

Alternative Silvicultural Practices in Irregular Boreal Forests: Response of Beetle Assemblages

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In the process of implementing sustainable management in the eastern Canadian boreal forest, we tested two selection cutting methods and compared them with two widely used practices in the boreal forest: clearcutting with protection of the advanced growth and soils and irregular shelterwood cutting leaving small merchantable stems. We used old-growth irregular stands as references in comparing the impact of these silvicultural treatments on the diversity and abundance of beetles. Three groups were targeted: saproxylic flying beetles, epigeaic saproxylic beetles and epigeaic non-saproxylic beetles. A sampling design including 320 pitfall traps and 80 multidirectional flight-interception traps was deployed in 2007. A total of 26 906 beetles was captured including 407 taxa distributed among 52 families. We found that clearcutting with protection of the advanced growth and soils and irregular shelterwood cutting leaving small merchantable stems had a greater impact on beetle communities than both selection cuttings. Canopy opening as well as the presence of snags and downed woody debris appear as important attributes for several saproxylic and non-saproxylic species. Beetle communities in selection cuttings remained more similar to those found in controls; these silvicultural treatments are new tools to implement ecosystemic and sustainable management in irregular boreal forests.

Keywords biodiversity, old-growth forest, irregular stands, selection cutting, coarse woody debris, sustainable management

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1 Introduction

Until 1990's, Canadian forestry was mostly focused on timber production (CCFM 2003). However, the concept of sustainable management, which aims to meet the needs of the present without compromising the ability of future generations to meet their own needs (Brundtland 1987), has required changes. Sustainable management of forest ecosystems has been defined to preserve ecological functions as well as the ecological processes supporting these functions. Biodiversity conservation has been recognized as a central criterion in all international initiatives to evaluate progress toward forest sustainable management (Simberloff 1999, 2001, CCFM 2003). In boreal forests, impacts of harvesting on faunal and floral diversity are known to be mainly due to the loss and fragmentation of old-growth forests combined with alteration of structural components and natural processes of this ecosystem (Bonan and Shugart 1989). Some species associated with old-growth forests may not persist under intensive harvesting regimes (Niemelä 1997, Pohl et al. 2007), particularly rare species (Spence et al. 1996). Thus, adapting forestry practices in order to maintain species associated with old-growth forests appears to be a major challenge of modern forestry (Niemelä 1997). To develop sustainable forest management, new silvicultural treatments are thus needed (Haila 1994, Groot et al. 2005).

Over the last 20 years, the concept of ecosystem management has also attracted much attention across the scientific community (Attiwill 1994, Angelstam 1998, Bergeron et al. 1999). It has been presented as the best approach to maintain the natural processes that regulate forest ecosystem dynamics (Attiwill 1994, Niemelä 1999, Simberloff 1999, Gauthier et al. 2009). Forest ecosystem management is based on natural disturbance regimes and it aims to maintain ecosystems within their natural range of variability, based on the pre-industrial period. Thus, species should not be exposed to conditions that they have never faced before (Hunter 1990). Such an approach takes into account the forest at both the stand and landscape scales (Bergeron et al. 1999, Harvey et al. 2002, Ruel et al. 2007). At the stand scale, forestry practices should attempt to maintain key structural attributes that are generated under natu-

ral disturbance regimes such as snags and coarse woody debris (Niemelä 1997, Harvey et al. 2002, Bauhus et al. 2009). At the landscape scale, the size and distribution of forest harvesting patches should reproduce the spatial arrangement generated by natural disturbances in order to preserve enough suitable habitats for maintaining species with low dispersal ability that would be otherwise at risk (Jonsson et al. 2005).

The dynamics of natural disturbances are strongly influenced by climatic conditions, which vary widely among regions. In the province of Québec, Canada, the eastern boreal forest is dominated by old-growth stands, which are characterized by irregular structures and a strong component of balsam fir (*Abies balsamea* (L.)) (Boucher et al. 2003, Bouchard et al. 2008). This results from an increasing gradient of precipitation from western to eastern Québec that lengthens the fire cycle up to 200–300 years (Bergeron et al. 2004) and even over 500 years in the most easterly part of the region (Foster 1983), compared with the 100–200 year cycle in western Québec (Bouchard et al. 2008). Such long periods without fire allow stands to reach the senescent stage, where trees die and develop in an irregular and more diversified structure (McCarthy 2001, Pham et al. 2004, McCarthy and Weetman 2006). Disturbances like wind, insects and diseases play an important role in the dynamics of this forest (Boucher et al. 2003). In the North Shore region of eastern Québec, 70% of the unharvested forest is composed of old-growth stands of irregular or uneven-aged structure (Boucher et al. 2003). This structural complexity, at both the stand and landscape levels, plays a key role in maintaining biodiversity because complex structures generate a greater variety of habitats, compared with regular even-aged stands, and should therefore host more species of plants and animals (Hansen et al. 1991). A recent study indicates that a combination of both structural and compositional habitat heterogeneity maximizes beetle richness in old-growth stands of the North Shore region (Janssen et al. 2009).

Most species found in forest ecosystems are arthropods, mainly insects (Kim 1993). Nearly 30 000 insect species were recorded in Canada 20 yrs ago (Danks and Footit 1989) and they account for 65 to 70% of overall forest species richness (Langor and Spence 2006). Several studies have focused on beetles, which are known as

efficient indicators of habitat changes (Niemelä 1997, Martikainen et al. 1999, 2000, Langor and Spence 2006, Pohl et al. 2007). These studies were generally conducted to identify the links between different forest attributes and communities of particular groups, such as carabid beetles (Niemelä et al. 1996, Halaj et al. 2008) or saproxylic beetles (Jonsell et al. 2004, Gibb et al. 2006, Halaj et al. 2009).

In our study, we examined the influence of four silvicultural treatments in irregular stands of the eastern boreal forest: two types of selection cutting, clearcutting with protection of the advanced growth and soils (in French, “Coupe avec Protection de la Régénération et des Sols; hereinafter CPRS) and irregular shelterwood cutting leaving small merchantable stems (in French, “Coupe avec Protection des Petites Tiges Marchandes; hereinafter CPPTM). Old-growth stands were conserved as controls. We hypothesized that silvicultural treatments that maintain the structural heterogeneity at the stand level should make it possible to maintain species richness and

assemblages of beetles at a level similar to that of the old-growth irregular forest of this region. Specifically, our objectives were to determine if these alternative silvicultural practices maintain attributes and biodiversity of the natural old-growth irregular forest. We addressed this issue by studying three groups of beetles: 1) flying saproxylic beetles, 2) epigeaic saproxylic beetles and 3) epigeaic non-saproxylic beetles.

