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Saproxylic beetle tolerance to habitat fragmentation induced by salvage logging in a boreal mixed-cover burn

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Abstract. 1. Saproxylic insect assemblages associated with burned forests are generally abundant and species rich, consisting of a mix of pyrophilous and secondary, opportunistic species depending on time elapsed since disturbance. Life-history traits associated with each group suggest that they may respond differentially to habitat fragmentation caused by salvage logging, with pyrophilous species having a much higher dispersal potential.

2. In a 2-year-old burn highly fragmented by pre- and post-fire logging, we sampled saproxylic beetles in coniferous and broadleaf burned residual stands along a gradient of spatial context including intensity of fragmentation and isolation from source habitat using Lindgren multiple-funnels traps.

3. Beetle assemblages differed in composition between coniferous and broadleaf burned stands, with secondary users dominating the latter. Pyrophilous species increased in abundance with distance from the edge and avoided unburned patches within the fire. Secondary users did not respond negatively to fragmentation or isolation of burned habitats, with one exception, the alleculid *Isomira quadristriata* (Couper), being overall diverse and abundant throughout the study area regardless of salvage logging prevalence.

4. No deleterious effects of isolation were thus detected in the occurrence patterns of secondary users, even up to 8 km from the edge. Our results suggest that older burns, especially those having some broadleaf cover, are intensively used by non-pyrophilous saproxylic species usually associated with dead wood in green forests and may contribute to maintain broader saproxylic assemblages than originally thought, especially when considering the importance of dead wood volume pulses associated with fire in boreal forests.

Key words. Dispersal, forest fire, habitat loss, isolation, pyrophilous insects, residual habitat, salvage logging, saproxylic insects.

Introduction

For thousands of years, fire has been a predominant component of North America's boreal forest dynamics (Johnson, 1992; Payette, 1992; Bergeron *et al.*, 2004a; Hély *et al.*, 2010). This disturbance, which causes important mortality in plant and animal communities and significantly alters habitat conditions, has left a major imprint on a variety of taxonomical groups and species. Hence, species have evolved an array of specialisation allowing rapid and efficient use of new habitats created by fire (e.g. serotinous cones in coniferous tree species, pyrophily in insects, numerical response, and reproductive output in

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birds) (Evans, 1966; Gauthier *et al.*, 1993; Schütz *et al.*, 1999; Suckling *et al.*, 2001; Hutto, 2008; Nappi & Drapeau, 2009), or at least some degree of tolerance and resilience to large-scale disturbances (e.g. forest bird communities) (Schieck & Hobson, 2000; Morissette *et al.*, 2002; Hannon & Drapeau, 2005; Smucker *et al.*, 2005; Kotliar *et al.*, 2007).

Fire also creates ecological legacies which persist in the ecosystem for several years as habitat elements, particularly dead standing trees (Siitonen, 2001; Pedlar *et al.*, 2002; Boulanger & Sirois, 2006; Nappi *et al.*, 2010; Angers *et al.*, 2011). Dead wood volume pulses associated with stand-replacing fires constitute the single most important dead wood recruitment event in the boreal forest successional processes (Siitonen, 2001). Although pyrophilous insect species generally use fire-created habitats or substrates only for one or two years (i.e. one generation), (Wikars, 2002; Saint-Germain *et al.*, 2004a,b,c; Boulanger & Sirois, 2007), coarse woody elements, like snags and logs, persist on a longer time frame and will eventually be used by non-pyrophilous saproxylic species (see Boulanger & Sirois, 2007; Nappi *et al.*, 2010). The value of recent burns for fire-associated species has been the focus of an increasing amount of literature in recent years (Hutto, 1995, 2008; Wikars & Schimmel, 2001; Wikars, 2002; Saint-Germain *et al.*, 2004a,b,c; Boulanger & Sirois, 2007; Toivanen & Kotiaho, 2007; Nappi & Drapeau, 2009; Boulanger *et al.*, 2010; Nappi *et al.*, 2010). Secondary use of these habitats by non-pyrophilous species, however, has received less attention, despite the fact that such habitat may be important (in terms of frequency, area, and volume of dead wood created) to the maintenance of their populations in ecosystems driven by large-scale disturbances such as boreal forests. Given that fire-killed trees persist for several years in the landscape, secondary users, which are not restricted to freshly killed wood, may be able to colonise and use this resource despite being dispersal-limited. Also, dead wood created by stand-replacing disturbances in the boreal ecosystem represents a larger part of the overall dead wood recruitment over a single developmental cycle (Siitonen, 2001).

Specific life-history traits have been associated with pyrophily in insects, such as high dispersal potential, sensitivity to specific chemical or thermal signals associated with fire, stressed-host wood-feeding behaviour (i.e. larval development only possible on heavily stressed or recently dead trees) (Saint-Germain *et al.*, 2004b; Boulanger & Sirois, 2007), and a somewhat variable life cycle length, specifically in terms of larval development (Evans, 1966; Wikars, 1994; Schütz *et al.*, 1999; Suckling *et al.*, 2001). Some of these traits significantly reduce dispersal constraints to new habitats created by fire. In contrast, some species or trophic guilds that can potentially colonise these habitats as secondary users are known to be poor dispersers. Schiegg (2000a) observed higher species richness and different species composition for saproxylic Diptera and Coleoptera in plots having higher connectivity between logs at a relatively small scale (150 m). Brunet and Isacsson (2009) detected lower dispersal capacity in red-listed saproxylic beetles. Other studies have detected a significant association of some species with habitat patches of larger size (Sahlin & Schroeder, 2010), for which disturbances reducing habitat cover, such as salvage logging, could pose problems. The colonisation dynamics of a recently burned forest is thus likely to differ between pyrophilous species and secondary users, as stronger dispersal constraints are to be expected for the latter. Hence, factors appearing as less restricting to pyrophilous species, such as fire size or burned habitat fragmentation induced by salvage logging, are likely to become more important to secondary colonisers. Pyrophilous assemblages should thus be expected to be more homogenous over space regardless of isolation, while secondary user assemblages should be more dependent on the proximity of source habitat (green forests).

