Boreal Carabid Beetles (Coleoptera, Carabidae) in Managed Spruce Forests – a Summary of Finnish Case Studies

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1 Introduction

Over 90% of the forests in Sweden and Finland are managed (Angelstam 1997, Sevola 1999) and form a mosaic of different successional stages (Hansson 1992). This is a consequence of forestry practices over several centuries, but the most drastic effects of forestry on forest biota have taken place during the past 50 years (Niemelä 1999). Over this period of time, the structures of the plant and animal assemblages of boreal forests have been strongly altered (Heliövaara and Väisänen 1984, Esseen et al. 1992, Niemelä 1997). Forestry is responsible for approximately 30% of the Finnish red-listed species being threatened (Rassi et al. 2000). Perhaps the most important reason for this is the fragmentation of old-growth forests. Habitat fragmentation is one of the most important causes of species declines and extinctions across the world (Saunders et al. 1991, Haila et al. 1994, Didham et al. 1996, Didham 1997a, Davies et al. 2000). In southern Finland, roughly 1% of forest cover is protected and only 5% of these are old-growth forests (Virkkala et al. 2000). Protecting all the remaining old-growth forests in these regions is an inadequate measure for the protection of old-growth forest specialists (e.g. Heikkinen et al. 2000). Thus, in addition to protection, the restoration of mature, managed forests and the improvement of the quality of the surrounding managed landscape matrix through the development of appropriate management methods are needed (Niemelä 1997, 1999, Nilsson 1997, Mönkkönen 1999).

Managed forests host fewer threatened forest-specialist species than do old-growth forests, and also many common species occur at low abundance in managed forests. Examples of this difference are e.g. bryophytes and epiphytic lichens (Söderström 1988, Andersson and Hytteborn 1991, Kuusinen 1994, 1996, Dettki and Esseen 1998), beetles living in dead wood (Väisänen et al. 1993, Siitonen and Martikainen 1994, Jonsell et al. 1998) and Mycetophilidae insects (Økland 1994). However, the long-term persistence of many forest species is dependent on populations living in managed forests (Lindenmeyer and Franklin 1997). The maintenance of these populations can possibly be achieved by ecological planning of forestry. Moreover, the importance of ecological forestry planning is not just to maintain old-growth forests but also to prevent the decrease of overall forest biodiversity at the within-stand, regional and national scales.

Keywords boreal, Carabidae, clear-cutting, edge, forestry, landscape, logging, management, retention felling, succession, selective felling

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Since maintaining viable populations of all species is of central importance in conservation, species that are most sensitive to fragmentation should determine conservation actions. Scarcity itself, however, makes studying these species difficult and costly. Therefore, intermediately common species, with strict microhabitat demands, can potentially be used as indicators of environmental quality in order to study e.g. whether or not new, modified management methods have an effect on forest-species assemblages (Haila and Kouki 1994). Such species can be found among carabid beetles (Coleoptera, Carabidae), although none of Finnish forest-carabid species are classified as threatened (Rassi et al. 2000). They are easy to collect in sufficient quantities using pitfall traps and form an ecologically and taxonomically well-known group (Niemelä et al. 2000), being often classified into forest, open-habitat and generalist species groups (e.g. Niemelä et al. 1988, 1993a, Niemelä and Halme 1992). Carabids also reflect changes in their environments and many intermediately common species with relatively strict microhabitat requirements occur (Thiele 1977, Lindroth 1985, 1986, Niemelä et al. 1992, Langor et al. 1994).

2 Aims of the Study

We summarise the main results of our four recent studies, focused on the effects of various logging regimes on boreal-forest carabid assemblages, and partly reanalyse the datasets. The biotic and abiotic effects of clear-cutting are well documented (e.g. Huhta 1976, Haila et al. 1994, Pettersson 1996, Davies and Margules 1998, Didham et al. 1998, Abildsnes and Tømmerås 2000), but the effects of modified logging methods are much less studied.

In this paper, three different modified logging methods are compared (for details of the treatments, see section 3). Firstly, gap felling may mimic natural gap formation (Sousa 1984, Attiwill 1994, Kuuluvainen 1994). Secondly, retaining small tree groups (e.g. 10–30 mature trees; 3–4 such groups per hectare) in the clear-cuts mimics small-scale disturbance events: such tree groups are often left in moist sites after fire (Vanha-Majamaa and Jalonen 2001). Retained trees may also act as stepping-stones or "lifeboats" for forest specialists (Franklin et al. 1997). Thirdly, carabid assemblages of stands where selective felling, aiming at an uneven age structure of trees, was applied were studied. Uneven age structure of trees is an important feature of naturally developing forests (Lähde et al. 1991, Esseen et al. 1997), but invertebrate studies concerning its importance are lacking. Studies concerning different thinning methods have mostly focused on their effects on tree growth.

