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Northern forestry and carabids: the case for concern about old-growth species

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Two studies in western Canada focus on whether carabid species specialize in use of old-growth forest habitats. In montane lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) forest, *Calathus advena* Lec., *Carabus chamissonis* Fish., *Leistus ferruginosus* Mnh., *Nebria intermedia* V. D., *Platynus decentis* Say, *Pterostichus brevicornis* Kby., *Pterostichus riparius* Dej., *Scaphinotus marginatus* Fisch. and *Trechus chalybeus* Dej. are common in post-rotation age forest with no history of harvesting, but scarce in or absent from regenerating sites, even 27 years after harvest. Residual populations of old-growth specialists in uncut fragments are exposed to increased contact with habitat generalists and open-habitat specialists from surrounding cut-overs and regenerating forests. Populations of several species of old-growth specialists in lodgepole pine live also in younger, fire-origin stands in boreal aspen (*Populus tremuloides* Michaux.) stands of the “mixedwood” zone. We hypothesize that they have recolonized from the large surrounding tracts of unburned residual forest remaining after fire. Thus, landscape-scale effects, resulting in changes in regional population size, may alter the probability of species retention in old-growth fragments, and of the recolonization of cut-blocks by particular species characteristic of old-growth.

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1. Introduction

World-wide concern is growing about the loss of old-growth forests as habitats for significant fractions of the earth's biota (Wilson 1992, Niemelä *et al.* 1993 ab, Berg *et al.* 1994, Haila *et al.* 1994, Noss & Cooperrider 1994). Much of the attention focuses on vertebrates because of their high apparency and their requirements for large, uninterrupted habitat patches (Schneider & Yodis 1994, Vickery *et al.* 1994, Newmark 1995). Clearly, however, deforestation also has been associated with impoverishment of invertebrate faunas (Warren & Key 1991, Esseen *et al.* 1992). It is appropriate to ask if such concerns are reasonably extended to carabids. Use of carabids as indicators of grassland conservation and management is well established in Europe (Eyre & Rushton 1989, Eyre *et al.* 1989) but less is known about the potential of carabids as environmental indicators in forested habitats. Some carabids appear to be sensitive to subtle habitat features such as those that distinguish old, undisturbed stands of trees from younger or more disturbed stands (Nield 1990, Szyszko 1990). Such species should have potential as indicator taxa (Frietag *et al.* 1973, Pearson & Cassola 1992, Niemelä *et al.* 1993b).

Concern for tropical forest faunas is exacerbated by alarming statistics about recent rates of tropical deforestation. Our colleagues with experience in tropical forests assure us that carabids are indeed at risk (e.g. Ball & Roughley 1982, Erwin 1991). In fact, the task of fully cataloging tropical insect faunas, including carabids, has been portrayed as a race of an undersized corps of systematists against hordes of loggers and land developers (Cotterill 1995). The argument is that tropical forests will be slow or unable to regenerate once they are cut down, and thus the animals, whose varied and largely unknown lifestyles depend on the forest's integrity, will be forever lost — perhaps even before the species are known to science (Wilson 1992, 1994). Presented with these stereotypes, the public of developed countries, when sensitive to the so-called biodiversity crisis at all, believe that the solution is largely about saving someone else's rain forests.

However, forests are being exploited wherever they occur, and local extinction of species is possible whenever a land base is allocated to harvest rotation (Noss & Cooperrider 1994). Boreal forest vegetation usually regenerates after logging, if given the opportunity, although the species complex that appears may not exactly replicate that of the progenitor (Barnes 1989). Thus, it may be argued that species like carabids that depend more on a forest "gestalt" than on specific plant species are safe. Developers claim that boreal forests have long regenerated naturally after periodic disturbances such as wildfire, and thus have a biota adapted to a shifting spatial mosaic of forest habitats. Nonetheless, recent work suggests that abundance and diversity of various saproxylic beetles have been reduced in northern European landscapes subjected to forestry over the past 300 years (Speight 1989, Väisänen *et al.* 1993, Siitonen & Martikainen 1994). Although carabids generally are not saproxylic, decaying woody material and leaf litter are crucial elements of habitat for many forest-dwelling ground-beetle species (Niemelä *et al.* 1992a, Haila *et al.* 1994). Furthermore, Halme and Niemelä (1993) have shown that some populations of forest carabids are reduced or eliminated in fragmented forests characteristic of modern land development.

Timber companies are just beginning the first cut in the extensive boreal forests of Alberta, Canada (Pratt & Urquhart 1994). This has prompted us to study the effects of forest harvesting and forest age on carabid populations. In this paper, we (1) ask whether there are species dependent upon these "old-growth" forests, (2) consider how forest fragmentation may affect the probability that these species will retain viable populations in the face of the increased logging activity, and (3) test the hypothesis that carabids are subject to edge effects, and thus sensitive to patterns of forest fragmentation that will result from logging. After presentation of our data, we place them in the context of other studies to assess the potential for negative impact of logging on boreal carabid faunas.