2 Materials and Methods

2.1 Study Area

The study was conducted in the North Shore region of Québec, Canada, which belongs to the eastern spruce-moss subdomain of the boreal forest. More specifically, the area was located in the Manicouagan reservoir sector, between the 49th and 52nd parallels (Fig. 1). The dominant tree species found in the area are black

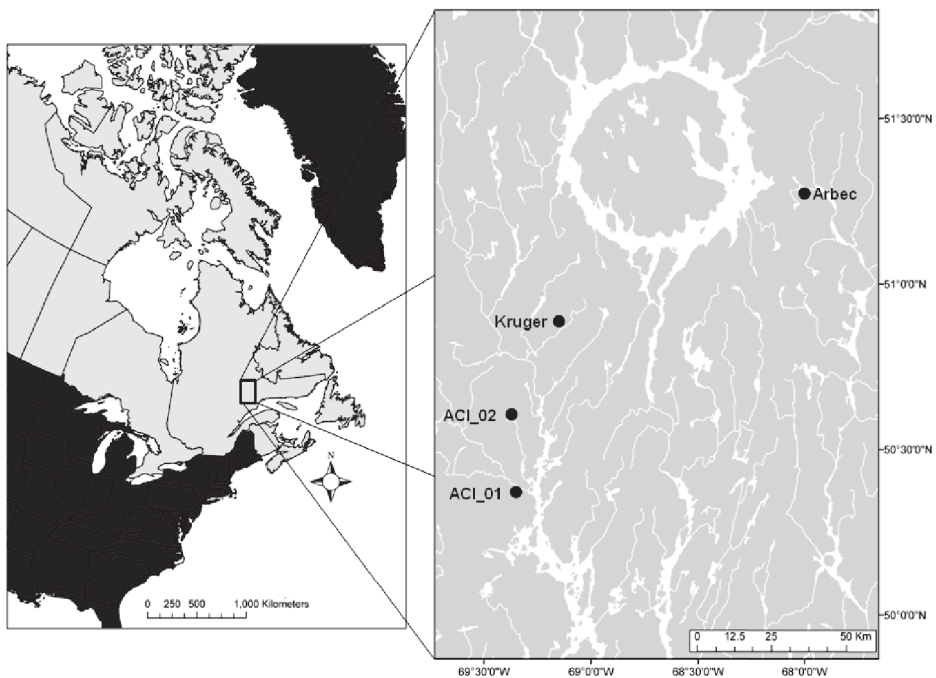


Fig. 1. Study area and distribution of experimental blocks in a forest matrix dominated by old-growth boreal forests in the North Shore region of Québec, Canada.

spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.).

2.2 Silvicultural Treatments and Experimental Design

Four 100 ha blocks were selected on territories managed by three forestry companies: Kruger (50°91'N, 69°17'W), Abitibi-Bowater (ACI_01 (50°38'N, 69°37'W) and ACI_02 (50°60'N, 69°37'W)) and Arbec (51°27'N, 67°99'W) (Fig. 1). These sectors had never been logged and were selected because of the presence of old-growth irregular stands that characterize the region. Blocks were established and harvested in 2004 (Kruger and ACI_01) and 2005 (Arbec and ACI_02). Each block contained a control and four silvicultural treatments, each applied on approximately 20 ha: CPRS, CPPTM and two types of selection cutting. CPRS is the most commonly used harvesting system in the boreal forest of Québec and it consists in harvesting all merchantable stems (diameter at breast height or DBH > 9 cm) while protecting the existing advanced regeneration (Groot et al. 2005). In the CPPTM treatment, trees with DBH ranging between 9 and 15 cm are left standing (Groot 2002), leading to harvesting 70 to 90% of the merchantable volume. This silvicultural treatment is currently used on an operational basis in irregular stands characterized by an abundance of small merchantable stems with an adequate crown ratio (Groot et al. 2005). The two selection cutting treatments were specifically designed to maintain the structure of irregular stands. The level of harvesting targeted for both of these treatments was similar but distributed in different spatial patterns. In the first one, an average of 43% of merchantable volume was harvested (Cimon-Morin 2009), skid trails were permanent, and trees were harvested across the entire stand area at the first entry (SCperm). Stems were selected on a single-tree basis, except in the secondary skid trails that provide access to the area located between primary skid trails. In the second type, an average of 44% of merchantable volume was also harvested (Cimon-Morin 2009) but skid trails were temporary (SCtemp)

and only half of the stand was treated at the first entry, leaving untouched strips for the next entry. Harvesting is thus more intensive in the treated parts at the first entry. Complete descriptions of these silvicultural treatments can be found in Ruel et al. (2007).

2.3 Insect Sampling

Four sampling plots located >100 m from each other and from the treatment edge were established in each experimental unit (treatment or control) (total of 80 plots). Beetles were collected from 5 June to 22 August 2007 with two types of traps: multidirectional flight-interception traps placed 0.5–1 m above ground for sampling flying beetles (Økland 1996) and pitfall traps (Multipher®; Jobin and Coulombe 1988) set into the ground for sampling epigeic beetles. Multidirectional flight-interception traps were built using four 15 cm × 40 cm panels (two made of mosquito net and two made of Plexiglas) mounted in a cross pattern, along a 10 cm diameter black ABS cylinder. Two funnels leading to collecting vials were located above and below the cylinder (Saint-Germain et al. 2004, Janssen et al. 2009). Pitfall traps were 10 cm diameter and screened with a wire mesh (10 mm × 10 mm) to reduce vertebrate captures. One multidirectional flight-interception trap and four pitfall traps were deployed in each plot, for a total of 80 multidirectional flight-interception traps and 320 pitfall traps. Inside an experimental unit, the position of the multidirectional flight-interception traps in plots varied among four positions, with each being used only once in each experimental unit. On each plot, the trap was randomly placed at 0 m, 5 m, 10 m or 15 m perpendicularly to the center of the skid trail. Pitfall traps were placed at 0 m, 5 m, 10 m and 15 m perpendicularly to the center of the skid trail in each plot. This setup allowed us to sample all conditions generated by the treatments and the same spatial layout of traps was used in controls, even in the absence of a skid trail. Samples were collected and pooled by experimental unit for further analyses.

A 40% ethanol solution with traces of household vinegar (5% acetic acid) was used as a killing and preserving agent in the traps. Traps

were serviced every 2 weeks and samples were sorted in the laboratory. Beetles were identified at the species (79%) or genus level (21%) according to resource availability. Identifications were cross-checked at the Canadian National Collection (CNC) of Insects, Arachnids and Nematodes (Ottawa, Canada) and at the René-Martineau Insectarium of the Laurentian Forestry Centre (Québec, Canada), where vouchers were also deposited.

2.4 Forest Structure and Composition

Four 400 m² plots were inventoried in each experimental unit. Plot form slightly differed, in order to represent the proportion of skid trails associated with each silvicultural treatment: CPRS, CPPTM and control (20 m × 20 m), SCperm (35 m × 11.43 m), SCTemp (30 m × 13.33 m). Although located within the same experimental units, plots used to characterize the treatments differed from those used for sampling insects in summer 2007. These plots were established and initially measured before harvesting and several were too close to treatment edges to ensure

an unbiased sampling of insects. However, the characterization data of the four plots of each experimental unit were pooled and expressed per hectare for further analyses (see Table 1).

To ensure that the same time elapsed after treatment, forest structure and composition was characterized in 2007 in two blocks (Kruger and ACI_01) and in 2008 for the two others (ACI_02 and Arbec). All merchantable stems (DBH ≥ 9 cm) were identified, their DBH was measured, and their vigor was estimated according to the Hunter (1990) classification (1 = healthy, 2 = moribund). Saplings (DBH ≤ 9 cm) were also inventoried in 100 m² circular sub-plots located at the center of each 400 m² plot; DBH, tree species and vigor of saplings were also recorded. The percentage of ground covered by ericaceous, latifoliate herbaceous, gramineous, sphagnum and mosses was estimated in nine sub-plots of 4 m² evenly distributed along the longitudinal axis of each 400 m² plot.

Volumes of coarse woody debris were estimated from inventories carried out during summer 2007 for downed dead wood (DDW) and during summer 2008 for snags. For DDW volume, only the northern quarter (100 m²) of each plot was

Table 1. Stand variables (average ± standard error) measured in the different silvicultural treatments applied in the old-growth boreal forest of the North-Shore region of Québec, Canada.