We also present results of studies where carabid assemblages at forest/clear-cut edges (Heliölä et al. 2001) and in a 60-year time scale of secondary succession, caused by clear-cutting (Koivula et al. 2002), were studied. Changes in abiotic and biotic conditions in the forest/clear-cut edge as compared to the forest interior are collectively called "edge effects" (Murcia 1995, Risser 1995). Clear-cutting creates relatively sharp habitat boundaries (ecotones) to which species may respond as conduits, filters or barriers, sources or sinks, habitat and feedback (i.e. edges amplify or reduce the intensity of ecological processes) (Kolasa and Zalewski 1995). To counteract the effects associated with edge, it is important to understand how species respond to the conditions at habitat edges (Haila et al. 1994). Forest edges harbour a rich invertebrate fauna (e.g. Helle and Muona 1985, Jokimäki et al. 1998), but very few of these species appear to be edge specialists (Didham 1997a, b).

Species' responses to habitat variability and natural and anthropogenic processes may be determined by different factors acting at different time (Niemelä 1999), and spatial levels (Addicott et al. 1987, Wiens 1989). It is, therefore, important to examine the ecological effects of logging at several scales (Haila and Kouki 1994). A temporal scale from days to hundreds of years, and a spatial scale from metres to hundreds of kilometres, form a relevant framework for studies concerning forest management and forest-species conservation; the "meso-scale" (Niemelä 1999). A 120-year time-scale, reaching from recently-logged to mature stands, covers the normal logging rotation (80–120 years) in southern and central Finnish spruce forests (Kuusela 1990).

3 Sampling Designs and Material

The summarised studies were performed in south-central Finland, at the border between the southern and middle boreal zones (Ahti et al. 1968). The study forests were spruce (*Picea abies*) dominated, *Myrtillus*-type forests (Cajander 1949). The natural succession of spruce forests begins with a deciduous phase and continues towards spruce dominance (Esseen et al. 1997). Mature stands had the age of the dominant trees being 90–120 years. Spruce was the dominant tree species, with pines (*Pinus sylvestris*), birches (*Betula* spp.) and aspens (*Populus tremula*) as an admixture. The herb layer was usually dominated by *Vaccinium vitis-idaea* and *V. myrtillus* dwarf shrubs, and *Dicranum*, *Pleurozium* and *Hylocomium* mosses covered most of the bottom layer. The sampling designs of the four studies are given below.

The beetles were collected using pitfall traps (Greenslade 1964, Southwood 1978). The nomenclature follows Lindroth (1985, 1986).

The short-term (two years after logging) responses of carabids to clear-cutting and two modified logging methods were studied in 1995–1998 (Koivula 2002a). The study was carried out at eight separate areas, each including four 1-ha study stands (+ adjacent surroundings, forming a total of 1.5–2 ha), each treated in different ways: i) control (uncut), ii) clear-cut, iii) gap felling with three 1600 m^2 openings per hectare, and iv) retention clear-felling, where 3–4 tree groups, each having 10–30 trees, per hectare were retained. In each stand, we had a total of 24 traps in six groups of four traps, each group in a 4 × 4 m square. The four-trap groups were placed at least 25–35 m apart from each other and from the nearest forest edge. In each retention-felled stand, three trap groups were placed in clear-cut and three in uncut sections. The dataset consisted of 21 650 carabid individuals representing 47 species.

The catches from selectively felled stands, with the aim of obtaining an uneven age structure of trees, were compared to uncut mature and clear-cut stands 1995–1998 (Koivula 2002b). In the selectively felled stands, 11–34% of the trees were cut, and accordingly, 433–1050 trees per ha were retained. Each treatment (represented by 1–2-ha stands) was replicated eight times. The adjacent surroundings of the selectively felled and uncut stands were mapped in order to study whether the landscape mosaic (distance to the nearest mature stand and to open habitat) influenced carabid abundance patterns. The number and the placement of the traps were as in Koivula (2002a). The carabid dataset consisted of 13 689 individuals representing 45 species.

