

Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia

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The effect of a forest harvesting system whereby small (typically 0.1–2.0 ha) patches of standing timber are retained inside of harvests, was compared to conventional clearcutting for its effect on ground beetle assemblages. Two seasons of pitfall trapping entailed 46 451 trap days, and yielded 15 799 individuals of 28 species; abundance was dominated by four species comprising 92.4% of the catch. Most species were known to have wide geographic distributions in Canada and Alaska but many species seemed to respond to disturbance on a site-specific basis. Contrary to findings of similar studies, no species could be characterized as “mature-forest specialists”, or “forest generalists”. Forest patches and edge habitats immediately inside the forest canopy contained assemblages more closely related to mature forest than to cleared areas. Harvested areas with patches yielded catches distinct from typical clearcuts, based primarily on changes in abundance of one common species. Climatic regimes and landscape disturbance levels were the two important factors distinguishing our study from others, and we have suggested that these may influence the degree to which patches are an effective conservation tool.

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Disturbance processes are integral components of ecosystems (Pickett and White 1985), and management for “natural” values increasingly considers the historical roles of disturbances in ecosystems. However, the scale and frequency of anthropogenic disturbances is such that we now suspect organisms, ecosystem processes and associated services (clean air and water, “aesthetics”, food, and more) to be endangered in many areas (Vitousek et al. 1997). Clearcut harvesting of forests in particular has been criticized for its failure to mimic natural processes (e.g. see Hammond 1991). Wildfires for example, are known to create understorey vegetation and stand structures quite different from clearcutting (Eberhardt and Woodward 1987). A number of alternative forest-harvesting practices, which reduce or reorganize patterns of tree removal relative to clearcutting,

are now being applied by land management agencies (e.g. see Vanha-Majamaa and Jalonen 2001).

“Patch retention” is the within-stand structural retention of patches 0.1–2.0 ha, maintaining 5–20% of pre-harvest volumes, with overall disturbance sizes averaging 40 ha (Fig. 1; Coates and Steventon 1995). Retention, or “clearcutting with reserves”, promotes an even-aged forest canopy interspersed with older and larger forest aggregates (Anon. 1995). The intent is to approximate natural disturbance patterns where wildfire, insect outbreaks or other patchy disturbances have been prominent stand-initiating agents (Coates and Steventon 1995). This definition is consistent with similar harvesting approaches such as “green-tree retention” in Scandinavia, which encompasses a variety of within-stand retention patterns, maintaining ca 10% of pre-harvest

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Fig. 1. Patch retention harvest near Smithers, British Columbia, Canada.

area in mature timber (Vanha-Majamaa and Jalonen 2001). Because these alternative strategies require increased levels of planning, they are more expensive (Hansen et al. 1995). From an economic and from a conservation standpoint, data indicating the efficacy of these changes are desirable.

There are already good data to suggest that patch and disturbance sizes are important factors governing the longevity of ground beetle populations (de Vries and den Boer 1990), and several North American studies indicate that ground beetles respond definitively to forest cutting. Spence et al. (1996) studied carabid beetle assemblages in a chronosequence of clearcut harvests in central Alberta, and found that several species might be unable to regenerate in clearcuts for as long as 27 yr following harvest. Further, conclusions reached by Haila et al. (1994) indicate that a variety of patch sizes at all scales of management are desirable for maintaining natural variation in ground beetle assemblages. However, at the scale of individual harvest, some studies have shown that typical methods of creating patches during harvesting are not distinguishable from standard clearcuts, when viewed from a bryophyte perspective (Jalonen and Vanha-Majamaa 2001), and from a ground beetle perspective (Koivula 2002).

In this study we examined the effect of patch retention harvests in promoting pre-harvest characteristics of ground beetle faunas. We did this as a comparison against the effects of standard clearcutting in high elevation forests in early stages of disturbance recovery (3–6 seasons). Our main hypothesis of interest was that the harvested areas in both types of harvest method would exhibit different faunal patterns during recovery, but we also wished to test whether catches from the insides of patches would be equivalent to those made beneath the forest canopy at harvest boundaries (edges).

