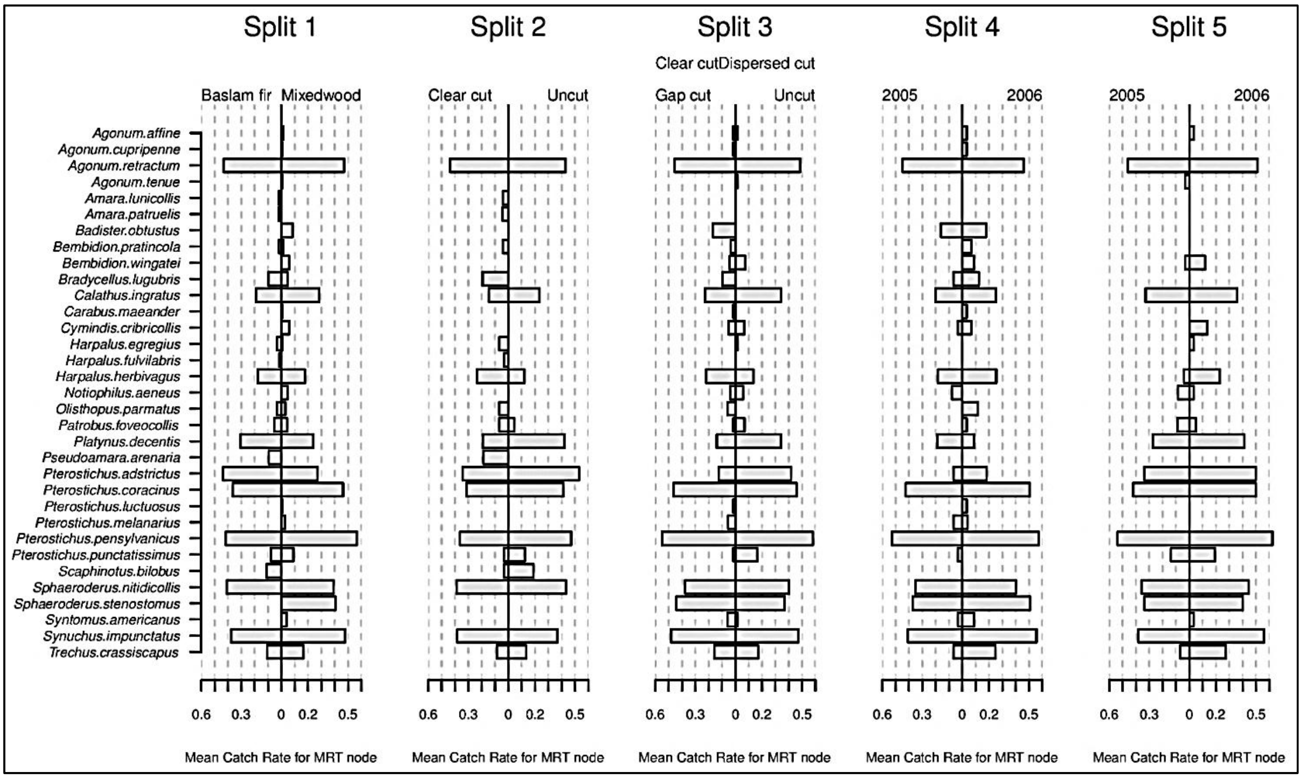
Table 3. Individual species variances by split within the ssMRT, total tree variance and total variance explained for the multivariate regression tree.

