CSIRO PUBLISHING

International Journal of Wildland Fire **2010**, *19*, 500–511 www.publish.csiro.au/journals/ijwf

Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds

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Abstract. Fire severity can vary greatly within and among burns, even in the Canadian boreal forest where fire regimes consist mostly of stand-replacing fires. We investigated the effects of fire severity on the long-term occupancy of burns by (i) saproxylic insects and (ii) three wood-foraging birds. Based on observations made 6 to 11 years after fire in burned conifer forests that varied in fire severity in Quebec, Canada, our results indicate that low-severity portions of the burns likely provided snag conditions suitable for the long-term presence of deadwood-associated insects and birds. The black-backed woodpecker, a post-fire forest specialist, was still abundant 6 and 8 years after fire. This pattern was likely explained by the persistence of several saproxylic insect species that are associated with recently dead trees and by the positive effect of lower fire severity on the abundance of *Arhopalus foveicollis*, a cerambycid with a long life cycle in dead wood. The American three-toed woodpecker and the brown creeper, and their associated prey (Scolytinae beetles), were more abundant in burned stands of lower *v.* higher severity. We conclude that less severely burned snags and stands within high-severity burns may favour the long-term presence of trophic webs that involve saproxylic insects and wood-foraging birds in burned boreal forests.

Additional keywords: American three-toed woodpecker, *Arhopalus foveicollis*, black-backed woodpecker, black spruce, brown creeper, Cerambycidae, *Certhia americana*, *Picoides arcticus*, *Picoides dorsalis*, Scolytinae.

Introduction

Fires in the boreal forest are typically characterised as severe stand-replacing disturbances that cause widespread tree mortality (Brown and Smith 2000; Bergeron *et al.* 2002). However, recent studies indicate these fires may vary spatially in their severity, leaving varying proportions of stands unburned or partially burned (Kafka *et al.* 2001; Bergeron *et al.* 2002; Schmiegelow *et al.* 2006). In eastern Canadian boreal forests, for example, zones of low burn severity where unburned trees dominate can comprise over 50% of the area affected by fire (Bergeron *et al.* 2002; Chabot *et al.* 2009). Such variation in fire severity can have a profound influence on forest dynamics and on the post-fire response of vegetation (Purdon *et al.* 2004; Jayen *et al.* 2006; Macdonald 2007) and wildlife (Smucker *et al.* 2005; Koivula and Spence 2006; Schmiegelow *et al.* 2006).

Burned forests represent high-quality habitats for many deadwood-dependent species (Hutto 1995; Wikars 2002; Hannon and Drapeau 2005; Saab *et al.* 2005; Nappi and Drapeau 2009). Wildfires, especially when severe, can generate sudden and massive increases in the availability of dead wood. High abundance and nutritional quality of fire-killed trees often lead to increased concentrations of wood-boring and bark beetle populations (Saint-Germain *et al.* 2004*a*, 2004*b*), which in turn attract wood-foraging birds such as several woodpecker species (Murphy and Lehnhausen 1998; Hoyt and Hannon 2002; Nappi *et al.* 2003; Koivula and Schmiegelow 2007).

Fire severity can affect both quantity and quality of fire-created snags and thus the response of deadwood-associated species to fire. For example, many deadwood-specialists respond positively to the increased availability of snags brought on by high-severity fire (Koivula and Schmiegelow 2007; Hutto 2008). At the same time, fire severity at the individual tree scale (e.g. trunk charring) can affect the quality of snags for saproxylic insects (i.e. species that are dependent on dead wood at least at some stage of their life cycle; Saint-Germain *et al.* 2007*b*) and thus for foraging woodpeckers. For example, severely scorched black spruce (*Picea mariana*) trees may support lower densities of saproxylic insects than more lightly affected trees (Nappi *et al.* 2003; Saint-Germain *et al.* 2004*b*). Therefore, the availability of suitable dead wood substrates may decrease beyond a certain threshold of fire severity.

 10.1071/WF08109 1049-8001/10/040500

Although several studies have documented the short-term effects of fire severity on saproxylic insects (Gardiner 1957; Ross 1960; Saint-Germain *et al.* 2004*b*) and wood-foraging birds (Murphy and Lehnhausen 1998; Koivula and Schmiegelow 2007), few have investigated the effect of fire severity on the long-term occupancy of burned forests by these species. Saint-Germain *et al.* (2007*b*) found that colonisation of black spruce snags by wood-feeding insects is generally limited to the early stages of snag degradation. As most trees die rapidly after severe fire, the presence of such insects is generally limited to the first few years after fire (Werner 2002; Saint-Germain *et al.* 2004*b*; Boulanger and Sirois 2007); this is also the case for wood-foraging birds (Murphy and Lehnhausen 1998; Nappi and Drapeau 2009). However, occupancy by these species may be quite different following fires of lower severity (i.e. fires that leave significant portions of partially burned stands). For example, tree mortality in less severely burned stands can be significantly delayed (Gardiner 1957; Dixon *et al.* 1984), thereby extending the availability of recently dead trees for saproxylic insects.

This study investigates the influence of fire severity on long-term occupancy of burned forests by deadwood-associated species based on observations made 6 to 11 years after fire in two burns that showed high variability in burn severity. Our main objectives were to (i) determine the presence and abundance of saproxylic insects and wood-foraging birds in these old burned forests, and (ii) assess the influence of within-burn variability in fire severity on the occupancy patterns of these deadwood-associated species. We hypothesised that lower fire severity in portions of these burned landscapes would contribute to the long-term presence of saproxylic insects and wood-foraging birds that are typically associated with initial post-fire conditions in high-severity burned forests.

Methods

Study area

This study was conducted in the black spruce–moss bioclimatic domain of north-western Quebec, Canada (Saucier *et al.* 1998; Fig. 1). Fire is the main natural disturbance in the region, which has and continues to experience the shortest fire cycle of Quebec's spruce–moss boreal forest (Lefort *et al.* 2004; Bergeron *et al.* 2006). The current fire cycle (1945–98) for the region is estimated at 136 years (Lefort *et al.* 2004). Forest cover of the study sites was codominated by black spruce and jack pine (*Pinus banksiana*). Other tree species included white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*) and tamarack (*Larix laricina*).

