ÉCOSCIENCE
19 (4): 398-403 (2012)

Causes of variation in wood-boring beetle damage in fire-killed black spruce (*Picea mariana*) forests in the central boreal forest of Quebec[1]

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Abstract: Burned trees in the boreal forest are quickly colonized by wood-feeding beetles after fire. Roundheaded and flatheaded borers (Coleoptera: Cerambycidae, Buprestidae) are common wood-feeding beetles whose larvae feed on the phloem in the first instars before entering the xylem, where they excavate galleries several centimetres deep. These organisms cause significant damage to post-fire salvaged wood. Recent studies show that a variety of environmental factors may create heterogeneous patterns of damage throughout burned landscapes. We evaluated the relationship between fire intensity (measured as bole scorch height), tree size, elevation, and the landscape-scale distribution of beetle damage in black spruce in four 2-y-old fires in the central boreal forest of northern Quebec. Beetle damage significantly increased with char height and elevation but not with distance from unburned edge. With regard to tree diameter, the number of entry holes increased with fire intensity for large trees, whereas it declined with intensity for small trees. The most remarkable result was that while a very large sample size enabled us to detect these significant patterns, the difference in predicted beetle attack rates across a wide range of parameter values was quite muted. Thus, managers cannot use these results to dramatically improve either the way in which they salvage or the strategy for set-asides intended to benefit beetles and their subsequent avian predators.

Keywords: boreal forest, fire intensity, forest fire, post-fire salvagewood-boring, xylophagous beetles.

Résumé : En forêt boréale, les arbres brûlés sont rapidement colonisés par les coléoptères saproxyliques. Les scolytes à tête ronde ou aplatie (familles Cerambycidae, Buprestidae) sont des coléoptères xylophages communs dont les larves se nourrissent de phloème durant leurs premiers stades. Ces larves pénètrent ensuite dans le xylème et y creusent des galeries de plusieurs centimètres de profondeur. Ces organismes causent d'importants dommages au bois récolté après feu. De récentes études ont montré que plusieurs facteurs environnementaux peuvent causer les patrons hétérogènes de dommages observés dans les forêts brûlées. Nous avons examiné la relation entre la sévérité du feu (mesurée par la hauteur à laquelle les aiguilles sont roussies), la taille des arbres, l'altitude et la distribution à l'échelle du paysage des dommages causés par le longicorne à l'épinette noire 2 ans après feu dans 4 sites brûlés dans le centre de la forêt boréale au Québec nordique. Les dommages causés par les coléoptères augmentaient de façon significative avec la hauteur à laquelle les arbres avaient été brûlés et avec l'altitude, mais pas avec la distance au périmètre du feu. Le nombre de trous d'entrée de larves augmentait avec la sévérité du feu pour les arbres de grands diamètres, mais ce nombre diminuait avec la sévérité du feu pour les arbres de petits diamètres. Le résultat le plus surprenant est qu'en dépit du très grand nombre d'échantillons ayant permis de détecter ces patrons significatifs, les taux d'attaque de coléoptères prédits à partir d'une vaste gamme de valeurs des paramètres présentaient des différences très modestes. Les gestionnaires ne peuvent donc pas utiliser ces résultats pour améliorer considérablement la manière dont le bois est récupéré ou la stratégie de conservation du bois brûlé visant à bénéficier les coléoptères et leurs prédateurs aviaires.

Mots-clés : coléoptères xylophages, forêt boréale, incendie de forêt, insectes perceurs, récupération du bois après feu, sévérité du feu.

Nomenclature: Marie-Victorin, 1995; Downie & Arnett, 1996.

Introduction

Trees killed or weakened by fire are often attacked by wood-boring insects. These attacks reduce the merchantability of salvaged wood as later instar wood-borer larvae tunnel within the bole (NLGA, 2010). Indeed, wood-boring larvae are the primary reason why forestry companies and governments prefer quick post-fire salvage despite the reductions in the natural regeneration of sexually reproducing plant species caused by this celerity (Lowell *et al.*, 1992; Saint-Germain & Greene, 2009).

