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Boreal carabid-beetle (Coleoptera, Carabidae) assemblages in thinned uneven-aged and clear-cut spruce stands

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Forestry has altered the boreal flora and fauna strongly during the 1900s. At present, logging methods other than clear-cutting are often applied but the ecological effects of these modifications are poorly studied. I collected carabid beetles in 8 uncut, 8 thinned (10%–30% of trees removed, with the aim of generating an uneven age structure) and 8 clear-cut, spruce-dominated stands, by using pitfall traps in central Finland during 1995–1998. The carabid species fell into three distinctive ecological groups in the multivariate analyses: forest, open-habitat and *Sphagnum* bog species. The forest species further formed a continuum from forest specialists to canopy-closure generalists. Logging affected the forest species slightly, while generalists and open-habitat species benefitted from clear-cutting. Thinning maintained the forest-floor carabid assemblage well. Site characteristics, such as the amount of trees and bottom and field-layer vegetation, were important determinants of carabid assemblages. Certain within-stand habitat types (e.g. spruce mires) were shown to be important for carabid diversity and should be managed with methods other than clear-cutting, in order to avoid extinctions of local populations. Increasing distance to the nearest source habitat had a negative effect on the abundance and distribution of carabids. Therefore, landscape-level forestry planning is also important for the maintenance of forest-species assemblages.

Introduction

The Fennoscandian boreal landscape consists mainly of managed forests of different successional stages (Hansson 1992). Over 90% of Finnish forests are managed (Sevola 1999) and usually cut at an age of 90–120 years (Kuusela 1990). Old-growth forests (for definition, *see* Aksenov *et al.* 1999) on the other hand, are extremely scarce in the southern parts of Fennoscandia; protected forests cover 1% of the forested area in southern Finland and only 5% of this represents old-growth forests (Virkkala *et al.* 2000). This is a consequence of the fragmentation process that has lasted several hundreds of years, but the most drastic effects of forestry on forest biota have taken place only during the last 50 years (Niemelä 1999). Fragmentation has strong effects on forest species; for example, in an experimentally fragmented tropical rain forest in Amazonia, Didham *et al.* (1998) showed that the abundances of 15 out of 32 abundant beetle species were significantly affected by forest fragmentation. Also extinctions occur (e.g. Saunders *et al.* 1991, Harrison & Bruna 1999) and over one-third of the Finnish red-listed species are threatened because of forestry (Rassi *et al.* 2000). The inadequacy of southern Finnish old-growth forests for the maintenance of old-growth forest specialists (e.g. Heliövaara & Väisänen 1984, Heikkinen *et al.* 2000) has led to demands to increase the amount of protected forests, restore mature managed forests and improve the quality of the surrounding managed landscape matrix (Niemelä 1997, 1999, Nilsson 1997). The latter two are thought to be best achievable by including natural processes and structural and compositional elements into the managed stands (Fries *et al.* 1997).

The long-term persistence of many forest species is dependent on populations which live in managed forests (Lindenmeyer & Franklin 1997). However, managed forests host less threatened forest-specialist species than old-growth forests do (e.g. Esseen *et al.* 1997) and also many commoner species occur there in low abundances. Examples are e.g. epiphytic lichens (Kuusinen 1994, 1996, Dettki & Esseen 1998), bryophytes (Andersson & Hytteborn 1991), beetles living in dead wood (Väisänen *et al.* 1993, Siitonen & Martikainen 1994) and Mycetophilidae insects (Økland 1994). Therefore, for the purposes of ecological studies, species with intermediate commonness and relatively strict microhabitat requirements may be useful indicators of environmental change. Such species can potentially be found among carabid beetles (Coleoptera, Carabidae). Boreal carabids can be roughly divided into open-habitat, (habitat-type) generalist and forest species (e.g. Lindroth 1985, 1986, Kinnunen 1999). Bortmann (1996) divided German beech-forest species further into forest-centre, forest-margin and clear-cut species. Niemelä *et al.* (1988, 1993a) made a similar division for boreal coniferous-forest assemblages, except that there were habitat generalists instead of margin species.