2. Material and methods

2.1. Study sites

We studied carabids in two types of boreal forest, representing a significant proportion of presently exploited timber reserves in western Canada (Fig. 1). Studies of lodgepole pine forests were carried out on the east slopes of the Rocky Mountains near Hinton, Alberta (53°22′N, 117°35′W). The overstory of these montane stands is dominated by lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelm.) with white spruce (*Picea glauca* [Moench] Voss) as a significant component in

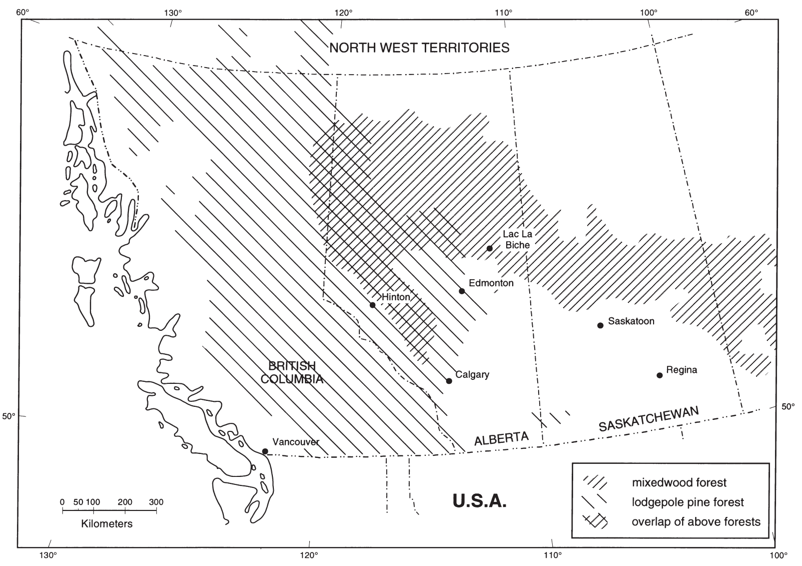

Fig. 1. Approximate distribution of mixedwood and lodgepole pine dominated forests in western Canada. The two main study sites were north and south of Hinton, Alberta and east of Lac La Biche, Alberta.

some areas; there is only a sprinkling of deciduous trees, mainly trembling aspen (*Populus tremuloides* Michx.). We compare the fauna collected from eight old (canopy trees > 80 yrs), never-logged stands with that of six nearby stands (9–27 yrs) regenerating to pine forest after clear cut logging. Logging has occurred in the Hinton area only since the late 1950's and we were unable to locate regenerating stands > 27 years of age for study. The sites and specific sampling design are fully described by Niemelä *et al.* (1993ab). In order to minimize geographic effects, we do not include data for mature stands in Swan Hills as was presented by Niemelä *et al.* (1993ab). Also, data for 1- to 2-year-old clearcuts north of Hinton were excluded from this paper because mixedwood stands of comparable age were unavailable for study.

We have also studied the carabid fauna of a boreal mixedwood site located in northeastern Alberta, near Lac La Biche (54°51′N, 111°27′W). These forests are composed mainly of trembling aspen, with balsam poplar (*Populus balsamifera* L.) co-dominant on moister sites; some older patches tend to white spruce through succession (Rowe 1972, Samoil 1988) although this process is more variable in both space and time than formerly supposed (Lieffers *et al.* 1996). In addition, succession to conifer-dominated stands was periodically set back in former times by frequent wildfire (Bonan & Shugart 1989).

In the mixedwood forest, we studied the effects of stand age, and assessed the early effects of clear-cutting on the carabid fauna by comparing samples among fire-origin aspen stands of three ages, and stands recently harvested. We sampled each of three age classes as follows: > 120 years (6 trap lines), ca. 60 years (6 trap lines), ca. 40 years (2 trap lines) since last disturbance by fire. We also ran trap lines in two stands, which had been harvested 8 years previous to initiation of the study. One of these stands (NCB) had been scarified and planted with lodgepole pine but was predominately characterized by naturally regenerating aspen, white birch (*Betula papyrifera* Marsh.) and willow (*Salix* spp.). The other 8 year-old stand (NCA) was unscarified and had regenerated naturally to a dense stand of aspen with lesser amounts of birch and willow. All stands sampled at Lac La Biche are located within a 40 km^2 area; see Spence *et al.* (1996) for a more detailed description of stands. Although trapping was concentrated in two even-aged stands for each of the oldest two age classes, trap lines within these stands were separated by > 150 m and we treat the catches as independent samples here.

2.2. Sampling method

Carabid assemblages were sampled using covered, pitfall traps (round 1-litre plastic containers, 10 cm in diameter) (Spence & Niemelä 1994). About 2.5 cm of ethylene glycol was added to the inner cup of each trap as a preservative. Plywood squares (15 × 15 cm) were suspended, on nails driven through their corners, ca. 2 cm above each trap to protect traps against rain and other disturbances. Six traps were set out in traplines, running linearly through the interior of each forest stand; traps were at least 50 m from the nearest edge and intertrap distances were 50–60 m so as to represent independent samples (Digweed *et al.* 1995).

