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Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes

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ABSTRACT

Saproxylic Coleoptera are diverse insects that depend on dead wood in some or all of their life stages. In even-aged boreal forest management, remnant habitats left as strips and patches contain most of the dead wood available in managed landscapes and are expected to act as refuges for mature forest species during the regeneration phase. However, use of remnant habitats by the saproxylic fauna has rarely been investigated. Our objective was to characterize the saproxylic beetle assemblages using clearcuts and forest remnants in western Québec, Canada, and to explore the effects of forest remnant stand characteristics on saproxylic beetle assemblages. We sampled both beetle adults and larvae, using Lindgren funnels and snag dissection, in five habitat locations (clearcuts, forest interiors of large patches, edges of large patches, small patches and cut-block separators) from three distinct landscapes. Adult saproxylic beetles (all feeding guilds combined) had significantly higher species richness and catch rates in small patches compared to forest interiors of large patches; the phloeophagous/xylophagous group had significantly higher species richness only. Small patches, cut-block separators and edges of large patches also had the highest snag density and basal area, increasing habitat for many saproxylic beetles. No significant differences in density of saproxylic larvae were found between habitat patches, but snag dissection nevertheless suggests that snags in forest remnants are used by comparable densities of insects. Saproxylic beetles appear to readily use habitat remnants in even-aged managed landscapes suggesting that forest remnants can insure the local persistence of these species, at least in the timeframe investigated in our study.

1. Introduction

Dead wood is a fundamental component of forest ecosystems, providing habitat for diverse organisms, and playing a vital role in the regulation of nutrient and carbon cycling, erosion, drainage and geomorphic processes (Harmon et al., 1986; Speight, 1989; Grove, 2002). Saproxylic organisms are dependant on dead or dying wood during some part of their lifecycle (Speight, 1989). One of the most diverse orders of saproxylic insects is Coleoptera, with entire families dependant on dead wood, usually in the larval stage, while adults are often short-lived and play a reproductive and dispersive

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role (Haack and Slansky, 1987; Speight, 1989; Hanks, 1999; Saint-Germain et al., 2006). Phloeophagous and xylophagous beetles are a functional group of saproxylic beetles that are typically the first organisms to colonize, feed and breed in recently dead or weakened trees (Harmon et al., 1986; Speight, 1989; Hanks, 1999; Grove, 2002).

The majority of studies on saproxylic insects have been conducted in northern Europe's boreal forest, where centuries of intense forest management and harvest have created a significant reduction in coarse woody debris and species diversity of saproxylic insects (Speight, 1989; Siitonen and Martikainen, 1994; Martikainen, 2001; Siitonen, 2001; Grove, 2002; Martikainen and Kaila, 2004; Lindhe et al., 2005). The rich aspen-dependant (*Populus tremula* L.) saproxylic fauna in Europe contributes disproportionately to threatened species lists (Siitonen and Martikainen, 1994; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002) and has been found predominantly in clearcuts that contain sun-exposed aspen snags (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005). Few studies on aspen-dependant saproxylic beetles have been conducted in the eastern boreal forest of North America (but see Saint-Germain et al., 2006, 2007a, 2007b). In Canada's western boreal forest, Hammond (1997) and (Hammond et al., 2001, 2004) obtained high saproxylic beetle diversity associated with trembling aspen in closed forests. In North American boreal forests, trembling aspen (*Populus tremuloides* Michaux) remains abundant and is among the most ecologically and economically important deciduous boreal tree species (Hogg et al., 2002; Hammond et al., 2004). In Fennoscandia, the aspen component of the boreal forest has been suppressed or eliminated due to low commercial value compared to conifers, disrupting the continuity of substrate for many saproxylic organisms (Siitonen and Martikainen, 1994).

It is therefore necessary and important to study the effects of forest harvest and management on saproxylic fauna to prevent their declines in North America's boreal forest. Patches of remnant forest left after clearcutting may create refuges for species not able to survive in harvested areas and may enhance population exchange between source forest areas and habitat remnants during the stand regeneration phase (Saunders et al., 1991). To our knowledge, there have been no published studies on the use of remnant forest patches by saproxylic beetles.

Increasing levels of 'green-tree retention' in coniferous stands in Finland, was found to promote species richness of red-listed and threatened saproxylic beetles in both burned and clearcut sites (Hyvärinen et al., 2006). In even-aged clearcut landscapes, cut-block separators are linear habitat remnants that can potentially function as corridors, directing insects to connecting large patches of uncut forest, which has been demonstrated with flies (Fried et al., 2005) and boreal forest moths (Mönkkönen and Mutanen, 2003). In Australia, Driscoll and Weir (2005) demonstrated that the greatest species richness of carabid, scarabid and tenebrionid beetles occurred in remnant mallee (*Eucalyptus* spp.) linear habitats in landscapes fragmented by grazed land and roads. In Tasmania, native linear forest remnants retained between plantations had similar Carabidae species richness as continuous native forest sites, but had intermediate species composition to that of plantation and native forest (Grove and Yaxley, 2005).

This study explores how habitat patches in this even-aged managed landscape are used by saproxylic beetles and how the forest mosaic affects beetle assemblages. The first objective of our study is to test if remnant forest patches within clearcuts (small remnant patches and cut-block separators) are used by saproxylic (all feeding guilds combined) and phloeophagous/xylophagous adult beetles and larvae in aspen-dominated stands in Canada's eastern boreal forest. The second objective is to determine what stand characteristics explain the distribution of saproxylic and phloeophagous/xylophagous beetles in this landscape.

2. Materials and methods

2.1. *Site description*

This study was conducted in the southern mixedwood boreal forest in the Abitibi region of northwestern Québec. Three geographically distinct sites were used for the study: Duparquet (48°28–29′N, 79°24–26′W), Magusi (48°23–29′N, 79°23–28′W) and Clericy (48°25′N, 78°33–35′W) (Fig. 1). Sites were pre-selected using digital cover maps (SIEF, 2002). Three landscapes of mixedwood composition, with uneven-aged stands, fragmented by clearcuts of 5–10 years of age and containing habitat patches of interest (cut-block separators, small and large remnant forest patches) were selected. Magusi is located approximately 10 km from Duparquet, and Clericy is located approximately 50 km from Magusi, Although located closer together, Duparquet and Magusi are considered independent landscapes.