Variables	Treatment				
	Control	SCTemp.	SCperm.	CPPTM	CPRS
Basal area (m ² /ha)					
<i>P. mariana</i> ^{a)}	11.42 ± 2.41 a	7.47 ± 0.90 a	9.19 ± 2.68 a	0.84 ± 0.27 b	0.68 ± 0.16 b
<i>A. balsamea</i> ^{a)}	15.82 ± 2.49 a	9.86 ± 0.91 b	13.59 ± 0.75 a	4.25 ± 0.69 c	1.82 ± 0.34 d
<i>B. papyrifera</i> ^{a)}	0.37 ± 0.09 ab	0.46 ± 0.09 a	0.49 ± 0.18 a	0.15 ± 0.8 bc	0.10 ± 0.06 c
Total	27.61 ± 0.98 a	17.79 ± 0.54 c	23.27 ± 2.12 b	5.24 ± 0.68 d	2.59 ± 0.47 e
Ground cover (%)					
Mosses	75.85 ± 1.95	59.42 ± 4.24	67.07 ± 4.67	50.83 ± 8.73	58.38 ± 10.36
Sphagnum	9.85 ± 1.23	15.27 ± 2.97	6.78 ± 4.64	5.08 ± 3.57	5.18 ± 2.00
Ericaceous	5.31 ± 2.89	3.84 ± 1.20	3.92 ± 1.77	2.69 ± 1.31	7.88 ± 2.50
Gramineous	0.00 ± 0.00	1.36 ± 0.78	2.28 ± 1.62	1.15 ± 0.55	0.94 ± 0.42
Herbaceous	9.30 ± 4.61	10.06 ± 1.90	6.56 ± 2.97	11.81 ± 5.09	8.85 ± 3.28
Dead wood (m ³ /ha)					
Young DDW	46.45 ± 14.39	45.37 ± 16.03	44.01 ± 10.15	45.54 ± 9.10	34.06 ± 9.71
Old DDW	56.59 ± 9.92	45.36 ± 5.22	49.32 ± 11.34	72.67 ± 19.93	48.02 ± 14.43
Young Snags ^{a)}	26.52 ± 4.66 a	21.98 ± 4.03 a	19.37 ± 4.44 a	4.51 ± 0.47 b	3.10 ± 2.38 b
Old Snags	9.09 ± 3.92	3.02 ± 1.01	4.54 ± 1.22	3.79 ± 0.95	2.06 ± 0.96
Overall CWD	138.64 ± 23.64	115.74 ± 15.75	117.24 ± 21.57	118.21 ± 27.92	87.22 ± 19.38

^{a)} Letters represent statistical differences at $\alpha < 0.05$. Anova's were done on log-transformed values.

considered. All woody debris on the ground with a diameter >9 cm was taken into account. The length, diameter at both ends, tree species (when-ever possible) and decay class (1 to 5 according to Hunter 1990) were determined. The volume was calculated using the equation of a truncated cone. Snag volume was estimated from inventories in the 400 m² plots in which the diameter at stump height (DSH, i.e. 30 cm above root collar), DBH, height, tree species and decay class (3 to 7; Hunter 1990) of every merchantable tree (DBH ≥ 9 cm) were recorded. Snag volume was estimated from the combination of a truncated cone for the lower part (length = 1 m, surfaces calculated at DSH and DBH) and for the upper part, a cone with its base surface at DBH and extending to the top. If the main axis of the snag was broken, the upper part was estimated as a truncate cone with DBH as basal diameter and an upper diameter estimated from a mean stem taper calculated with the entire snag measurements.

2.5 Statistical Analysis

All beetle species were retained for analysis, except for scavenger beetles that were excluded because they were not considered to be linked with the different silvicultural treatments, but rather with the presence of decaying material, which occasionally accumulated in some traps. Even if their impact on beetle assemblages was minimal, singletons were retained in all analyses, except for multivariate analysis in which rarely caught species could mitigate obtained patterns. Otherwise, singletons may contain rare species that are the most susceptible to local extinction as a result of forestry practices (Siitonen and Martikainen 1994). As a result, the presence or absence of these species might be of great ecological significance.

One-way ANOVAs were used to compare, for each type of trap as well as for all traps combined, the overall species richness and the overall beetle abundance between treatments. In the same way, we independently tested the richness and abundance of flying saproxylic beetles, epigeaic saproxylic beetles and epigeaic non-saproxylic beetles. According to Speight (1989), saproxylic invertebrates are defined as species “that are

dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylic organisms”. Beetles considered to be facultative saproxylics (species that may be found in dead wood but which not depend on it) were also included in these analyses as they tend to use dead wood resources. We also compared the percentages of ground covered by ericaceous, latifoliate herbaceous, gramineous, sphagnum, mosses and exposed humus. Finally, we compared the volumes of recent and old downed dead wood (respectively Hunter classes 1 and 2, and 3 to 5), recent and old snags (respectively Hunter classes 3 and 4, and 5 to 7) and of the overall downed dead wood, snags or all coarse woody debris combined. The least significant difference (LSD) at $P=0.05$ was calculated to compare differences among the means for each significant ANOVA. Data were log-transformed ($\log x + 1$) to satisfy the normality and homogeneity of variance assumptions of ANOVA. Analyses were performed using GLM procedure on SAS version 9.1 (SAS Institute 2004).

Rarefaction curves were used to compare the rate at which species accumulate as a function of abundance in each silvicultural treatment (Magurran 2004). This statistical method allows us to estimate the number of species present in random subsamples of varying size drawn from the larger sample (Magurran 2004) and allows us to compare samples of different sizes. The shape of the curves, reaching or not an asymptote, also allows us to estimate if the sampling effort provides a complete picture of species assemblages among treatments. Rarefaction curves were calculated using Biodiversity Pro (McAleece et al. 1997).

Multivariate analyses were used to determine which environmental attributes were the most important in explaining variation in species assemblages among the treatments. Redundancy analysis (RDA) was conducted on Hellinger-transformed data using the Vegan package (Oksanen et al. 2009) on R version 2.8.1 (R-Development Core Team 2008). The Hellinger transformation minimizes the importance of double-zeros, thus reducing the weight of rare species (Legendre and Gallagher 2001). Only species with overall abundance ≥ 5 were included to minimize bias

that might result from tourist species that would have been caught while travelling in a particular treatment without being linked to it. Three RDAs (flying saproxylic beetles, epigeaic saproxylic beetles and epigeaic non-saproxylic beetles) were used to encompass the species associated with mature forests and those associated with open environments. Centroids were used to represent the geometrical center of experimental units of each treatment. Environmental variables used in RDAs were the mean basal area of black spruce and balsam fir, the mean percentage of ground covered by ericaceous, latifoliate herbaceous, gramineous, sphagnum and mosses, the volume (m^3/ha) of recent (classes 3 and 4; Hunter 1990) and old (classes 5 to 7; Hunter 1990) snags and the volume (m^3/ha) of recent (classes 1 and 2; Hunter 1990) and old (classes 3 to 5; Hunter 1990) downed dead wood.

To identify species positively associated with a treatment or a combination of treatments, we used the point-biserial group-equalized phi coefficient (Pearson correlation) as described by De Cáceres and Legendre (2009). The MULTIPATT procedure was used in the Indicspecies package (De Cáceres 2008) of R version 2.8.1 (R-Development Core Team 2008). Correlation coefficients take into account absences outside the target groups (in our case a treatment or a group of treatments) as well as presences in sites of that group. Taking absences into account contributes to increasing the power of the associations and makes this analysis more context dependent than indicator value indices for the determination of species-habitat associations (De Cáceres and Legendre 2009). Analyses were performed on all identified taxa.