Traps were run continuously during the snow-free periods of May–October of 1989–90 (lodgepole pine forests) and 1992–93 (mixedwood forests). Traps were emptied at 2–4 week intervals, and all carabid adults were identified to species according to Lindroth (1961–69) and reference collections at the Strickland Museum, University of Alberta. Reference collections of voucher specimens from our studies have been established at the Strickland Museum and the Northern Forestry Centre, Canadian Forest Service, both located in Edmonton, Alberta.

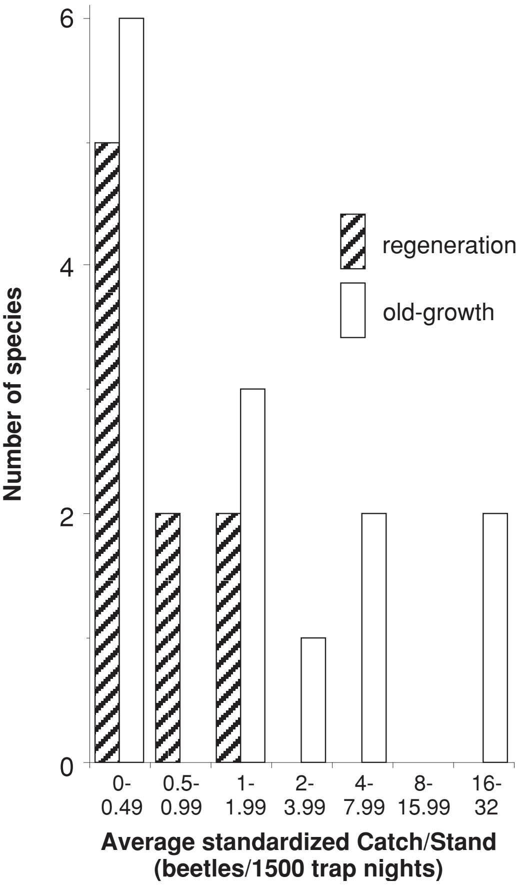

Fig. 2. Average activity-abundance of carabid species captured exclusively in either regenerating stands (9–27 years since harvest) or in old-growth stands (> 80 years since fire origin of stand) in lodgepole pine forests.

From 5 June to 14 October 1991, we undertook a separate study to determine whether carabids would be subjected to edge effects in fragmented lodgepole pine forest near Hinton. We trapped beetles in a pair 2-year-old clear-cuts and in their immediately adjacent residual blocks of old-growth lodgepole pine. Both cut blocks and residual stands in this area were about 1 000–1 200 m long × 500–600 m wide (i.e. 50–72 ha). The sites were located near the northern limit of active logging in the Weldwood Forest Management Area. The area to the north was mainly pristine, never-logged forest and to the south, ca. 40% of the landscape was previously clear cut patches.

Three lines of eleven pitfall traps were placed perpendicular to the southern edge of the residual stand at one site and two lines were placed similarly at the second site less than one km away. Trap lines were separated by a minimum of 100 m. Traps in each of the five lines were placed as follows: one trap, designated as 0, was located at the boundary of forest and clear-cut; five traps, F 1–5, respectively, were located 5, 10, 20, 40 and 80 m into the forest; five traps, C 1–5, respectively, were located 5, 10, 20, 40 and 80 m into the clear-cuts. For all lines, traps F5 and C5 were located > 100 m from any other habitat edge.

2.3. Calculations

In this paper we compare the relative abundances of common carabid species ($N > 15$ individuals captured in each two-year sample) among stands of different ages to judge if any are dependent on undisturbed, old-growth forest. “Old-growth” is a term with many different meanings (Barnes 1989). We use it to designate stands that have never been logged and that have existed relatively undisturbed for longer than the standard harvest rotation for a particular forest type. Harvest rotations are set at ca. 80 years for montane lodgepole pine in Alberta and for northern aspen stands; further south in the mixedwood zone to which Lac La Biche belongs, 40–60 year rotations are planned, depending on site. All old-growth stands that we studied had established naturally after wildfire.

Sampling effort (i.e. number of trap nights) varied among stands and years, and variable numbers of traps were lost, mainly through disturbance by wild mammals. Therefore, comparisons of abundance were based on the pooled data set from the two-year sample in each stand standardized to 1 500 trap-nights (number of traps × number of trap nights). A few, non-reproducing stragglers might be expected to disperse by chance into stands that do not support reproducing populations (see also Desender 1996). Therefore, we defined a species as dependent on old forest if ≥ 95% of the standardized catch for each forest type was obtained in old-growth stands. This “old-growth index” was calculated using the mean standardized catches of each species calculated over all old-growth stands or all regenerating stands in both study areas. In our calculations, the total standardized catch was taken as the sum of these means for each forest age class considered.

In comparing species richness among stands we further adjusted the data to compensate for varying sample sizes (i.e. beetle catch). These adjustments were made by rarefaction, a statistical method for estimating the number of species expected in a random sub-sample drawn from a larger sample (Simberloff 1978) using software in Krebs (1989). Estimates from all stands were adjusted to a sample size slightly less than the smallest actually observed so that measures of variance could be calculated for each rarefaction estimate.

