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# Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America

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## Abstract

Several insect groups have adapted to fire cycles in boreal forests, and can efficiently use new habitats created by fire. Our study aimed at producing a first characterization of post-fire Coleoptera assemblages of black spruce forests of eastern North America. For two years, we sampled Coleoptera using flight-interception traps in burned stands of contrasting age and structure in a 5097-ha wildfire and in neighbouring unburned mature stands. More than 40 species were exclusively captured in burned stands. Time elapsed since fire and proximity of unburned forests were the most significant parameters affecting Coleoptera assemblages. Stand age and structure had limited effects on assemblage structure; the Scolytid *Polygraphus rufipennis* Kirby was the only common species to clearly favor older stands. Fire-associated Coleoptera assemblages found in our study area were clearly distinct from those found in similar unburned stands; we should thus be conservative in our management approach concerning recently burned stands.

*Keywords:* Boreal forest; Forest fires; Habitat selection; Fire-associated Coleoptera; Salvage logging

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## 1. Introduction

Fire is a predominant disturbance factor in boreal forests; it profoundly alters the habitats it affects and, under natural dynamics, is a major determinant of forested landscape patterns (Zackrisson, 1977; Johnson, 1992; Payette, 1992; Bergeron et al., 2001). Fire can destroy large parts of the biotic components of a forested ecosystem (Danks and Foottit, 1989; Wikars, 1994; Paquin and Coderre, 1997). However, the newly created environment offers several unique conditions for opportunistic immigrants, such as habitats free of competitors and higher daytime air and soil temperatures (Wikars, 1992, 1994). It also provides an abundance of ephemeral substrata otherwise scarce and of unpredictable availability, such as recently dead wood of high nutritional value and exposed mineral soils (Jakubas et al., 1994; Pedlar et al., 2002).

Some insect groups have adapted to recurrent forest fires by evolving sensory organs and life strategies that allow them to exploit these high quality habitats efficiently. Pyrophilous Buprestids of the genera *Oxypteris* and *Merimna* and the Cerambycid *Arhopalus tristis* (F.) have been shown to respond physiologically to smoke and/or heat generated by fire, and use them as signals leading toward the newly created habitat (Evans, 1966; Schütz et al., 1999; Schmitz et al., 2000; Suckling et al., 2001). Pyrophilous species have high dispersal capabilities; some also use a risk-spreading reproductive strategy, adults emerging on a lengthened period, thus maximizing the probabilities that at least some fraction of their offspring may have access to high quality burned habitats (Wikars, 1994). Several other Coleoptera species uncommon in mature forests congregate in exceptionally high densities in burned stands. As their responsiveness to fire-created stimuli has not been demonstrated yet by physiological studies, such species will further be referred to as being fire-associated.

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Jonsell et al. (1998) hypothesized that fire-associated insect population dynamics were related to the source-sink type described by Pulliam (1988): high populations observed following recent forest fires would allow these species to persist in sub-optimal unburned habitats until the next regional disturbance. In landscapes where other types of disturbances are rare, this dependence on burned habitats would make them vulnerable to events affecting the fire cycle, either natural or of human origin, like climate change (Whitehouse, 2000), fire suppression or modern forestry practices (Anhlund and Lindhe, 1992; Wikars, 1992). Fire-associated invertebrates have shown a sharp decline in Fennoscandia in the last few decades as a result of efficient fire suppression (Anhlund and Lindhe, 1992; Wikars, 1992; Kaila et al., 1997; Jonsell et al., 1998).

Several factors could significantly lower burned habitat availability in boreal forests of eastern North America in the decades to come. Current models of climate change predict lower forest fire weather indices for eastern Canada in the future (Flannigan et al., 2001), and recent studies show a substantial decrease in fire frequency since the mid-19th century (Bergeron and Archambault, 1993; Bergeron et al., 2001). Furthermore, local governments are putting increasing pressure on the timber industry to salvage fire-killed trees as an alternative to declining stocks of wood (Quebec National Assembly, 2001). Salvage logging is a selective process where only merchantable wood (i.e. DBH over 10 cm) is harvested. Younger stands are left untouched, but their value as habitat for pyrophilous insects has not been assessed. North American pyrophilous insect communities are still poorly described and ecological factors affecting habitat use by these groups are largely unknown. Factors like fire severity, stand age and structure and spatial context within the landscape could affect stand colonization potential, egg-laying behavior of adults and subsequent larval development rate and survival (Dixon et al., 1982; Liu et al., 1991; Hanks, 1999).

Recently burned habitats present unique conditions in boreal forest succession and should be considered as key habitats. More knowledge is needed about post-fire insect communities and their habitat use patterns if we are to preserve this distinctive part of boreal forest biodiversity. A 5097-ha fire that took place in 1999 from May 30th to June 5th in the Grands-Jardins Provincial Park (Quebec, Canada) offered us an opportunity to study these insects. These forests have been exploited episodically since the 1950s and form a complex landscape. Our objectives were: (1) to provide a first description and characterization of pyrophilous Coleoptera communities of the boreal black spruce forest of eastern North America and (2) to determine how burned stand age, structure and spatial context affect species richness, abundance and community structure.