We selected burn sites according to several criteria. Burns had to be more than 5 years old, dominated by mature conifer stands, heterogeneous in burn severity, not or only lightly salvage-logged and accessible. Only two burns in the region met all these criteria. These represent two of several major fires that started in June 1996 and were located ~100 km north-west of the city of Chibougamau (Fig. 1). The largest of the two fires (Fire 392) started on 11 June and covered 24 995 ha between 50°15′ and 50°32′N and between 75°40′ and 75°50′W. The second fire (Fire 481) occurred ~5 km south-east of the first; it started on 12 June and burned 4641 ha. The area affected by the fires was composed mostly of mature stands of commercial value (>70 years). The two burned sites were considered together as they originated more or less simultaneously, were close to each other, and were similar in their prefire composition and fire severity patterns (Table 1).

A general assessment of the severity of these fires can be provided by the 'fire impact' evaluation made by the Quebec Ministry of Natural Resources and Wildlife (MNRW). Fire impact maps are made in the first weeks following fire via aerial surveys and provide a short-term evaluation of fire severity based on tree damage (green trees with intact crowns, trees with reddish crowns, charred trees with burned crowns, blowdown trees). Stands are classified into six fire impact classes based on the relative percentage of each tree damage category (based on percentage of crown cover; Table 1). The fire impact maps showed that the two burns were highly variable in fire severity and contained important proportions of partially burned stands (Table 1, Fig. 1). In both cases, approximately half of the burned landscape consisted of burned stands with a dominance of green trees (i.e. light impact class).

Vegetation sampling

A total of 80 sampling stations (60 in Fire 392 and 20 in Fire 481) were distributed at least 500 m apart within the burns. Fire impact maps were used to distribute these sampling stations and thereby ensure adequate representation across the full range of variation in fire severity. The MNRW fire impact evaluation only focusses on short-term effects of fire at a coarse resolution (>1 ha). To evaluate fire severity many years after fire (i.e. considering the subsequent mortality of trees) and at finer scales (stand and individual tree scales), we measured fire severity at these sampling stations in 2002 (6 years post-fire).

At each sampling station, vegetation measurements were taken within five 25-m-radius circular plots. The first plot was centred on the sampling station whereas the other plots were placed at 50 m from the centre of the station in each of the four cardinal directions. For each variable, the mean over the five plots was used in further analyses. Fire severity was estimated as the percentage of dead crown cover. Based on this percentage, each of the 80 sampling stations was then attributed to one of the following fire severity classes: unburned (0% dead), low (1–50%), moderate (51–99%) and high (100%). This classification of fire severity was further used for vegetation, insect and bird comparisons at the stand scale. Because we were interested in the characteristics of burned trees in relation to fire severity, we also measured the following four variables:

- Tree condition – proportion of trees in each of three classes of degradation: live trees, declining trees (alive but <20% of foliage intact, or broken top or other signs of severe damage), dead trees;
- Trunk charring – proportion of trees in each of four classes based on the percentage of trunk charred: uncharred, lightly charred (1–40% of the trunk charred), moderately charred (41–95% of the trunk charred) and severely charred (96–100% of the trunk charred);
- Bark loss – proportion of trees in each of four classes based on the percentage of bark lost (25% classes);
- Tree species – proportion of trees that were black spruce or jack pine.

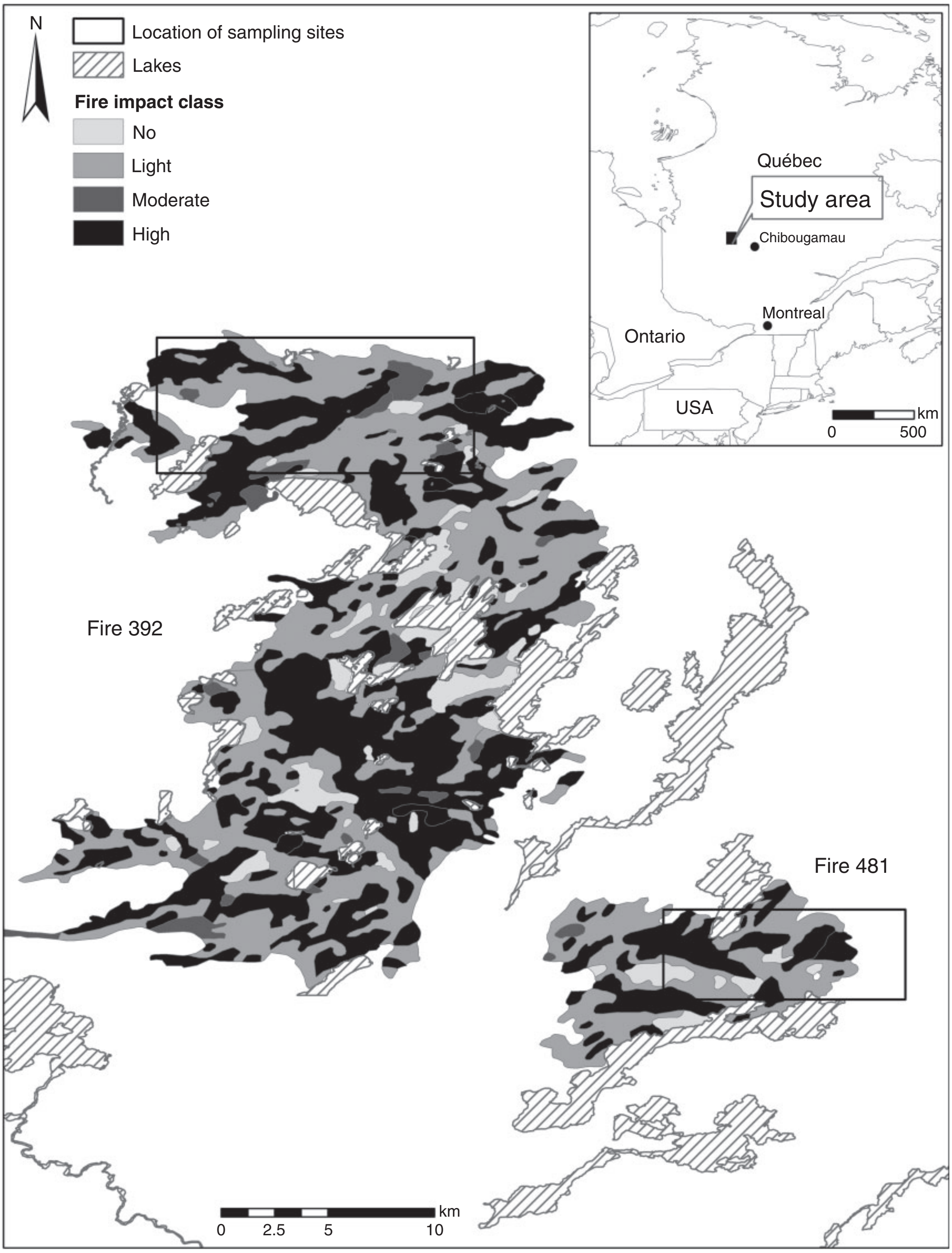

Fig. 1. Fire impact maps and location of the two studied burns in Quebec, Canada. See Table 1 for descriptions of the fire impact classification.

