Salvage Logging, Edge Effects, and Carabid Beetles: Connections to Conservation and Sustainable Forest Management

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ABSTRACT We used pitfall traps to study the effects of fire and salvage logging on distribution of carabid beetles over a forest disturbance gradient ranging from salvaged (naturally burned and subsequently harvested) to unsalvaged (naturally burned and left standing). Significantly more carabids were caught in the salvaged forest and the overall catch decreased steadily through the edge and into the unsalvaged forest. We also noted a strong negative correlation between carabid abundance and percent vegetation cover. Beetle diversity as measured through rarefaction was significantly greater at the edge relative to both the unsalvaged and salvaged forest. This stand level study suggests that the amount of edge habitat created by salvage logging has significant implications for recovery of epigaeic beetle assemblages in burned forests by inflating the abundance of "open habitat" species in the initial communities. Carabid beetle responses to salvage logging can differ from responses to harvesting in unburned boreal forest suggesting that management of postfire forests requires special consideration.

KEY WORDS carabid beetles, salvage logging, boreal forest, edge effects

Boreal forests are structured by cycles of wildfire and postfire regeneration (Larsen 1970, Bonan and Shugart 1989, Johnson et al. 1998), a disturbance regimen that is being altered by human activities. For example, postfire salvage harvesting recovers low-grade timber from the landscape in an attempt to minimize economic losses caused by fire. It is a relatively new disturbance, and the impact of salvage logging on wildlife in boreal habitats is poorly known (Harmon 2001, Nappi et al. 2004). Furthermore, salvaged areas fragment burned forest into patches that have higher amounts of distinct edge than in natural postfire situations in which the only edges occur along windfalls (Hunter 1993) and water bodies (Harper and Macdonald 2001).

Effects of fragmentation and direct loss of burned habitat resulting from salvage logging on the distribution, composition, and abundance of wildlife have not been studied in detail, except for birds (Haggard and Gaines 2001, Kotliar et al. 2002, Morissette et al. 2002). Work in Finland, however, provides examples of arthropod species declines as well as local extinctions being caused by such habitat changes in boreal forests (Rassi et al. 1992, Siitonen and Martikainen 1994, Niemelä 1997, Heliölä et al. 2001). Thus, it seems that invertebrates could be vulnerable to salvage logging.

In this study we compared the diversity, species composition, and abundance of carabids among three post fire habitats: (1) burned forest, (2) burned and then salvaged forest, and (3) the edge separating them. In addition, we studied associations between vegetation and carabid catch rates. Carabid assemblages are appropriate for disturbance studies because of their high abundance in boreal forests, their sensitivity to habitat change (Niemelä 1990, Niemelä et al. 1990, 1992, 1993, Abildsnes and Tømmerås 2000), and the efficiency with which they can be sampled (Spence and Niemelä 1994). The overall goal of this study was to determine if decisions about salvage logging might have conservation implications for carabid beetles and, perhaps, for other epigaeic organisms.

Materials and Methods

Study Area. The study was conducted ≈200 km northwest of Edmonton, Alberta, Canada, within the boundaries of the Chisholm fire, a severe, large-scale wildfire (≈120,000 ha) that burned during the spring of 2001. The specific sampling location was a burned white spruce [*Picea glauca* (Moench) Voss.] stand (≈35 ha) ≈7 km from the town of Chisholm, AB (54°55′ N, 114°10′ W). The forest companies involved in salvage logging in this area agreed to leave a portion of this stand (≈6 ha) for use in experiments, and this provided the unsalvaged habitat for this study.

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Sampling Design. Epigaeic beetles were captured using pitfall traps (Spence and Niemelä 1994) constructed by burying a 1-liter white plastic container (11.2 cm in diameter) even with the surface of the ground. A 0.5-liter inner plastic cup was placed tightly in this outer sleeve and filled with ≈150 ml of silicate-free ethylene glycol. Trapped specimens were removed periodically, and traps were refilled with fresh ethylene glycol. All traps were covered with a 15 by 15-cm plywood lid elevated several centimeters above the trap to reduce disturbance to trap catches and flooding by rain. Although data from pitfall traps is biased in some respects, they remain the most widely used technique for sampling epigaeic arthropod assemblages. We used pitfall catches, as recommended, to compare the relative abundances of a species among similar habitats (Niemelä et al. 1993).

