

# Carabid beetles (Coleoptera, Carabidae) in boreal managed forests – meso-scale ecological patterns in relation to modern forestry

Matti Koivula

This thesis is based on the following articles:

- 0) Summary
- I) Koivula, M.: Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). — Submitted manuscript.
- II) Heliölä, J., Koivula, M. & Niemelä, J.: Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest–clearcut ecotone. — *Conservation Biology* (in press).
- III) Koivula, M.: Boreal carabid-beetle (Coleoptera, Carabidae) assemblages in fresh clear-cuts and uneven-age structured stands. — Submitted manuscript.
- IV) Koivula, M., Punttila, P., Haila, Y. & Niemelä, J. 1999: Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. — *Ecography* 22: 424–435.
- V) Koivula, M., Kukkonen, J. & Niemelä, J.: Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. — Submitted manuscript.

# Contributions

The following table shows the major contributions of authors to the original articles (referred to as I–V)

	I	II	III	IV	V
Initiative	MK, JN	JH, MK, JN	MK, JN	YH, JN, PP	MK
Experimental design	MK, JN	JH, MK, JN	MK, JN	YH, MK, JN, PP	MK, JK
Data gathering	MK	JH	MK	MK	JK, MK
Analyses	MK	MK, JN, JH	MK	MK, PP	MK
Manuscript preparation	MK	JN, MK, JH	MK	MK, PP, JN	MK, JN, JK

Supervised by Prof. Jari Niemelä  
University of Helsinki  
Finland

Reviewed by Dr. Konjev Desender  
Royal Belgian Institute of Natural Sciences  
Belgium

Prof. Pekka Niemelä  
University of Joensuu  
Finland

Examined by Prof. John R. Spence  
University of Edmonton  
Canada

## Introduction

This thesis consists of five research papers (hereafter referred to as I–V) and a summary. The summary begins with a general background of the studies (forest fragmentation, management and their consequences) and reviews current knowledge concerning fauna of boreal managed forests. Further, the designs and main results of the studies I–V are presented, and these results are discussed in the context of forest management.

### *Forest fragmentation*

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). Forest fragmentation leads to isolation and reduction in size of mature-forest fragments and an increase in the proportion of edge habitat at the expense of interior habitat (Ranney et al. 1981, Harris 1984, Murcia 1995). Edge is a habitat on which an adjacent habitat has an effect e.g. through climatic alteration, whereas within interior habitat such an effect is not discernible. Deforestation and consequent loss of forest species in tropical forest ecosystems have received considerable attention (Laurance & Bierregaard 1997). Erwin (1982) estimated that tropical forests may host as many as 30 million arthropod species, while the number of all known species was estimated to be ca. 1.4 million at that time (Wilson 1988). Since recent extinction rates are more than 100 times greater than background geological ones (Pimm 1998), much of the tropical diversity is lost before it has been even discovered. However, boreal regions also host a rich fauna. For example, Hanski & Hammond (1995) suggested that boreal forests may house only seven times less beetle species than tropical ones.

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-caused fragmentation over several centuries but the most drastic effects of forestry on forest biota have taken place for only 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 & Väisänen 1984, Esseen et al. 1992, Niemelä 1997). Forestry is responsible for 30.7% 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. In southern Finland, roughly 1% of forest cover is protected and only 0.5% of these are old-growth forests (Virkkala et al. 2000). Obviously, 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).

### *Selecting the study subjects*

The long-term persistence of many forest species is dependent on populations living in managed forests (Lindenmeyer & Franklin 1997). Since maintaining viable populations of all species is of central importance in conservation, species that are most sensitive to fragmentation should determine conservation actions. However, 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 & Hytteborn 1991, Kuusinen 1994, 1996, Dettki & Esseen 1998), beetles living in dead wood (Väisänen et al. 1993, Siitonen & Martikainen 1994, Jonsell et al. 1998) and Mycetophilidae insects (Økland 1994). However, Martikainen (2000) showed that many saproxylic species can live in managed forests if they contain a sufficient amount of dead or dying wood.

Most forest species require specific elements of forests rather than “average forest” (Niemelä et al. 1996). Consequently, individuals of such species are more common in their favoured habitat and thus are distributed non-randomly among forest patches and within stands

(Niemelä et al. 1992a). Environmental diversity creates a richer within-stand habitat mosaic in naturally-developing forests compared to managed ones (Haila et al. 1994, Esseen et al. 1992, Dettki & Esseen 1998). Decaying wood, tree-species admixture and large trees, for example, are usually lacking from managed forests (Esseen et al. 1997, Niemelä 1997, 1999). Site characteristics may also appear different for different species. Consequently, some species with strict microhabitat demands occur in metapopulations (Hanski 1999), whereas for some other species with wider tolerances the environment may be divided into source and sink habitats (Pulliam 1988) with some species using several microhabitat and forest types. In a given habitat, colonisations and extinctions may occur, with the most successful species persisting for a longer time (Lockwood et al. 1997). The species in the forests thus form gradually changing assemblages rather than strict communities of species (e.g. Niemelä et al. 1990).

Intermediately common species, with strict microhabitat demands, can potentially be used as indicators of environmental quality in order to study whether or not new, modified management methods have an effect on forest-species assemblages (Haila & Kouki 1994). Such species can be found among carabid beetles (Coleoptera, Carabidae). 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 & 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. 1992a, Langor et al. 1994). Clear-cutting, for example, is shown to alter carabid assemblages (Haila et al. 1994, Didham et al. 1998).