At Duparquet, forests were dominated by trembling aspen (*P. tremuloides*) (31% of stems >10 cm DBH) and white birch (*Betula papyrifera* Marshall) (32%), and, in less abundance, white and black spruce (*Picea glauca* (Moench), *Picea mariana* (Miller)) (19%), balsam fir (*Abies balsamea* (L.)) (12%), balsam poplar (*Populus balsamifera* L.) (4%) and jack pine (*Pinus banksiana* Lambert) (2%). At Magusi, forests were composed of trem-

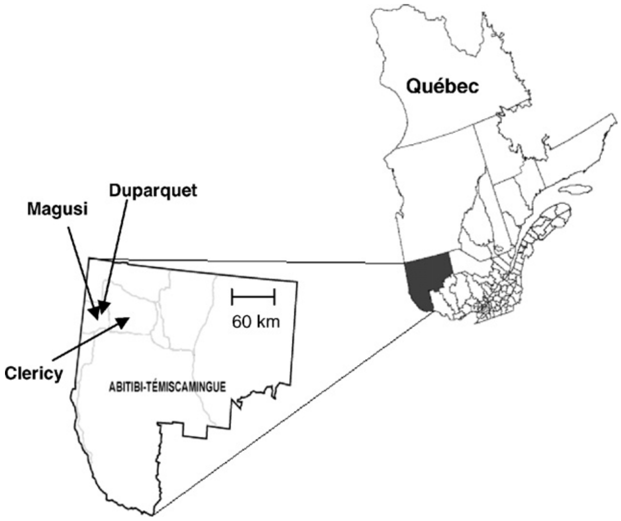

Fig. 1 – Location of sampling sites in the region of Abitibi-Témiscamingue, in the province of Québec, Canada.

bling aspen (54%), white and black spruce (17%), white birch (12%), balsam fir (9%) and jack pine (8%). At Clericy, forests were composed of white and black spruce (49%), trembling aspen (25%), balsam fir (23%), white birch (2%) and jack pine (1%).

2.2. *Sampling adult beetles with Lindgren funnels*

Lindgren funnel traps were used to capture adult saproxylic beetles and consisted of eight stacked black funnels that provide a long dark silhouette that mimics a tree or a snag (Lindgren, 1983). Lindgren funnels were installed 4–7 June 2005, removed 5–8 August 2005 and emptied every 2 weeks for a total of four sampling dates. The collection jar contained propylene glycol diluted with 50% water as a preservative. Lindgren funnels were baited with ethanol to increase saproxylic captures (Phero Tech Inc., Delta, British Columbia, Canada). Numerous studies have shown that saproxylic wood-feeders strongly respond to the ethanol emitted from decomposing deciduous trees (Allison et al., 2004).

There were three replicates of each habitat patch in each of the three sites (nine total treatment replicates per habitat patch). The selected habitat patches included the following: clearcuts of 5–10 years since harvest (clearcut area: Duparquet: 1.6–4.81 ha; Magusi: 25–29 ha; Clericy: 14–37 ha); 40–60 m wide cut-block separators that were connected to large patches; large patches of forest were greater than 80 ha; small remnant forest patches that were under 1 ha in area. Edges of large patches were sampled at approximately 20 m from the edge and interiors were sampled in the approximate center of the patch, situated at least 200 m from the edge. One Lindgren funnel was placed per habitat patch, except large patches where two Lindgren funnels were used (edge and interior), for a total of 15 Lindgren funnel traps per site. Beetles were sorted from the bulk samples and preserved in 70% ethanol.

2.3. *Sampling larvae by snag dissection*

To investigate actual use of remnant habitats by xylophagous and phloeophagous beetle larvae, 45 snags were cut down on 15 August 2005 and dissected, in Magusi only. As only larvae were targeted in this part of the study, sampling was done at the end of the summer because larger larvae are more easily identified then. The snags were taken from the same patches where the Lindgren funnels were installed. Five snags were cut from each habitat patch, which included cut-block separators, small patches and large patches, and replicated three times. Aspen snags were not present in clearcuts and this habitat patch was omitted from the experimental design. Following a transect along the edge of a large patch (approximately 20–30 m from the edge), snags were selected haphazardly until five snags of adequate quality and diameter were selected per patch. The majority of snags could be found on the patch-edge and due to physical constraints could not be carried long distances out of the interior of the patch. Snags of early–mid decay (Hammond et al., 2004; Lee et al., 1997) with standardized external characteristics (no twigs, 100% bark but slightly loose, treetop windblown) and diameter ranging from 14 to 49 cm were selected because the phloeophagous and xylophagous beetles are the earliest colonizers and old aspen snags were very rare, especially in small patches. Snags were cut from approximately 25 cm from the ground to 100 cm in height on the bole. Boles measuring 75 cm in length were debarked and larval beetle specimens were collected. Subsequently, 50 cm of the debarked logs was carefully dissected for larvae collection. The dissection consisted of cutting cross-sections of the boles with a chainsaw and using an axe to cut them into increasingly smaller pieces, removing the larvae from the galleries with forceps. Larvae were boiled in water for approximately 1 min and then placed in 70% ethanol for identification.

2.4. *Stand characteristics*

A 400 m^2 quadrat was created around each Lindgren funnel trap. Direction of quadrats was standardized by creating one north–south and one west–south transect, positioned in the middle of each side of the square. Intersecting these two transects, fallen dead logs and stumps (>5 cm diameter) were counted and diameter measured. A measure of relative log volume in a stand was calculated from these data using Harmon et al. (1986). Along the north–south transect inside the quadrat, shrubs and small understory trees that were touching the transect set at 1 m above ground were counted as either deciduous or coniferous as a measure of density. In addition, shrub density was estimated qualitatively using density classes, which were based on relative densities between habitat patches (0 = open, 1 = low density, 2 = medium, 3 = high, 4 = very high density).