Pitfall traps were deployed on three replicate transects 25 m apart and oriented perpendicular to the boundary (edge) between burned salvaged forest and standing burned forest. Unfortunately, replicate unsalvaged stands were unavailable for study, and thus we were restricted to replication of transects at three well-separated points (>25 m) across a single edge. Previous work has shown that traps placed 25 m apart in boreal mixedwood forest sample statistically independent populations (Digweed et al. 1995). We placed traps at intervals of 0, 10, 20, 30, and 40 m from the edge and into each of the two respective habitat types (Spence et al. 1996). Thus, each transect consisted of nine traps over a total transect length of 80 m. In our analysis, we regarded the traps at 0 m and those located at 10 m on either side as edge habitat, transitional between the salvaged and unsalvaged areas.

Beetles were collected continuously between 26 June and 22 August 2002. Traps were serviced at ~2-wk intervals. No traps were lost over the course of the experiment. After sorting, all carabids were subsequently identified to species according to Lindroth (1963–1969), and identifications were compared with reference specimens at the University of Regina, University of Alberta, and the Royal Saskatchewan Museum. Voucher specimens for all species are deposited in the E. H. Strickland Entomological Museum (University of Alberta) in Edmonton, Canada.

Vegetation Analysis. We estimated percent ground cover by vegetation, bare ground, and litter in a grid (1.0 by 1.0 m) around each pitfall trap. All plant species were identified according to Johnson et al. (1995).

Data Analysis. The effect of habitat type on beetle catch was analyzed using a one-factor analysis of variance (ANOVA). To minimize the potential effect of seasonal differences in carabid catches, data were summed across all sample dates for a given pitfall trap. Data for each habitat (unsalvaged, edge, salvaged) in a given transect were represented by a total seasonal catch of three traps. Therefore, replication within each habitat was at the transect level ($n = 3$). For the species-level catch data to meet the assumptions of normality and homoscedasticity, a $\log_{10}(n + 1)$ transformation was used.

Species richness estimates were obtained by rarefaction using internet-based software (Brzustowski 2003). Rarefaction corrects for sampling effort variability by modeling expected species richness as a function of subsamples of the original catch, thereby allowing comparisons between samples of similar size (Hurlbert 1971, Buddle et al. 2005). However, we calculated the Shannon-Wiener diversity index for each trap distance from the edge and used ANOVA to test for a significant effect of habitat on diversity.

To test for relationships between the carabid abundance and environmental variables studied (percent vegetation cover, percent bare ground cover, and percent litter), we calculated Pearson correlation coefficients (Zar 1999). However, because diversity did not meet the assumptions of parametric tests, Spearman's rank correlation was used to study possible correlations between environmental variables and carabid diversity (Zar 1999).

To test for species-level responses, a multivariate analysis of variance (MANOVA) (followed by Tukey's post hoc tests where appropriate) was performed on the five most abundant carabid species (≈87% of the total sample). Community-level responses were examined using nonmetric multidimensional scaling (NMS). This analysis was performed using the software package PC-Ord (McCune and Medford 1999) and Sørensen (Bray-Curtis) as the distance measure. To further examine carabid community responses to the three habitats, we used indicator species analysis (Dufrêne and Legendre 1997) to identify if species occurred predominately enough to be considered significant indicators of a given habitat. For all statistical tests, we used a rejection coefficient of 0.05.

Results

Species Occurrence Across the Edge. We captured a total of 2,494 carabid beetles representing 35 species during the study. Total carabid abundance was highest in the salvaged habitat, followed by the edge and lowest in the unsalvaged stand (Fig. 1). *Pterostichus adstrictus* Eschscholtz was the most abundant species (860 individuals comprising 34% of the total sample; Table 1), and *Sericoda quadripunctata* (DeGeer) was the second most abundant (680 individuals comprising 29% of the total sample; Table 1).