### *Effects of forest cutting on boreal carabids*

The biotic and abiotic effects of clear-cutting are well documented (e.g. Huhta 1976, Pettersson 1996, Davies & Margules 1998, Abilds-

nes & Tømmerås 2000) and the microclimates of clear-cut and closed-canopy sites differ (Matlack 1993). Open sites are windier and the diurnal light, temperature and humidity vary more; the sun dries and heats the ground, causing the decrease of dwarf shrubs (*Vaccinium* spp.) and forest mosses, and the drying of *Sphagnum* moss mires (Niemelä 1997, 1999). These factors affect carabid-beetle distribution directly and indirectly (Thiele 1977). Carabids are often more numerous and more speciose in open habitats than in forests (Niemelä & Halme 1992, Kinnunen 1999) but clear-cutting also has negative effects on the abundance of forest-specialist species (Niemelä et al. 1993a, b, Langor et al. 1994, Spence et al. 1996).

The effects of modified cutting methods are much less studied. For example, studies concerning thinning have mostly focused on its effects on tree growth. In this thesis, three modified cutting methods are examined (I, III). Creating openings of a few acres into stands may mimic natural gap formation (Sousa 1984, Attiwill 1994, Kuuluvainen 1994). Another method with small, retained tree groups has no obvious natural analogue but retained trees may act as stepping stones or “lifeboats” for forest specialists (Franklin et al. 1997). Finally, 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. In this thesis, beetle catches of stands where thinning (aiming at uneven age structure of trees) are studied (III).

Changes in abiotic and biotic conditions in the forest – clear-cut edge as compared to the forest interior are collectively called “edge effects” and are studied in paper II. 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 & 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 & Muona 1985, Jokimäki et al. 1998) but

very few of these species appear to be edge specialists (Didham 1997a, b). Invertebrate assemblages at habitat edges are mixtures of the species found on either side of the edge zone (Kotze & 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 & Husband 1998) and, consequently, such species may be lost if fragments become too small (Haila 1999).

### *Carabid beetles in the meso-scale framework*

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 effects of forestry at several scales (Haila & Kouki 1994). A temporal scale from days to hundreds of years, and a spatial scale from metres to hundreds of kilometers, form a relevant framework for studies concerning forest management and forest-species conservation; the “meso-scale” (Niemelä 1999). In this thesis, a 120-year time scale reaches from fresh clear-cuts to mature stands, covering the normal cutting rotation in southern and central Finnish spruce forests (Kuusela 1990). Short-term (two years after cutting) responses of carabids to clear-cutting and three modified cutting methods were examined in papers I–III. A 60-year time-scale was studied by comparing the carabid catches of clear-cut originated, *Myrtilus*-type stands that were from 5 to 60 years old (V). Two spatial levels were examined: within stand (site; alpha diversity) and between stands (area; beta diversity) (Magurran 1988). Environmental variables were used to explain carabid abundances at both site (II, III and IV) and stand (I and V) levels. In order to study within-stand factors affecting the abundance and habitat requirements of carabids,

vegetation with percentage coverages, and tree species with number per unit area were measured. Red wood ant (I–V) and springtail (V) catches were also recorded. Furthermore, to study the carabid catches in relation to landscape structure (area level), the sizes of the study stands, distances to nearest adjacent open habitat and to adjacent old stand were measured (III and V). These measurements were then used to study whether the beetle abundances in clear-cuts were affected by the surrounding habitats.

I focus on seven questions concerning carabid-beetle abundance in boreal managed forests. **(1)** In order to improve our knowledge of carabid ecology, which is important in conservation and the use of carabids as bioindicators (Niemelä et al. 2000), for example, I study whether the division of species into forest, generalist and open-habitat species is relevant in forest-carabid studies (I, III, V). Furthermore, I examine how carabids respond to moisture and light conditions (as indicated by vegetational variables) (I, III), to litter quality (IV), abundance of red wood ants and food (springtails) (I–V), the amount of trees shading the forest floor (I, III) and can any important within-stand habitat types be identified using carabid catches as a guideline (I–V). **(2)** Are there any carabid species that disappear from the clear-cut sites (I–III, V)? **(3)** Is the edge effect detectable in the carabid samples of forest/clear-cut edge (II)? **(4)** Can the mature or old stands act as sources for forest species occurring in adjacent clear-cuts (III, V)? **(5)** How does the carabid assemblage respond to clear-cutting in the short term and are the retained tree groups in the clear-cuts or small-scale cuttings of use for the maintenance of the original carabid assemblages (I)? **(6)** Does thinning change the forest-species assemblage in the short term (III)? **(7)** Do the abundances of species change along a 60-year succession gradient, and are there any critical phases of succession with radical assemblage changes (V)? Finally, I provide some practical guidelines for ecological forestry based on my studies.

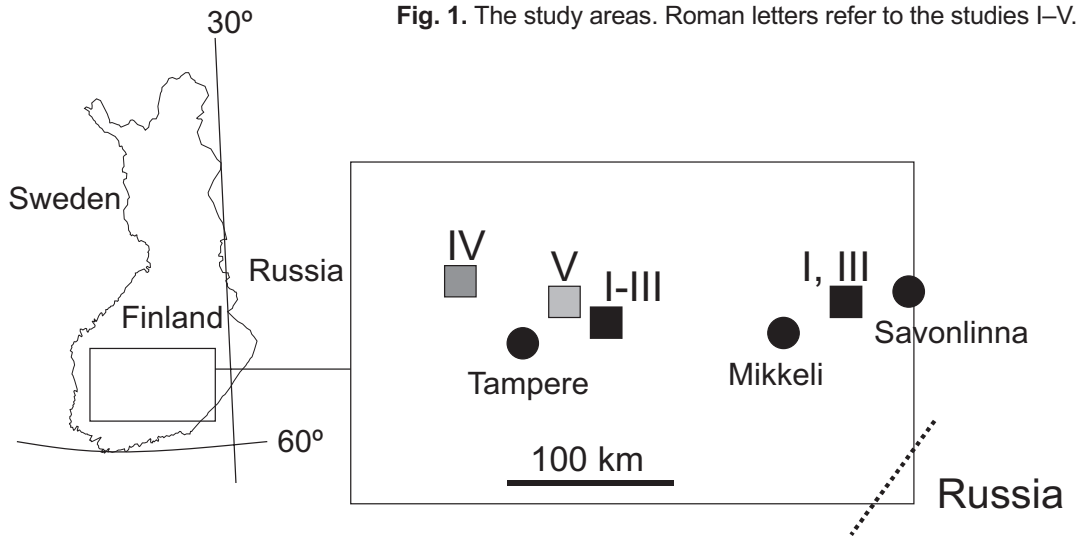


Fig. 1. The study areas. Roman letters refer to the studies I–V.