Methods and materials

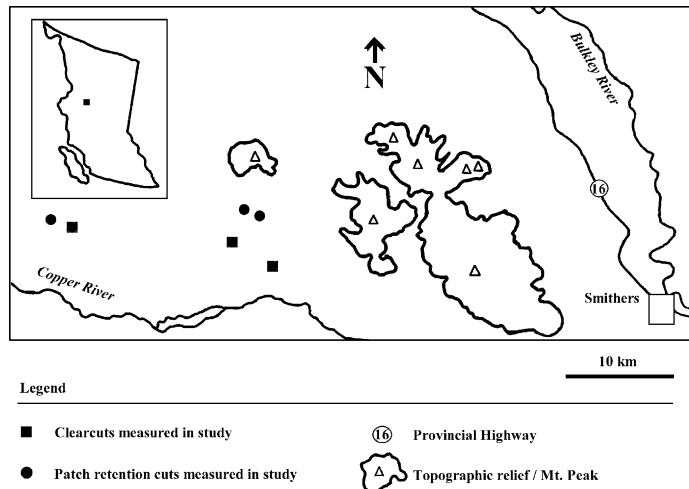
Study area

In the summers of 1995 and 1996 modified “Nordlander-type” pitfall traps (Lemieux and Lindgren 1999) were used to collect ground beetles from three paired “blocks” of patch retention and clearcut harvests. We collected in the Copper River Valley, near Smithers, British Columbia (Fig. 2; Lat/Long: 54°48'30"N to 54°50'24"/127°31'13"W to 127°44'20"W), one of the few areas in BC where patch retention harvests had been conducted prior to 1995. Study harvests were located in the lower elevations of the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (ESSF; Meidinger and Pojar 1991). The ESSF is widely distributed at higher elevations throughout British Columbia, and is commonly the highest forested system in mountainous and rugged terrain. This system is highly variable in timber production and tree density, as it reaches from several hundred meters below tree line, breaking into subalpine parkland near its boundary with alpine tundra. Climate is cold and snowy, with elevations of 1000–2000 m (Farnden 1994). Northern areas have mean annual temperatures near 0°C and up to two months of frost-free days (Farnden 1994); only tree species tolerating extended periods of frozen ground will occur there (Mackinnon et al. 1992). Overstorey is dominated by hybrid white spruce *Picea glauca* × *P. engelmanni*, and subalpine fir *Abies lasiocarpa*, with the former living longer and characterizing mature forests. Lodgepole pine *Pinus contorta* var. *latifolia*, is a common seral species in this zone, and both pine and western hemlock *Tsuga heterophylla*, can comprise minor stand components (Coupé et al. 1991).

Three paired replicates of each harvest type were chosen, so that in each geographical region one patch retention, and one clearcut harvest shared similar physical attributes including slope, aspect, harvest date, and elevation (Table 1, Fig. 2). We refer to these pairs in three “blocks” (Fig. 2). All areas of measurement had been harvested within 2–4 seasons of first being sampled in this study, by hand-felling and line-skidding to landings and roads. All harvests had been planted post-harvest with conifer species.

Clusters of five pitfall traps (plots) were placed in five treatment types: 1) in clearcuts, 2) open areas in patch-retention sites, 3) patches in patch retention sites, 4) interior habitats of undisturbed forest adjacent to both types of harvest, and, 5) areas at the edge of patch retention harvests, beneath intact forest canopy (in 1996 only; see below). Edge plots were established randomly around the circumference of each patch retention harvest, 10 m from the stand edge, on the forested side. Forest plots were also placed randomly, 100–300 m from stand boundaries. Within patch retention harvests there were often many small patches of timber remain-

Fig. 2. Study area, near Smithers, British Columbia, Canada. Numbered blocks refer to "Block" factor used in ANOVA models, indicating forest areas with similar physical and biological features, as listed in Table 1.



ing, of various shapes and sizes. We chose four in each harvest by aerial photograph interpretation, choosing sufficient sizes and shapes to encompass groups of traps. At least 10 m of standing forest existed between any trap and the patch edge; patches were sampled in their centres. In cases where there were more than four eligible patches, we used randomization to choose four. Harvested areas in both patch retention and clearcut harvests were sampled by randomly assigning trap locations.

The five traps in each plot were configured in a cross, with a central trap and four satellite traps, each 5 m from plot center. Traps were filled with saturated brine in 1995. In 1996 we used ethylene glycol-based antifreeze to reduce specimen decomposition. These two preservatives have been shown to produce statistically indistinguishable catches (Lemieux and Lindgren 1999). In each harvest area we randomly established four sample plots within the aforementioned broad habitat classes (mature forest, harvested areas, patch interiors, and forested edge areas in patch retention harvests). We established edge plots in 1996 only in patch retention harvests, in an effort to test whether responses from patches would mimic stand edges. Plot establishment within patches was not a randomized process, because the availability of suitable patches was limited. All other habitat types were sampled using a random sampling process to establish plot locations.

Collections were made on a bi- or tri-weekly basis over the sampling period 21 June–18 August 1995, and at one-month intervals, 6 June–13 September 1996. During 1995 traps were established asynchronously, as much as a month apart, but all patch retention/clearcut harvest pairs were established no more than seven days apart. In 1996, all traps were activated within three days of one

another, immediately following snow melt in early June. All traps were operated in 1996 until mid-September, at which point catches had become sparse.