Carabid Community Assemblages. Salvage logging in this stand resulted in an, increase of total carabid community catch (Fig. 1). MANOVA showed that habitat type significantly altered carabid community composition (Wilks lambda, treatment, $P = 0.01$). Salvage logging here increased carabid abundance and changed species composition by significantly increasing the catches of *P. adstrictus*, *S. quadripunctata*, and *S. bembidioides* across the edge (Fig. 2).

Carabid community similarity, depicted using NMS ordination analyses, between habitat types shows clear separation of unsalvaged habitat from the other treatments (edge and salvaged forest; Fig. 3). NMS resulted in a two-dimensional solution (final stress,

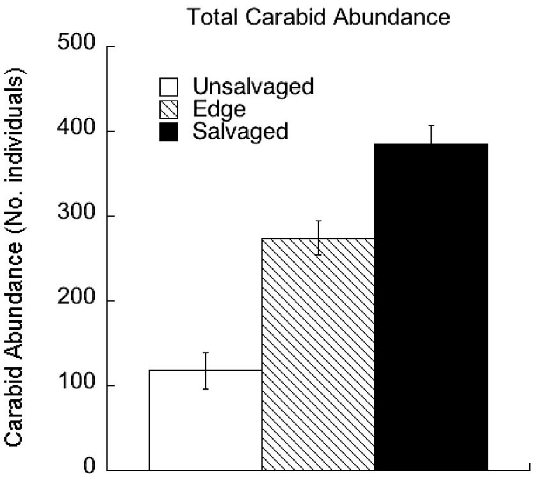

Fig. 1. Mean carabid abundance in unsalvaged, edge, and salvaged habitats. Bars are means ± SE for $n = 3$ transects.

7.44) that explained 92.4% of the total variance. This analysis showed that although there was overlap in carabid species composition between the salvaged and edge habitats, unsalvaged forest supported a distinct assemblage.

Carabid Abundance, Species Richness, and Environmental Variables. We found a significant positive correlation between total carabid abundance and distance from the extreme unsalvaged end of the gradient (Table 2). However, rarefaction analysis indicated that species richness was greater at the edge than in either the unsalvaged forest or the salvaged forest (Fig. 4). The unsalvaged forest and salvaged forest did not differ in species richness (Fig. 4), even though the data reflect contributions from different species in each habitat (Fig. 3).

Vegetation cover was inversely related to distance across the gradient (Table 2). Percentage cover was highest in the unsalvaged forest and decreased along transects to the interior of the salvaged forest (Fig. 5).

Forest floor characteristics were correlated with carabid abundance and diversity. We found a negative correlation between percent vegetation cover and carabid abundance (Table 2). In addition, amounts of both bare ground and litter were positively correlated with carabid abundance (Table 2). Carabid diversity was negatively correlated with percent vegetation cover and positively correlated with percent litter, but we found no relationship between diversity and percent bare ground (Table 2).

Species Responses to Habitat Type. Responses of individual species varied considerably across the gradient. However, a main component of the overall pattern was that species characteristic of "open" habitats were most abundant in the salvaged areas, which "forest" species tended to avoid. The intersection of both faunas in the edge areas led to higher diversity (see below and Fig. 4).

Several relatively uncommon species in our study (less than three individuals) were found only in the edge habitat [*Harpalus amputatus* Say, *Pterostichus pensylvanicus* LeConte, and *Syntomous americanus* (Dejean)]; however, no species occurred exclusively in edge habitat except for those represented by one to two individuals (Table 1).