## Material and methods

### Study areas

The studies were performed in central Finland, at the border between the southern and middle boreal zones (Ahti et al. 1968) (Fig. 1). The study forests were spruce (*Picea abies*) dominated, *Myrtillus*-type forests (Cajander 1949). The surroundings of the study stands varied from recently cut stands to mature (90–150 years) spruce forests.

In studies I–IV, the effects of various cutting regimes and leaf-litter addition on carabids were studied experimentally. Before the cuttings, the study stands were mature with 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 natural succession of spruce forests begins with a deciduous phase and continues towards spruce dominance (Esseen et al. 1997). In the study with different phases of clear-cut originated succession (study V), the 5 and 10 year-old stands were dominated by deciduous trees with plenty of birch and some spruce and pine saplings. Rosebay willowherb

(*Epilobium angustifolium*) and grasses (mainly *Deschampsia* and *Calamagrostis*) were abundant. The 20 and 30 year-old stands represented a mixture of deciduous (birches, willows *Salix* spp. and aspen) and coniferous (spruce and pine) saplings of natural origin. The field-layer vegetation was very dense in the 30 year-old stands with plenty of *Calamagrostis* grasses. The 60 year-old stands were spruce dominant with some pines and birches as an admixture.

### Sampling designs and analyses

The beetles were collected using pitfall traps (Greenlade 1964, Southwood 1978). The traps (sizes, see papers I–V) were partly filled with 25–30% ethylene or propylene glycol and detergent and covered with 10 × 10 cm plexi roofs to protect them from litter and rain. Trapping effort and total beetle catches in the studies are given in Table 1. The beetles were identified by MK in studies I, III and IV, by MK and Mr. Jarno Kukkonen in study V, and by Mr. Janne Heliölä in study II. The nomenclature follows Lindroth (1985, 1986).

The main statistical methods applied were analysis of variance (ANOVA), regression, correlation and multivariate analyses (Jongman et al. 1995). The statistical packages used were SYSTAT 8.0 (SPSS inc. 1998), STATISTIX 2.0 (Anon. 1998), CANOCO 3.15 (ter Braak 1987)

**Table 1.** Trapping effort (number of stands and traps used, and effort, i.e. thousands of trapping days), carabid catches (Indivs. = individuals caught) and species numbers.

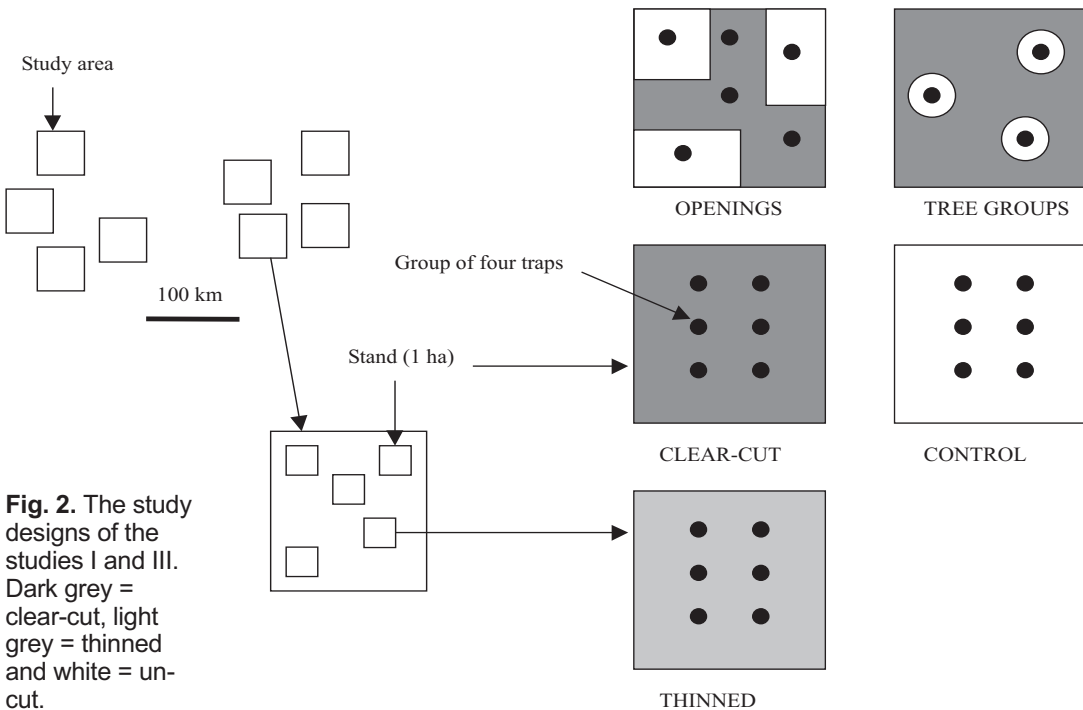
Study	Trapping effort				Carabid catch			
	Design		1,000 trapping days		Before		After	
	Stands	Traps	Before	After	Indivs.	Species	Indivs.	Species
I	32	768	81.79	258.43	4,350	23	17,300	47
II	6	324	–	26.13	–	–	5,609	34
III	24	576	61.34	132.77	3,402	16	10,287	44
IV	3	216	23.54	69.55	551	12	6,268	15
V	20	240	–	31.68	–	–	2,316	39

and CANOCO 4.0 (ter Braak & Šmilauer 1998).