3 Results

3.1 Overview

A total of 26 906 beetles belonging to 52 families and 407 taxa were identified; 285 taxa (14 344 individuals from 48 families) were captured in multidirectional flight-interception traps and 236 taxa (12 562 individuals from 36 families) in pitfall traps. Nearly 85% of the total abundance

was represented by seven families (Cryptophagidae, Curculionidae, Elateridae, Lathridiidae, Monotomidae, Nitidulidae and Staphylinidae). The SCtemp sites yielded the largest catches of beetles (28% of the overall), followed by the Control and SCperm sites (each 22%), and then by CPPTM (17%) and CPRS sites (11%). Overall, 27% of taxa caught were singletons and half were represented by fewer than five individuals; 21% of taxa were found in all silvicultural treatments. According to the available literature, 271 taxa (23 070 individuals) were considered to be saproxylic: 208 taxa (13 829 individuals) caught in multidirectional flight-interception traps and 142 taxa (9241 individuals) caught in pitfall traps. The other 126 taxa (2916 individuals) were non-saproxylic, consisting mainly of predators, fungivores, phytophages and bryophages (not associated with dead wood) that were mostly caught in pitfall traps. As previously mentioned, scavenger beetles were excluded from statistical analysis (920 individuals, 10 taxa).

3.2 Effects of Silvicultural Treatments on Forest Structure and Composition

As expected, total basal area was significantly higher in control, followed by selection cuttings, CPPTM and CPRS ($F_{4,12}=291.34$, $P<0.0001$) (Table 1). Significant differences were also found in the basal area of *P. mariana* ($F_{4,12}=31.92$, $P<0.0001$), *A. balsamea* ($F_{4,12}=61.54$, $P<0.0001$), and *B. papyrifera* ($F_{4,12}=3.89$, $P=0.03$) among treatments. For each tree species, the mean basal areas were similar in controls and selection cuttings (except for *A. balsamea* in SCtemp) but significantly lower in CPRS and CPPTM (Table 1). There were no significant differences among treatments for the percentage of ground covered by ericaceous ($F_{4,12}=0.57$, $P=0.69$), latifoliate herbaceous ($F_{4,12}=1.15$, $P=0.38$), gramineous ($F_{4,12}=1.18$, $P=0.37$), sphagnum ($F_{4,12}=2.04$, $P=0.15$), and mosses ($F_{4,12}=2.22$, $P=0.13$).

There were no significant differences between the overall amounts of DDW across treatments ($F_{4,12}=1.06$, $P=0.41$) (Fig. 2). Moreover, the volume of recent DDW ($F_{4,12}=0.64$, $P=0.65$) and old DDW ($F_{4,12}=0.81$, $P=0.54$) did not differ among treatments. However, total snag

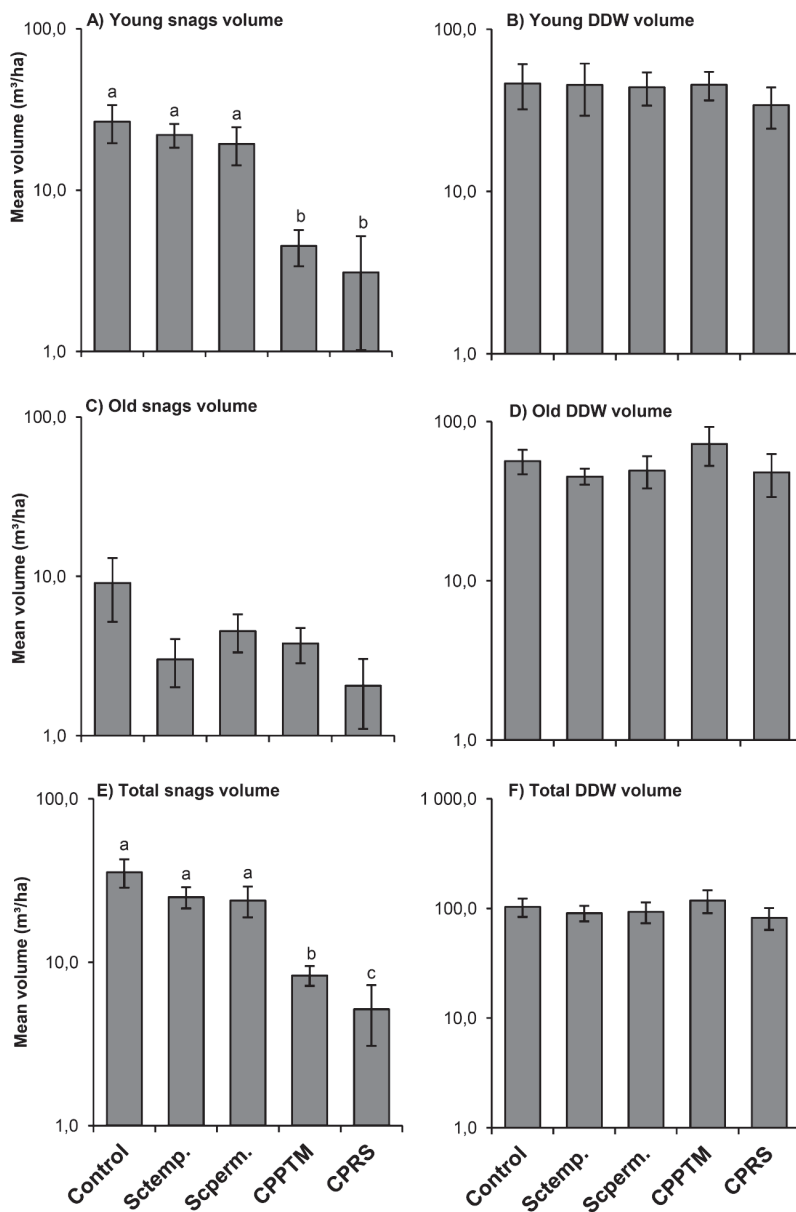


Fig. 2. Mean volume of young snags (A), young downed dead wood (DDW) (B), old snags (C), old DDW (D), total snags (E) and total DDW (F) in each treatment. Error bars represent standard error. Bars with different letters are significantly different at $\alpha < 0.05$. Anova's were done on log-transformed values.

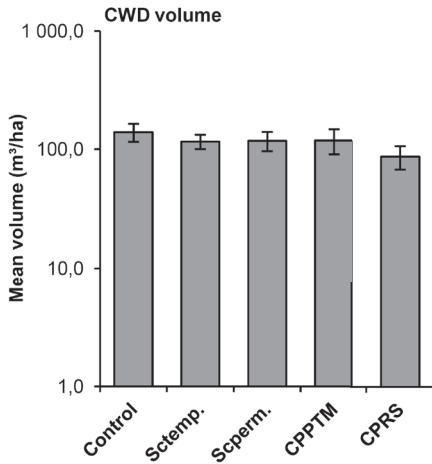


Fig. 3. Mean volume of coarse woody debris (CWD) in each treatment. Error bars represent standard error. Anova was done on log-transformed values.

volumes differed significantly among treatments ($F_{4,12}=33.33$, $P<0.0001$), with higher volumes being observed in controls and selection cuttings compared with CPPTM and CPRS. These differences were due to the number of recent snags that followed the same pattern ($F_{4,12}=14.58$, $P<0.0001$). No significant differences were observed in old snag volumes between treatments ($F_{4,12}=2.71$, $P=0.08$). Finally, the overall coarse woody debris volume (DDW and snags combined) did not differ significantly among treatments ($F_{4,12}=2.60$, $P=0.09$) (Fig. 3).