In this paper we also included previously unpublished carabid data of three stands where gap felling with mechanical soil preparation was applied. These stands were sampled in 1997–1998 in three of the eight study areas of Koivula (2002a, b). The stands, being 1–2 ha in size, had three 1600-m^2 openings. During the following summer after logging (1996), mechanical soil preparation was applied: the humus layer was partly removed in narrow (approximately 50 cm wide) strips. This is a common practice in Fennoscandia to help the saplings to establish. The number and the placement of the traps were as in Koivula (2002a). This dataset, together with those of Koivula (2002a, b) are used to analyse the possible differences among carabid catches of the studied logging and soil preparation regimes. These additional data consisted of 2307 carabids representing 23 species.

In addition to the above studies of the effects of logging, a 60-year time-scale, with comparisons of the carabid catches of different-aged clear-cut originated stands, was carried out by Koivula et al. (2002). Two spatial levels were examined: within stand (site; alpha diversity) and between stands (area; beta diversity) (Magurran 1988). Five stand-age classes (5, 10, 20, 30 and 60 year-old) were replicated four times for a total of 20 stands, within a 10 × 10 km area, during 1999. The sizes of the stands varied between 0.7 and 7.7 ha. In each stand there were three groups of four traps (in 4 × 4 m squares). The forest-carabid abundances in the stands of the three youngest age-classes were examined in relation to the distance to the nearest +40 year-old stand, to the amount of adjacent old forest and to the size of the study stands. This dataset consisted of 2316 carabid individuals representing 39 species.

The edge effect, caused by clear-cutting, was examined in six separate clear-cut stands in 1997, the second growing season after clear-cutting (Heliölä et al. 2001). This study was performed by using 120-m pitfall-trap grids, which extended 60 m into the clear-cut and 60 m into the adjacent forest. Nine groups of four traps were placed 15 m apart along each 120-m gradient. This dataset consisted of 5609 carabid individuals representing 34 species.

4 Results and Discussion

4.1 Responses of Carabids to Clear-cutting

Carabids are often more numerous and more speciose in open habitats than in forests (Niemelä and Halme 1992, Kinnunen 1999), but clear-cutting has negative effects on the abundance of forest-specialist species (Niemelä et al. 1993a, b, Langor et al. 1994, Spence et al. 1996). However, most spruce-forest species occurred also in recently clear-cut sites (Koivula 2002a, b). This pattern has at least three explanations. First, the individuals caught may be wanderers from nearby mature stands (Spence et al. 1996). Second, the catches may represent a population on its way to local extinction. Since some carabids may live for as long as 2–3 years (van Dijk 1996), these species may persist for some time in the clear-cuts, although they may not be able to reproduce there. Szyszko (1990) showed that the abundances of many forest carabids decreased three years after clear-cutting in Polish pine stands. If this is the case in boreal forests, the present time scales of 2–3 years (Heliölä et al. 2001, Koivula 2002a, b) would have been too short to demonstrate decreases. Indeed, Koivula et al. (2002) showed that populations of some forest species were much smaller in stands that were logged 5 years earlier than in stands where succession had proceeded 30–60 years. Third, some forest species may be adapted to natural disturbances (e.g. windthrows, forest fires) within a forested landscape and may survive in these clear-cuts.

Two years after logging, the total abundance of carabids had not changed significantly in the clear-cuts (Koivula 2002b). This contrasts with studies that have shown clear-cuts to host more individuals and more species (e.g. Niemelä et al. 1993a, Spence et al. 1996, Butterfield 1997). However, species richness was higher in the clear-cuts than in the other treatments (Koivula 2002a). A similar result was obtained when the catches of 5 and 60 year-old stands were compared (Koivula et al. 2002): the total catches were equal, while the former hosted more species. Open-habitat species predominantly occurred in clear-cuts and young sapling stands, and forest-succession generalists were most abundant in early and mid-successional stages (Heliölä et al. 2001, Koivula 2002a, b, Koivula et al. 2002).