Insect sampling

To identify the saproxylic insect species present in these burned areas and to investigate the effect of fire severity on their abundance at the stand scale, we captured insects using Lindgren funnel traps (Phero Tech Inc., Delta, BC, Canada) baited with semiochemical lures (α-pinene, ethanol and ipsenol). Semiochemicals were used to maximise catch rates of wood-feeding taxa that are often underrepresented in datasets collected through passive sampling (Chénier and Philogène 1989; Allison *et al.* 2001; Saint-Germain *et al.* 2006, 2007*a*). A total of 11 traps were placed in 2004 (8 years post-fire) at a subset of sampling stations selected to cover both low- and high-severity fire classes. Traps were set on

Table 1. Area covered by each fire impact class for the two studied burns

Fire impact class	Description	Fire 392		Fire 481	
		Area (ha)	Percentage of total area	Area (ha)	Percentage of total area
No impact	Patches of green trees (not affected by fire)	1642	6.6	397	8.6
Light impact	Mixed patches (green trees > trees with reddish crowns)	10 743	43.0	2394	51.5
Moderate impact	Mixed patches (trees with reddish crowns > green trees)	886	3.5	53	1.1
High impact (1)	Trees with reddish crowns and generally <25% blowdown	84	0.3	0	0.0
High impact (2)	Charred trees with burned crowns, often with detached bark; generally <40% blowdown	11301	45.2	1562	33.7
High impact (3)	Charred trees with burned crowns, bark is detached; generally >40% blowdown	339	1.4	235	5.1
Total fire area		24 995	100.0	4641	100.0

10 June using propylene glycol as preservative fluid and were emptied twice during the summer (15 July and 13 August).

Although indirect sampling techniques such as funnel traps are useful to document insect assemblages at the stand level, they may not provide an accurate portrait of the saproxylic insects present in the wood and cannot be used to investigate adequately the effect of tree-level variables (Saint-Germain *et al.* 2007*b*). Therefore, we used snag dissection to more precisely identify insect species present in burned snags and measure the influence of tree species and fire severity on insect abundance at the tree scale.

Two series of logs were dissected to investigate occurrence patterns of saproxylic insects. The first dissection series was conducted in 2004 (8 years post-fire) to identify and compare the abundance of saproxylic insects between black spruce and jack pine. We selected 10 trees of each of the two species in close proximity to funnel traps for wood dissection. Seven of these trees were observed being used by foraging black-backed woodpeckers and all sampled trees were located in known foraging areas. The effect of fire severity was controlled by selecting only lightly charred trees (burned at their base only, <40% charred, bark fully intact) of similar diameter (range 10.7–20.7 cm of diameter at breast height, dbh). With the second series of dissection, we evaluated the effect of fire severity on abundance of saproxylic insects. This was done in the summer of 2007 (11 years post-fire) in the same sector previously sampled. We selected 24 black spruce trees (range 15.9–30.9 cm dbh) showing contrasting levels of fire severity (12 lightly and 12 severely charred trees). In contrast to lightly charred trees, severely charred trees had lost most of their bark (>75%) with any remaining bark being completely charred. Overall, a total of 44 trees were used for wood dissection.

Tree felling and dissection took place between mid-June and mid-July. Each tree was felled and a 1-m bole segment was taken from the base (0–1 m above ground). These bole segments were put in plastic bags and taken to the laboratory for dissection. Bark was carefully removed and all larvae and adult invertebrates were collected. Segments were then cut into smaller pieces with hatchets, following insect galleries, and all insects found were collected. Specimens were conserved in 70% ethanol for preservation and later identified to family, genus or species.

Bird sampling

We examined the effect of fire severity on three bird species: the black-backed woodpecker (*Picoides arcticus*), the American three-toed woodpecker (*Picoides dorsalis*) and the brown creeper (*Certhia americana*). These species were chosen because they colonise recent burns (Hutto 1995; Hannon and Drapeau 2005), are wood-foragers and show differences in their foraging ecology and prey preferences (Murphy and Lehnhausen 1998; Hejl *et al.* 2002) that we expected would influence their response to fire severity.

Bird censuses were conducted during the summer of 2002 (6 years post-fire) using point counts (Blondel *et al.* 1970; Drapeau *et al.* 1999) and playbacks (territorial drumming and contact calls). At 80 sampling stations, all individuals of the three species were recorded during 5-min intervals for a total of 15 min. Each point count was then followed by a 1-min playback of each species successively (separated by a 1-min silent period) for an additional period of 6 min at each station. Only contacts made within the 75-m radius were considered. Each sampling station was visited twice during the breeding season. A sampling station was considered occupied by a focal species if it was seen in at least one visit. An additional survey was conducted during the summer of 2004 (8 years post-fire) to confirm the presence or absence of black-backed woodpeckers and American three-toed woodpeckers in the burned areas. This was done by visiting once a subset of 55 sampling stations. For this survey, we used 1-min playbacks (separated by 1-min silent periods) that we played twice for each species (total of 8 min per station). Surveys were conducted from sunrise to 1000 hours during days of low wind and no rain. All surveys were conducted between early June and early July, the period of peak breeding activity for these species in the region (Nappi and Drapeau 2009).

Statistical analyses

Comparisons of tree characteristics (tree condition, trunk charring, bark loss, tree species) among fire severity classes were assessed using Kruskal–Wallis tests. For saproxylic insects, we combined stands into two classes of fire severity (because of the low number of funnel traps) and compared insect captures using Mann–Whitney tests. The low-severity class included sampling stations with green tree dominance (range in dead crown cover: 14–47%) whereas the high-severity class included stations dominated by dead trees (range in dead crown cover: 75–100%). Analyses were conducted for saproxylic taxa with >20 captures. Densities of saproxylic insects in bole segments were compared between tree species or fire severity classes using Mann–Whitney tests. Insect density was calculated as the total number of individuals per cubic metre of wood. For each bird species, differences between frequencies of occurrence among fire severity classes were assessed using log-likelihood ratio (G) tests.