## 2. Materials and methods

Sampling was conducted in the Grands-Jardins Provincial Park (47°41′N; 70°43′W). It harbors the southernmost lichen woodland of eastern Canada, a legacy of its peculiar disturbance history (Payette et al., 2000a). This territory is especially fire-prone; recent fires have occurred within the park's boundaries or in its immediate vicinity in 1991 (2×), 1995, 1997 and 1999. Pure black spruce stands [*Picea mariana* (Mill.)] dominate the landscape, with the occasional presence of balsam fir [*Abies balsamea* (L.)], and tamarack [*Larix laricina* (Du Roi)], mostly in damp sites. We sampled insects in the 1999 burn during the summers of 2000 and 2001.

### 2.1. Stand selection and characterization

The stands that burned in 1999 originated mostly from a 1922 fire and two episodes of clear-cutting (1955–1964; 1979–1981) (Payette et al., 2000b). To cover the widest possible gradient of forest age and structure, we selected 5 stands originating from each of these disturbances. We also selected 5 unburned mature stands in the vicinity of the 1999 fire, for a total of 20 stands. Most of the unburned stands were initiated by distinct disturbances, their estimated age varying from 65 to 160-years-old. These groups will further be referred to as U80 for unburned mature stands, B80 for burned mature stands, B50 for burned stands originating from clear-cutting in the late 1950s and early 1960s and B20 for burned stands originating from the most recent clear-cutting episode.

In the approximate center of each selected stand, a 400 $m^2$ circular plot was established for stand characterization. Trees with a diameter at breast height (DBH) equal to or over 10 cm were counted and their DBH recorded. Trees of DBH $<$ 10 cm were counted in a 100 $m^2$ subplot. This data was used to calculate basal area and stem density (DBH $>$ 10-cm). Fire-killed stems were easily distinguished from those that were already dead before the disturbance using wood coloration and crown architecture. Percentage of charred bark was evaluated for each tree; the average of these values was used as an index of fire severity for each stand. Five trees were randomly selected from the dominant DBH class (5–10 cm, 10–15 cm, 15–20 cm or 20–25 cm). Their height was estimated using a clinometer and core samples were taken to age the trees.

Logs and stumps with diameters equal to or over 10 cm were counted within the plot. The shrub and herbaceous vegetation layers were characterized using the Braun-Blanquet cover-abundance scale (+: <1% cover; 1: 1–5%; 2: 6–25%; 3: 26–50%; 4: 51–75%; 5: 76–100%; Braun-Blanquet, 1964). Geographic Information System data was generated from aerial photographs of the fire taken in 1999 to provide measures of the landscape context surrounding each sampled stand. This data was analyzed using the software Arcview GIS 3.1 (Environmental Systems Research Institute, Inc., Redlands, California). The percentage of unburned matrix in a 250 m radius was calculated around each of the 20 stands. We also evaluated the shortest distance to continuous unburned matrix from each sampled stand. Since several unburned fragments that were too small to be considered as significant source habitat were present at or near the edge of the fire, we added a 500 m buffer to the burned polygons in order to exclude these fragments. This buffer allowed us to make objective decisions on where these shortest distances were. The 500 m scale was chosen as the most appropriate considering the spatial configuration of the fire/unburned matrix edge.

### 2.2. Insect sampling

Sampling was conducted from June 13th to August 16th in 2000 and from May 29th to August 13th in 2001. One multidirectional flight-interception trap was used in each stand. These traps were built using four $15 \times 40$ cm panels (2 made of Plexiglas® and 2 of mosquito net) mounted into a cross pattern, along a 10-cm diameter black ABS cylinder, with a funnel leading to the collecting vial. This "hybrid" trap (panels made of different materials) was designed to account for different behavioral responses shown among beetle families when hitting the interception panel. A solution made of 70% ethanol with traces of glycerine and household vinegar (5% acetic acid) was used as preservative. Glycerine was used to lessen evaporation in warm conditions and acetic acid to keep specimens flexible. Collecting vials were emptied once a week. Samples were sorted in the laboratory. Only Coleoptera were retained; species caught less than 4 times (less than 0.05% of total captures) were not included in the analyses, except for wood-feeding families (Buprestidae, Cerambycidae and Scolytidae). Most groups were identified to the species whenever actual literature allowed it, and identifications were cross-checked at the Canadian National Collection of insects, arachnids and nematodes (Ottawa, Canada), at the René Martineau insectarium of the Laurentian Forestry Center (Canadian Forest Service, Sainte-Foy) and at the Ouellet-Robert entomological collection (University of Montreal, Montreal). Vouchers are preserved at the René Martineau insectarium. Weekly samples were pooled by stand and sampling year for further analyses.

### 2.3. Statistical analyses

One-way ANOVAs were used to compare stand age, basal area, and stem, logs and stumps densities between types of stands. Two-way ANOVAs were used to compare species richness, Coleoptera capture totals, Elaterid capture totals and xylophagous species capture totals between types of stands and sampling year. All species caught over 50 times were independently tested for stand group preference with one-way ANOVAs (2000 and 2001 data pooled). Data were log-transformed to satisfy normality and homogeneity of variance assumptions when necessary. Tukey's Honestly Significant Difference tests were used for post-hoc multiple comparisons ($\alpha = 0.05$).