### Study I

Short-term responses of carabids to logging were examined with the “Before/After with Control/Impact” (BACI, Underwood 1991) design. Thus, I took samples before impact (1995), after impact (1996–1998), and from control (untreated) sites. The study was performed in eight separate areas, each containing four stands with different treatments, for a total of 32 stands. Each stand consisted of a one-hect-

are square and its adjacent surroundings, altogether 1.5–2 hectares. The treatments were (i) control, (ii) clear-cut, (iii) stand with three 1,600 m<sup>2</sup> openings (hereafter referred to as stand with openings) and (iv) stand with three approximately 15 × 20 m retained tree groups (hereafter referred to as modified clearfelling) (Fig. 2). Within each stand, 24 traps were placed in six groups of four traps, with the minimum distance to the stand edge and the nearest trap group being 25 m (Fig. 2). In treatments (iii) and (iv), three groups were placed in uncut and three in cut parts of the stands. Stand-specific averages



**Fig. 2.** The study designs of the studies I and III. Dark grey = clear-cut, light grey = thinned and white = uncut.

of plant-species coverages, tree variables and wood-ant catches were used in multivariate analyses to explain the carabid abundances at the stand level.

### *Study II*

The edge effect, caused by clear-cutting, was examined in four separate study areas in 1997, the second growing season after clear-cutting. This study was performed by using 120-m pit-fall-trap grids which extended 60 m into the clear-cut and 60 m into the adjacent forest. Nine groups of four traps each were placed along this gradient in each stand. The trap groups were in lines 15 m apart, with the traps in a line being 4–5 m apart. The vegetational gradient was examined by recording plant-species coverages and these were used together with the carabid catches in the multivariate analyses.

### *Study III*

With the BACI design, the catches from control (uncut) and clear-cut stands were compared to the catches from stands that were thinned with the aim of obtaining an uneven age structure of trees (hereafter referred to as thinned stands). I thus had data from before (1995) and after cuttings (1997–1998) (Fig. 2). The study was performed in eight separate areas, each subjected to all three treatments. The traps were placed as in treatments (i) and (ii) in study I. Here, multivariate analyses with block design were performed at the trap-group level with carabid data and environmental (vegetation, trees, and wood-ant catch) variables. Additionally, the adjacent surroundings of the stands were mapped in order to study whether the landscape mosaic influenced carabid abundance patterns. The distance to the nearest mature stand and to open habitat (and their forest types) were recorded and carabid assemblages were examined in relation to these distance gradients.

### *Study IV*

Small-scale variation within stands and leaf litter, which could potentially affect carabid abundance and distribution, were studied using artificially created aspen-litter patches (diameter 5 m) in Seitsemien National Park in central Finland between 1993–1996. A BACI design was

applied. Data were gathered before (1993) and after the litter addition (1994–1996). There were three control (no litter added) and three impact (litter added) plots in each of the three study stands. Three perpendicular plastic panes around groups of four traps (a total of 12 traps) were placed in each plot. The carabid catches of the control and impact patches were compared and vegetational data and wood-ant catches were used in multivariate analyses.

### *Study V*

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 in Häme, during 1999. The sizes of the stands varied between 0.7 and 7.7 ha. Three groups of four traps (12 traps in total) were placed in each stand, with the distance to the nearest adjacent trap group or stand edge between 25–75 m. Carabid catches in relation to environmental variables (stand-specific averages of vegetational variables, red wood ant and springtail catches) were studied. In order to study the source-sink effect, 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.

## Results and discussion

In the following, I present and discuss the main findings of the studies.

**(1) Forest carabids can be divided into open-habitat, generalist and forest species. Forest species can further be divided into forest generalists, species preferring sites with plenty of litter, those preferring mesic and luxuriant sites and mire species. Spruce mires, luxuriant sites and sites with deciduous trees are important for carabid diversity in spruce-dominated forests (I–V).**

The classification of carabids as open-habitat, generalist and forest species is not relevant when studying forested environments. The for-