Results

Fire severity and tree characteristics

Field measures of fire severity (% dead crown cover) 6 years after fire indicated that the heterogeneity reported by fire impact maps was still present many years after fire. Indeed, many forest stands were still characterised by mixed proportions of live trees and snags (Table 2). However, tree mortality at sampling stations was generally higher than what was reported by fire impact maps, especially for sampling stations originally classified within the light impact class.

Fire severity, as estimated by the percentage of dead crown cover, adequately reflected the effect of fire at the tree scale (all Kruskal–Wallis tests $P < 0.001$; Table 2). Proportion of live and declining trees tended to decrease with increasing fire severity whereas the opposite was observed for dead trees. Trunk charring was also clearly related to fire severity at the stand scale: trees that were moderately or severely charred increased in proportion from unburned to high-severity burned stands. The proportion of lightly charred trees showed a roughly modal distribution and peaked in moderate-severity burned stands. Bark loss was also well reflected by stand-level fire severity as the proportion of trees that retained their bark tended to decrease with increased fire severity. The two main tree species, black spruce and jack pine, were found in stands of all severity classes and stands were often mixed in their composition. However, there was a tendency for black spruce to increase in proportion in burned stands of lower severity. Despite these relationships between fire severity at the stand and tree scales, heterogeneity in tree characteristics was high within stands even in high-severity burned areas (i.e. total mortality). For example, even stands in moderate- and high-severity fire classes were characterised by an important proportion of trees that were lightly affected by fire (e.g. based on trunk charring or bark loss; Table 2).

Saproxylic insects

Thirty-three wood-feeding insect species belonging to the families Cerambycidae and Buprestidae, and the subfamily Scolytinae (family Curculionidae) were captured with funnel traps in the burned areas 8 years after fire (Table 3). Cerambycidae alone accounted for 71% of all captures of these three taxa and included mainly *Rhagium inquisitor* (L.), *Monochamus scutellatus* (Say), *Acmaeops proteus* (Kirby) and *Arhopalus foveicollis* (Haldeman). Together, these four species represented 88% of all Cerambycidae. The most abundant Scolytinae species were *Hylastes porculus* (Erichson), *Scolytus piceae* (Swaine) and *Polygraphus rufipennis* (Kirby), which accounted respectively for 52, 21 and 11% of insects belonging to this subfamily. Only eight Buprestidae individuals belonging to three species were collected. Bark beetle predators *Thanasimus dubius* (F.) and *Thanasimus undulatus* (Say) (Cleridae) were also abundantly captured throughout the burned areas. These two species represented 39% of all insects collected.

Table 2. Tree characteristics for different classes of fire severity based on field estimates 6 years after fire

Fire severity classes: unburned (0% of crown cover dead), low (1–50%), moderate (51–99%) and high (100%). Values are means (±1 s.e.)

Tree characteristics (percentage of trees in the stand)	Fire severity in forest stands of crown cover: Unburned ($n = 10$)		Low ($n = 17$)		Moderate ($n = 32$)		High ($n = 21$)	
Tree condition								
Live	84.1	(2.3)	60.6	(2.8)	17.7	(2.6)	0.1	(0.1)
Declining	8.7	(2.0)	8.0	(1.5)	4.1	(0.8)	0.4	(0.2)
Dead	7.1	(1.4)	31.3	(2.6)	78.2	(3.1)	99.6	(0.2)
Trunk charring								
Uncharred	99.4	(0.4)	64.0	(4.7)	14.7	(2.4)	0.0	(0.0)
Lightly charred	0.4	(0.3)	18.4	(3.0)	27.4	(3.3)	9.2	(2.1)
Moderately charred	0.1	(0.1)	10.3	(1.9)	33.2	(2.7)	38.8	(4.5)
Severely charred	0.1	(0.1)	7.2	(1.8)	24.7	(3.5)	52.0	(6.0)
Bark loss								
<26% of bark lost	97.5	(0.8)	88.7	(2.1)	60.7	(3.5)	20.7	(3.4)
26–50% of bark lost	1.1	(0.5)	5.4	(1.4)	17.8	(1.5)	23.2	(2.2)
51–75% of bark lost	0.7	(0.2)	2.5	(0.5)	12.9	(1.6)	27.3	(2.2)
>75% of bark lost	0.6	(0.2)	3.3	(1.2)	8.5	(1.8)	28.8	(3.8)
Tree species								
Black spruce	84.3	(5.8)	75.9	(6.1)	50.5	(5.2)	44.3	(6.8)
Jack pine	11.1	(5.5)	22.0	(6.3)	47.4	(5.5)	55.1	(6.8)

Table 3. Saproxylic insects captured in Lindgren funnel traps ($n = 11$) 8 years after fire

Effect of fire severity at the stand scale was assessed for taxa in bold

Taxon	Total number	Percentage of total
Cerambycidae	514	38.0
Acanthocinus pusillus	2	0.1
Acmaeops proteus	**79**	**5.8**
Anastrangalia sanguinea	4	0.3
Arhopalus foveicollis	**46**	**3.4**
Asemum striatum	2	0.1
Cosmosalia chrysocoma	5	0.4
Evodinus monticola	5	0.4
Gnathacmaeops pratensis	17	1.3
Monochamus mutator	9	0.7
Monochamus scutellatus	**142**	**10.5**
Neoclytus leucozonus	0	0.0
Pygoleptura nigrella	2	0.1
Rhagium inquisitor	**187**	**13.8**
Tetropium cinnamopterum	1	0.1
Tetropium n. sp.	5	0.4
Trachysida mutabilis	1	0.1
Xylotrechus undulatus	7	0.5
Buprestidae	8	0.6
Chrysobothris sp.	1	0.1
Dicerca sp.	5	0.4
Melanophila fulvoguttata	2	0.1
Curculionidae	282	20.9
Dendroctonus rufipennis[A]	1	0.1
Dryocoetes autographus[A]	4	0.3
Hylastes porculus[A]	**107**	**7.9**
Ips latidens[A]	3	0.2
Ips perroti[A]	11	0.8
Ips perturbatus[A]	1	0.1
Ips pini[A]	1	0.1
Orthotomicus caelatus[A]	4	0.3
Pityokteines sparsus[A]	2	0.1
Pityophthorus sp.[A]	4	0.3
Polygraphus rufipennis[A]	**23**	**1.7**
Procryphalus utahensis[A]	1	0.1
Scolytus piceae[A]	**43**	**3.2**
Scolytinae total	**205**	**15.2**
Pissodes sp.	76	5.6
Not identified	1	0.1
Cleridae	547	40.5
Thanasimus dubius	265	19.6
Thanasimus undulatus	267	19.7
***Thanasimus* spp. total**	**532**	**39.3**
Enoclerus sp.[B]	15	1.1
Anobiidae	1	0.1
Microbregma abbreviata	1	0.1
Total	1352	100.0

[A]Subfamily Scolytinae.
[B]Likely *Enoclerus* sp. but identification uncertain.