4.2 Recovery of Carabid Assemblages after Clear-cutting

In the early successional stands, the light, temperature and humidity vary more than in mature forest (Matlack 1993). The sun dries and heats the ground, causing the decline of dwarf shrubs (*Vaccinium* spp.) and forest mosses, and the drying of *Sphagnum* moss mires, but grasses are abundant (Heliölä et al. 2001, Vanha-Majamaa and Jalonen 2001, Fig. 1b). These factors affect carabid distribution directly and indirectly (Thiele 1977). In the multivariate analyses (presented in the summarized four papers), many species showed associations with certain within-stand site characteristics: *Sphagnum* bogs, and mesic and luxuriant sites, host distinctive carabid assemblages and are, therefore, important for the within-stand heterogeneity (Heliölä et al. 2001, Koivula 2002a, b, Koivula et al. 2002). However, such sites dry after logging (Heliölä et al. 2001), and carabid species associated with these microsites may decline or even disappear locally. It may take tens of years for such populations to recover after clear-cutting (Niemelä et al. 1993a, b, Langor et al. 1994). Although the spruce mire itself recovers after only a few decades (Fig. 1c), the recolonisation of species requiring such habitat depends on the availability of nearby source habitats (e.g. Spence et al. 1996). Also leaf litter is important for the boreal spruce-forest floor fauna, further indicating the importance of scattered deciduous trees within coniferous-dominated stands (Heliölä et al. 2001, Koivula

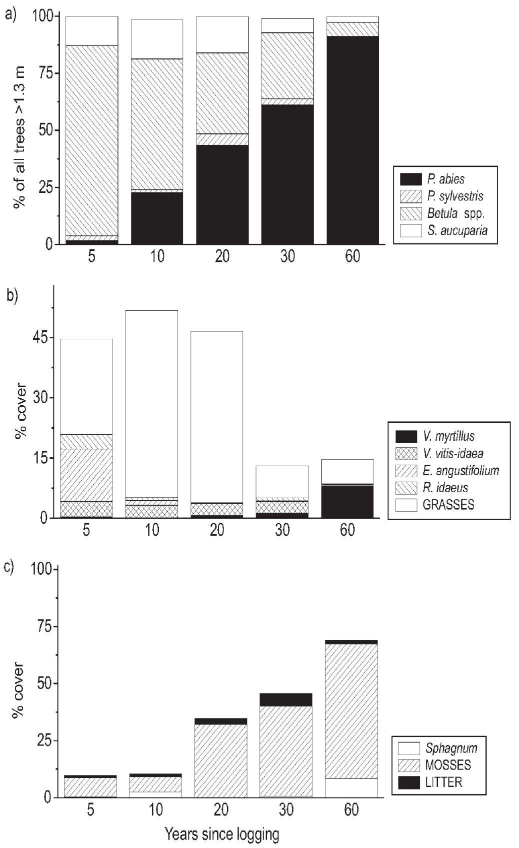

Fig. 1. Vegetational succession in 5, 10, 20, 30 and 60 year-old stands (time since clear-cutting), age-class specific averages presented. (a) The percentage proportions of the main tree species. (b) The percentage coverages of the main field-layer plant species or species groups. (c) The percentage covers of the bottom-layer elements (litter, mosses). Original data: Koivula et al. (2002).

et al. 2002; see also Niemelä et al. 1992). Interestingly, as a consequence of an experimental leaf-litter addition, the catches of *Calathus micropterus*, *Pterostichus oblongopunctatus* and *Cychrus caraboides* increased (Koivula et al. 1999). Deciduous-tree admixture and spruce mires are important also for, for example, epiphytic lichens, land snails and saproxylic beetles (Kuusinen 1996, Esseen et al. 1997, Niemelä 1997, Martikainen 2000, Siitonen and Saaristo 2000).

In the study comparing carabid assemblages 5–60 years post-harvest, species richness was highest in 5 and 10 year-old stands (Koivula et al. 2002). The species-rich assemblages of young, open stands are mostly due to the richness of open-habitat species that were associated with stands younger than 30 years. Eleven of such species were exclusively caught from 5 year-old stands (Koivula et al. 2002). These results are rather similar to several other studies (Szyszko 1990, Niemelä et al. 1993a, 1996, Haila et al. 1994, Butterfield 1997). The richness of open phases can be explained by favourable microclimate (Niemelä 1993) and perhaps decreased interactions between species (Loreau 1986, 1992). High daytime temperatures in the clear-cuts may favour diurnal *Bembidion* and *Amara* species (Lindroth 1985, 1986), although the grasses probably effectively shelter the ground. Increased vegetational richness in the field layer may be favourable directly (more seeds as food for *Amara* species) and indirectly (increased abundance of many invertebrates upon which carabids prey). Increased complexity of the field layer may also offer shelter against predation and climatic alterations, and more utilizable vertical space, enabling more species to occur simultaneously.