Within each quadrat, all live and dead standing trees were counted and characterized according to species and diameter at breast height (DBH >10 cm). Snag decay stage (early, mid, late) was estimated using external characteristics but these data could not be used due to the small sample size and high variance within and between habitat patches. Using a digital camera with an attached fish-eye lens, two hemispherical photographs were taken at each Lindgren funnel from about 1.5 m in height. The pictures were analyzed to obtain percent canopy openness with the software Gap Light Analyzer v. 2.0 (GLA, 1999).

2.5. *Beetle identifications*

All adult saproxylic beetles were identified to species or morphospecies (except for Staphylinidae). Phloeophagous and xylophagous beetles were analyzed separately, from total saproxylic Coleoptera, because this diverse functional group of large saproxylic beetles are most directly associated with dead wood and more taxonomic information and expertise can be obtained on species in this guild. Families that were considered part of the phloeophagous and xylophagous guild included Anobiidae, Cerambycidae, Curculionidae (including Scolytinae), Scarabaeidae, Lucanidae, Cephaloidae, Eucnemididae, Mordellidae, Pyrochroidae, Scraptiidae, Melandryidae, Alleculidae and Tenebrionidae.

Adult beetle specimens were either verified by S. Laplante, Y. Bousquet and/or cross-checked at the CNC (Canadian National Collection of insects, arachnids and nematodes, Ottawa, Canada). Cerambycid larvae were identified to species and phloeophagous/xylophagous larvae were identified to family. Larvae were verified by M. Saint-Germain and by Dr. V. Grebennikov (CNC). Adult beetle vouchers are deposited at McGill University's Lyman Entomological Museum (Ste Anne de Bellevue, Québec, Canada) and larvae vouchers are deposited at the CNC.

2.6. Analyses

2.6.1. Saproxylic beetle habitat-use

For each Lindgren funnel trap, samples from all sampling dates were pooled for analyses. Using SAS (Statistical Analysis Software, 2001), one-way ANOVA or Kruskal–Wallis tests were used to assess effect of habitat patches (small patch, cut-block separator, clearcut, large patch-edge and large patch-interior) on catch rate (number of individuals captured per habitat patch) and raw species richness (the number of species per habitat patch) of saproxylic and phloeophagous/xylophagous beetles. Normality and homogeneity of datasets was confirmed using a Shapiro–Wilk test and a Levene's test. Tukey's H.S.D. test ($\alpha = 0.05$) used for post-hoc comparisons of means follow ANOVA significant results. Post-hoc comparisons for Kruskal–Wallis tests were conducted using the Mann–Whitney test for pairwise comparisons. The probabilities for each pair were corrected using a Bonferroni adjustment.

Sample-based rarefaction, using the software *EstimateS* (Colwell, 2004), was used to compare species richness between habitat patches based on sampling effort (Gotelli and Colwell, 2001; Buddle et al., 2005). Rarefaction shows the rate of accumulation of new species as new samples are added, thereby verifying that enough samples have been collected to make accurate species richness comparisons (Gotelli and Colwell, 2001; Buddle et al., 2005). Sample-based was chosen over individual-based rarefaction because the samples were properly replicated with comparable sampling effort per habitat patch and there were no disturbed traps (Buddle et al., 2005).

Indicator species analysis was performed using PC-ORD v. 4.17 (McCune et al., 1999) to determine species with particular affinities for certain habitat patches. Each species is assigned an indicator value (I.V.), which is the percent of perfect indication based on combining the values for catch rate (average catch rate of a species in a habitat patch over the average catch rate of that species in all habitat patches) and relative frequency. A probability was assigned to each indicator value using a Monte Carlo test of 1000 permutations.

2.6.2. Saproxylic beetle responses to stand characteristics

Canonical correspondence analysis (CCA) (direct gradient analysis) was used to link possible measured explanatory variables in each habitat patch to the species data, using the software PC-ORD (McCune et al., 1999). CCA constrains a species matrix to an environmental matrix by multiple linear regressions. A Monte Carlo test (99 runs) was used to assess significance of the axes with the null hypothesis being there is no relationship between the species and environmental matrix. Forty-four samples with 186 species were used in this analysis, instead of 45 samples with 188 species, because it was not possible to collect stand characteristics from one habitat patch. The following stand characteristics were included in the environmental matrix: Deciduous tree density, coniferous tree density, snag density snag basal area, deciduous tree basal area, deciduous snag density, coniferous snag density, deciduous shrub density, coniferous shrub density, shrub density class, log volume and percent canopy openness (see Table 3). The final ordination plot was graphed using LC scores, which are fitted values of multiple regression with constraining predictor variables (as opposed to WA scores: weighted averages of species scores.).

The previous analysis on stand characteristics was supplemented with ANOVA or Kruskal–Wallis tests on the same stand characteristics by habitat patch followed by Tukey post-hoc test or a Bonferonni adjusted Mann–Whitney test.

2.6.3. Phloeophagous and xylophagous beetle aspen host-use

Kruskal–Wallis tests were used to determine effects of habitat patches on phloeophagous and xylophagous larval density and Cerambycidae larval density collected from snag dissections (Statistical Analysis Software, 2001). The proportion of snags in each habitat patch with phloeophagous/xylophagous and Cerambycidae larvae present was also tested with a Kruskal–Wallis test. Differences between beetle fauna caught using Lindgren funnels and snag dissections in the same habitat patches of the Magusi site were analyzed qualitatively.

3. Results

A total of 6620 adult saproxylic beetles, representing 188 species, was trapped in the 45 Lindgren funnels (Table 1). The most species-rich saproxylic beetle guild collected was the phloeophagous and xylophagous beetles, and the most abundant guild was the mycetophagous beetles (Table 1). The phloeophagous and xylophagous beetle guild had the lowest catch rate after the aquatic saproxylic beetles, which live and feed in water filled cavities of logs and snags as larva.