In the last decade, salvage logging has emerged worldwide as a widespread practice, aiming at reducing the negative impact of forest fires on the wood supply but also raising concerns about its effects on the biodiversity associated to post-fire environments (Saab & Dudley, 1998; Morissette *et al.*, 2002; Purdon *et al.*, 2002; Lindenmayer *et al.*, 2004, 2008; Nappi *et al.*, 2004; Hutto, 2006; Schmiegelow *et al.*, 2006; Saint-Germain & Greene, 2009). When accessible, high proportions of burned stands can be salvaged in the months following a fire, thus reducing the overall amount of burned forest into isolated remnant burned fragments and, hence, impinging dead wood availability for saproxylic organisms. This fragmentation does not affect colonisation *per se* by pyrophilous insects, because oviposition in these species is usually over by the time salvage operations can start (although it destroys the population that did colonise the salvaged stands). It could, however, significantly increase constraints on dispersal for less mobile secondary users, for which recent burn use is not as much restricted in time, and thus could render inaccessible burned habitat that possibly used to play a significant role in their population dynamics.

In 2007, a wildfire burned 64 450 ha of boreal mixedwood forest in western Quebec, Canada. It was relatively large, being approximately four times the average fire size for the region (Bergeron *et al.*, 2004b; Belleau *et al.*, 2007). In the western half of the fire, where our study was set, only 24.5% of the territory still had remnant burned forest cover over 7 m in height as the result of the combined effects of logging prior to the fire and salvage logging after the fire. This fire also burned a sizable proportion of broadleaf, aspen-dominated stands. Little research has been done to date on insect assemblages found after fire in broadleaf stands. Also, cumulative effects of logging and fire in this landscape offered an opportunity to test the response of insects to habitat loss and fragmentation of burned forests following such disturbances. Our objectives were thus twofold: investigate eventual dispersal constraints in saproxylic insects for both pyrophilous species and secondary users in this large, fragmented fire, and characterise the saproxylic entomofauna using coniferous and broadleaf remnant patches in a mixed-cover context. We hypothesised that: (i) pyrophilous species and secondary users should show differential responses to distance to source habitat and level of local fragmentation, with the latter showing negative response to both, and (ii) that species assemblages would be different between coniferous and broadleaf stands, with broadleaf assemblages being dominated by secondary users, mainly because primary stressed-host xylophagous and phloeophagous species, usually associated with immediate colonisation of post-fire disturbances, are few in aspen (Saint-Germain *et al.*, 2007a), and because fungal flora associated with dead wood is usually less affected by fire in broadleaf trees than in coniferous trees (Penttilä & Kotiranta, 1996), thus favouring mycophagous-associated insects, an important foraging guild of secondary users.

Methods

Study area

Our study was conducted in a burn near the town of Senneterre, Quebec, Canada. A total of 64 450 ha of coniferous, broadleaf, and mixed stands burned in May 2007. The centroid of all sampled plots was located at 76°42′W, 48°30′N. The study area is located at the transition zone between the balsam fir-paper birch and spruce-moss forest domains, where a gradual shift occurs from mixed-wood to continuous coniferous forests. Early seral stands are generally dominated by trembling aspen (*Populus tremuloides* Michaux), jack pine (*Pinus banksiana* Lambert), or black spruce [*Picea mariana* (Miller) BSP], depending on the disturbance type and intensity from which the stand initiated and the species composition before the disturbance, while late seral stands tend to be dominated by black spruce (Gauthier *et al.*, 2000; Lecomte *et al.*, 2006). Paper birch (*Betula papyrifera* Marshall) and balsam fir [*Abies balsamea* (L.) Miller] occur to some degree as secondary species. Mean annual temperature is 0.5 °C, and mean annual precipitation is 972 mm (Canada Climate Normals 1971–2000, Senneterre). In the 15 years preceding the fire within the 34 159 ha western part of the fire in which the study was conducted, 8313 hectares of mature forest had been harvested while 15 364 hectares were salvaged logged in the year following the fire. With these areas combined with water and unproductive terrain, only about 24% of the study area now has forest cover >7 m, mostly burned (Fig. 1). Therefore, the area can be considered as being highly fragmented, with a residual cover well below traditional habitat thresholds under which fragmentation effects (configuration and isolation) are believed to increase significantly for some taxa (e.g. <30%, Andrén, 1994; Betts *et al.*, 2007).