Abundance of the most commonly caught carabid, *P. adstrictus*, a habitat generalist (Lindroth 1969, Niemelä et al. 1993), differed significantly among the three habitat types (ANOVA, $F = 10.84$, df = 2,8, $P = 0.01$; Fig. 2). Tukey's test revealed that this species was significantly more common in the salvaged forest than in either the edge ($P < 0.05$) or the unsalvaged forest ($P < 0.01$), and along with *Amara torrida* Eschscholtz and *Sericoda quadripunctata* (DeGeer) are significant indicators of that habitat (Table 3). However, there was no significant difference in the abundance of *P. adstrictus* between the edge and unsalvaged forest.

Table 1. Pooled numbers of carabid individuals collected over the course of the experiment divided into unsalvaged forest trap lines, edge trap lines, and salvaged trap lines

	Number of Individuals[a]		
	Unsalvaged Forest	Edge	Salvaged Forest
Scientific name			
Agonum corvus (LeConte)	3	0	0
Agonum gratiosum (Mannerheim)	15	0	1
Agonum placidum (Say)	0	3	4
Amara farcta LeConte	1	0	0
Amara latior (Kirby)	2	4	9
Amara lunicollis Schiødte	0	0	1
Amara obesa (Say)	1	84	64
Amara sp.	0	1	0
Amara torrida (Panzer)	1	2	10
Bembidion bimaculatum (Kirby)	2	3	16
Bembidion grapii Gyllenhal	1	3	4
Bembidion nigripes (Kirby)	0	1	7
Bembidion nitidum (Kirby)	0	0	1
Bembidion praecinctum LeConte	0	1	1
Bembidion quadrimaculatum (Linnaeus)	0	1	1
Calathus ingratus DeJean	75	25	66
Calosoma calidum (Fabricius)	0	8	9
Dyschirius integer LeConte	0	0	1
Harpalus amputatus Say	0	1	0
Harpalus fuliginosus (Duftschmid)	0	0	1
Harpalus innocuous LeConte	1	0	0
Harpalus laticeps LeConte	0	1	1
Harpalus opacipennis (Haldeman)	1	0	0
Harpalus pleuriticus Kirby	0	0	1
Patrobus stigicus Chaudoir	6	1	0
Platynus decentis (Say)	71	16	15
Poecilus lucublandis (Say)	0	1	3
Pterostichus adstrictus Eschscholtz	113	276	471
Pterostichus pensylvanicus LeConte	0	1	0
Scaphinotus marginatus (Fischer von Waldheim)	16	1	0
Sericoda quadripunctata (DeGeer)	91	260	329
Sericoda bembidioides Kirby	3	161	210
Stereocerus haematopus (DeJean)	1	0	0
Syntomous americanus (DeJean)	0	2	0
Trechus apicalis Motschulsky	3	1	3
Number of individuals	407	858	1,229
Number of species	19	25	24

[a] Unsalvaged forest, traps 20–40 m into the standing burned forest habitat; edge, traps 10 m into the unsalvaged forest, traps on the edge, and traps 10 m into the salvaged forest; unsalvaged forest traps, 20–40 m into the salvaged forest habitat.