Data about standardized catches were used for cluster analyses to group age classes at Lac La Biche with respect to similarity of the carabid fauna. These analyses were based on the simple Bray-Curtis Index for percent similarity and clusters were formed using the unweighted group averaging option using the software in Ludwig and Reynolds (1988). Similar analyses are provided for the Hinton assemblage in Niemelä *et al*. (Fig. 2 in 1993b).

3. Carabids of lodgepole pine forests

3.1. Old-growth dependency

More than 4 000 individual carabids were collected in our two-year study of lodgepole pine forests at Hinton. We collected a total of 29 species and 2 941 individuals from the eight old-growth stands, in comparison to 34 species and 1 070 individuals from the six regenerating stands. The carabid fauna of lodgepole pine forests was dominated by a few common species; 66–86% and 85–96% of the catch was comprised of the five most abundant species in young and mature stands, respectively.

Nine species were restricted to the regenerating stands and 14 species to old-growth stands; however, these totals include rare species ($N \leq 15$ specimens). Although similar numbers of rare species with distributions restricted to one age class of forest were found in both groups of stands, some species with distributions restricted to old-growth stands were quite common (Fig. 2; n.b. especially *Pterostichus brevicornis* Kby. and *P. riparius* Dej., each with an average of 16–32 individuals captured/1 500 trap nights). At least 95% of the total standardized captures of nine common species occurred in old-growth stands (Table 1). It is reasonable to designate these species as dependent on old-growth lodgepole pine forest. Niemelä *et al.* (1993b) also designated *Agonum mannerheimi* Dej. a forest specialist; however, this species was not evaluated for old-growth dependency here because of its rarity. Also, Niemelä *et al.* (1993b) reported that *Trechus oregonensis* Hatch and *Pterostichus luctuosus* Dej. were old-growth specialists; however, these taxa were misidentified in the earlier paper and are hereby correctly identified as *Trechus chalybeus* Dej. and *Pterostichus riparius*, respectively.

3.2. Edge effects

Both carabid catches and diversity differed among groups of traps in relation to forest edge. The highest number of species was caught in traps located in the clear-cut areas (mean ± *S.E.*, 7.1 ± 0.26), followed by the edge traps (trap 0, 6.2 ± 0.62), and forest traps (traps F 1–5, 4.7 ± 0.25), respectively. The highest catches were from the clear-cut areas (40.0 ± 0.93 individuals/trap), followed by the forest traps (32.9 ± 0.84) and the edge traps (20.2 ± 1.33).

The pooled data from all five traplines suggest that habitat edge effects exist, but that they are variable and will be difficult to interpret generally for carabids. Of species collected frequently enough to allow interpretation, only two, *Scaphinotus marginatus* Fisch. and *Synuchus impunctatus* Say, were clearly limited with respect to habitat use on one side of the edge. *S. marginatus* was collected only in the forest and *S. impunctatus* only in the clear-cut area (Fig. 3). Three species, caught in the highest numbers on the clear-cut area and regarded as open-habitat species (Lindroth 1961–69), were captured also in the forest interior, two of them up to 80 m from the edge (Fig. 4A). Thus, forest assemblages may include open-habitat species in residual stands, even up to 160 m wide.

Table 1. “Old-growth index” (see Section 2.3 for calculations) for common carabid species collected from lodgepole pine and mixedwood forests. Blanks indicate that the species was not either absent or not sufficiently abundant for the analysis.

	% collected in post-rotation age stands		
		mixedwood forest, rotation	
	lodgepole pine forest	long	short
Agonum retractum Lec.	–	74	70
Bembidion grapei Gyll.	2	–	–
Calathus advena Lec.	100	–	–
Calathus ingratus Dej.	40	58	60
Calosoma frigidum Kby.	–	21	45
Carabus chamissonis Fish.	95	28	47
Harpalus fulvilabrus Mnh.	–	65	63
Leistus ferruginosus Mnh.	100	–	–
Miscodera arctica Payk.	26	–	–
Nebria intermedia V. D.	95	–	–
Notiophilus semistriatus Say	0	–	–
Patrobus foveocollis Esch.	56	33	67
Platynus decentis Say	100	43	52
Pterostichus adstrictus Esch.	18	28	47
Pterostichus brevicornis Kby.	100	–	–
Pterostichus haematopus Dej.	64	–	–
Pterostichus pensylvanicus Lec.	4	51	56
Pterostichus riparius Dej.	100	100	100
Scaphinotus marginatus Fish.	96	35	49
Synuchus impunctatus Say	8	49	55
Trechus chalybeus Dej.	95	–	–
Trichocellus cognatus Gyll.	2	–	–

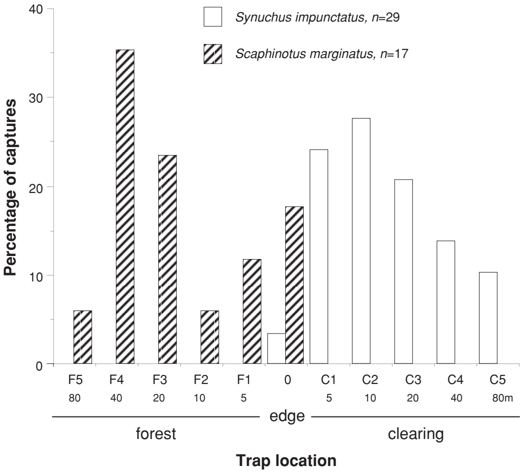

Fig. 3. Captures of *Synuchus impunctatus* and *Scaphinotus marginatus* in relation to forest edge. Percentages calculated over five trap lines.