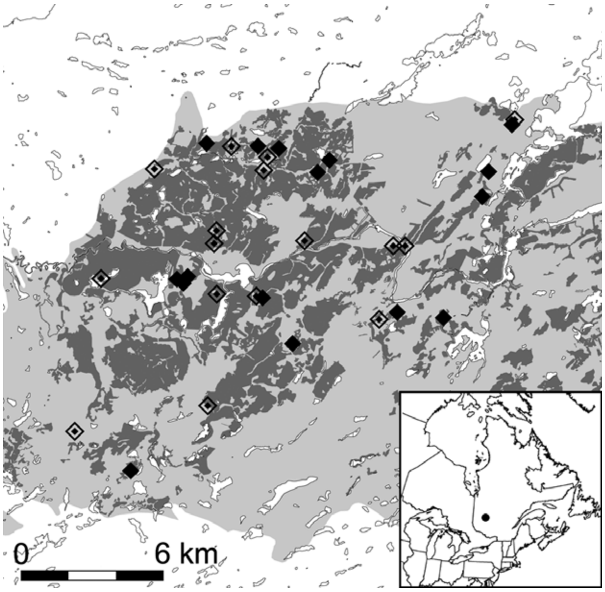

Fig. 1. Map showing part of the Senneterre 2006 fire (light grey area), areas that were salvage logged (dark grey areas), with broadleaf (closed symbols) and coniferous (open symbols) plots that were sampled.

Plot selection and characterisation

Forest inventory maps were used to locate broadleaf and coniferous-dominated residual burned stands. Only stands considered to be mature (i.e. 90 years or more for black spruce, 70 years or more for jack pine, 50 years or more for aspen or uncharacterised broadleaf stands) were chosen. To insure that we obtained gradients in patch size and degree of isolation among the plots selected, we classified potential plots into three groups: (i) near the edge of the fire, (ii) isolated, part of a large patch, and (iii) isolated, part of a small patch. Isolated plots were located at least 3 km from the closest fire edge. Small patches averaged in area 4.08 ha ($s_N = 4.69$) while large patches averaged 125.08 ha ($s_N = 96.23$), regardless of cover type. A total of 32 plots were selected, 16 coniferous-dominated and 16 broadleaf-dominated, with a near-equal representation for each type of spatial context for both cover types, with an extra plot near the edge of the burn for each cover type. Selected coniferous stands were either dominated by black spruce or jack pine, and most stands had both species co-occurring. Broadleaf stands were all dominated by aspen with a variable paper-birch component, which are the only widespread broadleaf species found in the biome. Stand level characterisation of each plot was conducted on a 10-m radius for tree species, tree diameter, and fire severity for all snags of dbh > 10 cm. We noted whether the trees were killed by fire or were already dead at that time. Coniferous, broadleaf, and total basal areas were calculated for both sources of mortality (fire or before). A visibility index was computed by measuring the distance from the trap (Lindgren multiple-funnel) in all four cardinal directions at which less than 50% of the funnels were visible, up to a maximum of 10 m, as high regeneration may hinder insect flight and reduce visual cuing. Landscape context of sampling plots was characterised at two spatial scales, i.e. some variables being measured within a 500 m radius, and others within a 5000 m radius. Local cover, salvage, and fire intensity were measured at the 500 m scale: % area salvaged, % area unburned, % of total and mature burned coniferous residual stands, and % of total and mature burned broadleaf residual stands. The 500 m scale was chosen as a compromise between spatial scales associated with pyrophilous species and less mobile secondary users (Schiegg, 2000a; Saint-Germain & Drapeau, 2011). At the 5000 m scale, a fire-edge proximity index was calculated as the % of a 5 km radius around each plot being outside the burned area. This approach was preferred to shear shortest distance to the edge, as this last metric is highly dependent on edge configuration. Also, to assess connectivity between source (unburned) habitat and sampled residual plots, we measured a series of cover and configuration variables using Fragstats 3.3 (McGarigal *et al.*, 2002) within a 5000 m radius: % residual cover, patch density (average number of patches per km^2), average patch size, large patch index (% of the area covered by the largest patch), and average Euclidean nearest neighbour distance. Most landscape metrics were calculated using forest inventory maps and a fire severity map produced by the Quebec Ministry of natural resources. Information on harvest history and salvage operations was kindly provided by P. Garneau of Tembec Inc., (Senneterre, Quebec, Canada).

Insect sampling

Starting from May 20 2009, flying insects were sampled using 12-units Lindgren multiple-funnel traps, with one trap suspended at the middle of each plot. Lindgren multiple-funnel traps were chosen because they often produce more specific results when sampling saproxylic Coleoptera with their tall vertical shape resembling a tree trunk (Chénier & Philogène, 1989). Fifty percent propylene glycol was used as a preservative. Traps were emptied once a month with the last collection made on August 22 2009. At each collection, samples were rinsed and transferred to 70% ethanol. In the laboratory, only Coleoptera were retained. Specimens were identified to species whenever possible, with identifications confirmed at the Ouellet-Robert insect collection (Université de Montréal, Montréal, Canada). Taxa representing 0.5% of captures or more were classified as pyrophilous species, secondary user or Elateridae based on capture data and life-history information given in Wikars and Schimmel (2001), Muona and Rutanen (1994), Saint-Germain *et al.* (2004b), Boulanger and Sirois (2007), Webb *et al.* (2008) and Boulanger *et al.* (2010). Species showing a strong numerical response to fire within a short time frame were classified as pyrophilous, while other species were classified as secondary users. Elateridae were kept apart because knowledge on their life history is lacking. They are usually abundant and diverse in recent burns, but whether they can detect fires (i.e. pyrophilous) or are just good dispersers has not been confirmed. Also, their larval ecology is extremely varied, some being predaceous in dead wood, some feeding in the soil, with species-specific information commonly lacking.