Variations in species composition and assemblage structure among sampling sites and their relationships with environmental factors were assessed using ordination techniques. A canonical correspondence analysis (CCA) was used to summarize the variation in species composition of insect assemblages and to assess the influence of environmental parameters on assemblage structure. Variables deemed important following the CCA were investigated further using linear regressions on fire-associated species and habitat generalists captures in burned stands. Ordination analyses were performed using Canoco 4.02 (ter Braak and Šmilauer, 1998). Analyses of variance and regressions were performed using SPSS 10.0.5 (SPSS Inc., 1999).

## 3. Results

### 3.1. Stand structure

Analyses of variance showed significant differences between types of stand for age of cored fire-killed trees ($F = 5.66$; df = 3, 16; $p = 0.008$), basal area ($F = 10,171$; df = 3, 16; $p = 0.001$), density of stems of DBH > 10-cm ($F = 15,383$; df = 3, 16; $p < 0.001$) and stump density ($F = 12,898$; df = 3, 16; $p < 0.001$). U80 and B80 stands cored fire-killed trees were significantly older than B20 stands trees, but B50 stands samples were not statistically different from either U80, B80 or B20. Total basal area was the lowest in B20 stands. Density of stems of DBH $\geqslant$ 10-cm was also lowest in B20 stands (Table 1). B50 stands were clearly more variable in age and structure. There were no statistical differences in log occurrence between stand groups ($p > 0.05$), but stumps were much more frequent in the B50 and B20 stands, which originated from clearcuts (Table 1). Ground vegetation was dominated by *Ledum groenlandicum* Oeder, *P. mariana* (Mill.) and mosses in unburned stands, and by *L. groenlandicum*, *Vaccinium angustifolium* Aiton and *Kalmia angustifolia* L. in all burned stand groups.

### 3.2. Insects

More than half of the 86 taxa captured in our study were restricted to burned stands. Total captures (tc) and

Table 1
Structural and spatial context variables measured in sampled stand groups, with standard deviation in parentheses or ranges in brackets

| Stands | Age | (%) Fire severity | Basal area ($m^2$/ha) | Density (10 cm + DBH stems/ha) |
|---|---|---|---|---|
| U80 | 83.9 (31.7) a | – | 17.2 (3.7) a | 875 (144.7) a |
| B80 | 88.0 (24.0) a | 90.2 [54.9–100] | 17.3 (4.5) a | 910 (194.9) a |
| B50 | 65.4 (25.4) ab | 100 [100–100] | 12.9 (5.1) a | 745 (346.1) a |
| B20 | 29.9 (12.3) b | 92.3 [80–100] | 4.5 (3.3) b | 75 (140.3) b |

| Stands | Logs/plot | Stumps/plot | Distance from unburned matrix (m) | % unburned matrix (250 m radius) |
|---|---|---|---|---|
| U80 | 4.6 (6.1) a | 1.6 (3.6) a | – | 77.8 [46, 9–98, 3] |
| B80 | 9.0 (5.2) a | 4.4 (4.2) a | 2967 [1931–4134] | 18.0 [0–52, 4] |
| B50 | 5.0 (2.4) a | 27.4 (12.1) b | 2884.8 [1505–4284] | 11.5 [0–27, 9] |
| B20 | 15.2 (12.5) a | 30.8 (13.4) b | 1911.6 [994–2772] | 4.9 [0–20, 4] |

Letters indicate statistical differences (Tukey HSD, $p = 0.05$).

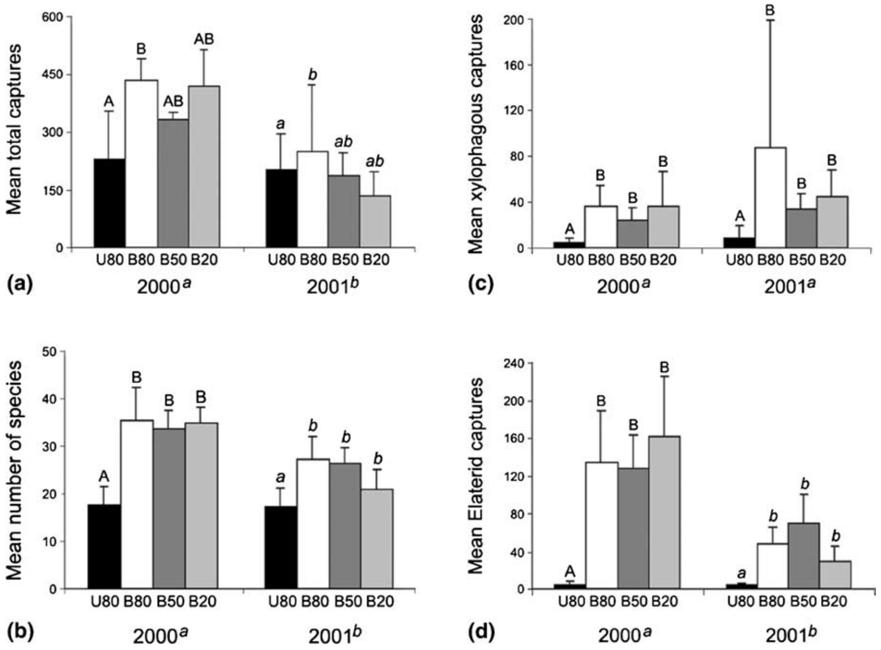

Fig. 1. Mean Coleoptera abundance (a), mean Coleoptera richness (b), mean Elaterid abundance (c) mean xylophagous species captures and (d) elateridae captures. Significant differences based on analyses of log-transformed data are indicated by letters (groups) and italics (year). (U80 – unburned 80-years-old forests; B80 – burned 80-years-old forests; B50 – burned 50-years-old forests; B20 – burned 20-years-old forests).