Most forest species require certain elements of forests rather than "average forest" (Niemelä *et al.* 1996). Forest-floor environmental factors create a heterogeneous mosaic of microsites and the resulting site characteristics may appear different for different species. Consequently, some species with strict microhabitat demands occur in metapopulations (Hanski 1999), whereas for some other species with wider tolerance, the environment may be divided into source and sink habitats (Pulliam 1988) and some may be able to utilize several habitat types. Carabids are distributed non-randomly among stands of different quality and also within the stands (Niemelä *et al.* 1992a). Factors such as moisture, temperature, food abundance and occurrence of red wood ants (*Formica rufa* group), affect the distributions and abundances of carabids and other invertebrates (Thiele 1977, Niemelä *et al.* 1986, 1990, 1992, Koivula *et al.* 1999, Laakso & Setälä 2000). Increased vegetational richness (Siemann *et al.* 1998) and herb-layer cover (Bortmann 1996) also affect invertebrate diversity. Logging affects the boreal carabids, for example, through changes in the above factors. They are often more numerous and form richer assemblages in open habitats than in forests (e.g. Niemelä & Halme 1992, Beaudry *et al.* 1997, Kinnunen 1999) though some species may suffer from clear-cutting (e.g. Langor *et al.* 1994, Spence *et al.* 1996). In Finland, regeneration clear-cutting makes up 40%–50% of the forest area of all annual logging, while thinning is almost equally commonly used with only a slight increase between 1970 and 1998 (Västilä & Herrala-Ylinen 1999). Although the ecological effects of clear-cutting are well documented (e.g. Huhta 1976, Niemelä *et al.* 1993a, 1993b, Pettersson 1996, Davies & Margules 1998, Abildsnes & Tømmerås 2000), the effects of other harvesting methods are much less studied. Studies concerning thinning have mostly focused on its effects on tree growth and studies concerning the importance of uneven age structure of trees for invertebrates are lacking.

In the present paper, I focus on four questions concerning carabid beetles in managed stands. (1) Is the species division into open-habitat, generalist and forest species relevant in forest ecology? (2) How much site variation is there in the study stands, and do the carabid catches reflect the microhabitat characteristics and logging? (3) Do the studied logging methods affect the carabid catches? (4) Does the quality of adjacent habitat matrix explain the abundance patterns of carabids? These questions are investigated using pitfall trappings over a short time scale, i.e. two years after logging. Species responses to habitat variability and natural and anthropogenic processes may be determined by different factors acting at different spatial levels (Addicott *et al*. 1987, Wiens 1989). It is therefore important to study the effects of forestry at several spatial scales (Haila & Kouki 1994, Niemelä 1999). Thus, logging is examined at within stand (site) and landscape (between study stands within an area) levels in this paper. In Finland, there are no red-listed (threatened) forest carabids (Rassi *et al*. 2000), but in this paper carabids are used as tools, rather than examples of endangered species, to study the effects of logging.

Material and methods

Study areas and sampling design

The study was performed in central Finland, on the border between the southern and middle boreal zones (Ahti *et al*. 1968), in eight separate areas. The areas were located within 100 × 300 km area (the latter being the east-west direction) in the municipalities of Heinävesi, Kerimäki, Keuruu, Kuorevesi, Längelmäki, Orivesi and Savonranta. The study forests represented 90–120 year-old Norway spruce (*Picea abies*) dominated, *Myrtillus*-type forests (Cajander 1949). The stands were previously managed but left intact (no thinning or other management activities) for at least 10 years before the experiment. Prior to logging, the herb layer was dominated by *Vaccinium vitis-idaea* and *V. myrtillus* dwarf shrubs, and *Dicranum*, *Pleurozium* and *Hylocomium* mosses covered most of the bottom layer. The surroundings of the study stands varied from recently cut stands to mature (90–150 year-old) spruce forests. The treated area within each study stand was a one-hectare square and its immediate surroundings. The distance to the nearest study stand (with different treatment) within a given area varied between 50 and 1500 m. Within the study areas, a road and/or different stand type (dissimilar in forest type, age and species distribution of dominant trees) always separated the study stands. Thus for carabids they were independent from each other and one treatment was randomly assigned to each stand. The randomisation was done simultaneously with the establishment of the study areas in spring 1995, before the experiment was started.