The effect of fire severity at the stand scale was assessed on total Cerambycidae, total Scolytinae, total *Thanasimus* spp. and seven individual species (Table 3). No differences between burned stands of low- and high-severity classes were found in total captures of Cerambycidae (Mann–Whitney test, $Z = -0.367$, $P = 0.714$; Fig. 2) or in captures of individual cerambycid species. Scolytinae abundance was higher in low- than in high-severity burned stands, although this difference was only marginally significant (Mann–Whitney test, $Z = -1.826$, $P = 0.068$; Fig. 2). Each individual Scolytinae species tested was more abundant in low- than in high-severity burned stands, although these differences were not significant except for *Polygraphus rufipennis*, for which the difference was marginally significant (Mann–Whitney test, $Z = -1.768$, $P = 0.077$). Trends in Scolytinae abundance were supported by similar effects of fire severity on bark beetle predators *Thanasimus* spp. (Mann–Whitney test, $Z = -2.739$, $P < 0.01$; Fig. 2).

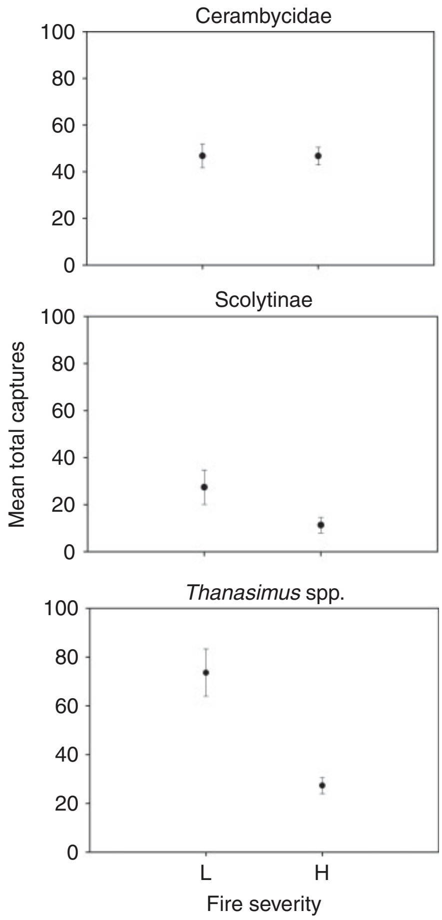

Fig. 2. Captures of Cerambycidae, Scolytinae (Curculionidae family) and *Thanasimus* spp. (*T. dubius* and *T. undulates*; Cleridae family) in Lindgren funnel traps for burned stands of low (L; $n = 5$) and high (H; $n = 6$) severity 8 years after fire. Numbers represent mean captures (±1 s.e.).

Most specimens captured from the bole segments 8 years after fire (snag dissection) were *Arhopalus foveicollis* (95% of all Cerambycidae; Table 4). We observed no significant difference in total Cerambycidae densities between lightly charred jack pine and black spruce 8 years after fire (Mann–Whitney test, $Z = -0.076$, $P = 0.939$; Fig. 3). *A. foveicollis* was also the main species collected from the bole segments 11 years after fire: these insects were found in different stages (adults, larvae and pupa) and represented 78% of all Cerambycidae captured (Table 4). Lightly charred spruce snags contained

Table 4. Saproxylic insects captured in 1-m bole segments of snags collected 8 years (2004 boles) and 11 years (2007 boles) after fire

Taxon	2004 boles ($n = 20$)		2007 boles ($n = 24$)	
	Total number	Percentage of total	Total number	Percentage of total
Cerambycidae	140	68.0	41	85.4
Acmaeops proteus	1	0.5	0	0.0
Anastrangalia sanguinea	1	0.5	0	0.0
Arhopalus foveicollis	133	64.6	32	66.7
Stictoleptura canadensis	0	0.0	8	16.7
Trachysida sp.	0	0.0	1	2.1
Lamiinae	2	1.0	0	0.0
Not identified	3	1.5	0	0.0
Buprestidae	2	1.0	0	0.0
Cleridae	2	1.0	0	0.0
Elateridae	1	0.5	0	0.0
Melandryidae	2	1.0	0	0.0
Salpingidae	16	7.8	0	0.0
Staphylinidae	2	1.0	0	0.0
Formicidae[A]	26	12.6	0	0.0
Others	15	7.3	7	14.6
Total	206	100.0	48	100.0

[A]Often found in colonies. Real abundance was higher than reported.

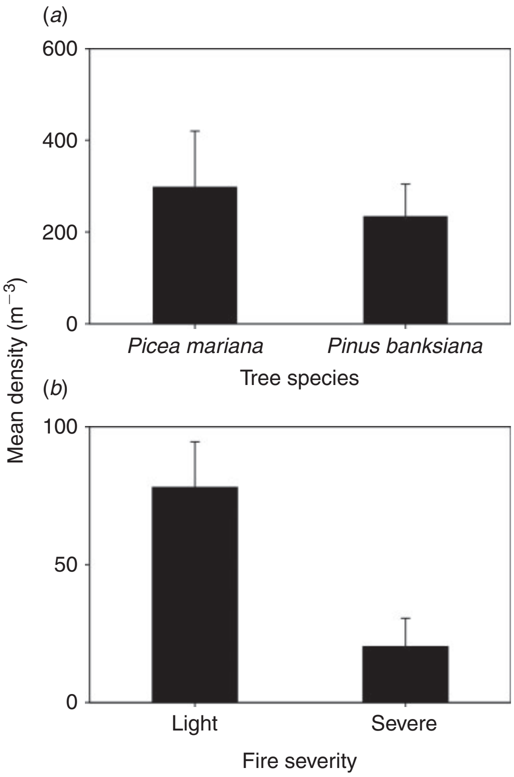

Fig. 3. Density of total Cerambycidae for (*a*) dissected bole segments from lightly charred black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) trees collected 8 years after fire ($n = 20$); and (*b*) dissected bole segments from lightly and severely charred spruce trees collected 11 years after fire ($n = 24$). Bars represent mean densities (+1 s.e.).

higher numbers of Cerambycidae when compared with severely charred ones (Mann–Whitney test, $Z = -2.5$, $P < 0.05$; Fig. 3).