species richness (sr) showed similar patterns, with significant differences between stand groups (tc: $F = 3072$; df = 3, 32; $p = 0.042$; sr: $F = 20,095$; df = 3, 32; $p < 0.001$) and sampling years (tc: $F = 27,708$; df = 1, 32; $p < 0.001$; sr: $F = 27,727$; df = 1, 32; $p < 0.001$), with a significant interaction between factors (tc: $F = 3061$; df = 3, 32; $p = 0.042$; sr: $F = 4155$; df = 3, 32; $p = 0.014$). We generally obtained more total captures in burned stands, with significantly higher captures in B80 stands than in U80 stands. There was a significant drop in captures the second year after the fire for all burned stands (Fig. 1(a)). The significant interaction between stand groups and sampling years seemed to be driven by total captures in unburned stands (U80) that did not suffer the same drop in 2001. Similar trends were observed for richness (Fig. 1(b)). All burned stand groups (B80, B50 and B20) had higher richness than unburned stands (U80) for both years, but a significant drop occurred in 2001. Again, the significant interaction between factors seems to be related to unburned stands which showed no drop in richness for 2001. Richness dropped more steeply in younger burned stands (B20) in 2001.

Elateridae was the most abundant family collected in our study. Most species were captured in much higher numbers in all burned stands than in unburned stands ($F = 47,218$; df = 3, 32; $p < 0.001$). Elateridae was also one of the families for which captures most drastically dropped in 2001 ($F = 45,901$; df = 1, 32; $p < 0.001$) (Fig. 1(c)). Wood-feeding species showed different dy-

Table 2
Total number of insects captured by family and species for each sampled stand groups

| Taxon | Sig. | U80 | B80 | B50 | B20 | Total |
|---|---|---|---|---|---|---|
| Buprestidae | | 1 | 5 | 8 | 4 | 18 |
| *Anthaxia inornata* (Rand.) | | 1 | 3 | 6 | 0 | 10 |
| *Melanophila drummondi* Kirby | | 0 | 1 | 1 | 1 | 3 |
| *Oxypteris acuminata* (DeGeer) | | 0 | 1 | 1 | 3 | 5 |
| Byrrhidae | | | | | | |
| *Cytilus alternatus* (Say) | | 0 | 2 | 1 | 2 | 5 |
| Cantharidae | * | 7 a | 7 a | 23 ab | 34 b | 71 |
| Carabidae | | | | | | |
| *Sericoda quadripunctata* (DeGeer) | | 0 | 1 | 1 | 2 | 4 |
| Cerambycidae | | 35 | 476 | 206 | 362 | 1079 |
| *Acmaeops proteus* (Kirby) | *** | 3 a | 75 b | 48 b | 58 b | 184 |
| *Anastrangalia sanguinea* (LeC.) | | 0 | 1 | 0 | 1 | 2 |
| *Asemum striatum* (L.) | | 0 | 0 | 1 | 1 | 2 |
| *Cosmosalia chrysocoma* Kirby | | 0 | 4 | 1 | 9 | 14 |
| *Evodinus monticola* (Rand.) | | 8 | 6 | 2 | 3 | 19 |
| *Gnathacmaeops pratensis* (Laich.) | *** | 19 a | 371 b | 137 b | 275 b | 802 |
| *Xestoleptura tibialis* LeC. | | 0 | 0 | 2 | 5 | 7 |
| *Monochamus scutellatus* (Say) | | 0 | 8 | 1 | 5 | 14 |
| *Pachyta lamed* Dejean | | 0 | 0 | 0 | 1 | 1 |
| *Pygoleptura nigrella* (Say) | | 0 | 0 | 1 | 0 | 1 |
| *Rhagium inquisitor* (L.) | | 4 | 8 | 9 | 2 | 23 |
| *Tetropium cinnamopterum* Kirby | | 1 | 2 | 4 | 2 | 9 |
| *Trachysida mutabilis* (Newman) | | 0 | 1 | 0 | 0 | 1 |
| Ciidae | | | | | | |
| *Orthocis punctatus* (Mellié) | | 3 | 2 | 2 | 0 | 7 |
| Cleridae | | 0 | 13 | 15 | 8 | 36 |
| *Thanasimus dubius* (F.) | | 0 | 4 | 4 | 1 | 9 |
| *Thanasimus undulatus* (Say) | | 0 | 9 | 11 | 7 | 27 |
| Corylophidae | | | | | | |
| Corylophidae sp.#1 | *** | 2 a | 58 b | 27 bc | 13 c | 100 |
| Cryptophagidae | | 26 | 21 | 10 | 6 | 63 |
| *Antherophagus* sp. | | 0 | 4 | 2 | 2 | 8 |
| *Atomaria* sp. | ns | 26 | 17 | 8 | 4 | 55 |
| Curculionidae | | 2 | 2 | 2 | 3 | 9 |
| *Hylobius congener* (DSM) | | 2 | 1 | 0 | 2 | 5 |
| Curculionidae sp.#1 | | 0 | 1 | 2 | 1 | 4 |
| Elateridae | | 40 | 904 | 985 | 955 | 2884 |
| *Agriotes collaris* LeC. | | 0 | 3 | 0 | 1 | 4 |
| *Agriotes limosus* (LeC.) | *** | 0 a | 59 bc | 32 b | 144 c | 235 |
| *Agriotes stabilis* (LeC.) | | 0 | 0 | 0 | 5 | 5 |
| *Ampedus apicatus* (Say) | ** | 0a | 20 b | 16 b | 24 b | 60 |
| *Ampedus deletus* (LeC.) | *** | 9 a | 38 ab | 70 b | 109 b | 226 |
| *Ampedus luctuosus* (LeC.) | | 0 | 8 | 4 | 7 | 19 |
| *Ampedus mixtus* (Hbst.) | | 3 | 1 | 6 | 8 | 18 |
| *Ampedus pullus* (Germ.) | | 0 | 5 | 12 | 29 | 46 |
| *Ampedus quebecensis* Brown | | 0 | 6 | 4 | 8 | 16 |
| *Ctenicera kendalli* (Kirby) | | 0 | 1 | 5 | 18 | 24 |
| *Ctenicera resplendens* (Esch.) | | 0 | 2 | 0 | 2 | 4 |
| *Ctenicera spinosa* (LeC.) | ns | 3 | 21 | 15 | 11 | 50 |
| *Ctenicera triundulata* (Rand.) | *** | 16 a | 651 b | 681 b | 459 b | 1807 |
| *Eanus decoratus* (Mann.) | *** | 1 a | 27 b | 36 b | 18 b | 82 |
| *Eanus maculipennis* LeC. | | 0 | 0 | 12 | 0 | 12 |
| *Limonius aeger* LeC. | | 0 | 1 | 5 | 2 | 8 |
| *Limonius* sp.#1 | | 6 | 0 | 0 | 0 | 6 |
| *Sericus incongruus* LeC. | *** | 2 a | 62 b | 87 b | 110 b | 261 |
| Laemophloeidae | | | | | | |
| *Laemophloeus biguttatus* (Say) | ns | 13 | 18 | 39 | 9 | 79 |