The addition of plastic cup inserts to traps was made in 1996 (e.g. Lemieux and Lindgren 1999), allowing trap emptying with minimal disturbance to the surrounding soil/vegetation (Spence and Niemelä 1994). All carabid specimens were identified by JPL; a subsample was kindly confirmed by George Ball (Univ. of Alberta, Edmonton, Alberta). Voucher specimens have been deposited at the Spencer Entomological Museum, Univ. of British Columbia, Vancouver, BC.

Analysis

Because of the difference in methods and trapping periods between years, we treated each year as a separate analysis. Catches at each site were counted as the sum of all five traps, pooled across all collection dates. Because some trap sites experienced disturbance from animals, each catch was standardized by the number of active trapping days used to generate it. A single response value for each species in each block was produced by averaging all four plots within a treatment type (see Fig. 3). We used two jackknife estimators to establish the expected number of species in our sampling region (Palmer 1990).

We used two separate analyses to discriminate among all of the disturbance types in our study. A single analysis comparing all treatment types was not possible since patch, edge, and harvested areas of patch retention are not completely independent from one another when being compared against clearcut harvests. To solve this, we compared species responses from harvested regions of either treatment (patch retention or clearcut) using

Table 1. Selected stand attributes of harvested sites studied near Smithers, BC.¹

Block	Harvest type ²	# growing seasons from harvest to 1st sample in this study ³	Area (ha) of opening including retention	Slope (%)/Aspect	Elev. (m)	Post-harvest treatments ⁴	Average diameter-at-breast-height all species (cm)	% Distribution overstorey conifer spp. by volume (Bl/Sx/Pl/Hw) ⁴	Density overstorey, all conifer spp. (stems/ha)
1	PR	3.5	48	5–25/S-SW	1000	Plant Pl Sx	28	55/21/23/1	654
1	CC	3.5	47	14/S-SW	1000	Plant Pl Sx	28	61/24/15/0	674
2	PR	2.5	45	5–30/N-NW	975	Plant Pl	29	60/24/8/8	656
2	CC	4	43	19/NE-N	975	Plant Sx Pl	28	58/22/19/1	748
3	PR	3	41	5–30/variable	900	Plant Pl Sx Bl	32	72/15/11/2	643
3	CC	2	49	5–35/S-SW	950	Plant Pl Sx	34	77/11/0/12	659

¹ Compiled from information contained in timber cruises and pre-harvest silviculture prescriptions, BC Ministry of Forests, Smithers, BC. ² PR = Patch Retention; CC = Clearcut. ³ Growing season includes the months of May–October (qualitative judgment based on field observations). ⁴ Species codes are as follows: Bl, subalpine fir (*Abies lasiocarpa*); Sx, hybrid white spruce (*Picea glauca* x *engelmannii*); Pl, lodgepole pine (*Pinus contorta* var. *latifolia*); Hw, western hemlock (*Thuja plicata*).

one sample t-tests, testing against a mean value of zero as a null hypothesis. Differences were taken within each block (Fig. 3B).

To examine the response of individual species to treatments within patch retention cuts, we used a General Linear Model procedure (Zar 1984, Anon 1997), initially testing the richest model: Species = Treatment + Block + Treatment × Block (Figs 2, 3C). We used a backward elimination procedure, reporting test values for treatment effect with all significant model terms included. When significant differences occurred, Tukey post-hoc multiple comparisons were used to contrast treatment means (Zar 1984). Data were log transformed to correct for non-normality and variance heterogeneity between treatment populations, (Zar 1984). Variance homogeneity was confirmed with a Levine test (Anon. 1997).

Additionally, we used the software program PC ORD (McCune and Mefford 1999) to describe our samples using non-metric scaling (NMS; Kruskal 1964), an ordination technique appropriate for non-normal data typical in ecological studies (McCune and Grace 2002). We used this technique to provide a multivariate comparison among all treatment levels, from both clearcut and patch retention treatments (Fig. 3A); results describe how plots are related to each other in “species space”. Data were log transformed and species were standardized to their own maxima. Species occurring in < 5% of plots were excluded from the analysis. These transformations reduce distortion that can occur in ordination when values between species range over several orders of magnitude (McCune and Grace 2002). We used a 2-dimensional solution in both years, chosen by examining plots of model fit that indicated where subsequent dimensions added little improvement (McCune and Grace 2002). We used 80 iterations to evaluate stability, and plots of iteration vs. model fit to ensure that our final solutions were stable.