	Split-1	Split-2	Split-3	Split-4	Split-5	Tree Total	Species Total
Agonum affine Kirby	0.020	0	0	0.030	0.030	0.080	0.684
Agonum cupripenne (Say)	0.005	0	0.015	0.030	0	0.050	0.352
Agonum retractum LeConte	0.100	0.001	0.050	0.005	0.063	0.218	1.342
Agonum tenue (LeConte)	0.005	0	0.015	0	0.030	0.050	0.352
Amara lunicollis Schiodte	0.028	0.043	0	0	0	0.071	0.499
Amara patruelis Dejean	0.035	0.052	0	0	0	0.088	0.613
Badister obtustus LeConte	0.514	0	1.543	0.008	0	2.066	3.661
Bembidion praticola Lindroth	0.001	0.043	0.060	0.121	0	0.225	1.135
Bembidion wingatei Bland	0.254	0	0.054	0.205	0.188	0.700	2.627
Bradycellus lugubris (LeConte)	0.168	0.994	0.490	0.087	0	1.738	3.507
Calathus ingratus Dejean	0.645	0.201	0.716	0.069	0.026	1.657	6.374
Carabus maeander Fischer von Waldheim	0.005	0	0.015	0.030	0	0.050	0.352
Cymindis cribricollis Dejean	0.247	0	0.015	0.030	0.483	0.775	2.043
Harpalus egregius Casey	0.046	0.121	0.015	0	0.030	0.212	0.999
Harpalus fulvilabris Mannerheim	0.020	0.030	0	0	0	0.050	0.354

Table 3. *Cont.*

	Split-1	Split-2	Split-3	Split-4	Split-5	Tree Total	Species Total
Harpalus herbivagus Say	0.001	0.354	0.371	0.134	0.948	1.808	4.152
Notiophilus aeneus (Herbst)	0.170	0	0.021	0.16	0.068	0.422	2.151
Olisthopus parmatus (Say)	0.001	0.121	0.185	0.37	0	0.679	1.924
Patrobus foveocollis (Escherholtz)	0.012	0.014	0.145	0.030	0.037	0.238	3.049
Platynus decentis (Say)	0.301	1.402	2.197	0.268	0.511	4.679	9.257
Pseudoamara arenaria (LeConte)	0.623	0.935	0	0	0	1.558	2.605
Pterostichus adstrictus Eschscholtz	1.909	0.906	4.57	0.35	0.690	8.425	10.462
Pterostichus coracinus (Newman)	0.686	0.256	0.001	0.18	0.150	1.27	2.827
Pterostichus luctuosus (Dejean)	0.005	0	0.015	0.030	0	0.050	0.352
Pterostichus melanarius (Illiger)	0.051	0	0.154	0.020	0	0.225	1.135
Pterostichus pensylvanicus LeConte	1.564	0.319	0.045	0.051	0.195	2.174	4.184
Pterostichus punctatissimus (Randall)	0.010	0.218	1.155	0.030	0.082	1.494	5.078
Scaphinotus bilobus (Say)	0.869	0.629	0	0	0	1.498	2.191
Sphaeroderus nitidicollis (Guérin-Méneville)	0.031	0.053	0.033	0.068	0.211	0.396	1.524
Sphaeroderus stenostomus (Dejean)	11.586	0	0.277	0.480	0.104	12.448	13.158
Syntomus americanus (Dejean)	0.107	0	0.102	0.078	0.030	0.317	1.749
Synuchus impunctatus (Say)	0.718	0.005	0.006	0.584	0.841	2.154	4.092
Trechus crassiscapus Lindroth	0.221	0.062	0.009	0.875	1.141	2.308	5.215
Total	20.958	6.760	12.278	4.325	5.856	50.176	100

Figure 7. Species means around ssMRT nodes indicating relative contribution to individual regression tree splits. Left and right bars correspond to left and right splits of the ssMRT.



The second (6.75%) and third splits (12.2%) of the ssMRT characterized differences between more intensive or more concentrated forms of harvesting. In the second split, clear cut and uncut balsam fir stands were differentiated based on relative higher abundances of *Platynus decentis* (Say) (1.40%), *P. adstrictus* (0.99%) and *S. bilobus* (0.63%), located in uncut stands, and *P. arenia* (0.93%) and *Bradycellus lugubrius* (LeConte) (0.99%), restricted to clear cuts. In the third split, clear cuts and gap cuts were differentiated from dispersed partial cuts and uncut stands within mixedwood stands. Uncut stands and dispersed cuts were characterized by relatively higher abundances of *P. adstrictus* (4.57%), *P. decentis* (2.20%), *P. punctatissimus* (1.15%) and *C. ingratus* (0.72%). Clear cuts and gap cuts were characterized by *Badister obtusus* (LeConte) (1.54%), which was absent from control stands and dispersed cuts.