Statistical analyses

Responses of pyrophilous species, secondary users, and Elateridae species to landscape variables including the fire-edge proximity index and fragmentation metrics (hypothesis 1) were assessed using stepwise linear regression (entry $P = 0.05$, exit $P = 0.10$). Specific relationships between species abundance and spatial metrics were assessed with simple linear regressions. Associations of species with broadleaf or coniferous habitats were assessed with indicator species analyses (Dufrêne & Legendre, 1997). Habitat associations used were coniferous/broadleaf, and then whether coniferous stands were dominated in terms of basal area by black spruce or jack pine, and broadleaf stands by aspen or paper birch, or mixed. Differences in abundance among these groups in coniferous and broadleaf stands were assessed with analyses of variance, and assemblage species composition between broadleaf and coniferous stands was compared using analysis of similarity (ANOSIM) (hypothesis 2). Species composition and community response to environmental factors were further assessed using canonical correspondence analysis (CCA) with Monte Carlo permutation tests (999 permutations) and downweighting of rare species (ter Braak & Smilauer, 1998). Species matrix included all 262 taxa found. Data from four plots (two coniferous and two broadleaf) were made supplementary to the CCA (excluded from the analysis but plotted on the biplot) because these traps suffered significant disturbance during the sampling period. Data from these plots were removed from all subsequent numerical analyses. Indicator species analyses were performed using IndVal 2.0 (M. Dufrêne), CCA with Canono for Windows 4.5 (ter Braak & Smilauer, 1998), ANOSIM with PAST 2.10 (Hammer *et al.*, 2001), and all other analyses with SPSS 10.0.5 (SPSS Inc, 1999).

Results

A total of 10 348 adult beetles were collected, consisting of 262 species or morphospecies. Of the 262 species, 31 represented more than 0.5% of the total captures and were classified as pyrophilous (6 spp., 4068 indiv.), secondary users (17 spp., 2371 indiv.), or Elateridae (8 spp., 2402 indiv.) for further analysis. These 31 species are listed in Appendix 1.

These three groups differed in their response to landscape and environmental variables in stepwise multiple linear regressions (Table 1). Pyrophilous species responded negatively to both % of unburned stands in a 500 m radius and the fire-edge proximity index. They were thus more abundant far from the border and tended to avoid unburned fire skips. Secondary users did not respond as a group to landscape level variables. They only responded (positively) to one stand level variable, the proportion of broadleaf basal area, and were thus commoner in broadleaf-dominated stands, as illustrated in Fig. 2. Finally, Elateridae species responded negatively to the proportion of broadleaf basal area and to the proportion of burned broadleaf residual forest in a 500 m radius. They were thus strongly associated with coniferous stands, and did not respond to other landscape level variables. Elateridae thus responded differently to environmental variables than both pyrophilous and secondary users. No significant response was detected in any species group to large-scale configuration variables in the multiple regressions, whether related to cover extent or connectivity aspects.

Few species responded individually to landscape level variables. *Isomira quadristriata* (Couper) is the only secondary user that showed a strong positive relationship to the fire/unburned forest fire-edge proximity index ($t = 4.28$; $R^2 = 0.585$; $P = 0.0009$), when considering only broadleaf stands (the species was mostly absent from coniferous stands) (Fig. 3). Also in broadleaf stands only, secondary users of the Aleocharinae subfamily (Staphylinidae) responded negatively to the border proximity index ($t = -2.48$; $P = 0.0291$). Elaterid *Ctenicera spinosa* (LeConte) ($t = -2.48$; $R^2 = 0.181$; $P = 0.0193$) and secondary user leiodid *Anisotoma globososa* Hatch ($t = -2.14$; $R^2 = 0.140$; $P = 0.0415$) responded negatively to the % salvaged in a 500 m radius. Bark beetle *Dryocoetes autographus* (Ratzeburg) was negatively affected by the % of burned broadleaf residual cover in a 500 m radius ($t = -3.17$; $R^2 = 0.456$; $P = 0.0080$). No species responded to the % of burned coniferous residual cover in a 500 m radius. *Ctenicera spinosa* (LeConte) responded negatively to the % unburned in a 500 m radius ($t = -2.28$; $R^2 = 0.156$; $P = 0.0307$). Although pyrophilous and secondary species did respond differentially to landscape variables, our predictions for our first hypothesis were only partially confirmed, as secondary species as a whole did not respond negatively to isolation nor fragmentation variables.

For all species combined, no significant differences were seen in mean abundance between coniferous (355.0 ± 121.5) vs. broadleaf (358.2 ± 142.0) plots ($F_{1,26} = 0.0041$; $P = 0.9492$) or in mean species richness (coniferous:

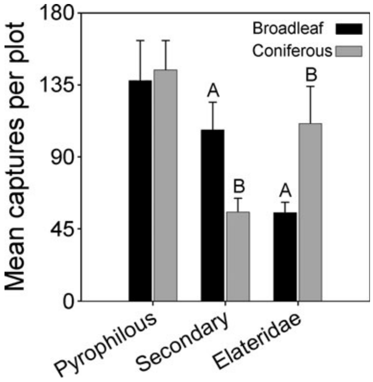

Fig. 2. Mean captures per plot for pyrophilous species, secondary users and Elateridae according to cover type. Only species representing at least 0.5% of total captures were included in these analyses.