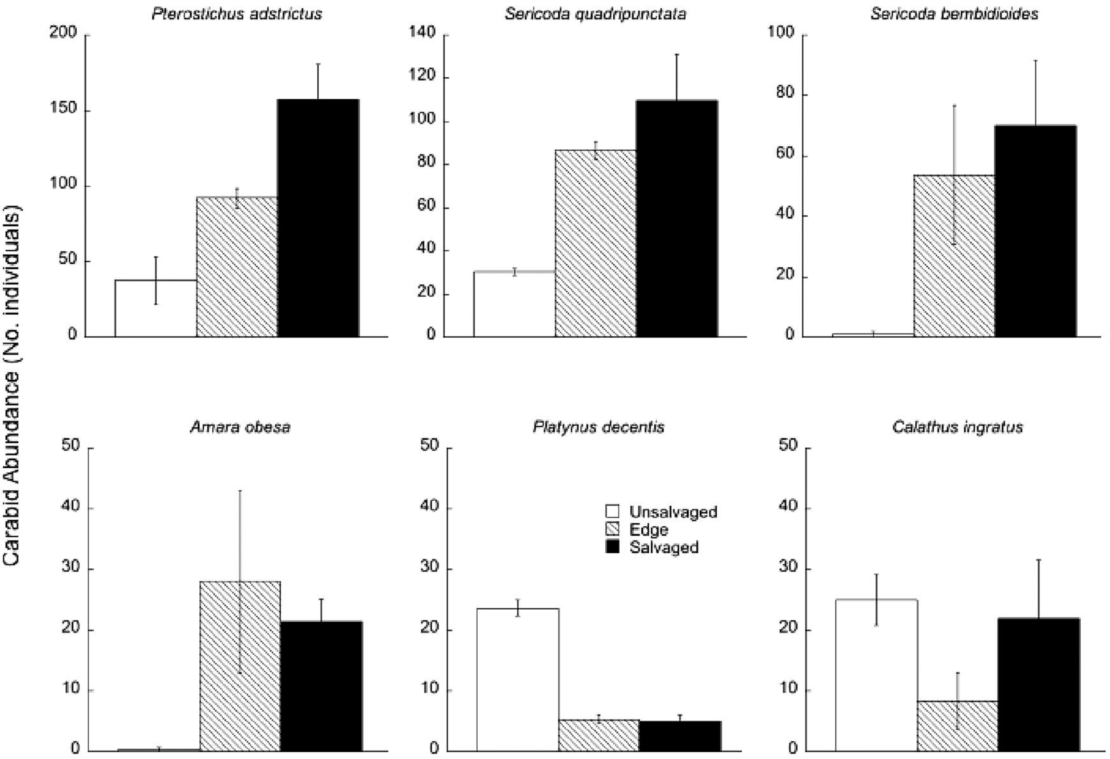

Fig. 2. Abundance of the most commonly caught carabid species in unsalvaged, edge, and salvaged habitats. Bars are means ± SE for $n = 3$ transects.

Despite this, total catch of *P. adstrictus* and that of the two *Sericoda* species seem to decrease from the interior of the salvaged forest to the interior of the unsalvaged forest (Fig. 2).

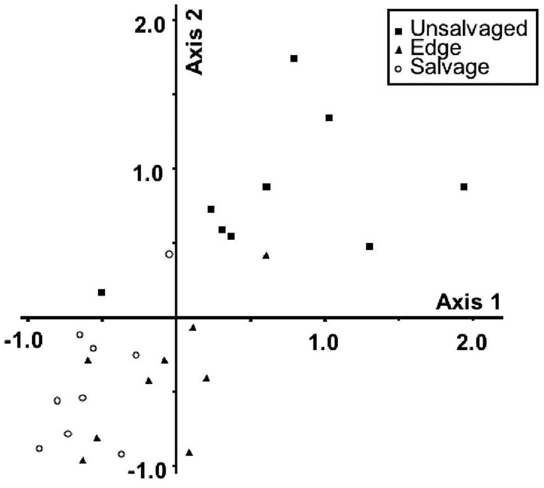

Fig. 3. Trap-level NMS ordination of carabid species in each habitat (final stress = 7.44; $P = 0.019$; cumulative explained variance = 92.4%). Each symbol represents the carabid species composition for the entire sampling period.

Amara obesa (Say) was an indicator species of the edge habitat (Table 3) because it was caught significantly more in the edge and salvaged habitat and only once in the unsalvaged habitat (ANOVA; $F = 24.91$, df = 2,8, $P = 0.001$; Table 1; Fig. 2).

Agonum gratiosum (Mannerheim), *Scaphinotus marginatus* (Fischer von Waldheim), and *Platynus decentis* (Say) were strongly associated with standing burned forest compared with either the edge or salvaged burned forest habitat. *A. gratiosum* and *S. marginatus* were found almost exclusively in the unsalvaged forest (Table 1), whereas *P. decentis* was captured significantly more frequently (ANOVA; $F = 39.24$, df = 2,8, $P < 0.001$) in the unsalvaged forest relative to the other two habitat types (Fig. 2). Indicator species analysis suggests that these species are significant indicators of standing burned forest (Table 3).