3.3 Abundance and Species Richness

The abundance of flying saproxylic beetles was significantly higher ($F_{4,12}=9.22$, $P=0.001$) in controls and selection cuttings than in CPPTM and CPRS but there were no significant differences in the species richness of this group among treatments ($F_{4,12}=2.60$, $P=0.09$) (Fig. 4). Abundance of epigeaic saproxylic beetles did not differ significantly among treatments ($F_{4,12}=2.60$, $P=0.09$) whereas species richness differed significantly ($F_{4,12}=4.06$, $P=0.03$). According to the least significant difference test, species richness was lower in CPRS and Control than in SCperm and CPPTM while SCtemp was only

significantly different from CPRS. Furthermore, no difference in epigeaic non-saproxylic beetle abundance was detected between treatments ($F_{4,12}=1.19$, $P=0.34$) although species richness was significantly lower ($F_{4,12}=7.88$, $P=0.002$) in Controls than in any other treatment. Moreover, species richness of epigeaic non-saproxylic beetles was significantly higher in CPRS than in SCtemp, which did not differ from SCperm and CPPTM. Finally, the model was not significant for the overall abundance of beetles ($F_{7,12}=2.69$, $P=0.06$) but Control showed a significantly lower ($F_{4,12}=5.08$, $P=0.01$) overall species richness than any silvicultural treatment.

Rarefaction curves indicate that the accumulation of species as a function of beetle abundance differed among treatments but showed the same pattern whether each type of trap was considered separately or not (Fig. 5). Beetle species richness increased slowly in old-growth forest (control), more rapidly in SCtemp and SCperm and reached its maximum rate in CPPTM and particularly CPRS. Rarefaction curves did not reach an asymptote in any treatment.

3.4 Beetle Assemblages and Environmental Attributes

The RDA ordination done on flying saproxylic beetles was significant ($F=1.65$, $p=0.04$, 999 permutations) with 49.7% of the variance being explained by the first two axes (Axis 1: 39.3%, Axis 2: 10.4%). The triplot showed centroids of closed forest habitats on the left (controls and selection cuttings) and centroids of open habitats on the right of the first axis. Closed habitats were related to vectors representing basal areas of *P. mariana* and *A. balsamea* and volumes of old and young snags (Fig. 6-A). The ericaceous vector was the most related to open habitats on the right of the first axis. The second axis was strongly linked to vectors of herbaceous plants, downed dead wood and old snags. The Monotomid *Rhizophagus dimidiatus* Mann. and the Nitidulid *Epureae planulata* Er. were closely associated with closed habitats while the Elaterid *Pseudanostirus triundulatus* (Rand.) was mostly found in open habitats.

The RDA done on epigeaic saproxylic beetles explained 40.5% of the overall variation, with

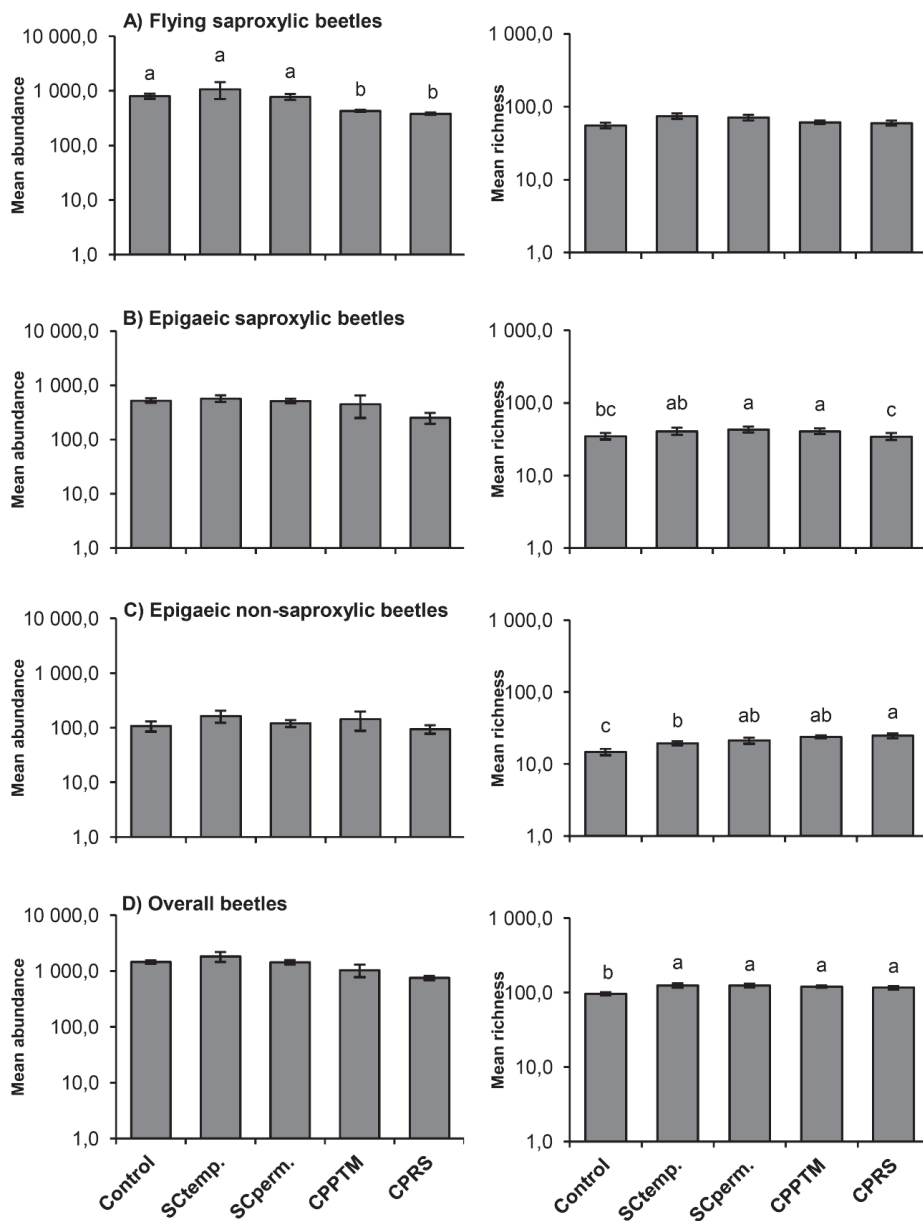


Fig. 4. Mean abundance (left) and richness (right) of flying saproxylic beetles (A), epigeaic saproxylic beetles (B), epigeaic non-saproxylic beetles (C) and overall beetles (D) in each treatment. Error bars represent standard error. Letters represent statistical differences among treatments at $\alpha < 0.05$. Anova's were done on log-transformed values.

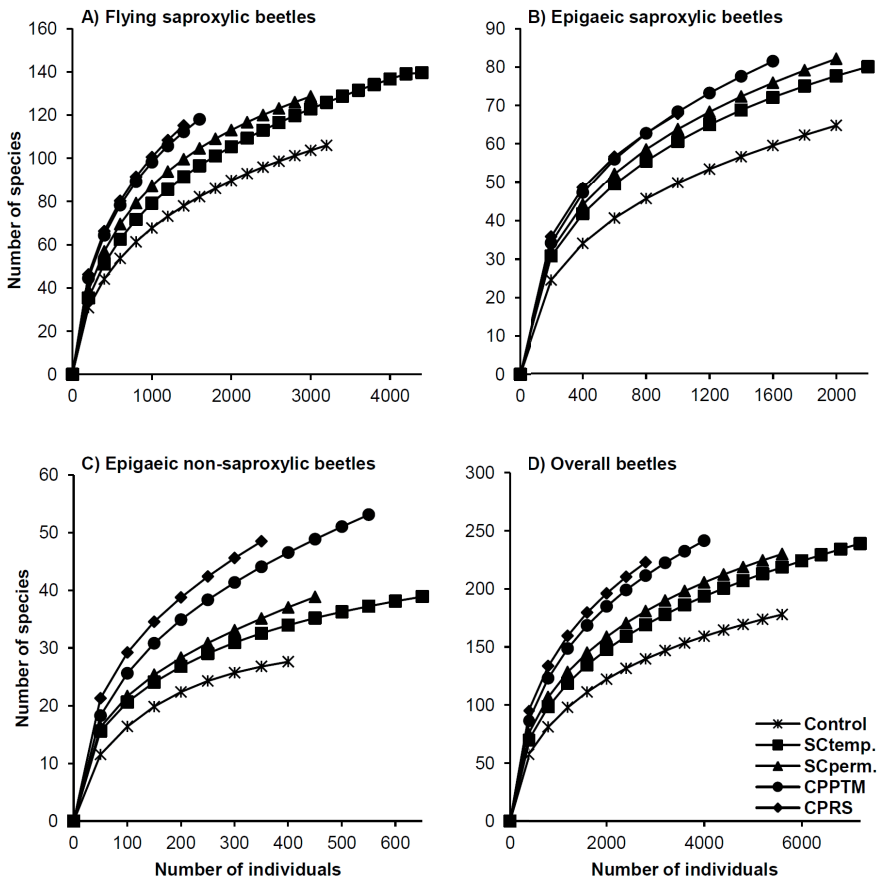


Fig. 5. Individual-based rarefaction curves for flying saproxylic beetles (A), epigaeic saproxylic beetles (B), epigaeic non-saproxylic beetles (C) and overall beetles (D) sampled across all treatments and in each stand type.