Table 2 (*continued*)

| Taxon | Sig. | U80 | B80 | B50 | B20 | Total |
|---|---|---|---|---|---|---|
| Lampyridae | | | | | | |
| *Ellychnia corrusca* (L.) | | 3 | 11 | 6 | 6 | 26 |
| Lathridiidae | | 110 | 328 | 225 | 308 | 971 |
| *Corticaria* sp. | *** | 24 a | 101 b | 93 b | 76 b | 294 |
| *Corticarina* sp. | *** | 16 a | 181 b | 99 b | 201 b | 497 |
| *Lathridius* sp. | ns | 31 | 12 | 15 | 22 | 80 |
| *Melanophthalma* sp. | ns | 39 | 34 | 18 | 9 | 100 |
| Lycidae | | | | | | |
| *Dictyopterus aurora* (Hbst.) | | 1 | 1 | 1 | 1 | 4 |
| Melandryidae | | | | | | |
| *Serropalpus coxalis* Mank | | 4 | 0 | 0 | 0 | 4 |
| Monotomidae | | | | | | |
| *Rhizophagus dimidiatus* Mann. | *** | 763 a | 182 ab | 119 b | 88 b | 1152 |
| Mordellidae | | | | | | |
| *Tomoxia borealis* LeC. | | 0 | 4 | 10 | 13 | 27 |
| Nitidulidae | | 611 | 226 | 106 | 46 | 989 |
| *Colopterus truncates* (Randall) | | 2 | 7 | 8 | 5 | 22 |
| *Epuraea* spp. | *** | 600 a | 209 ab | 79 bc | 34 c | 922 |
| *Glischrochilus sanguinolentus* (Olivier) | | 5 | 7 | 7 | 3 | 22 |
| *Glischrochilus siepmanni* Brown | | 2 | 0 | 2 | 1 | 5 |
| *Glischrochilus vittatus* Say | | 2 | 3 | 10 | 3 | 18 |
| Ptiliidae | | 3 | 4 | 3 | 1 | 11 |
| Salpingidae | | | | | | |
| *Sphaeriestes virescens* LeC. | *** | 3 a | 473 b | 462 b | 489 b | 1427 |
| Scolytidae | | 40 | 148 | 82 | 50 | 320 |
| *Cryphalus ruficollis* Hopkins | | 4 | 0 | 0 | 1 | 5 |
| *Dendroctonus rufipennis* (Kirby) | | 2 | 2 | 1 | 1 | 6 |
| *Dryocoetes affaber* (Mann.) | | 2 | 16 | 1 | 0 | 19 |
| *Dryocoetest autographus* (Ratze.) | ns | 10 | 17 | 17 | 8 | 52 |
| *Hylastes porculus* Erichson | | 0 | 1 | 0 | 1 | 2 |
| *Ips latidens* (LeC.) | | 0 | 1 | 0 | 0 | 1 |
| *Ips perroti* (Swaine) | | 0 | 1 | 0 | 1 | 2 |
| *Orthotomicus caelatus* (Eich.) | | 0 | 3 | 2 | 0 | 5 |
| *Pityokteines sparsus* (LeC.) | | 0 | 2 | 2 | 1 | 5 |
| *Pityophthorus* sp. | | 1 | 0 | 0 | 0 | 1 |
| *Polygraphus rufipennis* (Kirby) | *** | 3 a | 94 b | 49 bc | 24 ac | 170 |
| *Scierus annectans* LeC. | | 0 | 1 | 1 | 0 | 2 |
| *Trypodendron lineatum* (Olivier) | | 16 | 10 | 8 | 13 | 47 |
| *Trypophloeus* spp. | | 1 | 0 | 1 | 0 | 2 |
| *Xyleborus sayi* (Hopkins) | | 1 | 0 | 0 | 0 | 1 |
| Silvanidae | | | | | | |
| *Silvanus bidentatus* (F.) | | 3 | 13 | 9 | 4 | 29 |
| Staphylinidae | ns | 475 | 529 | 255 | 128 | 1387 |
| Total | | 2145 | 3428 | 2597 | 2532 | 10702 |