The most commonly collected species or morphospecies in Lindgren funnels were: *Melanophthalma* sp. 1 (Lathridiidae) (47.14% of the total number of individuals collected), *Glishrochilus siepmanni* W.J. Brown (9.94%) (Nitidulidae), *Triplax dissimulator* (Crotch) (Erotylidae) (3.85%), *Glishrochilus sanguinolentus* (Olivier) (3.41%) (Nitidulidae) and *Cerylon* sp. 1 (Cerylonidae) (3.35%). Other commonly collected beetles were those of the

Table 1 – Saproxylic beetle catch rate and raw species richness by larval feeding guild from 45 Lindgren funnels collected from habitat patches (small patch, cut-block separator, clearcut, large patch-edge, large patch-interior) of mixedwood boreal forest (*n* = 9)

Guild	Catch rate	Raw species richness
Phloeophagous/xylophagous	710	82
Mycetophagous	5069	54
Zoophagous	812	48
Aquatic[a]	29	4
Total	6620	188

[a] These species feed in water filled cavities of logs and snags as larvae.

closely related genera *Enicmus* and *Lathridius* spp. (Lathridiidae) (2.79%), *Mordella* sp. 1 (Mordellidae) (2.39%), and *Ampedus* sp. 1 (Elateridae) (2.30%).

Twelve species occurred only in one of the five forest patches more than once. However all were doubletons and tripletons, with the exception of the tenebrionid, *Upis ceramboides* (L.), which was captured eight times in Lindgren funnels placed in clearcuts.

3.1. *Saproxylic beetle habitat-use*

Significantly more saproxylic beetles were collected in habitat remnants (e.g., cut-block separators and small patches) compared to the interior of large patches (Table 2). As well, significantly more saproxylic beetle species were collected in cut-block separators than in interiors of large patches. For phloeophagous and xylophagous beetles, effect of habitat patch was non-significant for catch rate, despite greater numbers captured in clearcuts and cut-block separators than in other treatments. Significantly more species of phloeophagous and xylophagous beetles were collected in small patches than in interior of large patches.

Site effects were non-significant in ANOVA tests for saproxylic beetle catch rate (square root transformed data, $p = 0.19$; $F_{2,42} = 1.74$; means ± S.E.: Duparquet = 11.27 ± 0.56; Magusi = 12.9 ± 0.71; Clericy = 11.20 ± 0.88). For phloeophagous and xylophagous beetle catch rate, site effects were marginally significant (square root transformed data, $p = 0.04$; $F_{2,42} = 3.48$; means ± S.E.: Duparquet = 4.11 ± 0.33; Magusi = 4.11 ± 0.33; Clericy = 3.22 ± 0.30); however, the Tukey H.S.D. test did not detect significant differences between sites. Rarefaction curves showing the effect of site on species accumulation rate produced overlapping curves, suggesting no site effects on rarified species richness (data not shown). An NMS ordination demonstrated no clear patterns of species composition for sites (data not shown). Due to the lack of site effects on beetle catch rate, species richness and composition, analyses will focus on effects of habitat patches. Interactions between site and effects of habitat patches were explored but no clear patterns were detected.

As clearcuts differed in size, four separate linear regressions were performed to examine the relationships between clearcut size and catch of saproxylic beetles, catch of phloeophagous/xylophagous beetles, and saproxylic and phloeophagous/xylophagous beetle species richness. None of the regressions were significant.

The rarefaction curves (Fig. 2a) confirm the results found for saproxylic beetle raw species richness (Table 2). However, some caution is advised for the interpretation of these results as the rarefaction curves do not reach an asymptote, which suggests species remain to be captured with this sampling effort. At sample effort of nine traps per habitat patch, more saproxylic beetle species were caught in cut-block separators and small patches than in the interior of large patches (Fig. 2a). The rarefaction curve for phloeophagous and xylophagous beetles (Fig. 2b) also confirms patterns observed with raw species richness, where small patches and cut-block separators have higher species richness than interior of large patches.

Two indicator species with indicator values (I.V.) >50 were detected: *T. dissimulator* occurred largely in small patches (mean: 27.4 ± 7.43; I.V. 50.2, $p < 0.05$); and *Ampedus pullus* Germar (Elateridae) occurred dominantly in clearcuts (mean: 18.8 ± 7.94; I.V. 54.7, $p < 0.001$).

3.2. *Saproxylic beetle response to stand characteristics*

Table 3 details stand characteristic data averaged by habitat patch (nine replicates per habitat patch); these data were analyzed using CCA ordination and ANOVA. The CCA ordination only explained 12.1% of the total variance in the community data and only axis 1 ($p = 0.02$; Monte Carlo test) was found to be significantly different than could have been obtained by chance. Log-transformations, presence/absence, exclusion of rare species (i.e. singletons; singletons and doubletons) and analyzing the phloeophagous/xylophagous group separately were also attempted with no new pattern revealed or higher variance explained. Variables with intraset correlations of greater than 0.5 or smaller than −0.5 (on axis 1 or 2) were graphed (Fig. 3, Table 4). No clear species patterns result from

Table 2 – Results from one-way ANOVA and Kruskal–Wallis tests for the effects of habitat patches (small patch, cut-block separator, clearcut, large patch-edge, large patch-interior) on saproxylic beetle and phloeophagous/xylophagous beetle catch rate and raw species richness

	Habitat patch						
	Small patch	Cut-block separator	Clearcut	Large patch-edge	Large patch-interior	$F_{4,40}$ or $\chi^2_{4,40}$	*p* value
Mean saproxylic catch rate†	13.08 ± 0.82a	13.45 ± 0.85a	12.24 ± 0.87ab	10.95 ± 0.77ab	9.24 ± 0.92b	4.11	0.01
Mean saproxylic species richness*	29.67 ± 2.38ab	33.11 ± 1.06a	28.89 ± 3.42ab	25.11 ± 2.69ab	20.78 ± 1.71b	12.28	0.02
Mean phloephagpus/ xylophagous catch rate*	16.22 ± 1.91	19.44 ± 2.29	20.56 ± 5.57	13.00 ± 1.55	9.67 ± 1.85	8.47	0.08
Mean phloeophagous/ xylophagous species richness*	10.89 ± 1.05a	8.67 ± 0.97ab	8.22 ± 1.40ab	6.89 ± 0.92ab	5.11 ± 0.54b	14.59	0.01

Data are presented as means ($n = 9$) (±S.E.). Post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test ($\alpha < 0.05$). For Kruskal–Wallis tests, post-hoc tests are Bonferroni adjusted pairwise comparisons using the Mann–Whitney test.

* Kruskal–Wallis test.

† Square-root transformed data.