Wood-foraging birds

Six years after fire, the black-backed woodpecker was detected at 74% of the sampling stations. This species was the most abundant of the three wood-foraging species studied in the burned landscapes, representing 77% of all individuals detected. Although the black-backed woodpecker was more abundant in burned than unburned stands 6 years after fire ($G = 5.9$, d.f. $= 1$, $P < 0.05$), no significant difference in occurrence was observed among burned stands of different fire severity classes ($G = 2.0$, d.f. $= 2$, $P = 0.377$, Fig. 4). Despite lower sampling effort in 2004 (8 years post-fire), this species was nevertheless detected at 27% of sampling stations. No difference in occurrence was observed among burned and unburned stands ($G = 2.6$, d.f. $= 1$, $P = 0.108$) or among burned stands of different fire severity classes 8 years after fire ($G = 4.2$, d.f. $= 2$, $P = 0.123$).

The American three-toed woodpecker was rarely observed in our burned landscape. We observed only five American three-toed woodpeckers in 2002 (6 years after) and none in 2004 (8 years after fire). Although no significant difference in occurrence was found among the four classes of fire severity in 2002 ($G = 2.1$, d.f. $= 3$, $P = 0.553$; Fig. 4), the few observations of these birds were made in burned stands of low and moderate severity. The brown creeper was detected at 23% of the sampling stations 6 years after fire. Occurrence of this species decreased with increasing fire severity ($G = 11.6$, d.f. $= 3$, $P < 0.01$; Fig. 4).

Discussion

The burned forests we studied were characterised by high variability in tree characteristics many years after fire, which

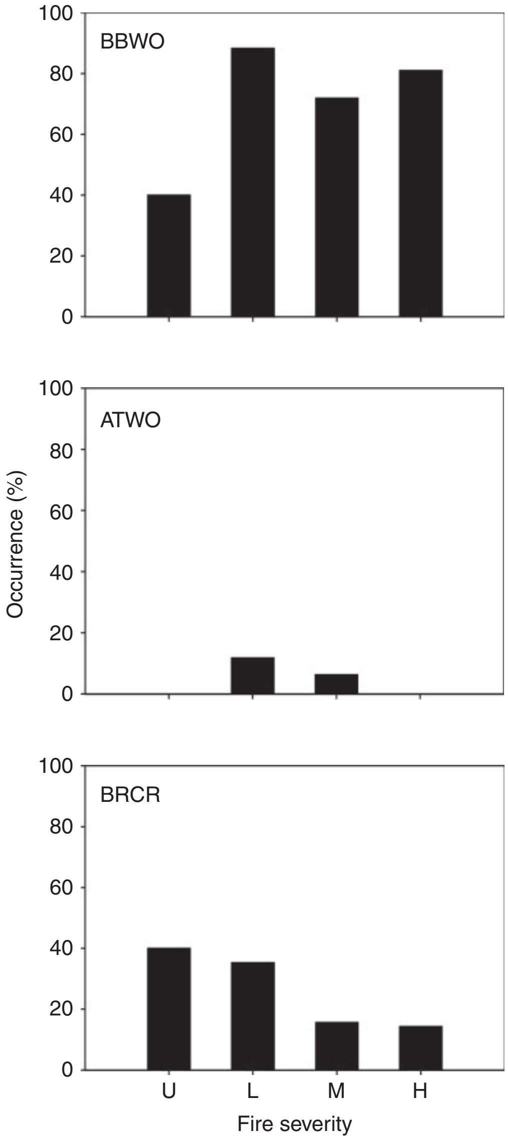

Fig. 4. Percentage of occurrence of the black-backed woodpecker (BBWO), the American three-toed woodpecker (ATWO) and the brown creeper (BRCR) in unburned stands (U; $n = 10$) and burned stands of low (L; $n = 17$), moderate (M; $n = 32$) and high (H; $n = 21$) severity 6 years after fire.

likely affected habitat conditions for saproxylic insects and wood-foraging birds. An important portion of these burns was covered by burned stands of low and moderate severity that supported mixed proportions of live, declining and dead trees. Conditions of snags were also very variable, these being affected to varying degrees by fire, even in high-severity burned stands (i.e. stands characterised by total tree mortality). Our results show that the low fire severity in some portions of these burns likely contributed to their long-term occupancy by wood-foraging birds and saproxylic insects, many of which have been typically associated with initial post-fire habitat conditions following severe stand-replacing fires (references below).

The black-backed woodpecker was the most abundant of the three bird species examined in these old burns. The black-backed woodpecker is a well-known fire specialist that typically occupies recently burned North American conifer forests (Hutto 1995, 2008; Murphy and Lehnhausen 1998; Saab *et al.* 2007). The high abundance of this woodpecker in recently burned forests is tightly linked to the high densities of saproxylic insects in burned conifer trees (Nappi *et al.* 2003; Saint-Germain *et al.* 2004*b*), in particular the cerambycid *Monochamus scutellatus*, which is often the black-backed woodpecker's main prey (Villard and Beninger 1993; Murphy and Lehnhausen 1998; Nappi and Drapeau 2009). In the North American boreal forest, the population decrease of black-backed woodpeckers in high-severity burned forests has been linked to the decrease of this insect in the first 3 years following fire (Nappi and Drapeau 2009). We found a relatively high abundance of the black-backed woodpecker 6 and 8 years after fire, a pattern that contrasts sharply with the short-term occupancy of this species documented in burns of the boreal spruce forest (Murphy and Lehnhausen 1998; Nappi and Drapeau 2009; but see Hoyt and Hannon 2002). This high abundance suggests that the lower severity of these burns provided extended foraging opportunities for this species. Our results suggest two factors that were likely responsible for this prolonged occupancy of the black-backed woodpecker.