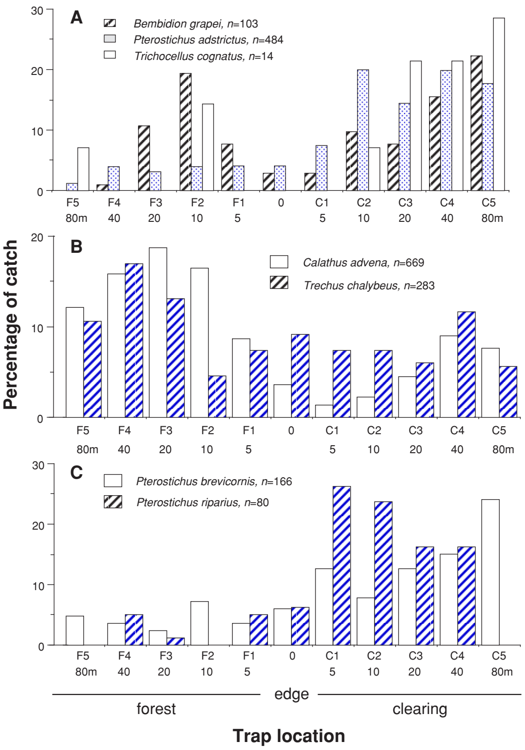

Fig. 4. Captures of open-habitat specialists (A) and old-growth specialists (B and C) in relation to forest edge. Percentages calculated over five trap lines.

Distributions of several species designated as old-growth forest specialists above (Table 1) were perplexing. For instance, *Calathus advena* Lec. and *Trechus chalybeus* were captured in the forest interior but also frequently in the clear-cut (Fig. 4B). Data for neither *Pterostichus brevicornis* nor *P. riparius* show any trend to increase toward the forest interior, and both of these species were collected most commonly in traps in the clear-cut (Fig. 4C). This appears to be consistent with observations that some forest specialists maintain populations in clear-cuts for 1–2 years after they are harvested (see Fig. 5 in Niemelä *et al.* 1993b). However, our earlier study suggests that such populations disappear from regenerating pine stands 9–27 years old. It is possible that increased capture rates observed for these species on the clear-cut reflect increased activity associated with attempts to locate more suitable microhabitats. Movement away from unsuitable habitat has been observed for carabids in other habitat types (Niehues *et al.* 1996, Riecken 1996). For most flightless beetles in the center of large clear-cuts, such attempts must be ultimately unsuccessful.

Data for *P. brevicornis* are particularly interesting and may represent a complex response. This species, the most widespread member of the subgenus *Cryobius*, is characterized as mainly a tundra inhabitant (Lindroth 1966); our study provides the southernmost records for this species. We captured *P. brevicornis* only in moist, cool forests or in recent clear-cuts. When clear-cuts appear, individuals of *P. brevicornis* may be attracted to them, a pattern perhaps reflecting primary adaptation to treeless, arctic environments. However, ultimately these colonists are unable to establish flourishing populations, perhaps because these areas dry out during relatively hot summers. Thus residual southern populations are maintained only in the cooler interiors of montane forests. Clear-cuts may be sinks for this species, and could significantly reduce populations in harvested landscapes.

In summary, our data suggest that carabid assemblages will be subject to edge effects that result from patchwork logging on the landscape (Fig. 5). Populations of some forest species seem to decrease near edges, but only within 5–10 m of a clear-cut edge. This suggests that fragmentation will not have much immediate negative consequence on forest species unless forest fragments are too small to retain viable population sizes at characteristic densities. However, many flightless individuals of forest species may perish in attempts to escape from clear-

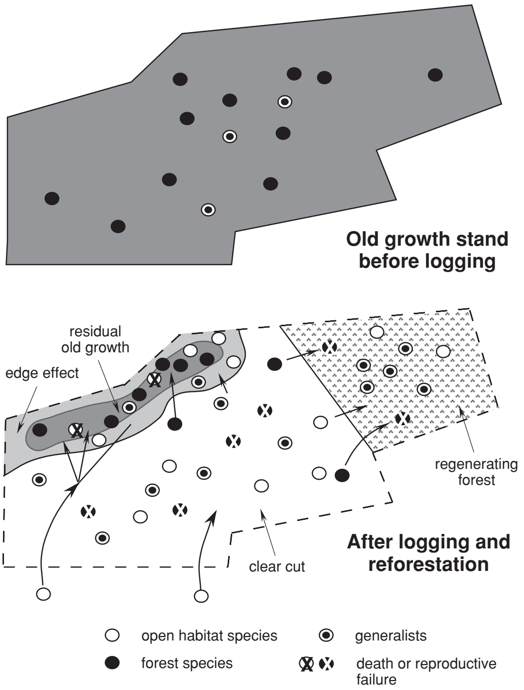

Fig. 5. Schematic diagram illustrating possible long-term changes in the carabid fauna of old-growth residuals after logging as a result of processes suggested by the edge study in lodgepole pine forests.