the first two axes explaining respectively 26.0% and 14.5% of the variance ($F=1.48$, $p=0.03$, 999 permutations). There was a canopy opening gradient from the bottom right of the triplot (Control), going through selection cuttings (near the center) and to the upper left (CPRS and CPPTM) (Fig. 6-B). All dead wood vectors were located in the lower portion of the triplot. Vectors related to closed habitats (snags, sphagnum, mosses, black spruce and balsam fir basal areas) were found on the right of the first axis while vectors representing attributes of open habitats (herbaceous, graminaceous, ericaceous) were located on the left of the first axis. Again, several species were associated with each type of habitat. The weevil *Hylobius congener* D. T., Sch. & Marsh. and the scolytid

Dryocoetes autographus (Ratz.) were closely linked to open habitats while the staphylinids *Proteinus* sp. and *Oxypoda grandipennis* (Casey) were related to closed habitats.

The last RDA ordination, on epigaeic non-saproxylic beetles, was significant ($F=1.52$, $p=0.02$, 999 permutations) and the first two axes explained 39.8% (axis 1 = 24.0%; axis 2 = 15.8%). Again, there was a clear gradient on the first axis from closed habitats on the left (along with vectors of basal areas of black spruce and balsam fir, sphagnum and moss coverage) to open habitats on the right with vectors of shrubs and lower plants (ericaceous, herbaceous, graminaceous). However, selection cutting centroids were near the CPPTM centroid but much closer to the

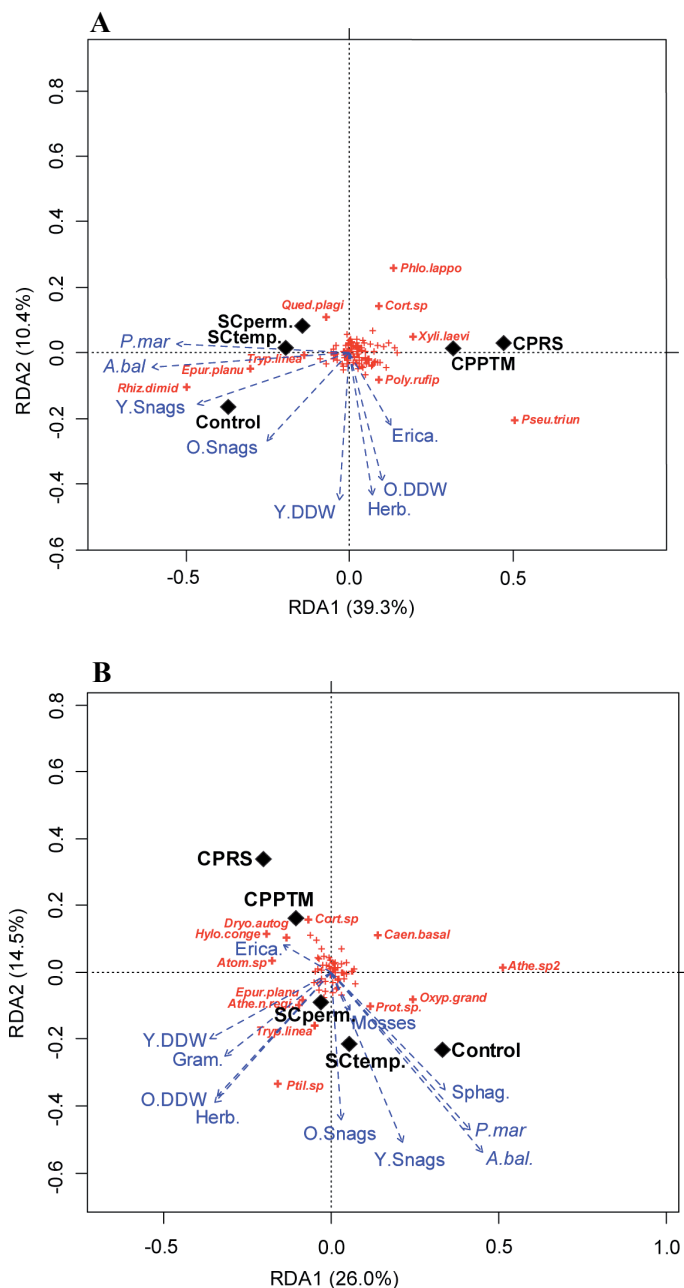


Fig. 6. RDA ordination of flying saproxylic beetles (A), epigeaic saproxylic beetles (B). Centroids of treatment are represented by a black rhombus. Species are marked with a red cross and the environmental variables with arrows. Only species clearly outside the cloud of species were identified. Label explanations: mean basal area (m^2/ha) of black spruce (P.mar) and balsam fir (A.bal); the mean percentage of ground covering ericaceous (Erica.), latifoliolate herbaceous (Herb.), sphagnum (Sphag.), (Mosses), the volume (m^3/ha) of young (Y.Snags) and old snags (O.Snags); the volume (m^3/ha) of young (Y.DDW) and old (O.DDW) downed dead wood.

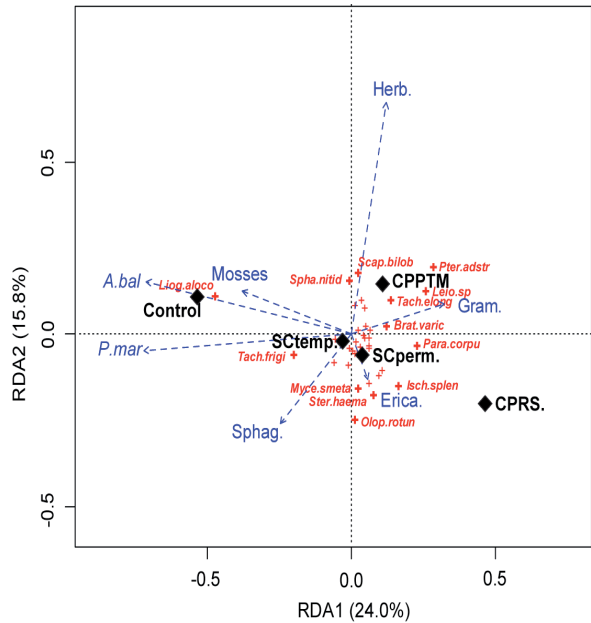


Fig. 7. RDA ordination of epigeaic non-saproxyllic beetles. Centroids of treatment are represented by a black rhombus. Species are marked with a red cross and the environmental variables with arrows. Only species clearly outside the cloud of species were identified. Label explanations: mean basal area (m^2/ha) of black spruce (P.mar) and balsam fir (A.bal); the mean percentage of ground covering ericaceous (Erica.), latifoliolate herbaceous (Herb.), gramineous (Gram.), sphagnum (Sphag.), (Mosses).

middle of the triplot (Fig. 7). Most epigeaic non-saproxyllic species were located to the right of the first axis mostly associated with open habitats. The staphylinids *Tachinus elongatus* Gyll. and *Ischnosoma splendidum* (Grav.) as well as the scydmaenid *Parascydmus corpusculus* (Casey) and the carabid *Pterostichus adstrictus* Esch. were associated with open habitats. Oppositely, the Staphylinids *Liogluta aloconotoides* Lohse and *Tachinus frigidus* Eric. were strongly correlated with the *A. balsamea* and moss vectors, characteristic of closed habitats.