Within burned areas, beetle damage is markedly heterogeneous, and authors have advanced 4 main causes for this variation. The first factor is tree size, with larger trees typically having greater beetle damage (holes·m^2) than smaller trees of the same species (Saint-Germain, Drapeau & Hébert, 2004a). Increased damage with size has been attributed to 1) better survival of larvae oviposited after the fire in the thicker phloem of larger boles (Cole, 1973;

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[1] Rec. 2012-08-09; acc. 2012-11-09.
Associate Editor: Pierre Drapeau.
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DOI 10.2980/19-4-3568

Cole & Jensen, 1979; Reid & Robb, 1999; Reid & Glubish, 2001) and 2) increased insulation from heat during wildfire due to the thicker bark of larger trees (Hare, 1965; Vines, 1968; Hengst & Dawson, 1994). A second factor affecting the spatial variation in attack rate is differing bole moisture content. For example, it has been argued that the probability of oviposition by wood-borers is proportional to moisture content (Dyer & Seabrook, 1978; Hanks *et al.*, 1999). In turn, moisture content declines quickly with time since fire. Boulanger and Sirois (2006) found a 50% decline in wood moisture 4 y after burning in a black spruce (*Picea mariana*) forest in Quebec. This is the other reason for rapid salvage: checking (the development of cracks in rapidly drying wood) increases rapidly after fire (Saint-Germain & Greene, 2009). A third reason for within-fire heterogeneity in attack rates is distance between viable host material and potential source populations of wood-borers. Saint-Germain, Drapeau, and Hébert (2004a) hypothesized that damage would be greater near the edges of burns, presumably due to a distance-decay function limiting overall oviposition rates of females as they dispersed into the burn from the adjacent green forest. Counter-intuitively, they found a slight positive relationship between beetle damage and distance to unburned matrix. The final factor mentioned in the literature as a cause of spatial heterogeneity in the density of entry holes is fire intensity. Saint-Germain, Drapeau, and Hébert (2004a) reported that wood-borer damage was proportional to fire intensity (they used the word "severity"), but within the single fire examined in their study, fire intensity was severe throughout the burn and thus their conclusions should be regarded cautiously. (Note that we use the descriptor "intensity" rather than "severity" because our measure—scorch height—is proportional to the energy output from the fire (*i.e.*, the fireline intensity: Michaletz & Johnson, 2003; Keeley, 2009).

Unhappily, these 4 factors contributing to spatial variation in beetle attacks within recent burns are intertwined. For example, the drying rate of burnt trees is assumed to be proportional to both fire intensity (Saint-Germain, Drapeau & Hébert, 2004b) and size, and it is possible that larger trees, with their thicker bark, will dry less than smaller trees exposed to equal fire intensity. Similarly, the outer edge of a fire, even with 100% tree mortality, experiences a markedly higher percentage of partially burned crowns than the fire interior does for distances between 50 to 100 m into the fire (Greene *et al.*, 2005). That is, distance from edge and fire intensity are linked.

Better prediction of the variation in beetle damage would be useful to minimize the salvage of downgraded wood. Such knowledge might also be useful during the rapid planning for post-fire salvage in that polygons on inventory maps that were considered to be at low risk for attack could be slated for later salvage, thus maximizing sexual recruitment by commercially valuable trees such as black spruce and jack pine (*Pinus banksiana*) and minimizing the need for subsequent planting (Greene *et al.*, 2006, Saint-Germain & Greene, 2009). Here we examine wood-borer attack rate, measured as the number of wood-borer entry holes, as a joint function of fire intensity, tree diameter, and site characteristics such as elevation or distance to unburned forests. More specifically, we hypothesize that lightly scorched (but nonetheless dead) trees will have more wood-borer damage than more heavily scorched trees due to increased oviposition and successful larval development. Additionally, we expect that, consistent with prior studies (Saint-Germain, Drapeau & Hébert, 2004a), wood-borer damage will be greater in larger diameter trees than smaller diameter trees. Finally, we expect that distance into the fire will be inversely proportional to beetle attack rate.

Methods

SITE SELECTION

We sampled wood-borer damage from 4 lightning-caused wildfires that burned in the spring of 2005 in northwest Quebec. Three of these fires (#256, #277, and #278 in the system of SOPFEU [Société de protection des forêts contre les feux], which burned from May 5th to June 23rd, May 5th to June 23rd, and May 5th to July 1st, respectively) were located approximately 100 km north of Chibougamau (Quebec, Canada), and a fourth wildfire (#298, which burned from May 31st to July 7th) was located 50 km south of Chibougamau. All were in black spruce–dominated central boreal forest, and all were extinguished by rain. Although modifications to the Forest Act of Quebec oblige logging companies to salvage fire-killed trees, a recent agreement between Quebec and the First Nations Cree bands states that harvesting on their land must be conducted in a mosaic pattern, leaving 50% of the mature productive burnt forest uncut. In the salvage of the fires used in this study, the forestry companies were further required to use partial-cutting on those parts of the mosaic that they were permitted to cut, leaving standing trees and snags within cutblocks.