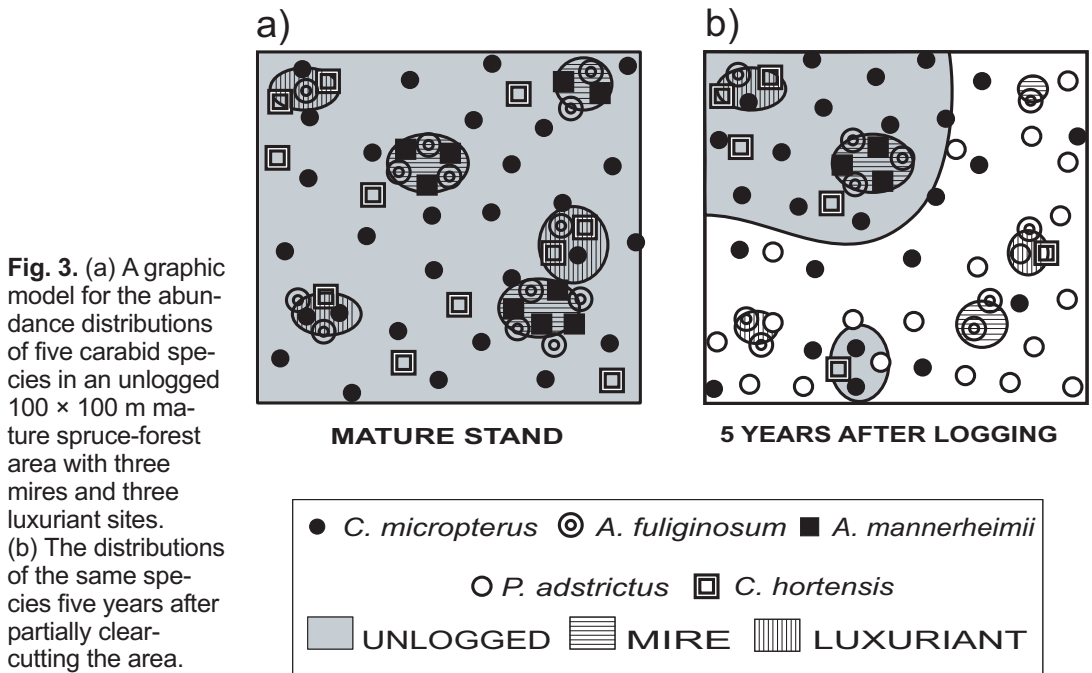


est species should be classified according to their preferences of the openness of forests (Bortmann 1996). Along a canopy-closure gradient (I, II, III, V), carabids were divided into closed-stand specialists, forest-habitat generalists and open-phase specialists (Table 2). This division corroborates those earlier proposed for forest species (Niemelä et al. 1988, 1993a, Niemelä & Halme 1992). Two species always showed a preference for closed canopy: *Carabus hortensis* and *Cychrus caraboides*, and probably also *Agonum mannerheimii*. However, the study with a 60-year succession period (V) indicated that both *Calathus micropterus* and *Carabus glabratus* also benefitted from closed canopy. Their populations thus survive at least 2–3 years in the clear-cuts (I, III) and decrease or disappear later (V), as has been earlier shown for *C. micropterus* (Abildsnes & Tømmerås 2000) and *A. mannerheimii* (Niemelä et al. 1993a). On the other hand, open-habitat species predominantly occurred in clear-cuts and young sapling stands (I–III, V). Of the 31 most numerous species, 13 were open-habitat species, the most abundant of these being *Amara lunicollis*, *Agonum sexpunctatum* and *Pterostichus adstrictus* (Table 2). Generalists were most abundant in early and mid-successional stages (V). Some generalists also showed increasing abundance with increasing openness of canopy (*Harpalus quadripunctatus*, *Pterostichus oblongopunctatus*, *Pterostichus niger* and *Pterostichus diligens*) while others showed the opposite trend (*Agonum fuliginosum*, *Notiophilus biguttatus* and *Patrobus assimilis*) (I, III, V).

Many species also showed clear preferences for certain site characteristics (Table 2). Wet *Sphagnum* sites, and mesic and luxuriant sites hosted distinctive assemblages and are thus important for the within-stand heterogeneity (I, III, V). Additionally, the amount of litter (and probably also its quality) is an important factor, further indicating the importance of scattered deciduous trees within coniferous-dominated stands. Five species preferred sites with plenty of litter (Table 2), and also Niemelä et al. (1992a) have shown that some carabid species are most abundant at sites with plenty of aspen litter. Interestingly, the experimental leaf-litter

addition affected carabid-assemblage structure by increasing the catches of *Calathus micropterus*, *Pterostichus oblongopunctatus* and *Cychrus caraboides* (IV). Also *Leistus terminatus* seemed to benefit from litter amount (V), whereas *Pterostichus oblongopunctatus* and *Pterostichus adstrictus* catches were highest in sites with plenty of logging residue (II). Sites with much field-layer vegetation (*Calamagrostis*, *Epilobium angustifolium* and *Rubus idaeus*) were favoured by *Trechus secalis*, *Harpalus quadripunctatus*, *Pterostichus diligens*, *Pterostichus adstrictus* and *Pterostichus strenuus* individuals (III, V). Mesic and luxuriant patches were favoured by *Pterostichus niger* (I), *Cychrus caraboides* and *Carabus hortensis* (I–III), and possibly also *Carabus glabratus* (I) and *Amara brunnea* (III). Finally, wet spruce mires often hosted distinctive assemblages with *Agonum mannerheimii*, *Agonum fuliginosum* and *Patrobus assimilis* (I–III, V) and also *Pterostichus diligens* (II). Deciduous-tree admixture and spruce mires are important for, for example, epiphytic lichens, land snails and saproxylic beetles (Kuusinen 1996, Esseen et al. 1997, Niemelä 1997, Martikainen 2000, Siitonen & Saaristo 2000). Since wet, mesic and luxuriant patches and leaf litter are important also for carabids, such patches should be left untouched or be managed with methods other than clear-cutting. Furthermore, my results indicate that tree-species admixtures should be favoured in managed forests.

The above mentioned habitat-preference patterns are summarised in a graphic model (Fig. 3). As shown in paper II, spruce mires and probably luxuriant within-stand sites dry after logging. The forest species, *Calathus micropterus*, decreases dramatically in the clear-cut (I, III, V) but is more abundant in the clear-cut the nearer the adjacent forest/clear-cut edge is, whereas the open-habitat specialist, *Pterostichus adstrictus*, increases especially in the central parts of the clear-cut but does not invade the remaining mature stand (I–III, V). *Agonum fuliginosum* appears to be a generalist in respect to canopy closeness but is dependent on *Sphagnum* mires (I–III, V). If any mire habitat remains in the clear-cut, *Agonum fuliginosum* will also persist there (Fig. 3b). Another mire specialist,



*Agonum mannerheimii*, on the other hand, disappears from the clear-cut (I–III, V, Niemelä et al. 1993a, b). The abundance of *Carabus hortensis* decreases in the clear-cut (I–III, V) but individuals may persist e.g. in the retained tree group or in mesic and luxuriant clear-cut sites. The model is rather similar to that of Spence et al. (1996) but with two major differences: firstly, open-habitat species do not colonise large forest stands, and secondly, the majority of forest species are assumed to survive in the clear-cut sites adjacent to mature stands. However, this model concerns only those carabid species that were studied in this thesis, and other taxa or carabid species may show different abundance patterns.