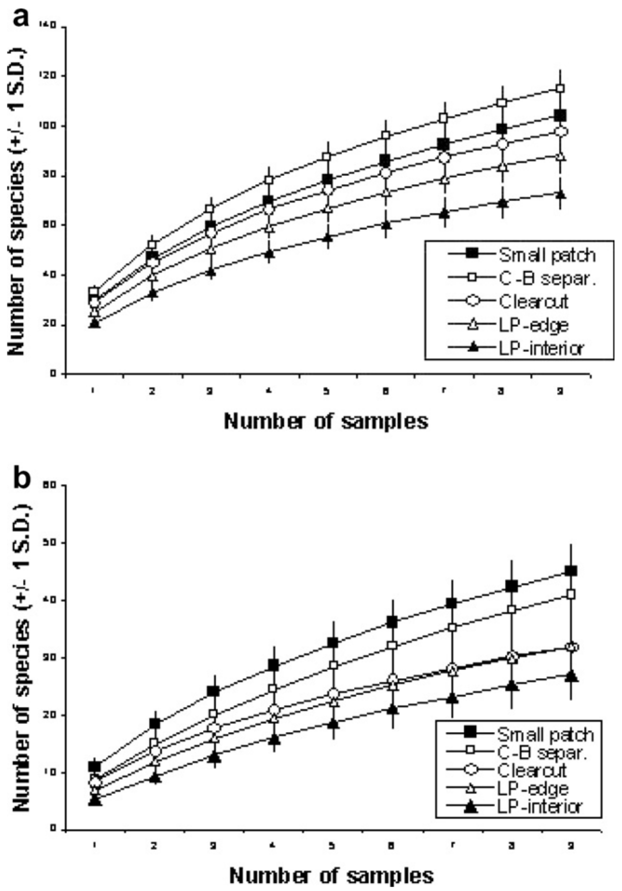

Fig. 2 – Sample-based rarefaction estimates (±1 S.D.) for number of saproxylic beetle species (188 species) (a) and phloeophagous/xylophagous species (53 species) (b) in habitat patches (small patch, cut-block separator, clearcut, large patch-edge, large patch-interior) using nine samples per habitat patch.

the CCA ordination, although cut-block separators, small patches and large patches appear to be loosely grouped away from clearcuts with some overlap. The interior of large patches have higher trap-to-trap variance than other habitat patches.

Coniferous tree and shrub density appear important in structuring beetle assemblages in large patches, small patches and cut-block separators. Deciduous shrub density, shrub density class and percent canopy openness vectors are associated with beetle communities in clearcuts while coniferous trees are negatively linked with beetle communities in clearcut areas. ANOVA results on stand characteristics by habitat patch explain these patterns further (Table 5). As expected, clearcuts have significantly more open canopy and lowest deciduous tree density, compared to other habitat patches. Small patches have the highest coniferous tree density and are significantly different from clearcuts. Small patches and cut-block separators have the highest snag density and snag basal area and are significantly different from clearcuts. Interior of large patches have the fewest snags after clearcuts; however, interior of large patches have the highest coniferous snag density, which is significantly different from clearcuts. In CCA, coniferous snag density had an intraset correlation that was close to the 0.5 cut-off for axis 1 but may still be ecologically important in explaining species variation.

3.3. *Phloeophagous and xylophagous beetle aspen host-use*

A total of 488 phloeophagous and xylophagous larvae, from families Cerambycidae (45.1% of total density), Melandryidae (42%), Tenebrionidae (7.4%) and Buprestidae (5.4%), were dissected from aspen snags. Two hundred and forty-six Cerambycidae larvae were dissected from snags and identified to species. The Cerambycidae species with the highest density was *Anthophylax attenuatus* (Haldeman) (48.5% of Cerambycidae density) followed by *Bellamira scalaris* (Say) (19.9%), *Trigonarthris minnesotana* (Casey) (4.1%) and *Trachysida mutabilis* (Newman) (1.3%). Density is presented in Table 6 to control for variation in diameter of the snags. Due to high variance in the data, no significant effects were found for phloeophagous/xylophagous larvae, Cerambycidae larvae and Melandryidae larvae although cut-block separators have

Table 3 – Average (n = 9) of measured stand characteristics by habitat patches (small patch, cut-block separator, clearcut, large patch-edge, large patch-interior)

	Habitat patches average				
	Small patches	Cut-block separators	Clearcuts	Large patch-edges	Large patch-interiors
Deciduous tree density	13.7	14.6	0.1	14.3	13.2
Coniferous tree density	17.2	10.3	2.2	10.1	10.8
Snag density*	10.2	10.7	3.3	9.1	6.7
Snag basal area (dm^2)	67.5	87.8	10.4	92.4	38.1
Deciduous tree basal area (dm^2)	316.8	405	0.2	422.1	298.6
Deciduous snag density	8	8.3	2.8	7.6	3.6
Coniferous snag density	2.1	2.2	0.4	1.2	3
Deciduous shrub density	15.2	16.7	26.4	15.4	18.4
Coniferous shrub density	4.6	2.7	3.8	5	6
Shrub density class	2.1	2.5	3.2	2.3	2.3
Log volume (m^3)	0.029	0.036	0.04	0.019	0.017
% Canopy openness	26	24.6	51.7	20.5	17.1

* Includes some snags that were too decayed to be classified as deciduous or coniferous.

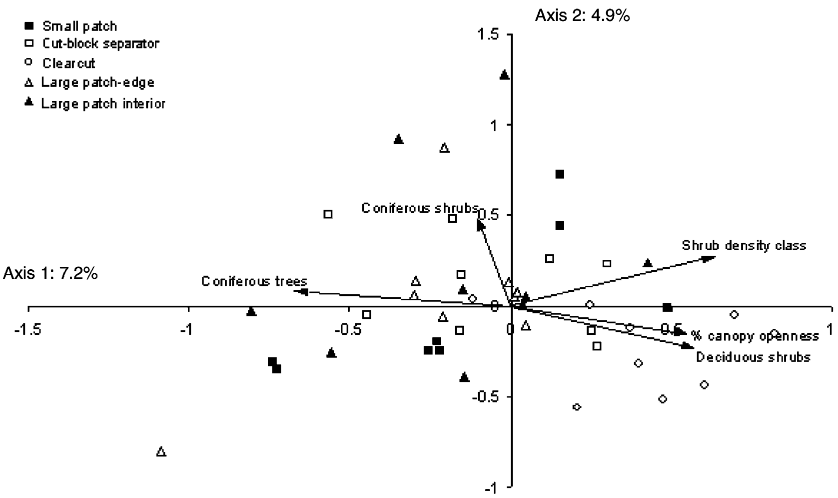

Fig. 3 – Canonical correspondence analysis of 11 measured environmental variables on 186 saproxylic beetle species captured in 44 Lindgren funnels ($n = 9$). Environmental variables with correlations >0.5 or <−0.5 on axis 1 or 2 are graphed.