A total of 749 trees were sampled in 2007. These trees were distributed among 75 sites in 4 fires, with 10 trees per site (with the exception of 1 site where 9 trees were sampled). We selected sites using information from forest inventory and fire intensity maps (created from aerial mapping shortly after each fire was extinguished) to ensure a broad coverage of fire intensities and tree sizes. Within each selected site, a centre point was arbitrarily set (marking the centre of a site) and the 10 nearest trees were chosen for subsequent analysis. We used an average of 19 sites per fire.

ESTIMATING THE RELATIONSHIP BETWEEN SITE- AND TREE-LEVEL PARAMETERS AND BEETLE DAMAGE

We related beetle damage to 2 site-level and 3 tree-level parameters using generalized linear mixed models (Pinheiro & Bates, 2000). For the site-level parameters, we estimated distance to the fire edge (nearest unburned forest) for each site using GIS data. We used a satellite image taken soon after the fire to verify that the estimated distance indeed reflected distance to the fire edge, and not to nearby residual (unburned) patches. We also estimated elevation from altitude values reported on the forest inventory map. For tree-level parameters, we measured scorch height and tree size (diameter at breast height). We used scorch (char) height as a proxy for fire intensity (Hely, Flannigan & Bergeron, 2003; Saint-Germain, Drapeau & Hébert, 2004b). Because scorch height varies by azimuth on the bole as a function of wind direction (Johnson & Miyanishi, 2001), we measured it both on the windward (low scorch) and leeward side (high scorch) of the bole (Johnson & Miyanishi, 2001). We used a digital clinometer to measure low and high scorch heights.

We assumed as did other authors that wood-borer damage was primarily due to *Monochamus* spp. We estimated wood-borer damage for these taxa by removing bark and counting all entry holes within the lowest 1.5 m of trunk. Due to the variable fire intensity (scorch height) observed among individual trees, entry holes were counted separately for the low scorch and high scorch side. Holes created by larvae as they enter the xylem are distinct from exit holes bored by emerging adults. Exit holes tend to be perfectly rounded for cerambycids or D-shaped when created by emerging buprestid adults. Gallery openings are at a right angle with the surface and easily distinguished from entry holes as the latter are oval in shape and enter the xylem at a more gradual angle.

In our model, we specified distance to unburned forest, size of tree (diameter at breast height, DBH), fire intensity (*i.e.*, scorch height), their interaction, and side of the tree (low scorch or high scorch) as fixed factors influencing hole density (DBH and elevation were centred). We used variation in and among individual trees and among sampling sites as random factors. We tested 2 basic model forms: the first included all variables as linear variables, while the second expressed scorch height both as a linear and as a squared parameter. We optimized parameter selection for each model using sequential ANOVAs. Models were estimated using the lme function in the nlme package (Pinheiro *et al.*, online) with the VarPower weight function to correct for heteroscedasticity. We compared final models using the second-order Akaike Information Criterion (AICc) (Sugiura, 1978; Hurvich & Tsai, 1989; 1991; Burnham & Anderson, 2002). Model selection was performed with the AICc function in the AICcmodavg package (Mazerolle, online). All analyses were performed using R (R Development Core Team, 2009).

Results

The model with all factors expressed as linear terms described the observed number of holes better than the model where scorch height was expressed as both linear and squared terms (Table I). Further model selection using sequential ANOVAs discounted distance from the forest edge as a meaningful parameter for the final model (Table II), leaving DBH, elevation, scorch height, scorch side, and the interaction of DBH and scorch height as meaningful explanatory variables (Table III; Figure 1). As shown

TABLE I. Comparison of 2 linear mixed models where scorch height was included as either a linear factor only (Model 1) or as both a linear and a quadratic factor (Model 2).

Model name	k	AICc	ΔAICc	w_i	Cumul w_i	Log-likelihood
Model 1	10	11 046.23	0.0000	0.9493	0.9493	–5513.036
Model 2	11	11 052.09	5.8587	0.0507	1.0000	–5514.949

TABLE II. Summary of sequential ANOVA significance test for variable selection (linear model, α = 0.05). Asterisks denote significance (alpha less than 0.05).