Table 2. Pearson and Spearman rank correlation coefficients between carabid abundance, species diversity, and distance along transect

Variables	Pearson abundance	Spearman	
		Diversity	Distance
Vegetation cover (%)	-0.573^{a}	-0.518^{b}	-0.755^{b}
Bare ground (%)	0.417^{a}	0.130^{c}	0.418^{a}
Litter (%)	0.35^{a}	0.496^{a}	0.596^{a}

Statistical significance: ^{a} $P < 0.05$, ^{b} $P < 0.01$, ^{c} $P > 0.05$. df = 2,8.

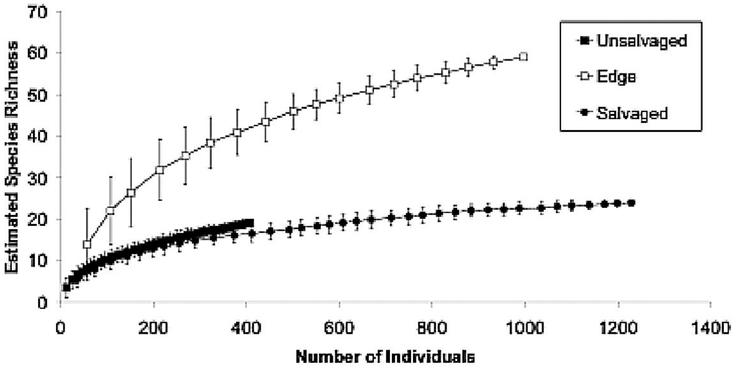

Fig. 4. Rarefaction curves of estimated carabid species richness in the unsalvaged, edge, and salvaged habitats.

Discussion

Carabid Abundance and Environmental Variables. Carabid abundance was highest in the salvaged forest and lowest in the unsalvaged forest along the gradient. This pattern was strongly related to percent vegetation cover that exhibited the opposite gradient (Fig. 5). Greenslade (1964) and others (see Spence and Niemelä 1994, Phillips and Cobb 2005) have suggested that vegetation density may affect catch rate of carabids in pitfall traps and thus bias estimates of abundance. However, at the scale of carabid movement, it seems unlikely that plant densities commonly observed at this recently burned study site could have such an impact. Instead, correlation between carabid abundance and diversity and percent bare ground and percent litter suggests that none of the environmental variables alone can account for the changes in carabid assemblages that we observed over the gradient.

Overall, the three environmental variables (percent vegetation, percent bare ground, and percent litter) taken together only accounted for ≈50% of the total variation in carabid abundance and diversity. Variables not included in this study, such as variation in prey availability, soil moisture, and temperature, may account for additional variation in each habitat (Lövei and Sunderland 1996). Also, increased scorched woody debris from salvage logging could explain the abundance of *Sericoda* species, as they seem to be associated with burned woody material (Lindroth 1969). Furthermore, Goulet (1974) found that *P. adstrictus* females oviposit in logs, and their larvae survive over a wide moisture range in these microhabitats. Despite the lack of clear mechanistic explanations, the strong responses observed here suggest that further study of salvaged systems might provide better understanding of local variation in carabid abundance.

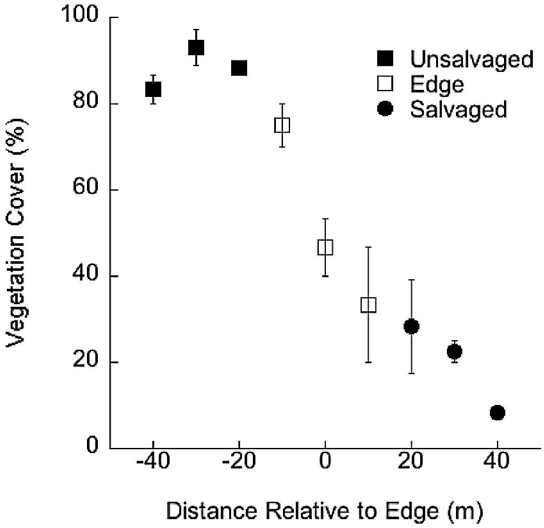

Fig. 5. Relationship between percent vegetation cover and distance across the edge. Values presented as means ± SE for $n = 3$ traps in a given transect.