There is usually a negative correlation between carabid and ant abundances (e.g. Thiele 1977). However, some species (*Notiophilus palustris*, *Notiophilus biguttatus*, *Calathus micropterus* and *Trechus secalis*) tolerated red wood ants (I and IV), whereas the majority of carabids avoided sites with many ants (I), as has also been shown by Niemelä et al. (1992a). The ant tolerance may depend on the activity of the carabid species (Punttila 1994). Diurnal ants may find the nocturnal carabids at their resting

sites, whereas diurnal carabids (*Notiophilus*) may be capable of avoiding ants. There are, however, exceptions. *Calathus micropterus* and *Trechus secalis* are nocturnal, but tolerate ants. Since clear-cutting and forest fragmentation are shown to affect wood-ant species composition (Punttila 1996), changes in ant abundance may have indirect effects on carabid abundances. Additionally, *Notiophilus biguttatus* showed a preference for sites rich in its preferred food, springtails (Hengeveld 1980), as did *Carabus hortensis*, for example, too (V).

**(2) Some forest carabids with poor dispersal ability preferred stands with a closed canopy, moist or mesic patches within stands or wet spruce mires (I, III).**

Some flightless forest specialists (*Carabus hortensis*, *Cychrus caraboides* and *Agonum mannerheimii*) preferred mesic and luxuriant patches or were restricted to spruce mires (Table 2, Fig. 3). These patches often dry due to the logging, and these species may therefore 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, the recolonisation of species which require such habitat depends on the availability of nearby source habitats (e.g. Spence et al. 1996). Therefore, at the landscape level, the continuity of stands with spruce mires should be guaranteed and at the within-stand level, mire sites as key biotopes should not be cut at all (Hallman et al. 1996, Savolainen 1997, Siitonen & Saaristo 2000). Furthermore, luxuriant sites should also preferably be managed with less destructive methods than traditional clear-cutting, in order to maintain the forest-floor flora and fauna.

Most forest species occurred in the fresh clear-cuts. This pattern has at least three explanations. Firstly, the individuals caught may be wanderers from nearby mature stands (Spence et al. 1996). This may be the case, for example, in sites close to mature-stand edges (Fig. 3). Secondly, 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. Szyszko (1990) showed that the abundances of many forest carabids in Polish pine stands decreased three years after clear-cutting. If this is the case in boreal forests, the present time scales (I–III) would have been too short to demonstrate dramatic decreases. Thirdly, some forest species may be adapted to natural disturbances (e.g. windthrows, forest fires) within a forested landscape and may survive in these clear-cuttings.

### **(3) Carabid assemblages in the clear-cut/mature-forest edges were more similar to forest assemblages than to clear-cut assemblages and open-habitat species in the clear-cuts did not penetrate the forest fragments (II).**

The edge ecotone between mature stands and adjacent clear-cuts was a barrier for open-habitat species, whereas forest species occurred in high numbers there (II, see also Kolasa & Zalewski 1995, Risser 1995). However, in studies III and V, evidence was found that the abundance of forest carabids may gradually decrease in the clear-cuts, with increasing distance from the forest edge.

The forest/clear-cut edge proved to be a sharp border for open-habitat carabid species (II). Carabid samples at the edges were similar to those within the forests, which corroborates results from Afro-montane forest-grassland edges in South Africa (Kotze & Samways 1999). These studies also showed that the edge was very abrupt for carabids. There were dramatic differences in the field- and ground-layer vegetation between the forest and clear-cut and most changes occurred right at the edge. In terms of vegetation, *Vaccinium* dwarf shrubs were 60–70% scarcer in the forest than in the clear-cuts (II). Grasses (*Deschampsia flexuosa*, *Calamagrostis* spp.) and rosebay willowherb (*Epilobium angustifolium*), on the other hand, were more common in the clear-cut than in the forest. Many open-habitat carabid species which were abundant in the clear-cuts occurred in small numbers in the edge zone ( $\pm 15$  m from the edge; II) 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. For example, the most abundant colonizer of the clear-cuts, *Pterostichus adstrictus*, decreased dramatically from the center of the clear-cut towards the edge, and did not penetrate the forest at all (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.

Forest-dwelling and generalist carabids appeared not to be affected by the edge zone, as beetle numbers did not increase or decrease near the edge (II). For example, *Agonum mannerheimii*, *Agonum fuliginosum*, *Pterostichus diligens* and *Patrobis assimilis* occurred both in the forest and in clear-cuts, showing no decrease due to logging. 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, continued fragmentation and decreasing size of fragments may in the long run threaten currently viable populations. For example, small forest fragments are more vulnerable to invasion by open-habitat species from the surrounding regenerating forests, probably due to habitat changes in

the remnants (Halme & Niemelä 1993). Furthermore, other taxa may be more sensitive to edge effects, as has been shown with bark beetles (Coleoptera, Scolytidae) in Finland (Peltonen & Heliövaara 1998).