The dominant species of the clear-cut originated stands seemingly change 5–10 years after logging, but a drastic assemblage-level change and decrease of beetle catches occurs 20–30 years after clear-cutting, which coincides with canopy closure and spruce dominance (Koivula et al. 2002, Fig. 1a). Canopy closure thus distinguishes the open-phase assemblages from the closed-phase ones (Niemelä et al. 1996). The majority of open-habitat species was scarce in or absent from the 30 year-old stands, as were many forest and generalist species. A similar decrease was reported by Szyszko (1990) for Polish pine forests. However, some species showed the opposite trend, e.g. *Calathus micropterus* and *Trechus secalis* were more abundant in these stands than in the other age classes. Clear-cutting may increase the within-genus component of species diversity, leading to a decrease in the numerical dominance of one species over the others (Lenski 1982). *Calathus micropterus* alone strongly dominated catches of stands older than 10 years, while the two youngest age classes (5 and 10 year-old stands) were dominated by three *Pterostichus* species (together with *Amara lunicollis*), supporting Lenski's (1982) view about several dominant species. The catches in 30 year-old stands (Koivula et al. 2002) support the view of Niemelä (1993) who suggested that the dominance pattern is perhaps a result of only a few species being adapted to the climatic harshness of boreal forests ("adversity selection").

4.3 The Short-term Effects of Retention-Felling Methods

No significant short-term changes in the carabid assemblages of selectively-felled stands were detected in Koivula (2002b). Also Atlegrim et al. (1997) reported similar results in thinned stands in Sweden. The retained trees (70–90%) in these studies thus seemingly sheltered the ground well enough for the maintenance of forest-species assemblages. However, thinning decreases the abundance of beetles that are dependent on deciduous trees (Økland 1995). Since the decrease of these species may be a result of thinning practices often reducing the amounts of decaying wood and deciduous trees, it is crucial to maintain structural heterogeneity within the managed spruce-dominated stands, e.g. decaying wood and deciduous tree admixture (Esseen et al. 1992, 1997, Dettki and Esseen 1998). Thus, retainment of components that may help sensitive species to persist in the managed landscape (Lindenmeyer and Franklin 1997) and avoiding homogenisation of stands (Law and Dickman 1998) are essential in management practices.

The catches of generalist carabids increased along a decreasing tree-density gradient in selectively felled (and uncut mature) stands (Koivula 2002b). Furthermore, many generalists were abundant in open phases of forest succession but scarce in 30 and 60 year-old stands (Koivula et al. 2002). These results indicate that habitat generalists actually are associated with openness rather than being true generalists in relation to canopy closure. Their population sizes thus increase after logging – an analogy with seed banks of several plant species.

Leaving uncut patches within stands probably contributes positively to the maintenance of forest species. In gap- and retention clear-fellings, open-habitat species were mostly associated with clear-cut sections of the stands, while generalists and forest species showed no association with either clear-cut or intact sites (Koivula 2002a).

The changes caused by logging, however, were not solely restricted to within-stand sites where trees were removed. The carabid assemblages of uncut sections of the gap-felled stands had also changed: many of these sites were colonised by open-habitat species. Moreover, the carabid assemblages of the tree groups (with 10–30 trees) in the retention clear-felled stands had altered even more, the change being again indicated by an increase of open-habitat species, and the catches being similar to those of the clear-cut stands (Koivula 2002a). The catches of selectively-felled stands, together with the more pronounced assemblage changes in the retention clear-felled than in the gap-felled stands, indicate that the more there are trees left in the stand, the better it maintains the original carabid assemblage. This result is similar to those earlier detected for the bottom- and ground-layer vegetation of the same stands (Vanha-Majamaa and Jalonen 2001).

4.4 DCA Analysis for the Logging-regime Datasets

We (re-) analysed the datasets of Koivula (2002a, b) with the three gap-felled stands with mechanical soil preparation applied, by using Detrended Correspondence Analysis (DCA; see e.g. Jongman et al. 1995) in order to directly compare the carabid catches of uncut, clear-cut, selectively felled, gap-felled and retention clear-felled stands. Only samples collected during the second and third summer post-harvest (1997–1998) were included, and samples from the same stand were pooled. We excluded from the analysis species with less than 5 individuals. The total inertia was 1.03, and the two first axes together explained 30.2% of the variation in the carabid dataset (Fig. 2).