Table 4 – Results and correlations from a CCA ordination of saproxylic beetles from 44 samples of untransformed data (correlations >0.5 or <−0.5 in bold)

	Axis	
	1	2
Eigenvalues	0.17	0.12
Species–environment relationship	0.88	0.80
Correlations[a]		
Dec. tree density	−0.12	0.08
Con. tree density	**−0.77**	0.11
Snag basal area	−0.05	0.14
Dec. tree basal area	−0.02	−0.04
Dec. snag density	0.06	0.15
Con. snag density	−0.45	0.25
Dec. Shrub density	**0.69**	−0.32
Con. Shrub density	−0.19	**0.65**
Shrub density class	**0.77**	0.39
Volume of logs	0.29	0.23
% Canopy openness	**0.64**	−0.22

[a] Snag density data were not included in the CCA as the deciduous and coniferous snag data provided more useful information.

considerably higher larval densities than large patches for these families (Table 6). Significant treatment effects were found for only Buprestidae larvae, which had equal densities in cut-block separators and small patches but were absent from large patches. Tenebrionidae larval density was marginally non-significant ($p = 0.05$) with small patches having the highest larval density and large patches the lowest larval density. The Kruskal–Wallis test on the proportion of snags with phloeophagous/xylophagous larvae present and Cerambycidae larvae present is also marginally non-significant ($p = 0.06$) but has high variance. Phloeophagous/xylophagous larvae and Cerambycidae larvae have increased larval presence per snag, in small patches and cut-block separators compared to large patches (Table 6).

The density of larvae of phloeophagous and xylophagous families in snags was compared with catch rate of beetles captured in Lindgren funnels from the same families and in the same habitat patches (Table 7a). Cerambycidae is the most abundant phloeophagous/xylophagous family collected by both sampling methods. Melandryidae were relatively more common in snag dissections than in Lindgren funnel traps. Tenebrionidae were never captured in Lindgren funnels of the Magusi site but were common in snag dissections. Buprestidae were absent from edges of large patches, were captured only once as adults and had low densities as larvae in the habitat remnants.

Among aspen-feeding Cerambycidae, *A. attenuatus* was the most abundant Cerambycidae dissected from snags but there were only three captures in Lindgren funnels (Table 7b). *Clytus ruricola* (Olivier), the most abundant Cerambycidae caught in Lindgren funnels was never found in snag dissections. Forty-five *B. scalaris* larvae were dissected from snags while only one was captured in Lindgren funnels. *T. mutabilis* and *T. minnesotana* were never caught in Lindgren funnels. Two additional species, *Psenocerus supernotatus* (Say), *Agomorphus modestus* Gyllenhal, were caught once each in Lindgren funnels but were never found in snags.

4. Discussion

4.1. *Use of habitat remnants by saproxylic beetles*

We predicted that remnant habitats would act as refuges for mature forest species during the regeneration phase of harvested stands in boreal forests of Northwestern Quebec. Our results showed that saproxylic beetles do use snags available in remnant habitats, as evidenced through snag dissection. We also found that the highest species richness of saproxylic and phloeophagous/xylophagous beetles was from habitat remnants. The greatest differences between habitat patches occurred between habitat remnants and interiors of large

Table 5 – Results from one-way ANOVA and Kruskal–Wallis testing for the effects of habitat patches (small patch, cut-block separator, clearcut, large patch-edge, large patch-interior) on stand characteristics

Stand Characteristic	Habitat patch							
ANOVA	Small patch	Cut-block separator	Clearcut	Lp-edge	Lp-interior	F, D.F.	F value	p value
Deciduous tree density	14.87 ± 3.14a	14.56 ± 3.83a	0.11 ± 0.11b	14.33 ± 3.03a	13.22 ± 2.54a	$F_{4,15.49}$	18.73	<0.0001*
Coniferous tree density	16.75 ± 4.19a	10.33 ± 2.11ab	2.22 ± 1.39b	10.11 ± 2.93ab	10.78 ± 2.86ab	$F_{4,18.54}$	5.07	0.006*
Snag density	10.63 ± 1.52a	10.67 ± 2.375a	3.33 ± 0.726b	9.11 ± 2.22ab	6.67 ± 1.08ab	$F_{4,18.44}$	6.45	0.002*
Snag basal area†	1.75 ± 0.13a	1.74 ± 0.17a	0.75 ± 0.18b	1.57 ± 0.27a	1.37 ± 0.17ab	$F_{4,39}$	4.62	0.004
Deciduous snag basal area†	1.45 ± 0.26	1.41 ± 0.23	0.70 ± 0.17	1.40 ± 0.28	0.86 ± 0.24	$F_{4,19.18}$	2.56	0.07*
Deciduous shrub density	8.53	0.07	26.44 ± 5.33	15.44 ± 3.44	18.44 ± 5.75	$F_{4,19.71}$	0.85	0.51*
Log volume‡	0.16 ± 0.02	0.18 ± 0.02	0.19 ± 0.02	0.13 ± 0.02	0.13 ± 0.01	$F_{4,19.14}$	2.64	0.07*
% Canopy openness	25.98 ± 3.37a	24.55 ± 1.30a	51.72 ± 4.15b	20.53 ± 1.67a	17.14 ± 0.83a	$F_{4,18.40}$	19.24	<0.0001*
Kruskal–Wallis	Small patch	Cut-block separator	Clearcut	Lp-edge	Lp-interior	χ^2 D.F.	χ^2 value	p value
Coniferous snag density	1.75 ± 0.84ab	2.22 ± 0.62ab	0.44 ± 0.44a	1.22 ± 0.55ab	3 ± 0.75b	$F_{4,39}$	10.27	0.04
Coniferous shrub density	4.56 ± 2.08	2.67 ± 1.17	3.78 ± 1.12	5.00 ± 2.24	6.00 ± 3.01	$F_{4,40}$	0.52	0.97
Density class	2.06 ± 3.5	2.50 ± 2.04	3.22 ± 0.31	2.28 ± 0.324	2.28 ± 0.383	$F_{4,40}$	7.95	0.09
Deciduous snag density	8.75 ± 2.05	8.33 ± 2.60	2.78 ± 0.494	7.56 ± 2.02	3.56 ± 1.13	$F_{4,39}$	8.53	0.07

Data presented as means ± S.E. post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test ($\alpha < 0.05$). For Kruskal–Wallis tests, post-hoc tests are Bonferroni corrected pairwise comparisons using the Mann–Whitney test.