Within the resulting ordination space, we rotated axes to maximize correspondence of a single axis to treatment groups (Dargie 1984), and used Pearson’s r^2 value to relate each species to the resulting axis (Zar 1984). To describe how well this rotation explained a linear disturbance gradient, we assigned an artificial linear set of numbers to code for treatment groups, based on obvious patterns from the ordination. We related those values to the rotated axis values, using Pearson’s r^2 : in the 1995 dataset we coded values from 1–4, corresponding to forest, patch, patch cut, and clearcut. For the 1996 data, we used values of 1–5 for: edge, forest, patch, patch cut, and clearcut. We used a non-parametric method, blocked multiple response permutation procedure (MRBP), to test whether treatments formed distinct multivariate groups (McCune and Grace 2002). “Block” was used as a blocking parameter.

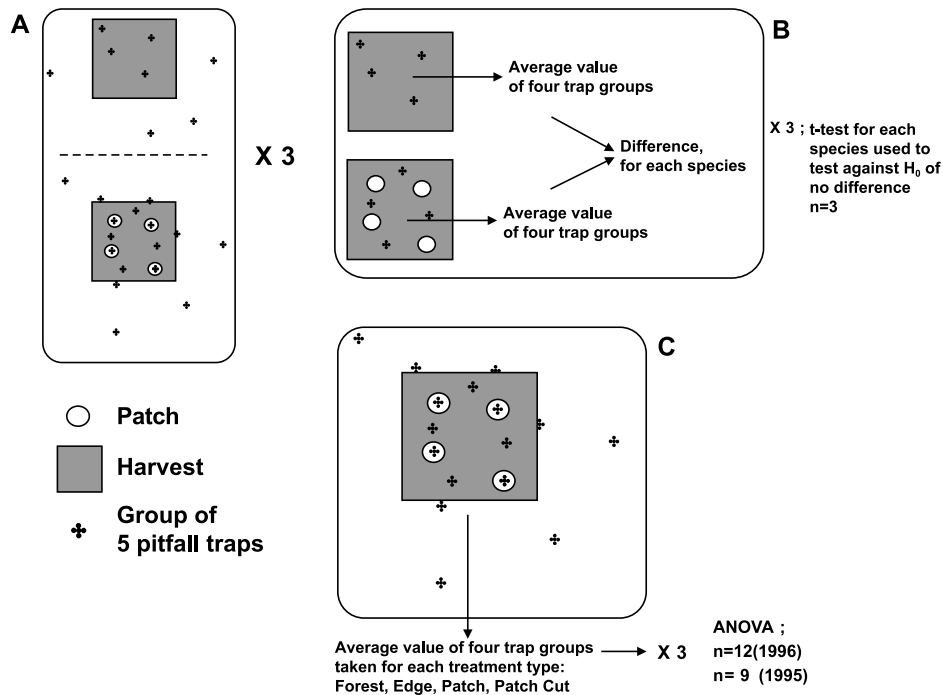


Fig. 3. Sampling regime used to collect ground beetles near Smithers, BC, Canada. The entire regime (A) was used in comparisons using non-metric scaling, but only certain subsets of the data were used to make comparisons of harvest areas (B), and all levels of treatments from patch retention harvests (C), using univariate statistics.

Results

Twenty-eight species of Carabidae in 17 genera were recorded over two seasons of trapping, comprising 46 451 trap days. First- and second-order jackknife estimates indicate that there may have been 33 or 34 species of carabids in the sampling region, respectively. Abundance was dominated by four species, comprising 92.4% of the catch (Table 2). No species were restricted to the forested, patch or edge locations, but eight species, caught in very low abundance, were unique to the harvested areas (Table 2). They indicate a tendency toward rarity in disturbed habitats in this system and should warrant future consideration by methods other than pitfall trapping.

Non-metric scaling (NMS) revealed two primary axes (Fig. 4) that explained 82% of the variation from the original data set (1995 data; 75% and 7%, respectively). Monte Carlo results of tests for whether axes represent non-random entities were $p = 0.02$ and $p = 0.04$ respectively; the second axis, accounting for a relatively small amount of information, may be less explanatory than indicated by the result. Rotation to maximum correspondence with treatment categories produced an axis that explained 55% of the variance in the original data, and which was highly related to linear coded values for treatment effects ($r^2 = 0.87$). The

second axis was poorly explained by the coded value of block ($r^2 = 0.07$).

There were also two primary axes formed from the 1996 data (Monte Carlo $p = 0.02$, both axes), explaining 80% (57 and 23%) of variance from original data set. Rotation produced an axis that explained 58% of variance from the original data set. In this configuration, the coded values we assigned to represent disturbance categories were well correlated with the first axis ($r^2 = 0.85$), and "block" codes were well correlated with the second axis ($r^2 = 0.81$).