Variable	Num df	Den df	*F*-value	*P*-value
(Intercept)	1	689	475.4768	<0.0001 *
DBH (cm)	1	616	303.0318	<0.0001 *
Elevation (m)	1	72	16.1514	0.0001 *
Scorch height (m)	1	689	7.3762	<0.0068 *
Scorch side (high or low)	1	689	16.4928	<0.0001 *
Distance to unburned (m)	1	72	0.4172	0.5204
DBH × Scorch height	1	689	40.3686	<0.0001 *

TABLE III. Summary of results from Wald's significance test for variables in final model (α = 0.05).

Fixed effects	Coefficients	SE	df	*t*-value	*P*-value
(Intercept)	29.225	1.422	689	20.559	<0.0001
DBH	1.846	0.166	616	11.098	<0.0001
Elevation	0.141	0.057	73	2.459	0.0163
Scorch height	0.011	0.082	689	0.139	0.8893
Scorch side (low)	–2.136	0.396	689	–5.397	<0.0001
DBH × Scorch height	0.090	0.014	689	6.342	<0.0001
Random Effects		SD			
Site	-	9.828	-	-	-
Tree	-	9.376	-	-	-
Residual	-	0.784	-	-	-

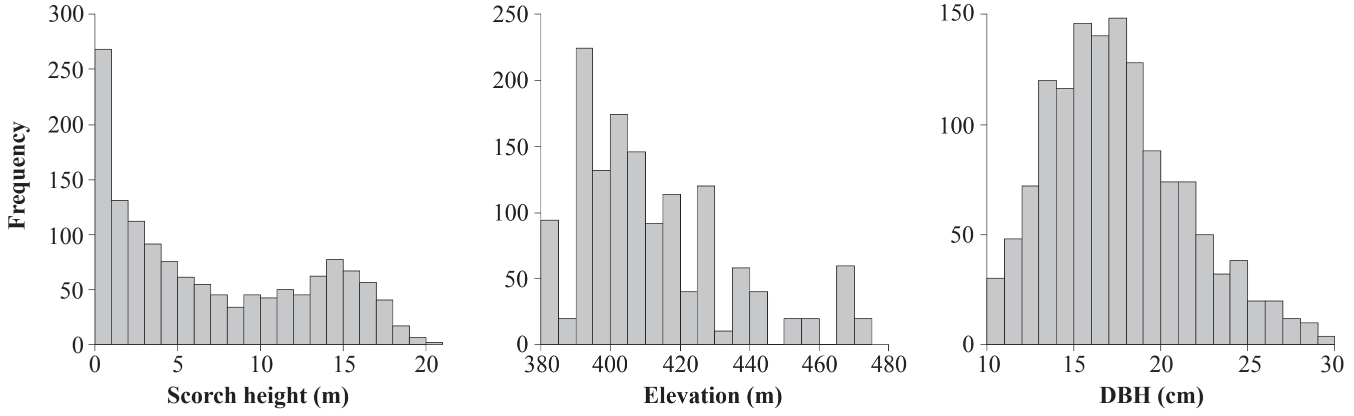

FIGURE 1. The observed frequency distribution of the model parameters scorch height, elevation, and diameter at breast height.

by the significant interaction term, the effect of scorch height did indeed vary with tree size (Figure 2). Contrary to expectations, smaller trees showed a negative response to scorch height, while this trend was reversed for larger trees. This final model indicated significant variability between sampling sites and among individual trees (Table III) but still provided a relatively good fit to observed data (Figure 3).

Increases in elevation also resulted in increased damage, although these changes were more modest given the model coefficient ($\beta_{elevation} = 0.138$) and the limited range of topography available in our study sites (Table III). Again, however, the effect, while significant, was modest, corresponding to a predicted difference of only 14 holes over the range of elevations. Large, highly charred trees had the greatest number of holes. While statistically significant, changes in hole number related to scorch height were modest: For example, our model predicted 120 entry holes (in the first 1.5 m of trunk) on a tree with low and high scorch heights of 10 m (DBH = 30 cm), compared to 144 entry holes for the same size tree with scorch heights of 20 m (Figure 3). Holes were also more prevalent on the leeward (high scorch) side of trees, although again these differences were modest and accounted for a predicted range of only 2.3 holes·1.5 m^{-1} bole sampled (Figure 3).