The overall result of the DCA indicates that logging affects carabid assemblages in the short term and that the assemblages of clear-cut and uncut mature stands host different carabid assemblages (Fig. 2). The retention-felling methods

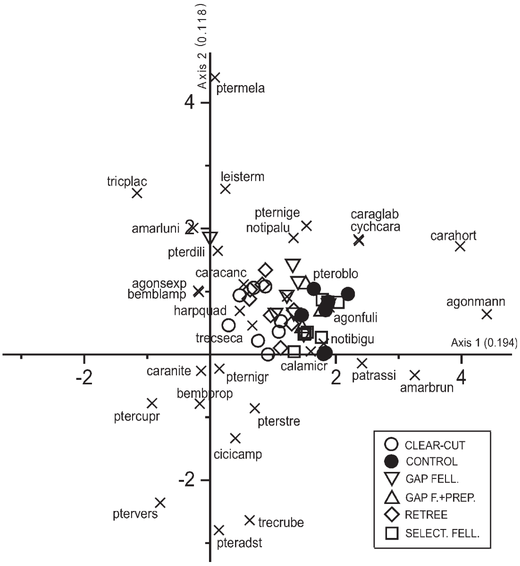

Fig. 2. DCA for carabids collected from differently treated stands in central Finland 1997–1998. Species are indicated with a cross and 4 + 4 letter abbreviations: e.g. calamicr = *Calathus micropterus*. For the rest of the species, consult Lindroth (1985, 1986). Original data: Koivula (2002a, b, unpubl.).

form a continuum. Retention clear-felling (with tree groups consisting of 10–30 trees) changes assemblages more than gap or selective felling (see above). In the DCA, the control-stand samples scattered to the right, while samples from logged stands were on the left side of the plot. There was also a lot of site-specific variation among the stands and in the compared treatments. Carabid species formed a continuum of forest specialists to open-habitat specialists. The majority of the open-habitat species scattered to the left side of the ordination, while forest specialists (*Agonum mannerheimii*, *Carabus hortensis*, *C. glabratus*, *Cychrus caraboides*, *Amara brunnea*) were to the right from the origin. The lengths of the gradients of the two first axes (2.20 and 1.87 SD units, respectively) indicate an overlap of the species composition among the samples, probably due to the shared common species.

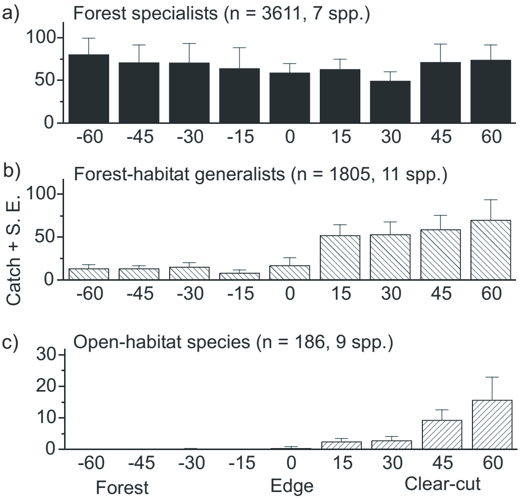

Fig. 3. Pooled catches (individuals caught in 1999) of three ecological groups of carabid beetles along a clear-cut/forest edge gradient. The species groupings, consult Koivula (2002a). Original data: Heliölä et al. (2001).

4.5 Carabids at the Forest/Clear-cut Ecotone

Invertebrate assemblages at habitat edges are mixtures of species found on either side of the edge zone (Kotze and Samways 1999). This implies that edges of forest fragments are easily invaded by invertebrate species from the surrounding matrix, and some species may continue beyond the edge "filter" into the forest interior (Spence et al. 1996). Edge habitat is unsuitable for species requiring interior habitat (Stevens and Husband 1998) and, consequently, such species may be lost if fragments become too small (Haila 1999).

Carabid assemblages in the clear-cut/mature-forest edges were more similar to forest assemblages than to clear-cut assemblages (Heliölä et al. 2001). The study also showed that the edge was very abrupt for carabids. Many open-habitat species occurred in small numbers in the edge zone (±15 m from the edge; Heliölä et al. 2001), and as only one individual of these species was found in the forest interior (30–60 m into the forest), it is evident that they entered the forest only sporadically (Fig. 3). As in boreal Canada (Spence et al. 1996), no carabid species were restricted to the edge and it seems that there are no "edge species" among boreal forest carabids. However, Koivula (2002b) and Koivula et al. (2002) found that the abundance of forest carabids gradually decreases in the clear-cuts, with increasing distance from the forest edge.

Forest-dwelling carabids appeared not to be affected by the edge zone, as beetle numbers did not increase or decrease near the edge (Fig. 3). For example, *Agonum mannerheimii*, *Calathus micropterus*, *Carabus glabratus* and *Cychrus caraboides* occurred both in the forest and in clear-cuts, showing no or only a slight decrease due to logging (Heliölä et al. 2001). Similar observations were made with forest species in Canada (Spence et al. 1996). Although these findings suggest that edges do not have much of a negative effect on forest carabids, other taxa may be more sensitive to edge effects, as has been shown with bark beetles (Coleoptera, Scolytidae) in Finland (Peltonen and Heliövaara 1998).