The study design follows a Before/After with Control/Impact design (BACI, Underwood 1991). I thus had data from both before and after the logging and control (not cut) and impact (clear-cut and thinned) stands. The study began in 1995 (pre-treatment study year) and the stands to be cut were felled the following winter (1995–1996). In each study area, there was a control stand, a clear-cut stand, and a stand where trees were cut with the aim of developing an uneven age structure of trees (hereafter referred to as thinned stands). In the latter, 10.9%–33.7% of the trees were cut and accordingly, 433–1050 trees per hectare were retained. The land-owning companies Metsähallitus, Metsäliitto, StoraEnso and Yhtyneet Paperitehtaat performed logging. The follow-up study was performed in 1997 and 1998.

The beetles were collected with pitfall traps (depth 68 mm, mouth diameter 66 mm). To ensure that the trapping sites would remain exactly the same before and after logging, I used 20-cm steel nails with a coloured plastic band to mark the trapping sites. In each stand, the traps were placed in six groups, each group with four pitfall traps in a 4 × 4-m square (one trap in each corner). The groups formed two rows, from which the distance to the nearest trap group was 25 m and 30 m to the adjacent row. The distance from every trap group to the nearest forest edge was at least 30 m. I had a total of 8 study areas × 3 treatments × 24 traps = 576 traps. The traps were partly filled with 30% propylene glycol and detergent and covered with 10 × 10-cm plexiglas roofs to protect them from litter and rain.

Each year the trappings covered the whole growing season (from late May to early September) and the traps were emptied once a month. This duration between visits is appropriate, since the cold climate and strong concentration of propylene glycol preserved the samples well. Additionally, catches of red wood ants were usually small and small mammals were only exceptionally caught, which could have filled the traps or further attracted carrion beetles and shrews into them.

I also gathered vegetational data (Appendix) and physiognomic (*sensu* Dunning *et al.* 1992) measurements from the stands. The former were inventoried in order to examine whether the treatments were similar before logging and whether the site characteristics explained the observed abundance patterns of carabids during the study years. The vegetation of the immediate surroundings of the four-trap groups was inventoried each year (1995, 1997 and 1998). The data consisted of percentage coverages (scale 0%–100%) of common plant species or plant-species groups within a 2-m radius and the amount of trees (height over 5 metres) within a 10-m radius, estimated from the centre of a trap group. The physiognomic measurements consisted of metric distances from the clear-cut stands to the nearest open habitat (forest road, clear-cut or sapling stand younger than 20 years) and to the nearest over 50 year-old spruce-dominated stand.

The analyses

The beetles were divided into three ecological groups (for the species, *see* Table 1) according to their considered canopy-closure preference (Lindroth 1985, 1986, Niemelä & Halme 1992, Niemelä *et al.* 1992, Koivula *et al.* 2001, and M. Koivula unpubl.). Species associated with a closed canopy are hereafter referred to as forest species, the other groups being generalists and open-habitat species in relation to canopy closure. The carabid data were transformed to individuals caught per 100 trapping days and log $(X + 1)$ transformed to improve the normalities of the distributions before the analyses.

First I studied whether the randomisation of the three treatments succeeded, or did the pre-treatment (1995) floristic and faunistic variation explain the possible differences among the treatments. This was done with Discriminant analysis, by using SYSTAT 8.0 software (SPSS Inc. 1998). The analysis provides linear functions of the variables that best separate the samples into predefined groups (the treatments). Jackknife technique, with Wilks' lambda and F-statistic, was applied to test the equality of the group centroids. The carabid, wood-ant and vegetational data from 1995 were included into the analysis, with the proviso that at least three stands had to have been occupied for a given species to become included into the analysis. I also performed a PCA (e.g. Jongman *et al.* 1995) for the same dataset, to study which variables explained the observed pre-treatment patterns best.

In order to study whether or not the overall catches among the three treatments differed significantly from each other, ANOVAs were performed. These analyses were applied for the total carabid catch, for those species caught in at least 75% of the stands and for forest, open-habitat and generalist species groups. For the purposes of the ANOVA, the within-stand catches were pooled because of the many zero catches in the dataset. The eight study areas formed blocks of three treatments. The catches of 1995 (before the cuttings) were used as covariates, except for the poor total catch of the open-habitat species group. An ANOVA with repeated measures was then performed. If the ANOVA indicated a difference between the catches of the compared treatments, a Tukey's post-hoc test was performed to localize the difference.