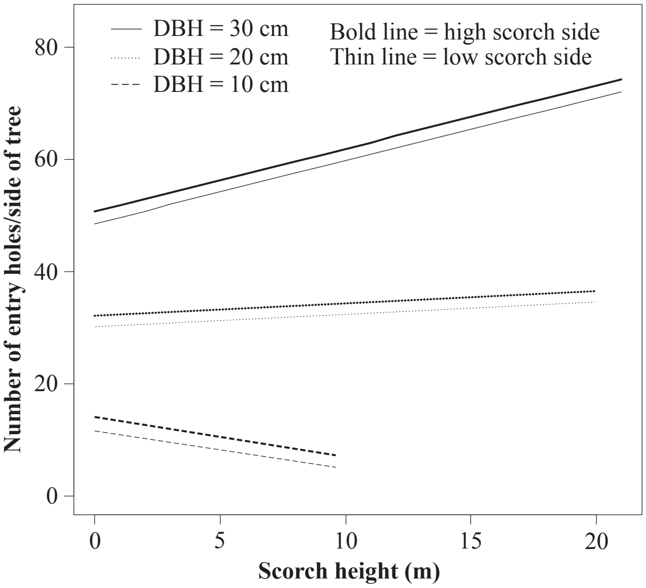

FIGURE 2. Model predictions for damage (holes per side per m of bole) *versus* scorch height (m) for different diameters when elevation was fixed at 412 m (mean elevation). Length of lines reflects realistic tree proportions (*i.e.*, DBH to height ratio).

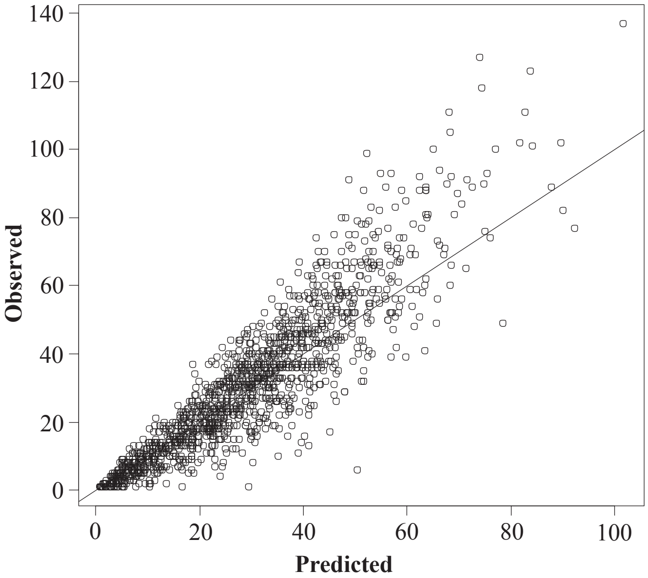

FIGURE 3. Observed number of holes *versus* predicted number of holes (model) from final generalized mixed model after variable selection.

Discussion

Saint-Germain, Drapeau, and Hébert (2004a) suggested that snags located near unburned matrix (residual patches or fire edge) were preferred oviposition sites as these offered easy access to the unburned needles and twigs required for the maturation feeding of recently emerged adults. Further, given that near sites require less energy expenditure by flying adults seeking oviposition sites than would sites in the burn interior, it follows that one expects higher attack rates near burn edges. However, we found no evidence that distance to unburned forest affected the number of holes in our study, despite a large range of distances (from a few metres to more than 1 km) to the nearest forest edge. It is possible that we could see little effect of distance because our fires were located within an unburned matrix dominated by relatively young forest that resulted from 2 decades of commercial logging, a situation not encountered by Saint-Germain, Drapeau, and Hébert (2004a). Younger stands have been deemed to represent poorer resources for adult beetles following fire (Holland, Bert & Fahrig, 2004). Conversely, it may be that distance is simply not an important factor as females search for oviposition sites. In the boreal forest, the remarkably invaginated edges of large (1000 to 100 000 ha) wildfires, coupled with the large number of residual stands, means that most points within a burn are within *ca* 300 m of a nominal fire edge or a green residual stand (Johnson & Greene, 1997), *i.e.*, the great majority of our sampling points were not far from an unburned stand. Such small distances may present only a modest challenge for the dispersal of such vagile species.

However, other physiographic features, such as elevation, did have muted effects on the degree of beetle damage sustained by individual trees. In our study, damage increased with elevation. This is contrary to the findings of Saint-Germain, Drapeau, and Hébert (2004a), who found a negative relationship between elevation and density of beetle galleries. They attributed this to the higher winds and colder temperatures observed at higher elevations, but this seems unlikely; the range of elevations examined within their study was only slightly larger than ours (maximum difference of <100 m). With regard to temperature, based on the adiabatic lapse rate, this slight difference in altitude translates to an average increase of approximately 0.6 °C from the highest to the lowest point (Gagnon, 1970; Han *et al.*, 2005). We think it more likely that the significant effect of local topography in our study (and in that of Saint-Germain, Drapeau & Hébert, 2004a) is actually related not to temperature but to hydrology. Although unmeasured in this study, we expect that even within this subdued topography, high points will tend to be drier than adjacent lowlands, and trees growing in the wetter (lower elevation) sites will tend to have lower DBH and, perhaps, lessened scorch.