First, our results suggest that the lower fire severity in some portions of the burns created delayed tree mortality, which likely maintained appropriate tree hosts for many saproxylic insects, thereby contributing to their long-term occupancy of these burns. Indeed, the presence of live trees in a declining stage in low- and moderate-severity stands shows that tree mortality was still ongoing within the burned landscapes. Many of the wood-feeding species we captured in these 8-year-old burns, such as *Acmaeops proteus*, *Monochamus scutellatus* and *Polygraphus rufipennis*, are typically associated with early post-fire conditions (Gardiner 1957; Saint-Germain *et al.* 2004*a*, 2004*b*; Boulanger and Sirois 2007). For instance, 11 of the 17 species of Cerambycidae and 9 of the 13 species of Scolytinae collected at our sites were also captured the first year following a severe fire in a conifer forest ~500 km south-east of our sites (Saint-Germain *et al.* 2004*a*). Most coniferophagous wood-feeding Coleoptera found in the Canadian eastern boreal forest, including the aforementioned species, are closely associated with the very first stages of decay of their tree hosts (Saint-Germain *et al.* 2007*b*). In experimental trials, ovipositing females of *Monochamus* rejected hosts that had been dead for over 1–2 months (Alya and Hain 1985). This association is likely due, in most cases, to the dependence of early-instar larvae on simple sugars still found in recently dead subcortical tissues. Most species we captured frequently have life cycles of at most 3 years (i.e. *Monochamus* in colder climate; Rose 1957). Therefore, the fact that these species were captured 8 years after fire in such abundance suggests that appropriate hosts (i.e. recently dead trees) were still available through delayed mortality several years after fire in these burned landscapes.

The second factor likely responsible for the long-term occupancy of the black-backed woodpecker was the high abundance of *Arhopalus foveicollis*. This insect was, by far, the most abundant saproxylic insect found in dissected snags, many of which were used by foraging woodpeckers before dissection. Larvae of this species were mostly longer than

1 cm, thus representing a substantial food resource for black-backed woodpeckers. Very little is known of the habits and life history of this species (formerly *A. agrestis*), but it was also found in recent burns in northern Ontario (Gardiner 1957) and in northern Quebec (Boulanger and Sirois 2007), suggesting an association of this cerambycid with post-fire forest conditions. The closely related *Arhopalus tristis* responds to smoke compounds of burned pines (Suckling *et al.* 2001) and colonisation by *Arhopalus* spp. typically occurs in the first weeks after tree death (Chararas 1981). The life cycle of *A. foveicollis* is not well known but we collected high numbers in burned trees 8 and 11 years after fire. Because most of the burned trees used for wood dissection likely died in the year following fire (based on dendrochronological analysis; Nappi 2009), this suggests that *A. foveicollis* larvae may remain in the wood for a much longer period (up to at least 11 years) than many other cerambycids.

Fire severity, at the tree scale, had a significant effect on the abundance of Cerambycidae larvae (the majority of these being *Arhopalus foveicollis*). The effect of fire severity on host quality (i.e. burned snags) for immediate colonisers has been well documented (Richmond and Lejeune 1945; Ross 1960; Furniss 1965; Saint-Germain *et al.* 2004*b*). For instance, spruce snags with less bark char are typically more efficient in keeping phloem and cambium moist and are thus more attractive to saproxylic insects (Ross 1960; Furniss 1965; Saint-Germain *et al.* 2004*b*). However, few studies have investigated the long-term effect of fire severity on host quality. Fire severity may influence the decay process itself, and thus host quality in the longer term for species with larval development that spans several years (e.g. *A. foveicollis*). In our study, severely charred trees typically lost their bark earlier than lightly charred trees. Maintenance of bark cover can alleviate variations in temperature and water content of underlying woody tissues – both these factors affect wood-boring beetles by influencing survival rates of larvae or fitness of survivors (Savely 1939; Chararas 1981; Hanks *et al.* 2005). Higher numbers of Cerambycidae in lightly *v.* severely charred spruce snags could be explained either by a higher density of colonists following fire or by lower mortality rates of insects in lightly charred snags. In any case, our results suggest fire severity at the tree scale may have an important influence on the long-term abundance of species with long life cycles such as *A. foveicollis*.

In burned forests of Alberta, Hoyt and Hannon (2002) also found a high abundance of black-backed woodpeckers 8 years after fire. They attributed this result to the presence of jack pines that they hypothesised could survive longer and provide more suitable conditions for wood-borers. Although the thicker bark of pines may be more efficient than spruce in preserving moist conditions for saproxylic insects (Gardiner 1957; Saint-Germain *et al.* 2004*b*), we found no effect of tree species on densities of Cerambycidae (i.e. mostly *Arhopalus foveicollis*) in lightly charred trees. We did not investigate differences between severely charred jack pine and black spruce, but we observed similar external wood conditions (extensive bark loss, high desiccation) for severely burned trees of these two species, which suggests the effect of increased protection in jack pine may be limited. Although more studies are needed to clarify the interaction of tree species and fire severity on the long-term quality of wood substrates for saproxylic insects, our results emphasise that less-severely burned trees of both species (black spruce and jack pine) are more likely to provide suitable foraging substrates for woodpeckers in the long term.

The presence of suitable foraging trees (i.e. recently dead and less severely charred trees) likely contributed to the overall high abundance of the black-backed woodpecker within the burned landscapes. Contrary to our expectations, however, we found no effect of fire severity on the abundance of this species at the stand scale. This pattern may be, in part, explained by the widespread distribution of lightly and moderately charred trees in burned stands of all severity: foraging trees that contained *Arhopalus foveicollis* were thus present in similar abundance within or in proximity to most sampling stations. We also observed no effect, at the stand scale, of fire severity on the abundance of total or individual cerambycid species, although we would have expected some of these species to be more abundant in low-severity (where recent snags are more likely to occur) than high-severity burned stands. This may be explained by our sampling approach (funnel traps likely captured insects in dispersal; Saint-Germain *et al.* 2006; Webb *et al.* 2008) and the relative inefficiency of cerambycids in identifying the sources of local host volatiles (host finding may thus require more dispersal in this family; Saint-Germain *et al.* 2007*a*).

The black-backed woodpecker has been typically associated with high-severity burned forests (Koivula and Schmiegelow 2007; Hutto 2008). Indeed, high snag densities within severely burned stands (i.e. stands with total tree mortality) provide, immediately after fire, important concentrations of potential foraging trees for this deadwood-dependent species. In the long term, however, some high-severity burned stands that only provide severely charred trees are not likely to represent suitable foraging habitat for this species. Although partially burned stands (i.e. stands with mixed proportions of live trees and snags) may provide less foraging opportunities in the short term than high-severity burned stands, prolonged recruitment of recent snags and relatively higher proportions of lightly charred trees in such stands likely maintain suitable habitat conditions over the longer term for saproxylic insects, and thus, for the black-backed woodpecker. Therefore, our results suggest that burned forests of lower severity represent an important long-term habitat for the black-backed woodpecker that contributes to the presence of this species within high-severity burned landscapes beyond the first few post-fire years.