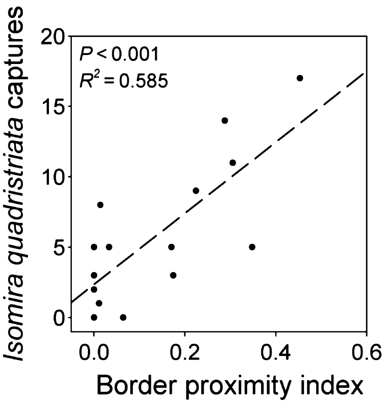

Fig. 3. Relationship between *Isomira quadristriata* captures and the border proximity index. *I. quadristriata* is the only species that showed a positive relationship with border proximity.

Table 1. Relationships between behavioural group abundance patterns and spatial/environmental explanatory factors determined with stepwise linear regressions (entry $P = 0.05$, exit $P = 0.10$). Only species representing at least 0.5% of total captures were included in these analyses.

Group	Step	Factor	*t*	*P*
Pyrophilous species	1	% Unburned stands (500 m radius)	−3.262	0.003
	2	Fire-edge proximity index	−3.221	0.003
Secondary users	1	Broadleaf/total basal area (plot)	2.738	0.010
Elateridae	1	Broadleaf/total basal area (plot)	−2.894	0.009
	2	Broadleaf/total forest remnants (500 m radius)	−2.082	0.050

53.3 ± 8.2; broadleaf: 59.9 ± 13.5) ($F_{1,26}$ = 2.3254; P = 0.1393). Species classified as pyrophilous did not differ in abundance between coniferous and broadleaf stands ($F_{1,26}$ = 0.2738; P = 0.6060). Secondary users, however, were significantly more abundant in broadleaf stands ($F_{1,26}$ = 5.5159; P = 0.0267), and Elateridae in coniferous stands ($F_{1,26}$ = 4.4390; P = 0.0468) (Fig. 2). The analysis of similarity showed that assemblages from coniferous and broadleaf burned stands differed significantly in species composition (R = 0.1774; P = 0.0007), confirming our prediction from hypothesis 2. The indicator species analysis found 16 species to be significantly associated with broadleaf stands, and 11 with coniferous stands. Species with indicator value of over 60 are listed on Table 2. Three species were associated with paper birch-dominated stands (*Disamara arenaria* LeConte, *Odontosphindus denticollis* LeConte, *Cucujus clavipes* F.) and one with jack pine-dominated stands (*Hylastes porculus* Erichson), but none of these species were caught in abundance (*Hylastes* being the most abundant with 10 total individuals).

Canonical correspondence analysis showed that assemblages found in coniferous and broadleaf stands were distinct, coniferous stands being concentrated on the negative side of the first axis and broadleaf stands being concentrated on the positive side (Fig. 4). The importance of cover type is confirmed by the strong association shown between the proportion of broadleaf basal area and the first axis (F = 3.52; P = 0.0005) (Table 3; Fig. 4). Figure 4 also suggests that assemblages for coniferous stands had higher within-group similarity. Other environmental factors that were found to be significant in the Monte Carlo permutation tests were old snag basal area (dead before the fire) (F = 3.19; P = 0.0100), which was strongly correlated with the second axis, and two others with marginal effects, the fire-edge proximity index (F = 1.66; P = 0.0065), and the mean residual patch size in a 5000 m radius (F = 1.56; P = 0.0225). Results from the logistic regressions suggest that the effect of the fire-edge proximity index detected in the CCA was not driven by ‘dispersal-limited’ secondary users, but rather by pyrophilous species that avoided fire edges. Figure 4 also shows relative positioning of species classified as pyrophylous, Elateridae, or secondary users as confidence ellipses (−1/+1 standard deviation). Pyrophylous species and Elateridae have smaller, rather linear, ellipses, with the latter shifted towards the coniferous-dominated side of the graph. The secondary users’ ellipse is larger, and is shifted towards the broadleaf-dominated side of the graph.

Table 2. Indicator species for broadleaf and coniferous-dominated burned stands identified using indicator species analysis (Dufrêne & Legendre, 1997). Only significant indicator species (P-level = 0.05) with an indicator value over 60 are shown, with calculated t.

Species	Family	Feeding guild	IV	t
Broadleaf stands				
Triplax dissimulator	Erotylidae	Mycophagous	91.3	5.679
Eusphalerum pothos	Staphylinidae	Unknown*	89.4	4.320
Ctenicera propola	Elateridae	Predaceous	86.7	5.750
Lordithon fungicola	Staphylinidae	Predaceous	79.4	5.390
Isomira quadristriata	Tenebrionidae	Saproxylic†	77.7	5.574
Sericoda quadripunctata	Carabidae	Predaceous	72.8	3.910
Glischrochilus siepmanni	Nitidulidae	Saprophagous	68.9	3.906
Agriotes fucosus	Elateridae	Unknown‡	60.5	4.234
Coniferous stands				
Xylita laevigata	Melandryidae	Wood-feeding	80.8	4.273
Ctenicera triundulata	Elateridae	Predaceous	69.3	2.243
Gnathacmaeops pratensis	Cerambycidae	Wood-feeding	66.0	4.176
Melanophthalma villosa	Lathridiidae	Mycophagous	62.6	2.429

*Adults anthophilous; larvae feeding habits unknown.

†Occurs in dead wood; relative contribution of wood and hyphae to nutrition unknown.

‡Larvae hypogeal; could feed on plant or animal material.