Edge Effects. Other studies of carabid edge response using transect methods have focused on a wide range of habitat and ecotone types (Table 4). Our compilation of these studies suggests that the effects of edge on carabid communities cannot be generalized with respect to pattern. Similar to the findings of studies of unburned forest edges (Spence et al. 1996, Heliölä et al. 2001, Koivula et al. 2004), we discovered no carabid species restricted to boreal forest edges created by salvage logging. Although "edge specialist" carabids have been identified from studies in Hungary of oak-horn beam/grassland interfaces (Magura and Tóthmérész 1997, Molnár et al. 2001, Magura et al. 2001, Magura 2002), such specialist species seem to be absent from boreal habitats. Heliölä et al. (2001) proposed that the different responses of carabids to edge habitats may be attributed to vegetation characteristics. This is supported by recent experiments showing that carabid catch rate in pitfall traps are heavily influenced by the vegetation in the immediate vicinity of the trap (Phillips and Cobb 2005). Because the carabid community here was strongly correlated with vegetation cover (Table 2), the effect of salvage logging may be a function of its impact on vegetation regeneration postfire. Furthermore, the edges in our study and those of other boreal forest studies (Spence et al. 1996, Heliölä et al. 2001) were abrupt, having been created by forest harvesting, whereas those stud-

Table 3. Significant indicator species for each habitat

Species	Treatment	Indicator value (obs.)	Indicator value from randomization	
			Mean ± SE	P
Agonum gratiosum (Mannerheim)	Unsalvaged	41.7	18.7 ± 0.28	0.045
Platynus decentis (Say)	Unsalvaged	69.6	41.6 ± 0.2	0.001
Scaphinotus marginatus (Fischer von Waldheim)	Unsalvaged	62.7	20.7 ± 0.27	0.003
Amara obesa (Say)	Edge	56.4	37.5 ± 0.3	0.047
Amara torrida (Panzer)	Salvaged	51.3	23.4 ± 0.26	0.013
Pterostichus adstrictus Eschscholtz	Salvaged	54.8	40.4 ± 0.13	0.005
Sericoda quadripunctata (DeGeer)	Salvaged	48.4	39.5 ± 0.12	0.016

Observed indicator values are presented as percent of perfect indication (Dufréne and Legendre 1997), and significance ($P < 0.05$) was determined using Monte Carlo randomization (1,000 permutations).

ied in Hungary (Magura and Tóthmérész 1997, Molnár et al. 2001, Magura et al. 2001, Magura 2002) were more gradual, with abundant bushes. Perhaps larger habitat areas associated with broad ecotones are required for beetle taxa to develop "edge" specialization.

In addition to identifying a significant burned forest edge indicator, *Amara obesa* (Table 3), we did find elevated species richness and species diversity at the edge relative to the other two habitats (Fig. 4), as predicted by the edge hypothesis of Odum (1971). In this regard, our results differ from others (Spence et al. 1996, Heliölä et al. 2001, Molnár et al. 2001), in which elevated species richness was maintained through the edge into the harvested habitat. However, the edge effect hypothesis of Odum (1971) was not completely supported by our results because carabid abundance was not elevated at the edge, nor was any abundant species found only in edge habitat. Salvage logging in this stand was associated with dramatic increases in relative abundance, and these more abundant beetles likely spilled across the edge and penetrated a short distance into the unsalvaged forest. *Amara, Bembidion, Calosoma,* and *Pterostichus* species found in higher abundance in the salvaged forest have all been described as favoring dry, open, and low vegetation (Lindroth 1963, 1968).