The American three-toed woodpecker was rarely observed in our burned landscapes. Although this species has often been reported in recent burns, this woodpecker is generally associated with old-growth forests (Hutto 1995; Imbeau *et al.* 1999; Hoyt and Hannon 2002; Imbeau and Desrochers 2002). Because of the short fire cycle in our study region (Lefort *et al.* 2004; Bergeron *et al.* 2006), old-growth forests occupy a smaller proportion of the forested landscape in comparison with other regions of Quebec's spruce–moss boreal forest (Bergeron *et al.* 2001). It may thus be hypothesised that population size is low at a regional scale, which would explain the low abundance of this species in these burns.

American three-toed woodpeckers forage mainly on recently dead spruce by flaking off pieces of bark and exposing Scolytinae beetle prey (Murphy and Lehnhausen 1998; Imbeau and

Desrochers 2002). In burned spruce forests, Murphy and Lehnhausen (1998) found that American three-toed woodpeckers fed mainly on uncharred portions of lightly to moderately burned spruce trees where Scolytinae beetle larvae were abundant. Although no significant difference was found in relation to fire severity, the few observations of these birds occurred in burned stands of low and moderate severity, which suggests that these retained better habitat conditions relative to high-severity burned stands many years after fire (i.e. higher abundance of lightly charred trees, declining trees and Scolytinae). Indeed, we observed an effect of fire severity at the stand scale for Scolytinae species. For *Hylastes porculus*, this effect of fire severity was probably caused by the higher proportion of live trees in low-severity burned stands, this species being known to feed on the roots of living trees (Erbilgin *et al.* 2001). In contrast, species such as *Scolytus piceae* and *Polygraphus rufipennis* are bole-feeders associated with heavily stressed and recently dead trees (Saint-Germain *et al.* 2007*b*). As life cycles of Scolytinae are typically short ($\leq$1 year), their presence in these stands was likely associated with the delayed mortality of trees that provided declining trees and recent snags.

Brown creepers are typically found in mature and old-growth conifer and mixedwood forests where they forage superficially on trunks of large trees and snags (Imbeau *et al.* 1999; Hejl *et al.* 2002). This species also uses recent burns, although this pattern is inconsistent among studies (see Hutto 1995; Schieck and Song 2006). In western boreal forests, this species is uncommon in burned forests without residual live trees but common in burns with large live trees (Schieck and Song 2006). Our results are consistent with this pattern as we found the brown creeper to increase in abundance with lower fire severity. Given that Scolytinae may be an important component of the brown creeper's diet (Otvos and Stark 1985), the higher occurrence of this species in burned stands of lower severity could be partially linked to higher foraging opportunities relative to high-severity burned stands. For the American three-toed woodpecker and the brown creeper, our results indicate that burned stands of lower severity may have contributed to the long-term occupancy of burns by these two species many years after fire.

Conclusion and management implications

Our results show that fire severity may be an important factor influencing the long-term presence of trophic webs associated with post-fire conditions that involve saproxylic insects and, in turn, several wood-foraging birds in burned forest landscapes. Variations in fire severity induce varying patterns of tree mortality and snag conditions many years after fire. Delayed mortality in burned stands of lower severity seems to have contributed to the presence of several saproxylic species associated with heavily stressed or recently dead trees many years after fire. Variation in fire severity at the tree scale also had an important effect on the abundance of insect species with long life cycles in dead wood such as the deep-borer *Arhopalus foveicollis*. As its main food source, the collective presence of these saproxylic insects in the burned landscapes contributed greatly to the high abundance of the black-backed woodpecker 6 and 8 years after fire. At the stand scale, fire severity influenced the abundance of Scolytinae and their insect predators (*Thanasimus* spp.), which were more abundant in low- than in high-severity burned stands. Bark-foraging birds such as the American three-toed woodpecker and the brown creeper that feed on Scolytinae responded similarly and tended to be more abundant in burned stands of lower severity. These results suggest that portions of stand-replacing fires with lower severity may provide suitable long-term post-fire habitat conditions for deadwood-associated species in the boreal conifer forest. Our study further supports the idea that fire severity is an important determinant of species responses to fire (Smucker *et al.* 2005).

Fire severity is an important factor to consider in the management of burned forests. As in many parts of the world (Lindenmayer *et al.* 2004), there is increasing economic pressure to intensify post-fire salvage logging in the boreal forest (Nappi *et al.* 2004; Schmiegelow *et al.* 2006). This management practice is often conducted with few guidelines targeting the conservation of post-fire legacies and natural processes (Morissette *et al.* 2002; Nappi *et al.* 2004; Hutto 2006; Schmiegelow *et al.* 2006). Results of the present and other recent studies show that fire severity has a major influence on species responses to fire (Smucker *et al.* 2005; Kotliar *et al.* 2007). Because species found in post-fire forests have different habitat requirements, we consider that a coarse-filter approach that focusses on conserving large forest patches representative of all severity classes (including merchantable stands) is necessary to maintain biodiversity and ecological processes, such as trophic webs, in managed burned forest landscapes (see also Koivula and Schmiegelow 2007). Differences in species composition or responses among post-fire studies also emphasise the need for conservation strategies to be applied to all burns under management (Nappi *et al.* 2004). For instance, one of the most abundant saproxylic insects present in this study (*Arhopalus foveicollis*) was not present in another study conducted ~500 km from our study area (Saint-Germain *et al.* 2004*a*, 2004*b*). Further studies are clearly needed to better understand the effects of factors such as prefire composition, fire severity, time since fire and fire location on species responses to fire. Such studies would contribute to the development of science-based strategies for post-fire harvesting that maintain fire-associated biodiversity.

Acknowledgements

We are thankful to François Gagnon, Jocelyn Thibault, Marjorie Gobeil, Nicolas Luigi, Simon-Pierre Babski, Réjean Deschênes, Alexandre Giroux, Élise Bolduc, Alexandre Roby and Simon Laurin-Lemay for their invaluable assistance in the field, Dave Gervais and Tim Work's laboratory for their help with wood dissection, and Mélanie Desrochers for producing Fig. 1. Earlier drafts benefited greatly from the suggestions of Tyler Rudolph, Ronnie Drever, Sylvie Gauthier, Tim Work and Richard Hutto. We also thank two anonymous reviewers who provided insightful comments on this manuscript. Financial support was provided by the Fondation de la Faune du Québec, the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) – Programme Actions Concertées – Fonds Forestier, the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, a Discovery Grant (P. Drapeau) and a Postgraduate Scholarship (A. Nappi) from the Natural Science and Engineering Research Council of Canada (NSERC).

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Manuscript received 21 June 2008, accepted 20 October 2009