For ground beetles and other litter arthropods, removal of the forest overstory often provokes a generalized response pattern, whereby species associated with closed canopy forest are reduced and open-habitat species are promoted [53,54]. Retaining 50% or more of stand basal area generally allows forest associated species to persist following harvesting [20,55], although in some cases, remnant populations may persist in reduced numbers (Graham-Sauvé *et al*, submitted manuscript). The differences in ground beetle assemblages that we observed between gap and dispersed cuts suggests that in addition to the overall level of retention maintained post-harvest, the distribution of standing residual trees within harvested blocks is also an important factor for groups, such as litter-dwelling arthropods. Similar responses have been reported elsewhere. Klimasewski *et al*. [56] found that two large gaps, equivalent to 45% removal of the pre-harvest basal area, harbored ground beetle assemblages that were more similar to clear cuts than to uncut stands. In the same experiment, these authors also reported that increased number of smaller gaps, which maintained the same overall basal area, maintained beetle assemblages that were more closely related to uncut stands [56], thus corroborating the trend we report here. Ground beetles may be responding to the same set of factors that promote understory vegetation, such as increases in light, temperature and moisture.

How retention is distributed throughout harvested sites has implications for the effectiveness of partial cutting as a conservation tool, particularly with increased interest in the development of continuous cover forestry practices [57]. For example, if residual retention is to be left in order to maintain assemblages consistent with uncut forests, gap cuts may be largely unsuccessful, despite relatively high levels of retention. However, in the context of ecosystem management, partial cuts in mature aspen stands should aim at maintaining attributes and processes similar to those created by insect outbreaks or other small scale disturbances. Leaving gaps to encourage open-habitat species may be desirable. This serves to underscore the importance of the forest overstory and standing retention not only in maintaining forest species, but as a means of attenuating open-habitat species.

Splits four (4.32%) and five (5.59%) of the ssMRT characterized interannual variation and were dominated by greater catch rates of particular species in 2006. Within the mixedwood clearcuts and gap cuts, relatively more *S. impunctatus* (0.58%) and *Trechus crassiscapus* Lindroth (0.87%) were collected in 2006 than in 2005. Within uncut mixedwood stands and those stands with dispersed cut, relatively more *T. crassiscapus* (1.42%), *Harpalus herbivagus* (Say) (0.98%), *S. impunctatus* (0.84%), *P. adstrictus* (0.69%) and *P. decentis* (0.51%) were collected in 2006 than in 2005.

The final splits of the ssMRT imply that the ground beetle assemblages are changing with time. However, at this point, we are unable to discern whether this reflects simple interannual variation or whether this reflects recovery or further diversion of assemblages in harvested stands.

4. Conclusions

Changes in control stand characteristics over the eight year period indicate that the even-aged aspen cohort of these stands was on the verge of breaking up. The canopy was opening up, and stand composition was moving towards softwood dominance. In this context, removing 40% and 50% of the basal area mostly accelerated stand break up, while recuperating what could be qualified as imminent mortality. Similar to what has been observed in natural stands following forest tent caterpillar outbreaks, partial harvesting promoted the establishment of a second cohort of aspen able to compete with the pre-established balsam fir regeneration. However, clear cutting was also beneficial to both aspen and balsam fir regeneration. The value of partial harvesting over clear cutting is evidently in the recruitment of large trees, snags and downed logs. How these residual structures are distributed is of consequence for stand succession and species diversity. Ground beetle assemblages and, to a lesser extent, deadwood dynamics and regeneration, responded to the distribution of residual stems. It is conceivable that gap and dispersed harvesting could push succession dynamics in two different directions, with dispersed cuts accelerating the transition to balsam fir and gap cuts retaining more aspen in the stand. Nonetheless, the study confirms that partial harvesting is an ecologically sound approach in aspen-dominated mixed stands and could contribute to maintaining the distribution of stand ages at the landscape level. As the region in which this study was undertaken was recently affected by a two to three year FTC outbreak, there exists an opportunity to compare mortality, recruitment and growth patterns following different intensities and configurations of partial harvesting with those patterns induced by tent caterpillar defoliation and to adapt partial cutting prescriptions to better reflect natural disturbance dynamics.

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Conflict of Interest

The authors declare no conflict of interest.

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