3.5 Associated Species

The species-habitat associations analysis (Pearson's point-biserial correlation) revealed that 16

species were associated with Control, SCtemp, SCperm or combinations of these treatments which maintained $>50\%$ of the canopy and can be considered as closed habitats. The other 7 species were associated with CPRS or a combination of CPRS and CPPTM, which left $<20\%$ of the canopy and which can be considered as open habitats (Table 2). Of these 23 significantly associated species, 22 were saproxyllic beetles, with the other one being a non-saproxyllic predator. The three species associated with old-growth forests (control) were staphylinids, with the strongest association being found for *Oxypoda grandipennis* (Casey). Several species were associated with diverse combinations of selection cutting treatments and the control (closed habitats) but no species were simultaneously associated with closed habitats and open habitats. Five species

Table 2. Beetle species significantly associated ($P < 0.05$) with untreated stands (Control), with a particular silvicultural treatment or with a combination of treatments in the old-growth boreal forest of the Cote-Nord region in Quebec, Canada. Total catch refer to the number of individuals captured for each taxa across treatments and the Phi coefficient is the point-biserial group-equalized phi coefficient (Pearson correlation; see De Cáceres and Legendre 2009 for details) which is an estimate of the strength of an association.

Treatments	Family	Taxa	Number of individuals	Phi coefficient	p
Control	Staphylinidae	<i>Oxypoda grandipennis</i> (Casey)	150	0.781	0.003
	Staphylinidae	<i>Atheta strigulosa</i> Casey	16	0.716	0.024
	Staphylinidae	<i>Proteinus</i> sp.	308	0.669	0.012
SCtemp.	Anobiidae	<i>Xestobium gaspensis</i> R.E. White	16	0.673	0.041
	Staphylinidae	<i>Phloeopora</i> sp. Er.	13	0.666	0.043
SCperm.	Lathridiidae	<i>Corticaria</i> sp. Marsham	1612	0.720	0.010
Control + SCtemp.	Lathridiidae	<i>Corticaria gibbosa</i> (Hbst.)	16	0.718	0.015
Control + SCperm.	Scydmaenidae	<i>Stenichmus turbatus</i> (Casey) ^{a)}	84	0.730	0.010
SCtemp. + SCperm.	Scaptiidae	<i>Canifa pallipes</i> (Melsh.)	10	0.690	0.021
	Anobiidae	<i>Microbregma e. emarginatum</i> (Dufts.)	14	0.650	0.038
	Carabidae	<i>Platynus decentis</i> (Say)	9	0.637	0.039
Control + SCtemp. + SCperm.	Monotomidae	<i>Rhizophagus dimidiatus</i> Mann.	4649	0.797	0.002
	Nitidulidae	<i>Glischrochilus sanguinolentus</i> (Oliv.)	118	0.776	0.003
	Cryptophagidae	<i>Cryptophagus</i> sp.	61	0.753	0.010
	Nitidulidae	<i>Epureae planulata</i> Er.	3708	0.675	0.025
	Curculionidae	<i>Dryocoetes affaber</i> (Mann.)	170	0.614	0.040
CPRS	Cerambycidae	<i>Trachysida aspera brevifrons</i> (Howd.)	3	0.840	0.027
	Cucujidae	<i>Pediacus fuscus</i> Er.	17	0.795	0.007
	Staphylinidae	<i>Gyrophaena</i> sp.	13	0.742	0.017
	Salpingidae	<i>Sphaeristes virescens</i> LeC.	23	0.719	0.015
	Elateridae	<i>Ampedus prob. nigrinus</i> (Hbst.)	81	0.696	0.008
CPPTM + CPRS	Melandryidae	<i>Xylita laevigata</i> (Hell.)	90	0.709	0.017
	Elateridae	<i>Sericus incongruus</i> (LeC.)	26	0.706	0.018

^{a)} Non-saproxylitic beetle

CPRS: clearcutting with protection of the advanced growth and soils ; CPPTM: irregular shelterwood cutting leaving small merchantable stems; SCperm: selective cutting with permanent skid trails; SCtemp: selective cutting with temporary skid trails; Control: untreated stands.

were associated with the combination of the three closed habitats: *Rhizophagus dimidiatus* Mann. (Monotomidae), the most abundant species caught in the study, showed the strongest association. The species with the highest association with CPRS was *Trachysida aspera brevifrons* (Howd.) (Cerambycidae), a species caught on only 3 occasions but always in that treatment and in 3 out of the 4 replicates. No species were only associated with CPPTM while only two species were associated with the combination of CPPTM and CPRS.

4 Discussion

Our study showed that habitat modifications induced by different silvicultural practices in irregular boreal forests that had never been harvested previously influenced saproxylitic and non-saproxylitic beetle assemblages. All treatments increased overall species richness, compared with the old-growth stands (control), and modified beetle assemblages, particularly CPRS and CPPTM which induced the largest changes while

selection cuttings maintained assemblages similar to those found in old-growth stands. As CPRS and CPPTM are silvicultural treatments that severely open the canopy, they generate new ecological niches that could be colonized by open habitat species that are uncommon in closed canopy old-growth forests. Recent results obtained in the same experimental units also showed that selection cuttings maintained a similar stand structure, based on tree diameter distribution, to that found in controls while CPPTM and CPRS significantly differed (Cimon-Morin 2009). Meanwhile, the number of recent snags is reduced after CPRS and CPPTM, which is detrimental to several saproxylic species associated with this resource. The communities found after CPRS and CPPTM would be a mixture of ubiquitous species found in the original old-growth matrix, as well as open habitat species found in disturbed parts of the matrix resulting from windthrows or localized insect outbreaks. It is known that the irregular boreal forest of the North Shore area is regulated by gap dynamics that generate structural heterogeneity, characteristic of old-growth forests, and thus provide a higher diversity of habitats than even-aged stands (Kuuluvainen 2002, Pham et al. 2004).

Our results indicate that closed habitat associated species were much less abundant and in some extreme cases completely absent 2–3 years after CPRS or CPPTM. As observed previously for carabids and staphylinids (Niemelä et al. 1993, Spence et al. 1996, Pohl et al. 2007), low populations of old-growth forest specialists survive a few years after harvesting but they eventually disappear. Our results suggest that within 3 years after treatment, the decrease in abundance of closed habitat (control and selection cuttings) species was much faster than the increase in abundance of open habitat (CPRS and CPPTM) species. This may explain why overall species richness was similar among treatments while abundance was generally lower in open habitats. As shown by rarefaction curves, this resulted in a faster accumulation of species in open habitats than in closed ones. A good example is *Pseudanostirus triundulatus*, an elaterid species of the Canadian boreal forest that seems to be favoured by open habitats (Azeria et al. 2009) and which is also dominant in recently burned forests (Saint-Germain et al.