In order to study whether the carabid catches from the clear-cuts in 1997 and 1998 were dependent on the distance to the nearest

Table 1. The red wood ant (*Formica rufa* –group) and carabid-beetle catches during the study years. Carabid nomenclature follows Lindroth (1985, 1986). The HAB column refers to the species' habitat preferences (F = forest, G = generalist and O = open-habitat species). CONTR = control stands, THINN = stands with uneven age structure of trees (thinned) and CLEAR = clear-cut stands.

Group/Species	HAB	1995			1997			1998			
		(CONTR)	(THINN)	(CLEAR)	CONTR	THINN	CLEAR	CONTR	THINN	CLEAR	TOTAL
Formica rufa group		163615	227676	151094	92287	337468	129038	155715	292214	76640	1625747
Carabid beetles, total		1090	1241	1071	1558	1824	2500	1249	1624	1532	13689
Forest species		603	840	745	1050	1393	1109	843	934	313	7830
Generalist species		487	401	326	499	424	1195	405	687	814	5238
Open-habitat species		0	0	0	9	7	196	1	3	405	621
Calathus micropterus (Dft.)	F	435	647	640	834	1224	1045	702	743	272	6542
Pterostichus oblongopunctatus (F.)	G	441	313	204	294	256	773	361	521	531	3694
Carabus glabratus Payk.	F	70	44	52	70	46	23	53	70	20	448
Trechus secalis (Payk.)	G	17	8	84	45	27	119	10	34	88	432
Agonum fuliginosum (Pz.)	G	4	7	12	92	67	160	4	21	54	421
Pterostichus niger (Schaller)	G	23	54	20	43	35	57	20	83	61	396
Carabus hortensis L.	F	42	70	13	64	54	4	28	18	–	293
Notiophilus biguttatus (F.)	F	20	18	13	31	36	21	22	23	9	193
Amara brunnea (Gyll.)	F	10	47	8	14	22	3	19	62	4	189
Agonum sexpunctatum (L.)	O	–	–	–	3	–	96	–	–	74	173
Amara lunicollis (Schiødte)	O	–	–	–	1	–	12	–	2	149	164
Cychrus caraboides (L.)	F	26	13	18	30	5	8	19	13	7	139
Harpalus quadripunctatus Dej.	G	1	7	1	9	17	29	6	15	30	115
Pterostichus adstrictus (Eschtz.)	O	–	–	–	–	2	32	–	–	40	74
Patrobus assimilis Chaudoir	G	–	10	4	9	18	15	2	8	6	72
Cicindela campestris L.	O	–	–	–	2	–	1	–	–	52	55
Trichocellus placidus (Gyll.)	O	–	–	–	–	–	2	–	–	49	51
Pterostichus strenuus (Pz.)	G	–	–	–	4	2	13	–	4	16	39
Pterostichus cupreus (L.)	O	–	–	–	–	–	15	–	–	14	29
Pterostichus versicolor (Sturm)	O	–	–	–	–	1	11	–	–	12	24

Continued

Table 1. Continued.