4.6 The Importance of Forest-Landscape Structure

Forest-carabid abundance in the clear-cuts and young sapling stands increased with decreasing distance to the nearest source habitat (old stand), indicating an edge effect reaching from the forest to the clear-cut and possibly a source-sink situation (Pulliam 1988, Koivula 2002b, Koivula et al. 2002). Furthermore, the catches increased with decreasing size of clear-cut and increasing amount of surrounding old forest, albeit statistically non-significantly (Koivula et al. 2002). Nevertheless, the majority of these species seemed to maintain populations all along the 60-year succession gradient. The catches of *Calathus micropterus*, however, were poor in the 5 and 10 year-old stands but then subsequently increased. According to Koivula (2002a, b), *Calathus micropterus* was not significantly affected 2–3 years after clear-cutting, but another study indicated that the population decreases remarkably later, perhaps 3–5 years after logging (Koivula et al. 2002). A drastic population decline can lead to local extinction (e.g. Hanski 1999).

In a heavily managed landscape with clear-cuts larger than the studied ones, forest specialists may be absent from the central parts of clear-cuts and restricted to scattered mature stands and their adjacent surroundings, where large trees shelter the ground. This may be the case for strict forest-habitat specialists with poor dispersal ability (Desender et al. 1999), e.g. *Carabus hortensis*, *Cychrus caraboides* and *Agonum mannerheimii* (Lindroth 1985, 1986). Within a heavily fragmented landscape, species dispersal abilities and the distance between their utilized habitat patches are critical for the maintenance of populations (den Boer 1990a, b, Fahrig and Merriam 1994, With et al. 1997, Hanski 1999). Flightless carabids may move up to a few hundred metres by foot (Mascanzoni and Wallin 1986), but these movements are probably seldom target-oriented at the scale of tens of metres (Wallin 1986). The continuous availability and connectivity of mature stands should thus be guaranteed, and the distance between these stands should not exceed 50–200 metres.

The large area of clear-cut habitat and young sapling stands at the landscape level, functioning as source habitats for open-habitat species, can be profitable for these species (e.g. Spence et al. 1996). Open-habitat species were commonly found even in the most isolated clear-cuts (over 200 m to the nearest clear-cut) (Koivula 2002b). Similarly, in a Finnish forest/field mosaic, Kinnunen et al. (1996) observed that, although non-isolated and large fields hosted more individuals and more species than isolated and small ones, flightless open-habitat species were commonly found even in the most isolated fields. Kinnunen et al. (1996) concluded that dispersal by air is perhaps the most important means of colonisation: the majority of the open-habitat species caught in the present studies were long-winged, thus being potentially good dispersers (den Boer 1970, 1990a, b, Thiele 1977, Ranta and Ås 1982). Additionally, the increase of the total length of the Finnish forest-road network from a few hundreds of kilometres in 1950 to the present over 120 000 km (Västilä and Herrala-Ylinen 1999; see an example in Martikainen 2000) enhances the rapid colonisation of open-habitat species to recent clear-cuts by offering dispersal corridors and habitat for such species (Vermeulen 1995, Koivula 2002c).

4.7 A Summary of the Spatial Responses of Carabids to Logging

We briefly summarize the above-discussed habitat-association and logging-response patterns of carabids by using five example species (Koivula 2001). A forest species, *Calathus micropterus*, decreased in the clear-cuts (Koivula 2002a), but was more abundant in the clear-cuts the nearer the adjacent forest/clear-cut edge was (Koivula et al. 2002). An open-habitat specialist, *Pterostichus adstrictus*, increased especially in the central parts of the clear-cuts, but did not invade the remaining mature stand (Heliölä et al. 2001). *Agonum fuliginosum* appeared to be a generalist in respect to canopy closeness, but was dependent on *Sphagnum* mires (Koivula 2002a, b, Koivula et al. 2002). If any mire habitat remains in the clear-cut, *A. fuliginosum* will also persist there. Another mire specialist, *Agonum mannerheimii*, on the other hand, disappears from the clear-cuts (Niemelä et al. 1993a, b). The abundance of *Carabus hortensis* decreased in the clear-cuts (Koivula 2002a, b, Koivula et al. 2002) but individuals may persist e.g. in the retained tree-groups or in the mesic and luxuriant forested parts of the retention-felled stands. These patterns are rather similar to those of Spence et al. (1996), but with two major differences: firstly, open-habitat species did not colonize large forest stands (Heliölä et al. 2001), and secondly, the majority of forest species survived in the clear-cut sites adjacent to mature stands (Koivula 2002a, b, Koivula et al. 2002).