Unfortunately, only a single burned and salvaged white spruce stand was accessible in the Chisholm Fire when the study began in 2002. Although pitfall traps placed 25 m apart are considered statistically independent with respect to carabid sampling (Digweed et al. 1995), the fact that our study could only be applied within this single stand constrains our ability to generalize conclusions about salvage logging edge characteristics. However, the single stand studied here provides the most homogeneous background conditions possible to examine carabid responses to edge habitat created by salvage logging and basis for future studies of salvage logging. Because there is so little literature concerning the effects of salvage logging, studies such as ours are crucial to evaluate impacts and develop best practices for salvage logging. Our study provides a clear hypothesis that may be extended in comparison with future studies to develop more robust inferences about the general impacts of salvage logging and edge effects in burned stands.

Conservation Implications. According to the NMS, carabid assemblages along edges grouped together with those from salvaged forest (Fig. 3). This similarity in species composition differs from the results of other studies of carabids and edge effects. Heliölä et al. (2001) found that carabid assemblages associated with edge habitats grouped more closely with the natural forest interior assemblages rather than the clear-cut assemblages. Our results suggest that carabid assemblages may respond differently to logging practices in postfire habitats than in prefire forests. After salvage logging in this stand, edges with unharvested areas

Table 4. Carabid responses to edge between open habitat and forest: studies over various habitats

Country	Authors	Date	Species richness	Total abundance	Number of stands	Number of transects	Habitats
Hungary	Báldi and Kisbenedek	1994	+	+	1	3	Forest/agriculture
United Kingdom	Bedford and Usher	1994	+	NR	2	2	Forest/agriculture
Switzerland	Hänggi and Baur	1998	−	−	1	3	Forest/grassland
Finland	Heliölä et al.	2001	−	+	6	9	Forest/clearcut
Finland	Koivula et al.	2004	NR	+	8	2–4	Forest/agriculture
South Africa	Kotze and Samways	2001	−	NR	6	5	Forest/grassland
Hungary	Magura	2002	−	NR	1	2	Forest/grassland
Hungary	Magura and Tóthmérész	1997	−	+	1	1	Forest/grassland
Hungary	Magura et al.	2001	−	NR	1	3	Forest/grassland
Hungary	Moln½r et al.	2001	−	NR	1	2	Forest/grassland
Canada	Spence et al.	1996	−	+	1	3	Forest/clearcut
Spain	Taboada et al.	2004	−	NR	4, 4	1	Oak, beech/grassland

+, edge elevated over open or forest habitat, gradient, open to forest; −, edge not elevated over open or forest habitat, not gradient, open to forest; NR, paper did not report.

clearly amplified numbers of "open habitat" species and reduced numbers of some species associated with the logged but burned forest. Further study is necessary to identify ecological responses to salvage logging before widespread salvage logging takes place under the guidelines put in place for unburned boreal forest harvesting.

Continuing fragmentation of postfire boreal forest is likely of particular threat to specialists that seem to require the natural burned habitat (Holliday 1991). We found that *A. gratiosum*, *S. marginatus*, and *P. decentis* were abundant in the unsalvaged forest, but drastically reduced in both the edge and salvaged forest (Table 1) and can be used here as indicator species (Dufrêne and Legendre 1997) to characterize natural, unsalvaged habitat (Table 3). Populations of these carabids would likely be adversely affected by the loss of suitable natural burned habitat. Policy solutions require one to prioritize and balance the importance of preservation of native biodiversity, faunal abundance, food webs and successional sequences against the economic value of burned stands in a single, integrated value system.

Structure and identification of an ecotone depends on the time at which the interactions between those two habitats are observed (Kolasa and Zalewski 1995) and clearly invertebrate assemblages inevitably change over time (Wolda 1992). Therefore, to understand if the ecological phenomena we observed continue, long-term studies are imperative to determine the overall impacts of fragmentation of postfire forests on the succession of those habitats. Although we have no choice but to manage now according to the best ecological information available, present pressures to manage are a weak argument against support of long-term studies. Meaningful and widespread adoption of the "triple bottom line" under which social and environmental issues are explicitly balanced against the economic picture seems to be our present best hope to ensure sustainable forest management.

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