Blocked multiple response permutation procedure (MRBP) provides a Monte Carlo p-value describing the likelihood of an equal or smaller effect size "A" than that measured by the procedure (McCune and Grace 2002). The effect size is the value 1-(within group heterogeneity/randomly expected heterogeneity). When $A = 1$, there is perfect within group agreement, and when $A = 0$ within group agreement is equal to random expectation. A significant effect size of 0.1 is commonly observed in community data (McCune and Grace 2002). The effect sizes, A, observed in our study were 0.23 ($p = 0.02$, 1995) and 0.26 ($p = 0.00$, 1996).

The most abundant species in the study, *Scaphinotus angusticollis* occurred more frequently in harvests with patch retention than in clearcuts, 1996 data ($p = 0.05$, $DF = 2$), and was the only species that showed a

statistically significant difference between treatments. Mean values and standard deviations of species with p-values less than or equal to 0.25 are listed in Table 3.

GLM and Tukey post-hoc multiple comparison results are given in Table 4. Most species were caught variously among several treatments, and few if any can be described as forest generalists or mature forest specialists, as expected from previous studies (Craig 1995, Spence et al. 1996). Some species were restricted to open habitat areas (see Table 2), but most were observed in a gradient sense, with stronger values either in forests or clearcuts, but still present in substantial quantities in all treatments. The majority of positive test values occurred in 1996, though the order of means among treatments was often consistent between years, suggesting common year-year responses.

Discussion

We observed consistent community level trends from year to year, though resolution for individual species was better in 1996; we believe this to be an artifact of our more limited sampling in 1995. It is possible that treatment effects may increase through time for carabid beetles (Koivula 2002), although the 2–6 yr post-harvest interval for our measures is consistent with other studies that have shown dramatic difference (Craig 1995, Spence

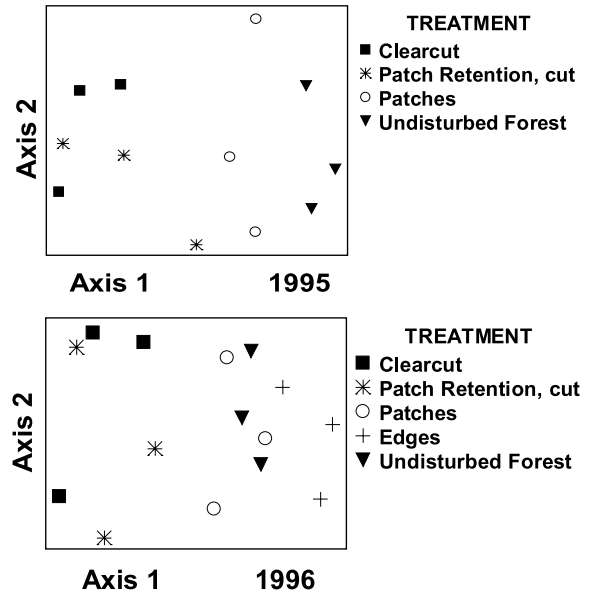


Fig. 4. Non-metric scaling (NMS) ordination for carabid species caught near Smithers, BC, 1995 and 1996.

et al. 1996). The strong trends revealed by non-metric scaling (NMS) show that disturbance-related patterns account for the majority of variance in our catches, and that “block” was an independent but significant source of variation; useful for modeling in our linear models.

Table 2. Carabidae from pitfall traps near Smithers, BC. Data are pooled over all catches and expressed as counts of each species and percentages of total catch, all species.

Taxon	Clearcut	Patch retention, harvested	Patch	Edge	Forest	Total caught	% of catch
* <i>Agonum metallescens</i>	2	1	0	0	0	3	< 0.50
* <i>Amara erratica</i>	2	0	0	0	0	2	< 0.50
* <i>Amara sinuosa</i>	5	8	0	0	0	13	< 0.50
<i>Bembidion fortetrium</i>	0	2	5	0	0	7	< 0.50
* <i>Bembidion grapei</i>	1	2	0	0	0	3	< 0.50
<i>Bembidion incertum</i>	4	22	4	0	0	30	< 0.50
* <i>Bembidion incrematum</i>	0	4	0	0	0	4	< 0.50
<i>Bembidion oblongulum</i>	60	34	37	1	37	169	1.07
<i>Calathus advena</i>	189	171	959	1372	537	3228	20.42
<i>Calathus ingratus</i>	0	1	1	0	0	2	< 0.50
<i>Elaphrus americanus</i>	0	1	0	0	0	1	< 0.50
<i>Elaphrus clairvillei</i>	11	53	1	3	0	68	< 0.50
* <i>Harpalus laticeps</i>	0	1	0	0	0	1	< 0.50
* <i>Harpalus nigratarsus</i>	3	1	0	0	0	4	< 0.50
<i>Leistus ferruginosus</i>	1	0	1	0	3	5	< 0.50
<i>Loricera decempunctata</i>	2	10	2	0	0	14	< 0.50
<i>Nebria gyllenhali</i>	2	2	3	3	4	14	< 0.50
<i>Notiophilus sylvaticus</i>	19	17	50	12	44	142	0.90
* <i>Patrobus fossifrons</i>	0	1	0	0	0	1	< 0.50
<i>Pterostichus adstrictus</i>	125	124	4	4	3	260	1.65
<i>Pterostichus castaneus</i>	77	81	55	22	54	289	1.83
<i>Pterostichus empetricola</i>	4	6	11	3	5	29	< 0.50
<i>Pterostichus riparius</i>	25	45	22	2	31	125	0.79
<i>Scaphinotus angusticollis</i>	462	1291	1761	1684	3666	8864	56.08
<i>Scaphinotus marginatus</i>	279	162	84	79	404	1008	6.38
<i>Syntomus americanus</i>	2	1	2	0	0	5	< 0.50
<i>Trachypachus holmbergi</i>	0	2	0	0	0	2	< 0.50
<i>Trechus chalybeus</i>	672	427	218	25	164	1506	9.53
Carabidae	1947	2470	3220	3210	4952	15799	