cuts and, because these species seem unable to establish populations in regenerating stands ≤ 27 years old (Niemelä *et al.* 1993b), cumulative losses could be significant over a harvested landscape. Both open-habitat species and habitat generalists penetrated into forest stands to the limit of our trapping (80 m), suggesting that species composition of forest carabid assemblages in fragments will differ markedly from pristine, old-growth forest. The absence of forest specialists from some old-growth fragments south of Hinton (Niemelä *et al.* 1993ab) could reflect action of such community level processes over time, especially in association with microclimatic changes in isolated stands.

4. Carabids of mixedwood forest

More than 15 000 individual carabid beetle adults were collected during the two-year study (5 525 in 1992 and 9 786 in 1993), including representatives of 31 species. Number of species collected per stand ranged from a two-year low of 10 in 1993 for 40–45 year-old stands, to a high of 17 in the youngest stands, also during 1993. The identity of the abundant species was remarkably similar across all stands. The only striking effect of stand age in our data is that species richness was clearly higher in the new cutovers than in the three older age classes of fire-origin stands (Fig. 6). Overall, the five most abundant species comprised > 80% of the catch. Fourteen species were collected in only one age class, but these were all uncommon and, unlike at Hinton, not disproportionately represented in old-growth stands.

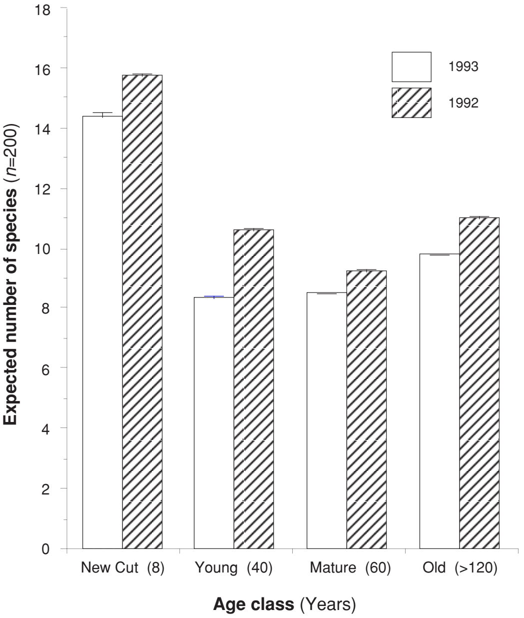

Fig. 6. Results of rarefraction analyses of carabid diversity in four age classes of mixedwood forest. Error bars are standard deviations.

Stand age affected carabid abundance, but standardized catches in the 65 year-old stands were greater than those in the old-growth forest (Fig. 7). Furthermore, among species that achieved proportional dominance (> 5% of all captures) in one or more of the three oldest age-classes of forest, there were no obvious tendencies to fare best in the oldest stands. For example, *Pterostichus adstrictus* Esch. was a dominant species in all age classes of forest but was quite uncommon in the new cuts at Lac La Biche. In contrast, its closely related congener, *P. pensylvanicus* Lec., although also dominant in the forest stands was overwhelmingly dominant in the new cuts accounting for ca. 55% of the total carabid catch in both years. Even among the larger-bodied spe-

Fig. 7. Activity-abundance of all carabids in four age classes of mixedwood forest.

cies, *Calosoma frigidum* Kirby, *Carabus chamissonis* Fish., and *Scaphinotus marginatus*, there was no tendency for captures to be concentrated in old-growth stands (Fig. 8a–c).

Cluster analysis of carabid communities reveals a clear difference in similarity between recent cutovers and established forests (Fig. 9). The assemblages of the new cutovers clustered with the three forested habitats at only ca. 20%. The carabid faunas from the three older age classes clustered at a higher level of similarity (60–80%), providing little evidence that the oldest forests support unique assemblages of carabids. In contrast, samples of the old-growth fauna of lodgepole pine forests near Hinton clustered with those from younger stands at similarity levels of only 10–30% (Fig. 2 in Niemelä *et al.* 1993b).

Because the rotation periods to be employed for aspen harvest in Alberta vary between 40 and 80 years, we did the analysis in two ways (Table 1). First, to test for old-growth specialists relevant to long rotations, we compare the data averaged over both 40 and 60 year old stands with that averaged from stands > 120 years old. Second, to test for old-growth specialists in the context of the shorter rotation periods proposed, we compare the average abundance of each species from the 40 year old stands with an average obtained over the set comprised of the 60 and > 120 year old stands. The only possible old growth specialist identified by the analysis using the 95% criterion is *P. riparius*. However, data for this species are somewhat enigmatic, and thus do not compel us to name this species as an old-growth specialist. All but one of the 38 individuals taken came from a single trap and were collected over one four-week period in 1993.