Statistical differences are indicated by letters (Tukey HSD, $p = 0.05$) and significance level by stars for species captured more than 50 times (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.00$).

namics. Although their captures were significantly higher in burned stand groups ($F = 18,423$; df $= 3$, 32; $p < 0.001$), their abundance did not drop in 2001 ($p > 0.05$) (Fig. 1(d)).

Several species clearly favored burned habitats. The following species were solely or mostly (95%+) captured in burned stands (further referred as fire-associated species): Cerambycids *Acmaeops proteus* (Kirby) and *Gnathacmaeops pratensis* (Laicharting), Elaterids *Agriotes limosus* (LeConte), *Ampedus apicatus* (Say), *Ampedus deletus* (LeConte), *Ctenicera triundulata* (Randall), *Eanus decoratus* (Mannerheim) and *Sericus incongruus* LeConte, Salpingid *Sphaeriestes virescens* LeConte and Scolytid *Polygraphus rufipennis* (Kirby).

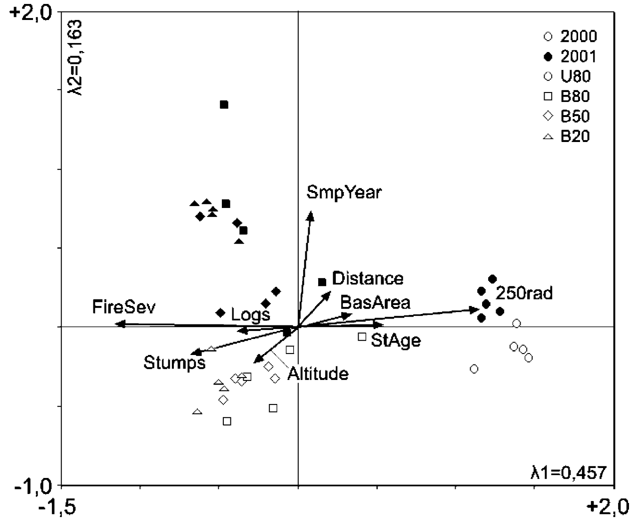

Fig. 2. CCA biplot combining sample scores and environmental variables vectors from analysis made using Coleoptera abundance with 2000 and 2001 results separated. Open symbols represent results from 2000, and solid symbols from 2001. (BasArea – stand basal area; 250Rad – % unburned forest in a 250 m radius; FireSev – fire severity; StAge – stand age).

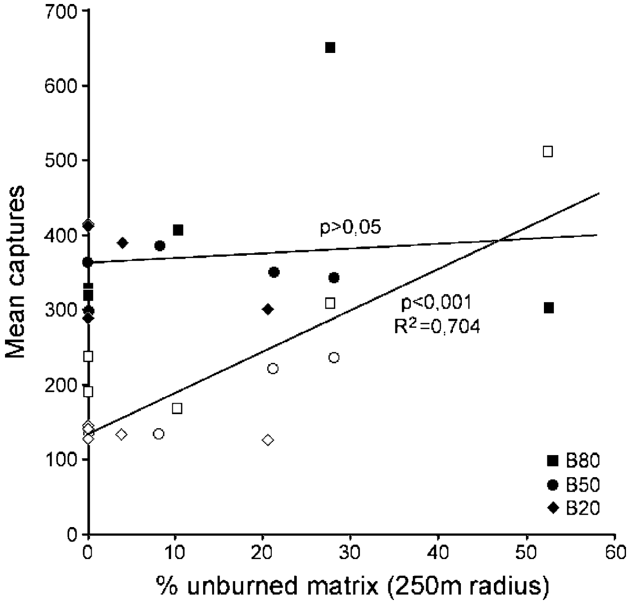

Fig. 3. Effect of the percentage of unburned forest in a 250 m radius on the abundance of fire-associated species (solid symbols) and habitat generalists (open symbols) in burned stands.