Discussion

Patch isolation and habitat fragmentation effects

In recent years, research on the consequences of salvage logging on biodiversity has mostly focused on organisms that colonise burns immediately after fire (Lindenmayer *et al.*, 2004, 2008; Nappi *et al.*, 2004; Hutto, 2006). Less work has examined the consequences of salvage logging of standing dead wood for organisms that colonise post-burned habitats after the initial wave of fire-associated colonists. As mentioned earlier, pyrophilous species are by definition highly mobile, as they are usually time-limited to converge towards new fire-created ephemeral habitats (Wikars & Schimmel, 2001; Saint-Germain *et al.*, 2008; Boulanger *et al.*, 2010), and are thus thought to be less susceptible to fragmentation effects. In opposition, multiple studies have shown that some non-pyrophilous saproxylic taxa are clearly restricted in their dispersal (Schiegg, 2000a,b; Grove, 2002; Brunet & Isacsson, 2009). We thus expected different responses from pyrophilous species and secondary users to environmental variables related to habitat fragmentation and patch isolation.

Contrarily to these predictions, secondary users were diverse and abundant, and as a whole did not respond to any environmental variable related to habitat loss, fragmentation or isolation. Overall, assemblages observed at the core of the burn, about 8 km from the nearest fire edge, were similar to those observed near the border. A single species, *Isomira quadristriata*, showed a positive

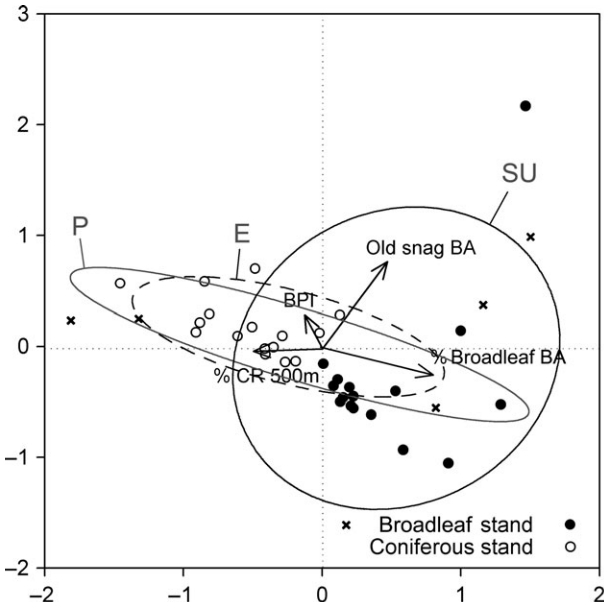

Fig. 4. Canonical correspondence analysis biplot showing sample scores (closed symbol for broadleaf plots, open for coniferous plots) and significant environmental variable vectors (according to Monte Carlo permutation tests). Confidence ellipses ($P = 0.6827$) show positioning of pyrophilous species (P), Elateridae (E), and secondary users (SU). (Old snag BA: plot-level basal area of snags dead before the fire; % broadleaf BA: broadleaf basal area/total basal area, plot-level; BPI: Border proximity index, or % of a 5000 m radius outside of the fire; % CR 500 m: percentage of coniferous-dominated forest remnants in a 500 m radius)

Table 3. Results and correlation matrix from canonical correspondence analysis including Coleoptera assemblages from 32 sampled plots (16 coniferous-dominated and 16 broadleaf-dominated). Environmental factors shown were significant in Monte Carlo permutation analyses.

	Axes			
	1	2	3	4
Eigenvalues	0.219	0.164	0.091	0.073
Species-environment correlations	0.980	0.979	0.949	0.932
Cummulative percentage variance of				
Species data	15.4	26.9	33.3	38.4
Species-environment relation	22.0	38.3	47.5	54.8
Environmental factors – axes correlation matrix				
% Broadleaf basal area	0.7713	−0.3015	−0.3544	−0.1172
Old snag (pre-fire) basal area	0.4849	0.7217	−0.1292	0.0497
Fire-edge proximity index	−0.1001	0.3096	−0.3968	−0.0626
Mean patch size (5000 m radius)	0.0962	0.2219	−0.6422	0.2516

relationship with our fire-edge proximity index. Little is known about the ecology of this species beyond that it is found associated with dead wood and is saprophagous. Why this species showed limited dispersal potential while other saprophagous species did not, cannot be explained using current knowledge of these species. These results show that, in general, amongst the species that did colonise the burned habitat, dispersal was not a limiting factor within the time frame of the study. Salvage logging thus did not have a negative influence on the accessibility of remnant patches for these secondary users even though our investigation was conducted in an environment (24% of remnant burned habitat) that can be considered highly fragmented (Andrén, 1994; With & King, 1999; Fahrig, 2002; Betts *et al.*, 2007). We should also note that secondary users were not significantly associated with unburned fire skips within the fire (measured as % of unburned stands within 500 m radius), which could also be considered as potential sources of colonists. As post-disturbance colonisation patterns by organisms in fires rely in part on the organisms' dispersal ability (Brotons *et al.*, 2005), our results indicate that secondary species probably have a dispersal potential higher than generally expected for mycophagous and other saprophagous species associated with dead wood.

It is, however, important to point out that these observations of successful colonisation of isolated residual habitat patches in no way establish that habitat loss by salvage logging does not have a negative influence on these species' populations on the longer term. Salvage logging removes the breeding substrate (fire-killed trees) on a temporal scale that will affect numerous successive generations of saproxylic insects. Hence, the lack of statistical relationship between distribution patterns of non-pyrophilous saproxylic insects and spatial configuration variables does not rule out the possibility that the important reduction of standing deadwood following salvage logging in burns may play a significant role in their population dynamics on larger spatial and temporal scales. The role of older burns in these species' population dynamics needs further clarification.