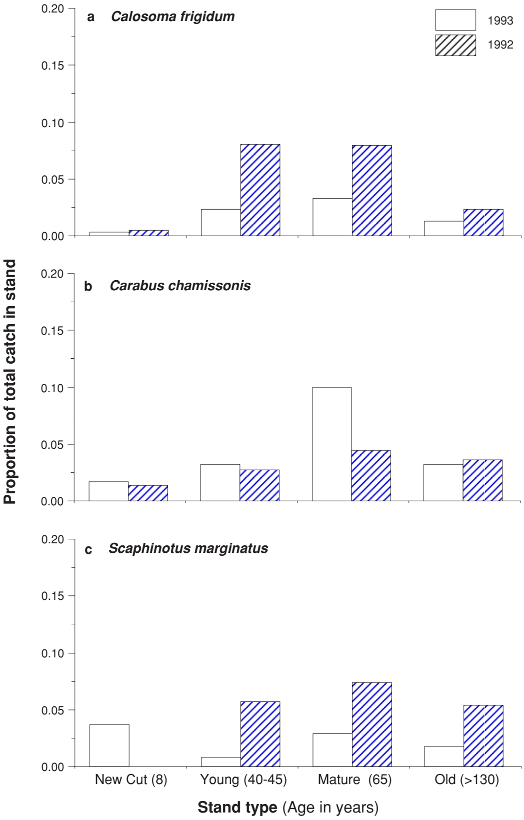

Fig. 8. Relative abundances of five species in four age classes of mixedwood forest. Species represented in panels a–c were all identified as old-growth specialists in lodgepole pine forest (see Table 1).

5. Synthesis

5.1. Comparison of carabid assemblages between two forest types

A greater overall species richness was observed in the lodgepole pine forests, despite the fact that only about one third as many individual carabids were collected there as in the mixedwood forest. This difference in species richness is not explained by year-to-year variation as the difference between years is quite small (Fig. 6). The carabid fauna at Lac La Biche also seems somewhat depauperate in comparison to that revealed by other studies. For example, Holliday (1991) reported ca. 70 species from aspen forest in central Manitoba and Niemelä *et al.* (1992b) reported 54 species from a site in central Alberta. However, these two studies included a number of hygrophilous species characteristic of habitats not sampled at Lac La Biche; only 17–30 species were collected from comparable habitats in central Alberta (Niemelä *et al.* 1992b, Niemelä & Spence 1994). The greater diversity at Hinton did not result from sampling a greater array of potential microhabitats but clearly reflects existence of a more diverse upland assemblage.

We offer a three lines of possible explanation for this finding, the first two having historical connections. First, transcontinental boreal faunal elements (Danks & Foottit 1989) are mixed with both northern (e.g. *Pterostichus brevicornis*, *P. haematopus* Dej.) and western (e.g. *Leistus ferruginosus* Mnh., *Nebria intermedia*) forest assemblages on the eastern slopes of the Rocky Mountains. The fauna at Lac La Biche, in contrast, includes mainly transcontinental species characteristic of the boreal zone, though a few northern (e.g. *Pterostichus riparius*) and western species (e.g. *Scaphinotus marginatus*) are shared with the Hinton assemblage. Second, the climatic warming trend experienced during the Altithermal Period could have caused losses of some cold-adapted species in the lowland fauna of these northern forests but left the fauna of higher elevations relatively unaffected.

A third possible explanation for the difference observed in species richness between lodgepole pine and mixedwood forest invokes landscape effects of forestry practices operating in ecological time. The fauna at Hinton included three times as many open-habitat species representing *Amara*, *Bembidion*, *Harpalus* and *Notiophilus* than that at Lac La Biche (18 vs. 6 spp.), possibly reflecting the much larger portion of recent clearcuts and regenerating stands at Hinton (Niemelä *et al.* 1993b). Canopy closure comes slowly in these montane pine stands and was not complete even in the oldest regenerating stands, cut ca. 30 years earlier. In contrast, at Lac La Biche, where only a small percentage of forest has been cut or burned in recent time, there may not have been opportunity for establishment of local populations of open-habitat specialists sufficient to mount wide colonization responses to clear-cuts. Alternatively, we note that much less open soil is exposed in logging operations in aspen forest, due to lack of scarification, and that dense thickets of aspen, willow and birch establish naturally shortly after logging operations. Holliday (1992) suggested that few carabid species colonize such dense young stands. Thus, the ultimate response of open-habitat species to logging in the mixedwood zone will likely depend upon the silvicultural options employed in regenerating stands.

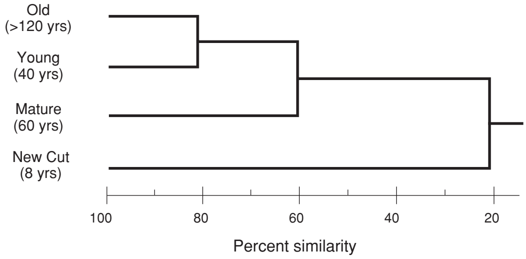

Fig. 9. Cluster analyses of Bray-Curtis measures of percent similarity for the carabid assemblages of four age classes of mixedwood forest.