Table 3
Results and correlation matrix obtain from a CCA performed on all sampled stands (burned and unburned) using untransformed Coleoptera abundance of 2000 and 2001 separated

| | Axis | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Eigenvalues | 0.457 | 0.163 | 0.117 | 0.052 |
| % Species data explained | 29.1 | 39.5 | 47.0 | 40.3 |
| % Species-env. relation | 49.4 | 67.1 | 79.7 | 85.3 |
| *Correlation matrix* | | | | |
| Basal area | 0.2270 | 0.0575 | −0.1209 | −0.2389 |
| Altitude | −0.2286 | −0.2521 | 0.5381 | 0.1318 |
| % Unburned matrix | 0.8968 | 0.1284 | −0.2945 | 0.0144 |
| Stand age | 0.3951 | 0.0094 | 0.3776 | −0.5804 |
| Distance | 0.1482 | 0.2243 | −0.6753 | −0.1323 |
| Fire severity | −0.9045 | 0.0259 | −0.2047 | −0.1156 |
| Logs | −0.2665 | −0.0056 | 0.3840 | 0.4784 |
| Stumps | −0.5190 | −0.1881 | 0.1246 | 0.2033 |
| Year of sampling | 0.0623 | 0.8018 | 0.1377 | −0.0549 |

Of these species, only *P. rufipennis* favored older stands (B80). Surprisingly, several other species seemed to favor younger stands (*A. limosus*, *A. deletus* and Cantharidae) (Table 2). *Rhizophagus dimidiatus* Mannerheim (Monotomidae), *Epuraea* spp. (Nitidulidae) and Staphylinidae were abundant taxa that were mainly captured in unburned forests.

When assemblages were compared, three distinct groups emerged in the CCA diagram (Fig. 2). Unburned assemblages were tightly grouped, regardless of the year of sampling, on the right end of the first axis. On the left side of the diagram, burned assemblages formed two groups distributed along the second axis, consisting respectively of the 2000 and 2001 burned stand assemblages. B20 stands were more tightly grouped than other burned stands, which indicates less between-site variability. Fire severity and sampling year were highly correlated with the first two axes. Distance from unburned matrix and stand age were the parameters most highly correlated to the third and fourth axes, but they explained much less of the species-environment relationships (Table 3). The percentage of unburned forest in a 250 m radius was closely correlated to fire severity in the CCA, and its effect on the abundance of fire-associated insects and taxa common to both burned and unburned forests was further investigated in burned stands only. Abundance of species common to both habitats were highly correlated to this variable ($p < 0.0001$; $R_2 = 0.704$; $y = 133.54 + 554.39x$), especially in older stands. However, it had no apparent effect on fire-associated species captures ($p > 0.05$) (Fig. 3). Although the positive effect of adjacent unburned forest on the abundance of generalists seemed to vary in intensity between stand groups (B80 > B50 > B20; Fig. 3), this phenomenon could not be independently analyzed due to lack of replication.

## 4. Discussion

### 4.1. Activity level, community composition and structure

Most studies carried out in burned forest ecosystems report drastic increases in the activity level of several insect groups after fire (Anhlund and Lindhe, 1992;

Muona and Rutanen, 1994; Dajoz, 1998); it was also the case in our study. Burned forests provide concentrations of substrata (i.e. stressed or dead wood and roots) at density levels rarely seen in other succession phases of boreal forest development (Pedlar et al., 2002). This resource concentration, combined with the long-distance signal emitted by the fire and the sensorial and dispersal capabilities of some insect species, probably lead to the convergence of individuals distributed over thousands of hectares of neighboring unburned forests toward the burned habitat. The open structure of burned stands, characterized by higher temperatures, also account for increased levels of insect activity (Wikars, 1994). Most species found to be associated with burned stands in our study depend largely on dead wood (Cerambycidae, Scolytidae) or stressed roots (some Elateridae). Some subcortical predators were also captured (Cleridae, Salpingidae).

The fire-associated Coleoptera assemblage captured in the Grands-Jardins provincial park is closely related to those observed in other parts of the boreal forest around the northern hemisphere. Wood-boring Cerambycid genera *Asemum*, *Monochamus*, *Rhagium*, *Tetropium* and Scolytid *Dryocoetes* are common to burned forests of Quebec, Fennoscandia and China (Liu et al., 1991; Wikars, 1994). Muona and Rutanen (1994) also recorded higher captures of the Scolytids *Polygraphus* and *Trypodendron*, soil-dwelling Elaterids *Eanus* and *Sericus*, Cryptophagid *Atomaria*, Salpingid *Sphaeriestes* and Lathridiid *Corticaria* in burned forests of Finland. A pyrophilous life strategy implies constant long-distance dispersal that is probably responsible for the enormous ranges covered by these taxa.

### 4.2. Temporal dynamics of fire-associated assemblages

Several fire-associated insect groups probably produce only one generation in a single burn (Wikars, 1992). In wood-boring Coleoptera, all pyrophilous species are dependent on heavily stressed or recently dead trees. Only one generation is possible after a fire for most of these species, since the structure and the nutritive value of subcortical tissues rapidly deteriorate (Haack and Slansky, 1987; Hanks, 1999).