Pyrophilous species responded to the fire-edge proximity index, but negatively (i.e. which translates in a lower abundance near the edge), and to the percentage of unburned stands (fire skips) in a 500 m radius. Lower abundance near unburned fire skips suggests that these areas were somewhat avoided by pyrophilous species. Fire skips may be indicative of areas of lesser overall fire severity, and pyrophilous species or assemblages have been reported to respond strongly to fire severity which affects the quality of the subcortical environment where larvae are to develop (Saint-Germain *et al.*, 2004a,b,c). The death of trees that were only lightly affected by fire is frequently delayed, which in the case of a spring fire, desynchronises the death of the tree and the flight period of the insect adults in search of oviposition substrate. This frequently results in very low colonisation densities in lightly affected trees (L. Morneau, Quebec Ministry of Natural

Resources, unpubl. data). As for the distribution of these species within the fire, our results echo previously reported observations that confirm the high motility of these species, which were as abundant at the core of the fire, up to 8 km from the fire edge.

Amongst all 31 species representing more than 0.5% of total captures, only one individual species (*Anisotoma globososa*) responded negatively to salvage logging intensity (i.e. % salvaged within a 500 m radius). This general lack of response to habitat fragmentation could be explained (i) by the apparent absence of dispersal constraints discussed earlier, and (ii) by the fact that, in general, saproxylic species are dependent on a single habitat element (e.g. a snag) to complete their life cycle. Thus, the spatial context by itself, once the insect has colonised the patch, may be of little relevance to the local survival of the species. *Anisotoma* are in general myxomycete feeder. Myxomycetes are frequently found on dead wood and are thus generally associated with closed forest settings with low exposition. The negative impact salvage had on *Anisotoma globososa* may thus be linked with the habitat requirements of its feeding substrate.

The results reported here apply for species that have at least some moderate dispersal potential, as we sampled insect assemblages using a trap type targeting flying insects. Only species having relatively good flying capabilities could possibly be represented in the samples. Perhaps other methods of sampling not based on activity, such as extractors used for dead wood that literally extract insects from their substrate, could have yielded different results by sampling species that are more constrained in their dispersal abilities leading to stronger fragmentation effects with variables of spatial configuration and isolation of remnant burned stands.

Forest cover type effects

Little to no information has been reported thus far in the literature about insect assemblages found in recently burned broadleaf stands (but see Holliday, 1992 on ground beetles). Based on current knowledge, species composition and abundance of two major insect groups should diverge among the two cover types. In coniferous stands, post-fire saproxylic assemblages are in part dominated by stressed-host wood-feeding taxa (i.e. species associated with recently killed trees) and dependant species (e.g. predators, parasites, commensals) (Saint-Germain *et al.*, 2004b; Boulanger & Sirois, 2007), similar to what is seen in dying trees in unburned forests (Saint-Germain *et al.*, 2007a). This type of community does not seem to have an equivalent in aspen, as studies that have investigated aspen-associated saproxylophagous insects in green forests have shown that occurrence of wood-feeders is rather concentrated in late-decay snags (i.e. dead-host species) (Saint-Germain *et al.*, 2007a,b). Secondly, mycophagous species tend to be closely associated with a specific array of fungal species (Jonsell *et al.*, 2005). The fungal flora is usually highly dependent on host tree species, and Penttilä and Kotiranta (1996) reported higher survival to fire in fungal flora associated with broadleaf vs. coniferous trees. It would thus be expected to see a significant partitioning in the mycophagous group between broadleaf and coniferous stands, and a richer fauna in the former.

Assemblages from both cover types showed equal richness and abundance. Species composition, however, diverged significantly, as illustrated by both the ordination results and the indicator species analysis, despite that the two most abundant pyrophilous taxa, *Sphaeriestes viridescens* and *Corticaria* spp., were almost as abundant in both cover types. Secondary users were diverse and abundant in broadleaf burned stands, regardless of the degree of isolation from unburned and edge forests, while Elateridae were more closely associated with coniferous burned stands. This divergence is to be expected, for qualitative resource availability for saproxylic insects should be distinct in broadleaf and coniferous snags, as mentioned above. In recently dead trees, very few saproxylophagous species, if any, are known to be able to consume both broadleaf and coniferous woody tissue (Saint-Germain *et al.*, 2007a). No common wood-feeder was found to be abundant in both broadleaf and coniferous burned stands, and no wood-feeding species came out as an indicator species for broadleaf burned stands. The close association between the secondary users and the broadleaf burned stands 2 years after the fire could be linked at least in part to the observations reported by Penttilä and Kotiranta (1996), which showed that the fungal flora was less disturbed by fire in broadleaf trees than in coniferous trees. Based on these results, the resources used by mycetophagous species in our study could have been more abundant and diverse in broadleaf burned stands than in the coniferous burned stands. Also, the broader ellipse in the CCA biplot associated with secondary users may suggest that these species use a broader range of resources, among them trees that were already dead before the fire, an environmental factor that was to some degree correlated with axis 2 (Table 4; Fig. 2). Although, indicator species identified for both coniferous and broadleaf assemblages were functionally diverse, the role of the fungal community appears to play a central role in structuring communities. Indicator species *Triplax*, *Glischrochilus,* and *Melanophthalma* are all mycophagous. *Xylita* and *Isomira*, while often classified as xylophagous, probably obtain a significant part of their nutrition from fungal hyphae consumed with the dead wood. Finally, some predators, like *Lordithon*, are predaceous specifically on fungi.