2004) colonized by ericaceous and herbaceous plants. In our study, it was the most abundant species in CPRS with 384 captures, which is much higher than the 62 specimens captured in controls (increasing ratio of 6.2). On the other hand, *Rhizophagus dimidiatus*, the most abundant species in controls with 1640 captures, was drastically less abundant in CPRS with only 111 individuals captured in this treatment (decreasing ratio of 14.8). To determine if old-growth forest specialists on the irregular boreal forest of the North Shore region will be maintained in harvested stands in the medium and long terms, future sampling will be necessary to document the ecological trajectory of species succession over time.

Several studies have shown the importance of coarse woody debris (CWD) for maintaining saproxylic beetle diversity (Økland 1996, Esseen et al. 1997, Niemelä 1997, Siitonen et al. 2000, Siitonen 2001, Jonsell and Weslien 2003, Gibb et al. 2006). Significant reductions in the amounts and the alteration of some properties (size, decaying stage and moisture) of CWD in managed forests have been associated with significant decreases in abundance and richness of saproxylic beetles (Martikainen et al. 1999, Siitonen 2001, McGeoch et al. 2007). Our results showed that flying and epigeic saproxylic beetle assemblages of old-growth stands were generally maintained, on a short-term, in both selection cutting treatments. The lower harvesting intensity (proportion of living trees removed) in these stands and the presence of recent snags allowed to maintain closed forest saproxylic species, while their abundance was significantly reduced in CPRS and CPPTM. The high dispersal capacity of adult flying beetles could have mitigated the response of this group at the stand level, explaining that there was no difference in species richness of flying saproxylic beetles among treatments. Recent results of Jansen et al. (2009) showed that the richness of flying beetles in irregular boreal forests was a function of both stand and landscape attributes. Adult flying saproxylic beetles may be attracted by warmer conditions in harvested stands or by the presence of flowering plants that are more abundant after canopy opening. Several beetle taxa, such as Lepturinae (Cerambycidae), Mordellidae and Melandryidae, are known to be floricolous (Arnett et al. 2002). This might also explain why seven

saproxylic species were clearly associated with open habitats, even if none were abundant. Two of these species, *Sphaeristes virescens* and *Sericus incongruus*, have been reported to be very abundant in recently burned forests (Saint-Germain et al. 2004), another type of open habitat. Azeria et al. (2009) also found them among a group of flying coleoptera associated with open habitats. Nevertheless, the most abundant saproxylic beetle caught in our study was *Rhizophagus dimidiatus*, a predator of bark beetles that was also associated with closed habitats (control and selection cuttings). Its abundance was lower after CPRS and CPPTM, practices that severely open the habitat and remove the recent snags on which this predator usually finds its prey. Other species of *Rhizophagus* have been reported to be associated with abundant coarse woody debris after disturbance in Europe (Bouget 2005). Interestingly, in our study, downed dead wood did not seem to be a key attribute for maintaining flying saproxylic beetle assemblages while snags seem to be of greater importance (Fig. 6-A). This is in agreement with previous studies that demonstrated the major role of snags for conservation of flying saproxylic species (Martikainen et al. 1999, Gibb et al. 2006, Jacobs et al. 2007).

Dead wood also influenced epigeaic saproxylic beetle assemblages, especially the species of the genus *Ptiliolum* (Ptiliidae) that were correlated with old CWD and old snag vectors. Most ptiliid species feed on the spores produced by the fruiting bodies of fungi (Arnett and Thomas 2001), which are often found on old dead wood. Even if the amount of old dead wood was similar among treatments, the quality of that resource may have been altered by the opening of the habitat following silvicultural treatments. Dead wood located in open habitats is more exposed to wind and sun, which may modify some characteristics of this resource, particularly its moisture content. In RDA triplots, if we consider mosses and sphagnum vectors as indicators of stand moisture, CPPTM and CPRS were clearly drier habitats. Moisture content has been shown to be related with the abundance of the saproxylic *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae) (Mitgaard et al. 1998). Jonsell et al. (2001) also reported that several saproxylic beetles living in polyporous fungi were found at

different height above ground, which is an indirect measure of microclimatic effects (temperature and moisture). Moisture also affects the substrate temperature, which influences the development of wood-decaying fungi on which feed saproxylic fauna (Jonsell and Weslien 2003). Therefore, in addition to the maintenance of appropriate amounts of dead wood, conservation of saproxylic beetle diversity must also involve the quality of dead wood. Of the 23 associated species found in our study, 22 were saproxylic beetles showing the essential role of dead wood attributes in irregular boreal forest.

Based on results arising from RDA (Fig. 7), a slightly different pattern was observed for assemblages of epigeaic non-saproxylic beetles because they were clearly favored by silvicultural treatments. Selection cuttings and CPPTM produced different assemblages but CPRS was the treatment that caused the largest changes. This suggests that this group takes advantage of forest openings but that the maintenance of a residual forest cover keeps some species associated with closed forests. Moreover, a less invasive treatment (SCtemp.) showed significantly fewer species than CPRS but more than the control. In fact, it appears that the increasing trend in species richness of epigeaic non-saproxylic beetles follows a gradient in canopy opening generated by the different silvicultural treatments (see Fig. 4c). In several boreal forest studies, forest harvesting decreased abundance and richness of epigeaic beetles, such as carabids and staphylinids (Buddle et al. 2006, Pohl et al. 2007, Halaj et al. 2008). Many species of these two families are considered as predators, notably *Pterostichus adstrictus* (Heliola et al. 2001, Cobb et al. 2007, Pohl et al. 2007), *Ischnosoma splendidum* and *Tachinus elongatus* (Pohl et al. 2007), and rapid colonizer species associated with open habitats. On the other hand, the two most abundant non-saproxylic species in our study, the staphylinids *Liogluta aloconotoides* and *Tachinus frigidus*, were strongly correlated with closed habitats in the RDA. The biology of *Liogluta aloconotoides* is unknown (Majka and Klimaszewski 2008) but *Tachinus frigidus* is known to be associated with balsam fir forests (Janssen et al. 2009) and decaying mushrooms (Pohl et al. 2007). Due to their lower mobility compared with flying beetles, responses of epi-

gaic beetles reflect variation in microhabitats at finer scales (Niemelä et al. 1996). This might be the case of the staphylinid *Oxypoda grandipennis*, an epigeaic saproxylic beetle for which we captured 150 individuals, 146 in closed habitats (109 in controls, 37 in selection cuttings) distributed over 23 different plots but only four individuals in CPPTM and none in CPRS. In another study on the North Shore region, this species has been found among a group of ground-dwelling beetles associated with closed-canopy balsam fir-white birch forests (Azeria et al. 2009). This species is widely distributed in Canada and has been found in different types of forest but it would be most abundant in unharvested stands (Klimaszewski et al. 2006). Therefore, even if it is obviously not a specialist of old-growth forests, it seems to be a good indicator of closed canopy forests.

5 Implications for Management

Our study showed that selection cuttings retaining >55% of the forest cover and better maintained beetle assemblages of the old-growth boreal forest than CPRS and CPPTM which retained <20% of the forest cover, at least on a short-term and at the stand level. This was a first step in assessing the usefulness of these alternative silvicultural practices and, as they fit into the concept of ecosystem management, they should be integrated into management plans in order to implement sustainable management in the irregular boreal forest of eastern Canada. Whether these assemblages will be maintained on a long-term and at the landscape level remains to be determined. We identified several indicator species to be associated with old-growth forests and/or with selection cuttings (referred as close-canopy forests) that should make it easier to monitor the impact of these silvicultural treatments on a long-term. Most of these indicator species were also found in groups associated with close-canopy forests in another study in the North Shore region (Azeria et al. 2009). This study showed that a set of 28 beetle indicators could predict as much as 80% of species richness among North Shore forest stands. Therefore, beetles are powerful indicators

and those identified in our study should also be useful to assess the usefulness of selection cuttings as tools to reduce landscape fragmentation and thus maintain biodiversity associated with old-growth forests.

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