*Indicates species caught only in harvested areas.

The substantial effect sizes we observed with blocked multiple response permutation procedure (MRBP) indicate that the overall distinction among treatment types was relatively strong when compared against typical community data.

These patterns are based on a good catch where we believe we have represented all species that would be common enough for the analyses we used; jackknife techniques indicated that there should be a few more species in the region, but we expect they would be trapped in incidental quantity. Our catches bear an average species richness and are consistent in some respects with studies from other northern forests. Craig (1995) lists 28 species from a full year of intensive pitfall trapping on Vancouver Island, BC, Niemelä et al. (1993) trapped 39 species from a multi-year and regionally broad study near Hinton, Alberta, and Duchesne and McAlpine (1993) list 28 species from a single summer of pitfall trapping in eastern Ontario jack pine forest. Abundant species and those that were used for analysis in this study were also those with wide regional distributions (Lindroth 1961–1969); incidental species tended to have been reported as having limited or patchy ranges, a trend previously reported for ground beetles in boreal forests (Niemelä and Spence 1994). Because of this our study considers species that have been examined elsewhere in western Canada and as far east as Ontario. Our comparisons against those studies indicate some important trends for the conservation of individual species, especially considering the effects of patch retention.

Assemblages from Duchesne and McAlpine (1993), Niemelä et al. (1993), Craig (1995), Spence et al. (1996), as well as from Niemelä et al. (1992) have been resolved to distinct response categories of: forest generalists (species abundant through a range of local forested habitats), mature-forest specialists (species confined to specific forested habitats) and open-habitat specialists (species occurring primarily in open areas). However, none of the species in our study displayed distributions that could be interpreted as mature-forest specialist or generalist; no species were restricted to mature forest. The fauna we examined appears to have had a more

generalist nature, and the majority of distinct contrasts occurred where species were caught prevalently in harvested areas. Instead of a suite of specialists and non-specialists, many of the species we observed could be better described along a habitat gradient, illustrated in our multivariate analysis (Fig. 4). The ecological basis for such a gradient is obvious, being related primarily to light, moisture and temperature gradients created from the process of canopy removal, but possibly also to structural features like dead wood and soil compaction. The gradient confirms that patches tend to house intermediate assemblages, and that there is some slight distinction between clearcuts and patch cuts when all species are considered in unison. With the exception of those species occurring in incidental quantity (Table 2), we can classify species as having no particular association, responding to environmental gradients across a range of disturbances, and those showing especially abundant responses in either patches or edges. Large catches of *S. angusticollis* and *Calathus advena* in edges contributed to the strong “edge effect” observed in our 1996 samples (Fig. 3). We have considered that inordinate catches at stand edges may have been influenced by a “rebound” effect, where species preferring forested habitats are caught disproportionately when they turn away from stand edges (e.g. Duelli et al. 1990). Edge treatments were also characterized by a paucity of the smaller, more vagile species that were more abundant in forests and cleared areas than in edges: notably *Bembidion oblongulum*, but also *Notiophilus sylvaticus* and *Trechus chalybeus* (Table 4). These species could be excluded by the larger, predatory species that we caught there, though there is little experimental evidence to support competitive exclusion as a mechanism for such interactions (Loreau 1990, Niemelä et al. 1997).

That we observed less dramatic responses compared with other studies is compounded by the fact that many of the species were common to those studies. One of the central themes in Lindroth’s (1961–1969) ecological descriptions of ground beetles is the tendency for forest species to emerge into open habitat in certain limits of their distributions; often western. This may underlie a

Table 3. Mean, standard deviation and test values from t-tests used to compare harvested areas of patch retention sites with clearcuts.