At the scale of individual trees, diameter was positively related to beetle damage, a trend that has been recorded elsewhere in eastern boreal forests (Saint-Germain, Drapeau & Hébert, 2004a). As tree diameter is highly correlated with bark and phloem thickness, larger trees provide overall more phloem for developing wood-borer larvae, and, in turn, this enhanced resource likely increases larval survival (Amman, 1972; Haack, Foltz & Wilkinson, 1984; Haack *et al.*, 1984; Haack, Wilkinson & Foltz, 1987; Haack *et al.*, 1987; Hanks, Paine & Millar, 1993; 2005). Thicker outer bark may also have helped preserve moisture in the phloem.

While factors such as the windward or leeward side of the tree had significant but minor effects on overall beetle damage and demonstrate that adult wood-borers may be capable of detecting very local variations in fire intensity (*i.e.*, windward *versus* leeward side), perhaps most surprising was the relationship between entry hole number and scorch height (our proxy for fire intensity: Van Wagner, 1973; Hely, Flannigan & Bergeron, 2003). For larger trees, ovipositing adults preferred those stems more intensely damaged by fire. This "choice" cannot be due to avoidance of resin production as all our trees were dead regardless of scorch height. We saw the opposite trend for small-diameter trees: as intensity increased, there was less oviposition. Higher intensity will lead to drying of the phloem, an effect that should be accentuated in small boles. With very large boles, the thicker bark will better insulate the phloem, and thus one should expect less effects of intensity on phloem quality.

The different trends observed for large and small trees suggest that phloem quality (as perceived by beetles) is altered by fire intensity. Host selection, constrained by the needs of first instars, is reliant upon the palatability of the phloem. Fire intensity has been shown to affect host selection and larval survival, but no study has examined the direct effect of fire intensity on phloem water content. Similarly, fire-related changes in the nutrient content of phloem have not been evaluated. Considering the varied responses of beetle attacks to fire intensity reported in this and past studies, clarification of the relationship between fire and phloem quality is vital.

From the point of view of maximizing profitability, given that the bigger trees constitute the more profitable parts of the salvage harvest, the harvest of heavily scorched large trees should be prioritized. Accelerating the harvest of the most valuable trees would minimize losses due to insects. Conversely, from the point of view of conserving xylophagous beetles (as well as their avian predators), a manager should delay harvesting the more intensely burned large trees. This is particularly relevant in areas where existing laws prohibit complete salvage, such as on the territory covered by the James Bay and Northern Quebec Agreement (JBNQA), and the manager seeks a means of determining which stands should be left as prime conservation habitat. Harvesting part of each heavily scorched tree (in effect creating residual patches of tall stumps) should also be considered as a compromise between economic and conservation priorities. This practice, more common in unburned forests in Scandinavian countries, has been shown to sustain several red-listed saproxylic beetle species (Schroeder *et al.*, 1999; Jonsell, Nittérus & Stighäll, 2004).

This almost reflexive appeal to management concerns, however, risks masking the remarkably invariant results we obtained. While some variables were significant and others were not, the most fundamental result we obtained in our examination of 75 sites distributed among 4 fires was that the difference in infestation rates tended to be quite subdued essentially everywhere. Neither distance to edge nor diameter nor fire intensity nor elevation led to dramatic differences in hole density. It follows therefore that our best advice to managers is that decisions regarding which parts of a burn should be preserved should not be based on the needs of saproxylic beetles or their subsequent predators. Rather, the needs of other, more demanding taxa should guide the spatial and temporal (delayed salvage) pattern of set-asides. For example, the damage done to plants reliant on sexual reproduction by salvage can be ameliorated through consideration of seedbed quality and issues such as distance from edge (Saint-Germain & Greene, 2009).

Acknowledgements

We thank G. Gélinas and C. Alder for their assistance in the field and M. Mazerolle for help with statistical analyses. This study was funded by the National Sciences and Engineering Research Council of Canada and a collaborative research grant via the CRSNG-UQAT-UQAM Chaire en aménagement forestier durable.

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