**(4) 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 (III, V).**

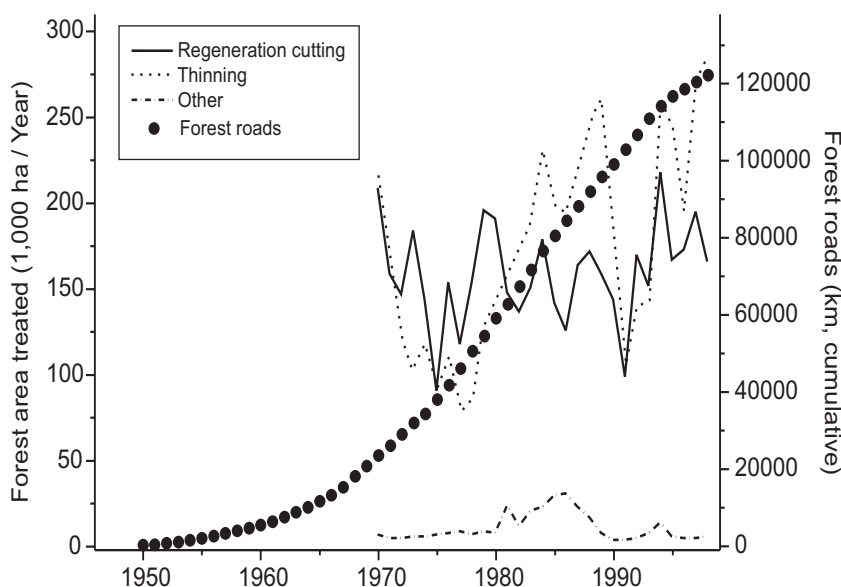
Catches of forest species in the clear-cuts decreased with increasing distance from adjacent old stands (III and V, Fig. 3). Furthermore, the catches increased with decreasing size of clear-cut and increasing amount of surrounding old forest, albeit statistically non-significantly (V). The majority of these species nevertheless seemed to maintain populations all along the 60-year succession gradient (V). The catches of *Calathus micropterus*, for example, strongly decreased in the 5 and 10 year-old stands but then subsequently increased. Such a drastic decrease can cause local extinctions (e.g. Hanski 1999). Also, in a managed landscape with clear-cuts larger than the studied ones, forest specialists may be absent from the central parts of such areas 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 (Lindroth 1985, 1986), e.g. *Carabus hortensis*, *Cychrus caraboides* and *Agonum mannerheimii* (Table 2). Within a heavily fragmented landscape, species dispersal abilities and the distance between preferred habitat patches are critical for the maintenance of populations (den Boer 1990a, b, Fahrig & Merriam 1994, With et al. 1997, Hanski 1999). Flightless carabids may move up to a few hundred metres by foot (Mascanzoni & 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.

**(5) In the short term, open-habitat species and habitat generalists benefit from logging and were abundant in traditionally clear-cut stands and in modified clearfellings, whereas forest species showed no clear responses to cutting (I, II, III).**

The large area of clear-cut habitat and young sapling stands at the landscape level, functioning as source habitats, can be profitable for

**Fig. 4.** The yearly forest area treated by regeneration (traditional) clear-cutting, thinning and other logging methods (left axis; seed-tree cutting and logging on scrub lands excluded from the figure) and the cumulative amount of forest roads (right axis) in Finland during 1950–1998. Source: Finnish Forest Research Institute.



**Table 3.** The three ecological groups of carabids and their short-term responses to different logging methods (Modif = modified clearfellings, Thinn = thinned stands, Open = stands with openings, and Clear = traditional clear-cuts), and long-term responses to clear-cutting in a 60-year time scale with their abundance trends at different phases of succession (5–10 y = catches in 5 and 10 year-old stands compared to the other age classes, 20–30 y = same for 20 and 30 year-old stands, and 60+ y = same for over 60 year-old stands). The symbols indicate the following. ++ = strong (statistically significant) preference for the treatment or age class, + = weak (nonsignificant) preference (larger total catch than in the compared treatments), ± = no preference, -- = strong (statistically significant) avoidance or absence and – = slight avoidance (poorer total catch than in the compared treatments).

	Short term (2–3 years after logging)				Long term (clear-cutting)		
	Modif	Thinn	Open	Clear	5–10 y	20–30 y	60+ y
Open-hab. spp	++	±	+	++	++	–	--
Generalists	±	±	±	+	+	±	±
Forest spp	±	±	±	±	–	±	±

open-habitat species (e.g. Spence et al. 1996). In the Fennoscandian managed forest landscape, open habitats are continuously available for species which prefer them. Open-habitat species were commonly found even in the most isolated clear-cuts (over 400 m to the nearest clear-cut) (III). 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 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 (Table 2), thus being potentially good dispersers (den Boer 1970, 1990a, b, Thiele 1977, Ranta & Ås 1982). Additionally, the dense forest-road network (Fig. 4, Västilä & Herrala-Ylinen 1999, Martikainen 2000) enhances the rapid colonisation of open-habitat species to fresh clear-cuts by offering dispersal corridors (Vermeulen 1995).

The abundance of habitat generalists increased as the distance to the nearest potential source (open habitat) decreased and as the density of trees decreased in control and thinned stands (III). Furthermore, many generalists were very abundant in open phases of forest succession but scarce in 30 and 60 year-old stands (V). These results indicate that habitat

generalists actually prefer openness rather than that they were true generalists in relation to canopy closure. Indeed, multivariate analyses indicated that many generalists – *Harpalus quadripunctatus*, *Pterostichus strenuus*, *Pterostichus diligens*, *Agonum fuliginosum*, *Trechus secalis*, *Pterostichus oblongopunctatus* and *Notiophilus biguttatus* – may benefit from the increased openness caused by logging (III, V).

**(6) In the short term, thinning and the creation of small openings only moderately changed the forest-species assemblage, while traditional and modified clearfellings caused more profound alterations (I, II, III, V).**

Only moderate effects of thinning on carabid assemblages were found in this study (III, Table 3). Similar results have been reported by Atlegrim et al. (1997) for Swedish forests. The retained trees (70–90%) in my study may thus shelter the ground well, or the carabid assemblages may respond to the cuttings over a longer time-scale than two years. However, the catches of habitat generalists increased as the density of trees decreased in thinned (and control) stands (III). Thus, the amount of trees removed may indicate a threshold below which open-habitat species begin to invade the stand. Thinning is shown to decrease the abundance of beetles which are dependent on deciduous trees (Økland 1995). Since the decrease of these spe-

cies 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 & Esseen 1998). Thus, retainment of components that may help sensitive species to persist in the managed landscape (Lindenmeyer & Franklin 1997) and avoiding homogenisation of stands (Law & Dickman 1998) are essential in management practices.