Species (yr)	Treatment in which species was caught in most abundance	Mean difference between treatments \pm SD (individuals/trap/day)	p-value
<i>Scaphinotus angusticollis</i> (1995)	Patch retention	0.239 \pm 0.189	0.21
<i>Scaphinotus angusticollis</i> (1996)	Patch retention	0.251 \pm 0.088	0.05
<i>Bembidion oblongulum</i> (1996)	Clearcut	0.015 \pm 0.013	0.19
<i>Bembidion incertum</i> (1996)	Patch retention	0.008 \pm 0.007	0.19
<i>Trechus chalybeus</i> (1995)	Clearcut	0.083 \pm 0.085	0.23

Table 4. Commonly occurring species (> 50 individuals) captured in pitfall traps near Smithers, BC, 1995/6. Treatment codes with a continuous underline were not significantly different from one another (Tukey, $\alpha = 0.05$). OP = open areas in patch retention; P = patch; E = edge; F = undisturbed forest. Non-metric scaling (NMS) axis r^2 values are the correlation between species values and treatment scores on axis one.

Species	Year	NMS axis r^2	Mean \pm SD (individuals/trap/day)				p-value treatment effect
<i>Bembidion oblongulum</i>	1995	0.12	0.014 \pm 0.006 P	0.012 \pm 0.009 OP	0.002 \pm 0.004 F		0.04
	1996	0.18	0.012 \pm 0.009 P	0.011 \pm 0.013 OP	0.008 \pm 0.009 F	0.000 \pm 0.001 E	0.22
<i>Calathus advena</i>	1995	0.23	0.269 \pm 0.216 P	0.111 \pm 0.117 F	0.041 \pm 0.032 OP		0.08
	1996	0.28	0.851 \pm 0.796 E	0.305 \pm 0.240 P	0.092 \pm 0.052 F	0.062 \pm 0.038 OP	0.00
<i>Elaphrus clairvillei</i>	1995	0.20	0.004 \pm 0.005 OP	– P	– F		0.08
	1996	0.12	0.021 \pm 0.028 OP	0.001 \pm 0.002 E	0.000 \pm 0.001 P	– F	0.13
<i>Notiophilus sylvaticus</i>	1995	0.32	0.001 \pm 0.002 F	– P	– OP		0.42
	1996	0.00	0.021 \pm 0.021 P	0.011 \pm 0.005 F	0.008 \pm 0.005 OP	0.008 \pm 0.006 E	0.34
<i>Pterostichus adstrictus</i>	1995	0.76	0.022 \pm 0.017 OP	0.001 \pm 0.001 P	– F		0.01
	1996	0.65	0.050 \pm 0.023 OP	0.003 \pm 0.003 E	0.001 \pm 0.002 P	0.001 \pm 0.001 F	0.00
<i>Pterostichus castaneus</i>	1995	0.19	0.016 \pm 0.015 OP	0.011 \pm 0.007 P	0.007 \pm 0.003 F		0.11
	1996	0.22	0.033 \pm 0.025 OP	0.023 \pm 0.008 P	0.013 \pm 0.009 E	0.011 \pm 0.009 F	0.00
<i>Pterostichus riparius</i>	1995	0.02	0.018 \pm 0.021 P	0.017 \pm 0.012 OP	0.008 \pm 0.013 F		0.56
	1996	0.75	0.014 \pm 0.008 OP	0.004 \pm 0.006 F	0.002 \pm 0.001 E	0.001 \pm 0.002 P	0.04
<i>Scaphinotus angusticollis</i>	1995	0.56	0.408 \pm 0.159 F	0.339 \pm 0.263 OP	0.331 \pm 0.149 P		0.57
	1996	0.73	1.031 \pm 0.450 E	0.743 \pm 0.249 F	0.675 \pm 0.063 P	0.428 \pm 0.158 OP	0.05
<i>Scaphinotus marginatus</i>	1995	0.00	0.045 \pm 0.040 F	0.027 \pm 0.043 P	0.018 \pm 0.028 OP		0.60
	1996	0.06	0.080 \pm 0.067 F	0.071 \pm 0.079 OP	0.050 \pm 0.034 E	0.029 \pm 0.032 P	0.65
<i>Trechus chalybeus</i>	1995	0.81	0.115 \pm 0.007 OP	0.078 \pm 0.055 P	0.019 \pm 0.015 F		0.00
	1996	0.50	0.158 \pm 0.077 OP	0.063 \pm 0.018 P	0.036 \pm 0.017 F	0.019 \pm 0.018 E	0.00

simple moisture requirement, which is met in coastally-influenced western areas but not in more continental ranges. In contrast to the cool wet conditions of the Copper River Valley, Spence (pers. comm.) has described the post-harvest conditions of pine stands of his Alberta studies to have been xeric. Perhaps because of late snowmelt and low temperatures at high latitude and altitude, we observed mesic or even hygric conditions through much of the trapping season in all habitats.