† Log transformed.

‡ Square-root transformed.

* Welch's F statistic and p = value used to correct for inequality of variance.

Table 6 – Results from Kruskal–Wallis tests for the effects of habitat patches (small patch, cut-block separator, large patch-edge) on aspen-feeding beetle larval density and larval density by family, for snag dissections

	Habitat patch				
	Small patch	Cut-block separator	Large patch- edge	$\chi^2_{2,42}$	p value
Mean aspen-feeding beetle larval density	0.52 ± 0.17	1.18 ± 0.60	0.31 ± 0.15	4.42	0.11
Mean Cerambycidae larval density	0.25 ± 0.14	0.45 ± 0.26	0.20 ± 0.14	4.22	0.12
Mean Buprestidae larval density	0.054 ± 0.03	0.054 ± 0.02	0	7.08	0.03[a]
Mean Melandryidae larval density	0.13 ± 0.05	0.63 ± 0.52	0.088 ± 0.05	1.76	0.41
Mean Tenebrionidae larval density	0.094 ± 0.03	0.040 ± 0.01	0.016 ± 0.01	5.91	0.05
Proportion of snags with aspen-feeding beetle larvae present	0.17 ± 0.02	0.15 ± 0.02	0.09 ± 0.03	5.68	0.06
Proportion of snags with Cerambycidae larvae present	0.11 ± 0.03	0.09 ± 0.03	0.03 ± 0.02	5.73	0.06

Results from Kruskal–Wallis tests for effects of habitat patches on the proportion of snags with aspen-feeding beetle larvae and Cerambycidae larvae present. Data presented as means ($n = 9$) ± S.E. Post-hoc tests performed with pairwise comparisons using a Bonferroni adjusted Mann–Whitney test.

a Post-hoc test does not detect significant differences with Bonferroni adjustment.

patches; the latter had the lowest catch rates and species richness of saproxylic and phloeophagous/xylophagous beetles.

The low species richness and low catch rates of beetles in the interior for forest patches may be explained partially by the relatively low snag density (deciduous), and low snag basal area, since saproxylic are dependent on this habitat. In contrast, small patches and cut-block separators had the highest snag density and basal area, increasing habitat for many saproxylic beetles. Increased edge around these remnant habitats can increase environmental variation in wind and temperature, and trees there are susceptible to mechanical damage from harvesting (Peltonen, 1999). Although some authors have documented increased snag densities at the forest-clearcut ecotone (Peltonen, 1999), it is not always the case.

When searching for mechanisms to explain patterns in species diversity in our harvested landscape, we face a key problem with the lack of life history information about saproxylic beetles. In North America, with the exception of the few economically important species, there is little natural history known about the species we collected, even though indicator species analysis revealed some species-specific patterns. *T. dissimulator* (Erotylidae) was a significant indicator of small patches and was very rarely collected in clearcuts. Some species of the genus *Triplax* are endangered or threatened in European countries (Franc, 1997). Mycetophilous beetles, which include *Triplax,* are considered indicators of well-preserved ecosystems in Europe (Franc, 1997). In North America, genus *Triplax* is generally distributed and larvae feed on soft bracket fungi, primarily of the genus *Inonotus* and *Pleurotus* (Arnett et al., 2002).

4.2. *Use of clearcuts by saproxylic beetles*

Clearcuts had intermediate species richness (for both saproxylic and phloeophagous/xylophagous beetles) and

Table 7 – Comparison of aspen-feeding xylophagous/phloeophagous families (Duparquet) (a), and total aspen-feeding Cerambycidae (b) captured in Lindgren funnels ($n = 3$) or density (/dm^3) dissected from snags ($n = 3$) in same habitat patches in the Magusi site

	Lindgren funnels (Adult catch rate)					Snag dissections (Larval density/dm3)			
	Small patch	Cut-block separator	Large patch-edge	Large patch-interior	Total	Small patch	Cut-block separator	Large patch-edge	Total
(a)									
Cerambycidae	12	32	22	15	81	3.8	6.8	3.0	13.6
Buprestidae	0	1	0	0	1	0.8	0.8	0.0	1.6
Melandryidae	13	4	7	6	30	1.9	9.4	1.3	12.6
Tenebrionidae	0	0	0	0	0	1.4	0.6	0.2	2.2
(b)									
A. attenuatus	1	0	2	0	3	0.4	5.3	0.9	6.6
B. scalaris	1	0	0	0	1	2.1	0.6	0.0	2.7
T. mutabilis	0	0	0	0	0	0.1	0.1	0.0	0.2
T. minnesotana	0	0	0	0	0	0.3	0.2	0.0	0.6
C. ruricola	8	32	17	15	57	0.0	0.0	0.0	0.0
P. supernotatus	0	0	1	0	1	0.0	0.0	0.0	0.0
A. modestus	0	0	1	0	1	0.0	0.0	0.0	0.0

moderate catch rates (for only saproxylic beetles) compared to habitat remnants and forest interiors, but there was no significant difference between habitat patches for these response variables (Table 2). For the phloeophagous and xylophagous beetles, clearcuts had the highest catch rate (also non-significant). Although the highest density of woody debris was found in clearcuts, only a fraction of the beetle fauna may be able to use them as hosts, as the debris was small, highly decomposed and covered by thick vegetation. Having high densities of deciduous shrubs, clearcuts areas may have an important role for anthophilous saproxylic species. Flowering plants may provide resources necessary for many adult saproxylic species, while larvae of the same species might prefer snags located in edge habitat. Although catch rates in clearcuts were relatively high, they by themselves do not represent egg-laying habitat for most saproxylic species. Caution is thus needed in the interpretation of catch rate data from clearcut habitat.