In stands with openings and in modified clearfellings, open-habitat species preferred clear-cut parts of the stands, while generalists and forest species showed no preference between these site types (I). Open-habitat individuals also colonised many uncut parts of stands with openings. Generalists increased less in the small openings than in the large (one-hectare) clear-cuts. These results indicate that the cutting of small openings maintains the original assemblages better than if the clear-cuts were large or if modified clearfelling was applied. However, the assemblages of uncut parts of the stands with openings had changed somewhat. On the other hand, the retained tree groups in the clear-cuts were too small to maintain the original assemblages. Leaving uncut patches within stands probably contributes positively to the maintenance of forest species.

Two years after logging, the total abundance of carabids did not increase much in the clear-cuts (III). 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, the species richness was higher in the clear-cuts than in the other treatments (III). A similar result was obtained when the catches of 5 and 60 year-old stands were compared (V): the total catches were equal, while the former hosted much more species but the total catch decreased later (20–30 years after logging).

**(7) In a study comparing carabid assemblages 5–60 years post-harvest, species richness was highest in 5 and 10 year-old stands. A drastic assemblage-level change and decrease of beetle catches occurred 20–30 years**

**after clear-cutting, which coincided with canopy closure (V).**

Open-phase and closed-canopy carabid assemblages were very distinctive and non-overlapping in terms of species composition. However, the two dominant species were usually shared (I–III). Young, open stands (5 and 10 year-old) hosted rich carabid assemblages (36 species) compared to the closed 30 and 60 year-old stands (20 species) (V), mostly due to the richness of open-habitat species that preferred stands younger than 30 years. Eleven of these species were exclusively caught from 5 year-old stands. These results corroborate other forest-carabid 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 the cuttings, but the most beetle-poor phase, with dramatic changes in assemblage structure, begins 30 years after logging (V), supporting the view that canopy closure distinguishes the open-phase assemblages from the closed-phase ones (Niemelä et al. 1996). The majority of open-habitat species were 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* strongly dominated catches of stands older than 10 years, while the two youngest age classes (5 and 10 year-old stands) were dominated by *Amara lunicollis* and three *Pterostichus* species (V), supporting Lenski's (1982) view about several dominant species. The boreal forests are usually dominated by a few species, while other species are scarce and intermediately common ones may be lacking (Niemelä 1993). The catches of 30 year-old stands (V) support the view of Niemelä (1993) who also suggested that the dominance pattern is perhaps a result of only a few species being adapted to the climatic harshness of boreal forests.

## Conclusions

Landscape heterogeneity and the continuity of mature and old-growth forests are important for the dynamics of forests (Fahrig & Merriam 1994, Esseen et al. 1997), as the present results with carabids also indicate (I–III, V). 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 management regulations towards an ecologically more sustainable direction (Hallman et al. 1996, Angelstam & Pettersson 1997, Savolainen 1997). In Finland, clear-cut size is usually less than 3–4 hectares, above which the economical benefit/cost relationship does not increase markedly (Parviainen & Seppänen 1994, Imponen & Kaila 1988). The use of modified logging methods in Finland has not, however, increased at all between 1970 and 1998, being 2–8% p.a. of the managed forest area (Fig. 4). On the other hand, thinning is as widely used as clear-cutting with both methods constituting 30–50% p.a. of the logged forest (Fig. 4, Västilä & Herrala-Ylinen 1999). In addition to modified harvesting methods, new applications also include the retention of ecological corridors and maintenance

of certain key habitats (Hallman et al. 1996).

The importance of ecological forestry planning is not just to maintain old-growth forests but also to prevent the gradual decrease of overall forest biodiversity at the within-stand, regional and national scales. Since the level of wood material removed yearly from the forests will probably remain constant in the near future, applying thinning and other "ecological" methods, increases the total land area that has to be managed to produce the same economical benefit as before. Furthermore, creating small openings within otherwise intact forests also increases the amount of edge habitat and may therefore have cumulative consequences on boreal biota in the long term. For example, open-habitat carabids invade small openings but also the uncut sections of the same stands (I). At first this seems to contrast with the results in the paper II but the uncut sites in these studies were very different. In study II, the forest interior reached at least 60 metres from the edge, while in studies I and III the uncut fractions were much more open, their breadth being often only 20–40 m, 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 & Franklin 1997). However, the carabid assemblages of studied tree groups had altered much (I), probably because of their size being too small to function as an efficient shelter for the forest floor. One possible method to try to incorporate species conservation into forest management might be strip clear-cutting, though this method is yet to be studied. Also increasing the period between clear-cutting operations 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 2000). Additionally, if soil is strongly altered (e.g. by heavy ploughing), populations of some forest-specialist carabids may not recover even within a few centuries after clear-cutting (Desender et al. 1999).



Within-stand site variation is important for the spatial distribution of many forest species (Niemelä et al. 1992a) and for overall forest-species diversity (Esseen et al. 1992, 1997), as has been shown with carabids (I–V). 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). These restoration efforts 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). At the stand level, the new logging methods studied (I, III) may benefit some forest species, since retained trees shelter the ground layer from direct sunlight and, to some extent, from microclimatic alterations. However, the sheltering efficiency depends on the number of trees retained (as indicated by the relationship between generalist carabids and tree density; III), and the degree of exposure and geographical position of the site. The most valuable within-stand sites in the spruce forest, e.g. luxuriant sites and spruce mires (I–III, V), should preferably 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, for example by leaving large enough fragments for forest-interior specialists to persist (Spence et al. 1996, Burke & Goulet 1998). Finally, the results presented in this thesis concern only the forest-floor fauna. Since it is possible that species which live in trees (polypores, epiphytic lichens, saproxylic species) are more sensitive to logging than carabids, modified management methods should also be examined in relation to these species.

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