Where prevailing climatic and forest regimes differ, species may be expected to behave quite differently to disturbances. For example, Craig (1995) reported a high abundance for *S. angusticollis* in Vancouver Island forests, BC, with virtually no occurrence in cleared areas of young stands, 3–8 yr after harvest. She classified it as a forest generalist, recovering gradually with stand succession. Our data indicate that *S. angusticollis* does not respond as a “forest species” under our study conditions, that it appears to use harvested areas successfully, and may have some predisposition toward occurring in high densities at stand edges. This is corroborated by observations from southeastern British Columbia, where abundance decreased in clearcuts vs surrounding forests, but not in a statistically significant manner (Lavallee 1999). However, this species was also the only one showing difference between harvested areas of patch retention and clearcut harvests (Table 3). We believe this species above all others to be very sensitive to habitat changes, but able to use clearcut habitats in our study area because of wet or mesic conditions that occur there. We caught a large number of gastropod slugs in harvested regions ($n = 4388$ for clearcuts, 1758 for harvested plots in patch retention harvests, 124 in patches, 113 in mature forest and 19 at edges), which are an important food item for this genus (Digweed 1993), and which are absent from drier forests in Alberta (Spence pers. comm.)

Likewise, *Scaphinotus marginatus* has been observed as a forest generalist (Niemelä et al. 1992, Spence et al. 1996), nearly absent from sites at ages of two years post-harvest (Niemelä et al. 1993, Spence et al. 1996), and 3–8 yr in southern coastal forests (Craig 1995). Our data indicate that this species was a generalist with uniform abundance across disturbance types. Lindroth (1961–1969) indicates the species to be more restricted to forests in southern areas, occurring above timberline in the Rocky Mountains, and throughout open tundra on the Aleutian Islands, Alaska.

Both *Pterostichus riparius* and *Trechus chalybeus* were considered threatened species from multiple pass rotations of forest harvesting in Alberta lodgepole pine forests, (Spence et al. 1996), but we collected these abundantly in harvested areas. Both species responded strongly to treatments, decreasing in abundance in plots with intact forest canopies (Table 4). Lindroth (1961–

1969) indicates that both species will occur above timberline or in certain open areas.

Calathus advena has been collected as a forest specialist (Spence et al. 1996), threatened by short rotation intervals in Alberta, and by Duchesne and McAlpine (1993) as a species characterizing clearcuts in eastern Ontario. Our data, the westernmost collection of the three, indicate that this species is a generalist with high population densities in patch and edge environments. Lindroth (1966–1969) lists this species as primarily a forest insect, in shaded, mesic habitats but also in open meadows in the Aleutian Islands, AK.

Elaphrus clairvillei was collected as a forest specialist (Niemelä et al. 1992), but we collected it abundantly in openings, although the use of ANOVA does not discriminate among treatments. *Pterostichus adstrictus* is a well known denizen of open and grassy habitat, but it is known to lay its eggs in moist, woody debris (Goulet 1974). We observed this species responding very strongly to a disturbance gradient, and markedly associated with harvested areas. A similar response was observed by Heliölä et al. (2001) in Fennoscandia, but other studies from western Canada have reported this species as an overall generalist, occurring across a range of forest succession stages (Niemelä et al. 1993, Spence et al. 1996).

The extent to which our results contradict other studies surprised us, but we note also that our study landscape was relatively undisturbed at the time of measurement. Spence et al. (1996) proposed that the failure of forest specialists like *S. marginatus* to recolonize harvests even 27 yr post-harvest, was due to dwindled source populations in the landscape. This insufficiency was thought to result from habitat loss and the insularization of remaining mature forests. Additionally, we noted a lack of open habitat specialists reported from those same studies. Typically, forest openings or forest meadows are dominated by members of the carabid genera *Amara* and *Harpalus* (Craig 1995, Duchesne and McAlpine 1993, Niemelä et al. 1992, 1993, Spence et al. 1996). The almost complete absence of these groups in our study might indicate a more general absence of open habitat specialists from a broad array of taxa that could compete with the established fauna. We suggest that landscape history may influence the way in which species respond to local disturbance patterns by adjusting the degree of competition for resources.

Some ground beetle species in our study seemed less at risk from harvesting when compared to reports of the same species in other studies; but the presence of patches did nevertheless influence the fauna in regenerating areas. And because even small patches more closely emulated a mature forest fauna than openings, the retention of patches without a corresponding increase in harvest size or number should help to maintain

pre-harvest conditions. If our speculation is correct, the effect of the method should change with the frequency of disturbance in the landscape, and with changes in prevailing climatic conditions.

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