5.2. Old growth specialists

Carabids that require attributes of old-growth forests are especially vulnerable to forest harvesting. Four of the nine species identified as old-growth specialists in lodgepole pine forests (*C. chamissonis*, *P. decentis*, *P. riparius*, *S. marginatus*) also occurred in aspen stands at Lac La Biche but did not show similar specialization in old-growth stands. Thus, apparent specialization in old-growth is not strictly a species characteristic, but appears to result from some interaction between a species and characteristics of the forest type itself. This interaction could relate to detailed habitat requirements of carabid species that reflect both age and structure of forest stands. Future work on implications of old-growth forest habitats for carabids might profitably focus on how responses of particular species are affected by stand structure and how these effects vary with spatial scale (e.g. Niemelä & Spence 1994).

Our study of old-growth specialization may be biased because we studied harvest-origin regenerating stands at Hinton, whereas all but the youngest stands at Lac La Biche had originated after wildfire. Possibly forest specialists re-colonize stands disturbed by fire more quickly than those harvested, scarified, and planted. However, the available evidence suggests that this cannot explain the differences between our two forest types with respect to number of old-growth specialists. A carabid assemblage from a 33 year-old fire-origin stand of lodgepole pine south of Hinton did not have a higher proportion of forest specialists than assemblages in 27-year-old harvested stands (D. Langor & J. Spence, unpub.). Our results from aspen stands are also similar to what is known about faunal build-up in stands regenerating after a burn. Holliday (1992) showed that carabid assemblages of burned aspen stands converge on those of unburned stands rather quickly. Although numbers of both individuals and species were lower in the fire-origin stands than in an unburned control, the common species had re-established populations eleven years after burning.

As noted above, landscape effects of forestry practices may be important determinants of the occurrence of open-habitat species. Similarly, landscape effects could also contribute to the observation of putative forest specialists in young aspen stands. Presently at Lac La Biche, young, fire-origin aspen stands are generally small islands in a landscape comprised mainly of older age classes. Thus, forest specialists may more regularly colonize these young stands and appear to use them more extensively than in landscapes, such as those at Hinton, where young stands predominate and are more likely to be adjoined by other young stands. The data about *P. adstrictus* at Lac La Biche show how population process and landscape configuration could interact to dramatically reduce the regional pool of colonizers under extensive harvesting. Although abundant in all forest age-classes, only a few *P. adstrictus* were trapped on the new cutovers at Lac La Biche. Larvae of this species depend on coarse woody debris as habitat (Goulet 1974). If such material were removed over wide areas through harvesting, adult recruitment could fall below replacement rates over much of a regional landbase, causing lags in re-colonization of regenerating stands and slowing population rebound even after sufficient coarse woody debris becomes available. The possibility of such landscape level phenomena, mediated primarily by changes in the relative abundance of colonists from the regional source pool, underscores arguments for harvesting patterns that are spatially similar to natural disturbance patterns (e.g. fire; Hunter 1993, Haila *et al.* 1994), and justifies leaving significant amounts of residual material on the land after harvest. Fortunately, this latter approach has been adopted by the companies harvesting the mixedwood forest in Alberta.

5.3. Edge effects and fragmentation

Although forest edges provide suitable habitat for species such as deer and elk (Alverson *et al.* 1988), they appear unsuitable to species requiring interior forest environments. Our data, although not extensive, suggest that forest carabid assemblages will be subject to edge effects, such as colonization by open-habitat species and changes in habitat quality or microclimate, in the face of harvesting. For example, Chen *et al.* (1995) reported that microclimatic effects typically extend 30 m to > 240 m into residual Douglas fir stands left after harvest in Washington and Oregon. These microclimatic changes may make the edges of forest patches more suitable for open-habiatat species and habitat generalists, and encourage their movement into forest fragments, as is suggested by recent data of Halme and Niemelä (1993).

In addition, fragmentation may be associated with changes in colonization rates and in competition within altered communities. Patches of uncut forest simply may be too small to maintain viable populations of old growth specialists. Depending on the extent of local harvest, distances between suitable patches may become too large to allow re-colonization by old-growth specialists, even when habitats are suitable. Many carabid species that occupy relatively stable habitats, like old-growth forests, are characterized by large body size and wing reduction (Den Boer 1970, Holliday 1991) and species characteristic of old woodlands are generally poor colonists (Nield 1990). Such species will be unable to colonize small patches of residual old-growth once local populations have been extirpated and some critical limit to interpatch distance is exceeded (Den Boer 1990, De Vries & Den Boer 1990). In contrast, we expect that habitat generalists will colonize residual patches of old-growth at increasing rates as a landscape is fragmented, homogenizing the fauna over broad areas.

We predict that most of the short term impact of fragmentation on carabid assemblages will result from increases in diversity associated with invasion of forest stands by habitat generalists and open-habitat specialists that colonize cutovers. It is presently unknown if forest specialists will be negatively affected by these changes in community structure. Our ability to predict such changes depends on achieving a firm understanding of factors that structure carabid assemblages. Thus, there are no substitutes for detailed ecological studies.

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