5 Within-stand and Landscape Variation and Conclusions

At the stand level, the studied retention felling methods, compared to the clear-cutting, contribute positively to the maintenance of forest-carabid assemblages. Retained trees shelter the ground layer from sunlight and, to some extent, from microclimatic alterations and changes in the bottom- and field-layer vegetations. However, the sheltering efficiency depends on the number of trees retained, as indicated by the relationship between generalist carabids and tree density (Koivula 2002b), and the degree of exposure and geographical position of the site. The most valuable within-stand sites in the spruce forest, e.g. spruce mires, should be managed by applying methods other than traditional clear-cutting or by leaving these sites intact. Forest management should also aim at minimising adverse edge effects. The best option is to leave large enough fragments for forest-interior specialists as source areas (Spence et al. 1996, Burke and Goulet 1998). Finally, the results presented in this paper concern only a fraction of the forest-floor fauna. Since species that live in trees (polypores, epiphytic lichens, saproxylic species) are probably more sensitive to logging than carabids, modified management methods should also be examined in relation to these species.

Compared to the effects of clear-cutting, logging gaps within intact forests increases the amount of edge habitat more and may, therefore, have cumulative consequences on biota in the long term. For example, open-habitat carabids had invaded small openings, but also the narrow uncut sections of the same stands (Koivula 2002a). At first this seems to contrast with the results in Heliölä et al. (2001), but the uncut sections next to the small openings were only 20–40 m wide, thus having no interior habitat and being much more well-lit. Retained trees and vegetation in logged sites may nevertheless act as a buffer for adjacent forest reserves, by decreasing edge effects and increasing the effective area of interior reserves (Lindenmeyer and Franklin 1997).

One possible method for incorporating species conservation into forest management might be strip clear-cutting, although this method remains to be studied. Also increasing the logging rotation time to 150–200 years may enable some important within-stand elements (e.g. spruce mires, the amount of decaying wood, very large trees and trees with cavities) to develop. For example, when an old-growth forest is clear-cut, the pre-cutting amount of decaying wood is not achieved within 200 years (Siitonen 2001). Additionally, if the soil is strongly altered (e.g. by being taken to agricultural use), populations of some forest-specialist carabids may not recover even within several centuries post clear-cutting (Desender et al. 1999).

As shown in this paper, within-stand site variation is important for the spatial distribution of boreal forest carabids, and for overall forest-species diversity (Esseen et al. 1992, 1997). Forest biodiversity can probably best be maintained if forest management mimics natural processes, blends natural structures and includes natural composition within the stands (Fries et al. 1997).

Landscape heterogeneity and the continuity of mature and old-growth forests are important large-scale features of boreal forests (Fahrig and Merriam 1994, Esseen et al. 1997), and of importance also for within-stand level abundance patterns of forest species, as the present results with carabids also indicated. Therefore, the management approach should be to maximise regional-scale habitat diversity and guarantee the availability of old-growth forests (Niemelä et al. 1993a, b). Swedish and Finnish management guidelines and forestry laws have recently changed their focus towards an ecologically more sustainable direction (Hallman et al. 1996, Angelstam and Pettersson 1997, Savolainen 1997). In Finland, for example, clear-cut size is usually less than 3–4 hectares, above which the economical benefit/cost relationship does not increase markedly (Imponen and Kaila 1988, Parviainen and Seppänen 1994). Management guidelines also include the retainment of ecological corridors and maintenance of certain key habitats (Hallman et al. 1996). The use of logging methods other than clear-cutting and thinning has not, however, increased at all between 1970 and 1998 in Finland, being 2–8% per year of the managed forest area, but thinning is as widely used as clear-cutting, with both methods constituting 30–50% per year of the logged forest (Västilä and Herrala-Ylinen 1999).

Since the level of wood material removed yearly from the Fennoscandian forests will probably remain constant in the near future, applying widely ”ecological” methods – like retention felling – increases the total land area that has to be managed to produce the same economical benefit as before. This can probably be, at least to a certain extent, offset by the restoration efforts that probably benefit the threatened forest species best if applied in forests adjacent to existing reserves, rather than if they were spread evenly (and thinly) over whole countries (Hanski 2000).

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