This trend was most obvious in our results for xylophagous species in Scolytidae, which abundance clearly declined in 2001. These insects are characterized by short life cycles. In opposition, Cerambycidae abundance showed no trend during the two years of sampling. These larger species have life cycles of variable lengths (from 1 to 5 years or more depending on species and individuals) (Raske, 1972; Hanks, 1999). Also, the larval development time of wood-borer species is known to vary between regions, depending largely on climatic factors (i.e. *Monochamus scutellatus*; Raske, 1972). The climate of the Laurentian Plateau, being especially cold, probably lengthened the average larval development time of most species. Since most Cerambycid life cycles are, in these circumstances, as long or longer than our sampling period, no decline in their abundance was to be expected.

Elateridae exhibited the most drastic decline in abundance among beetle families in 2001. The ecology of boreal Elaterids is much more obscure than that of wood-borers. Most species of the genera *Agriotes*, *Ctenicera*, *Eanus* and *Sericus* are believed to feed on underground roots in their larval form (Muona and Rutanen, 1994). It is possible that "stressed-host species" also exist for root-feeders, warranting a one generation only strategy. Also, Elateridae generally exhibit short larval development time (~1 year). Changes observed in the herbaceous and shrub layers and the arrival of more competitive but slowly dispersing species in years following the fire probably also affect many species (Wikars, 1994).

### 4.3. Effects of ecological variables on habitat use in burned stands

Even if our stand groups exhibited contrasting structures, their respective Coleoptera assemblages did not greatly differ from one another, either in species composition or activity level. These results are most surprising for wood-feeding species. Tree caliber is usually an important factor in host selection for several xylophagous groups (Zhang et al., 1993; Hanks, 1999). Bigger trees mean higher wood volumes for wood-borers, and the thicker bark usually offers better conditions for egg-laying, especially when burned (Gardiner, 1957; Zhang et al., 1993). The Scolytid *P. rufipennis* was the only xylophagous species to favour older stands. However, the two other dominant wood-feeders captured in our study were small, subcortical Cerambycid species (*A. proteus*; *G. pratensis*). Tree diameter may be less important for species feeding exclusively in the subcortical region (Gardiner, 1954; Wikars, 1992). Larger, more structuring species, like *Monochamus* and *Tetropium*, were common on the site as seen in a concomitant rearing experiment, but they may have been less efficiently sampled by our flight-interception traps. As for the poorly known soil-living Elaterids, we can speculate that they either feed on roots of fire-killed spruce, or on roots of the fire-favored species of *Vaccinium* (Ericaceae). In either case, we have no indications that the quality or the availability of these resources differ accordingly to stand age.

Among the other variables incorporated in the CCA, sampling year and the percentage of unburned forest in a 250 m radius had important effects. The percentage of unburned forest in a 250 m radius had divergent effects on fire-associated taxa and habitat generalists using both burned and unburned stands. Several Cryptophagidae, Lathridiidae, Nitidulidae and Staphylinidae were common to both types of stands. Although they were sometimes abundant in burned stands, the proximity of unburned forest was significant in explaining their number of captures. Several of these groups feed primarily on fungi or decaying organic matter (Dajoz, 1998), resources that can be abundant in burned forests (Wikars, 1994; Dajoz, 1998). Some mycetophagous taxa probably find suitable habitat in burned forests, but are restricted in their distribution by limited dispersal capabilities (see Jonsell et al., 1999). Since fungi and decaying organic matter are generally abundant in mature forests, long-distance dispersal and sensorial capabilities were probably not selected as predominant life history traits in their evolutionary process (Jonsson, 2000).

Other parameters seemingly had limited effects that were restricted to specific groups or species. Some Elateridae, especially in the genus *Ampedus*, did favour younger stands, and seemed closely tied to stump densities. Most of the Elaterid genus *Ampedus* is composed of saproxylic species (Nilsson and Baranowski, 1997). Higher number of captures observed in younger burned stands could be related to higher availability of decaying wood (logs and stumps) left by clearcuts.

### *4.4. On the conservation of burned forest ecosystems*

Our results demonstrate that fire-associated Coleoptera assemblages are fundamentally different from those found in similar unburned forests. Although post-fire Coleoptera assemblages harbor several species sometimes found in other types of disturbances (i.e. *Monochamus* species, *C. triundulata*, *P. rufipennis*), forest fires are by far the most important disturbance in black-spruce dominated landscapes of northeastern Canada. Forest fires also differ from other stand replacement disturbances by the mechanisms leading to colonization, as the smoke plume generally travels much longer distances than host volatiles could.

There are currently no management guidelines regularizing salvage logging operations in the province of Quebec. Our results indicate that younger burned stands generally left behind by salvage logging operations could be adequate habitat for some fire-associated insect species. However, these stands are probably not suitable for deep-boring species or other organisms which need high caliber dead trees to complete their life cycles. Moreover, we currently have no understanding of the impact of the loss of a sensible fraction of the population due to salvage logging, which transforms source habitats to sinks, on the long-term persistence of these species. Although more studies are needed to draw a more comprehensive portrait of post-disturbance insect communities in the boreal forest, we believe we should be conservative in our management approach concerning recently burned stands.

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