The results from the multivariate ordination, which help decipher responses of saproxylic beelte composition in relation to landscape features, demonstrate a separation between the composition of beetle assemblages collected in clearcuts compared to interiors of large patches (Fig. 3). Clearcuts exhibited less trap-to-trap variance in species composition than other habitat patches, especially compared to interiors of large patches. Remnant habitats and uncut forest supported more variable assemblages of species than clearcuts, which depicted a homogenous assemblage composition. This corroborates work with saproxylic beetles from Fennoscandia that document differences in species composition between clearcuts and uncut forest (Kaila et al., 1997; Sverdrup-Thygeson and Ims, 2002).

One of our objectives was to test if our measured environmental variables were able to predict differences in species composition using CCA (Fig. 3). Here, percent canopy openness and deciduous shrubs affected the species composition in clearcuts. These findings are consistent with the use of clearcut habitats by anthophilous species, which will often feed on flowering shrubs such as *Ledum groendlandicum* Oeder and *Rubus* spp. (Bonds and Philips, 1999). Alternatively, we can hypothesize that the silhouette of a snag or Lindgren funnel may be more visible while in flight in a clearcut or edge habitat than in forest interiors, making it easier for a flying beetle to locate a host in open habitats. Some saproxylic beetles use visual cues on a landscape scale to search for a silhouette of a snag and individual tree hosts by selection through trial and error landing (Chenier and Philogene, 1989; Saint-Germain et al., 2006, 2007a). Despite lower snag densities, the probability of capturing beetles may be higher in a clearcut, where the Lindgren funnel is more visible and there are fewer potential hosts to land on. Higher temperatures in clearcuts may have also increased the activity of insects (Kaila et al., 1997).

4.3. *Saproxylic beetle response to stand characteristics*

There were weak species–environment relationships in the CCA ordination, although species composition in deciduous and coniferous sites was dissimilar in relation to canopy openness. One explanation, regarding the lack of strong relationships between stand characteristics and adult beetle captures, is that the composition of host trees may not affect adults dispersing at local scales in this managed system (high small-scale heterogeneity in forest cover?). An alternative explanation is that Lindgren funnels may not be the appropriate sampling device to measure local responses of saproxylic insects to dead wood availability.

The lack of clear relationships in our CCA analysis may relate to spatial scale of observation. Økland et al. (1996), for example, documented stronger relationships between species data and stand characteristics at the landscape scale compared to the stand scale. Availability of habitat for survival of saproxylic species appears important at 1–10 km^2 scales in Sweden (Gibb et al., 2006). This may be due to better correspondence with activity ranges of saproxylic beetles, less influence of local heterogeneity and a better relationship between sampling scale and scale of ecological differences on the landscape (Økland et al., 1996). Furthermore, beetles' species-specific responses to their environment are highly scale-dependent (e.g., Cerambycidae responses vary from 100 to 1600 m, Holland et al., 2005). Larger beetles typically have responses to habitat at larger spatial scales, and there was great variation in size among the species sampled in this study. A larger larvae dataset from snag dissection, which efficiently characterizes the use of local habitat elements by these species, identified to at least the generic level, may relate more strongly to stand characteristics such as those used in our CCA analysis.

4.4. *Saproxylic beetle habitat-use versus aspen host-use*

Snag dissections and Lindgren funnels collected very different phloeophagous/xylophagous families and Cerambycidae, in terms of species and the number of individuals collected. We believe there are three main reasons for these differences. First, flight traps capture beetles that are actively dispersing and collect many species that are not resident in the patches where traps are deployed. Second, the probability of collecting certain species is increased in snag dissections, as beetles may spend several years in the larval stage. The same species may only fly for a few weeks of the summer, making a Lindgren funnel capture less likely. Therefore, if a species is rarely captured in a flight trap, it does not necessarily mean it is rare in that habitat, as larvae may be living in nearby snags. Third, the larval stage of some species may use an area higher on the bole than was sampled during snag dissections (i.e. 25–100 cm above ground). Vance et al. (2003) reported that *C. ruricola* was more often collected in the canopy than understory flight-intercept traps. *A. attenuatus* was exclusively captured in the understory by Vance et al. (2003) and was abundant in the lower bole samples dissected in our study. Although time consuming, snag dissections are a promising method for studying saproxylic beetles in boreal forests, as captures of beetles *in situ* are a direct representation of host-use (Saint-Germain et al., 2007b).

5. Conclusions

The highest saproxylic beetle species richness and catch rate was collected in habitat remnants, which also had the highest snag densities. Comparable densities of larvae were dissected from snags supporting patterns found in Lindgren funnel captures. This suggests that habitat remnants are used readily by saproxylic insects in even-aged managed landscapes and that the amount and distribution of remnant patches are an important factor in conserving beetle assemblages in managed landscapes. Dead wood in clearcuts tends to be slash debris of poor quality with very little standing dead wood, which is concentrated in forest edge and remnant habitats. Suitable dead wood habitat for a given insect species is highly ephemeral, and adequate spatial and temporal connectivity is needed in even-aged managed landscapes. We suggest that a network of remnant habitats in clearcut landscapes will help provide this connectivity.

To conserve the saproxylic fauna, and prevent species declines as experienced in Europe's boreal forest (Jonsson et al., 2005), it is necessary to know what species exist across the entire landscape, and knowledge about species habitat requirements is needed. A more natural stand structure during regeneration of the clearcut may be ensured using remnant forest patches as biological legacies (*sensu* Franklin et al., 2000), offering habitat to an increased diversity of organisms than clearcutting alone. We also expect that diversification of forest management using an uneven-aged approach (Bergeron, 2004; Gauthier et al., 2004; Bergeron et al., 2007), such as partial cut and selective cut practices, may provide a wider range of habitat and host types for the diverse needs of boreal saproxylic fauna, than with clearcutting alone.

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