Management implications

The use of older burns by secondary saproxylic species generally associated with dead wood in green forests is somewhat new information, and it raises the question whether older burns play a significant role in their overall

Table 4. Landscape descriptors used in habitat loss and fragmentation analyses.

Variable	Minimum	Maximum	Average	SD
Fire-edge proximity index (%; 5000 m radius)	0.0	45.8	15.0	16.8
% Residuals (500 m radius)	7.0	61.6	28.1	15.7
% Residuals (5000 m radius)	17.1	30.8	23.9	4.0
Patch density (per km^2)	4.6	9.6	6.5	1.1
Large patch index (%)	2.4	13.8	5.6	2.3
Euclidean nearest neighbour average	64.5	81.1	72.7	3.6

population dynamics and long-term maintenance within the boreal landscape. In our study, no major negative effect of habitat fragmentation was detected on saproxylic beetles using a salvage logged burn, whether in pyrophilous species or secondary users. These observations echo to some degree what has been reported in a study of pyrophilous insects in a recent burn relative to the distance to the fire edge (Boulanger *et al.*, 2010), in which distance to unburned forest did not affect insect occurrence or abundance. To this point, our study provides empirical evidence that functional connectivity exists between residual burned stands even at high levels of habitat loss and fragmentation, at least for secondary saproxylic insects. This allows some flexibility with regard to how retention of burned forests may be spatially organised in salvage logged burns. It is clear, however, that patch retention targets of burned forests in fires submitted to salvage logging operations should draw on the ability of deadwood-dependent species to persist in this altered landscape. Results reported here, however, should not be seen as support for large-scale salvage operations, as, although several group of organisms have been showed to persist in salvaged burns (insects, birds), at least to some degree, the importance of burns to their long-term population dynamics and the impact of a widespread reduction in the reproductive output associated with these habitats are not known and could affect these species in the long term. Studies conducted at multiple scales within and between wildfires are needed to bring a better understanding of these species' dispersal and population dynamics and provide an empirical evaluation of the importance of older burns in the long-term maintenance of their populations.

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Appendix 1

Mean abundance by cover type with SD in parenthesis and classification of species representing over 0.5% of total capture (P: pyrophilous; S: secondary user; E: Elateridae).

Taxon	Cl.	Coniferous stands	Deciduous stands
Alleculidae			
Isomira quadristriata (Couper)	S	0.3 (0.6)	5.5 (5.1)
Carabidae			
Sericoda quadripunctata DeGeer	P	1.2 (1.1)	3.7 (2.9)
Cerambycidae			
Gnathacmaeops pratensis (Laicharting)	P	3.4 (5.6)	0.1 (0.3)
Cerylonidae			
Cerylon castaneum Say	S	0.6 (0.8)	2.6 (4.2)
Corylophidae			
Molamba fasciata (Say)	S	7.9 (4.4)	6.3 (6.9)
Cryptophagidae			
Atomaria spp.	P	1.8 (1.1)	1.8 (1.6)
Curculionidae			
Dryocoetes autographus (Ratzeburg)	P	4.1 (2.6)	1.8 (2.7)
Elateridae			
Agriotes limosus (LeConte)	E	3.2 (3.8)	0.6 (0.9)
Ampedus fusculus (LeConte)	E	5.6 (7.3)	2.7 (2.6)
Ampedus luctuosus (LeConte)	E	1.9 (2.0)	1.8 (2.4)
Ampedus nigrinus (Herbst)	E	2.9 (3.7)	1.7 (1.3)
Ctenicera nitidula (LeConte)	E	2.6 (5.8)	3.1 (2.8)
Ctenicera propola (LeConte)	E	0.5 (0.7)	5.4 (4.2)
Ctenicera spinosa (LeConte)	E	4.9 (4.7)	3.0 (2.8)
Ctenicera triundulata (Randall)	E	89.2 (80.8)	34.7 (16.8)
Erotylidae			
Triplax dissimulator (Crotch)	S	1.2 (2.4)	11.2 (11.3)
Lathridiidae			
Corticaria spp.	P	30.6 (23.4)	30.1 (16.5)
Melanophthalma pumila (LeConte)	S	7.1 (12.4)	6.3 (5.6)

Appendix 1 (Continued)

Taxon	Cl.	Coniferous stands	Deciduous stands
Melanophthalma villosa Zimmerman	S	3.9 (4.5)	1.1 (1.3)
Leiodidae			
Agathidium exiguum Melsheimer	S	4.4 (5.1)	5.6 (3.4)
Anisotoma globososa Hatch	S	3.1 (4.3)	2.8 (2.0)
Catopocerus spp.	S	7.6 (8.6)	16.9 (43.8)
Melandryidae			
Xylita laevigata (Hellenius)	S	6.9 (8.8)	0.5 (0.7)
Nitidulidae			
Glischrochilus siepmanni Brown	S	0.6 (1.2)	5.7 (8.5)
Salpingidae			
Sphaeriestes virescens LeConte	P	103.6 (64.6)	88.6 (68.2)
Silvanidae			
Dendrophagus cygnaei Mannerheim	S	2.3 (2.5)	2.2 (2.5)
Staphylinidae			
sf. Aleocharinae	S	4.9 (2.1)	7.4 (5.6)
Eusphalerum pothos Mannerheim	S	0.8 (1.2)	14.1 (20.7)
Lordithon fungicola Campbell	S	0.6 (1.2)	5.5 (5.3)
Nudobius cephalus (Say)	S	2.3 (1.4)	2.1 (1.6)
sf. Pselaphinae	S	1.3 (1.3)	2.6 (2.3)

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