Group/Species	HAB	1995			1997			1998			
		(CONTR)	(THINN)	(CLEAR)	CONTR	THINN	CLEAR	CONTR	THINN	CLEAR	TOTAL
Agonum mannerheimii (Dej.)	F	–	–	–	6	5	5	–	5	1	22
Pterostichus nigrita (Payk.)	G	–	–	–	–	–	11	–	–	10	21
Pterostichus diligens (Sturm)	G	–	–	1	1	–	6	–	–	12	20
Carabus cancellatus Ill.	O	–	–	–	2	–	12	–	–	1	15
Leistus terminatus (Hellw. *in* Pz.)	G	1	2	–	2	–	5	2	–	3	15
Bembidion lampros (Herbst)	O	–	–	–	–	–	4	–	–	7	11
Trechus rubens (F.)	G	–	–	–	–	2	3	–	1	1	7
Bembidion properans (Stephens)	O	–	–	–	–	1	3	–	–	1	5
Carabus nitens L.	O	–	–	–	1	–	3	–	–	1	5
Bembidion quadrimaculatum (L.)	O	–	–	–	–	–	3	–	–	–	3
Notiophilus germinyi Fauvel	O	–	–	–	–	3	–	–	–	–	3
Notiophilus palustris (Duft.)	O	–	–	–	–	–	1	1	–	1	3
Loricera pilicornis (F.)	G	–	–	–	–	–	2	–	–	–	2
Pterostichus melanarius (Ill.)	G	–	–	–	–	–	–	–	–	2	2
Trechus rivularis (Gyll.)	F	–	1	–	–	1	–	–	–	–	2
Amara communis (Pz.)	O	–	–	–	–	–	–	–	–	1	1
Amara eurynota (Pz.)	O	–	–	–	–	–	–	–	–	1	1
Anisodactylus binotatus (F.)	O	–	–	–	–	–	–	–	–	1	1
Bembidion bruxellense Wesm.	O	–	–	–	–	–	1	–	–	–	1
Dromius agilis (F.)	F	–	–	–	1	–	–	–	–	–	1
Leistus ferrugineus (L.)	O	–	–	–	–	–	–	–	–	1	1
Notiophilus aquaticus (L.)	O	–	–	–	–	–	–	–	1	–	1
Notiophilus reitteri Spaeth	F	–	–	1	–	–	–	–	–	–	1
Pterostichus vernalis (Pz.)	G	–	–	–	–	–	1	–	–	–	1
Synuchus vivalis (Ill.)	G	–	–	–	–	–	1	–	–	–	1

mature (over 90 year-old) stand or to the nearest open habitat, I applied analysis of covariance (ANCOVA) with repeated measures, where the catch from 1995 and the distance were covariates. Additionally, I studied whether the amount of trees (density; trees per hectare) in the control and thinned stands from 1995, 1997 and 1998 had a relationship with carabid-group catches. I analysed the dataset using ANCOVA with repeated measures, areas formed eight blocks with two nested treatments and the amount of trees was a covariate.

Multivariate analyses (Jongman *et al.* 1995) were used to search for ecological and physical gradients in the carabid dataset and similarities between the sites (trap groups). Species with similar habitat preference and sites with similar species assemblages in the dataset, aggregate close to each other in the correspondence analyses. The analyses were performed at the trap-group level, with CANOCO 4.0 software (ter Braak & Šmilauer 1998a). I calculated percentage proportions of individuals caught per trap group ($n_{\text{trap group}}/n_{\text{total}} \times 100$) for each species, and used these values to rule out the potential dominance of a few very abundant species in the analyses below. I first studied whether or not the assemblages of different treatments differed from each other after logging. This question was examined by performing a BACI-CA with the total beetle data. Area (the eight study areas) and Stand (blocks; the 24 study stands) were used as covariates in order to eliminate their effects in the analysis. Furthermore, I performed a BACI-CCA (Jongman *et al.* 1995, ter Braak & Šmilauer 1998b) in order to study the significance of environmental variables in explaining the observed carabid patterns. The covariates were the same as those used in the BACI-CA. Twenty-six environmental variables (Appendix) were included in the analysis. The statistical significances of these variables were examined by Monte-Carlo randomisations (ter Braak & Šmilauer 1998b), by including variables one by one until the next variable to be added was not statistically significant. A total of 23 carabid species, whose total catches exceeded 19 individuals, were included in the BACI-CA and BACI-CCA analyses and the data were centered by species.

Results

Overall patterns in the dataset

Red wood ants dominated the catches with ca. 1.6 million individuals (Table 1). Carabids were represented by 13 689 individuals and 45 species and the catches of 13 species exceeded 100 individuals. The yearly catches varied between 3402 and 5882 individuals. The most numerous species were *Calathus micropterus* and *Pterostichus oblongopunctatus*, which constituted 47.8% and 27.0% of the total catch, respectively. Forest species, with 7830 individuals and 10 species, constituted 57.2% of the total beetle catch. The open-habitat species catch was 621 individuals and 20 species (4.5% of the total catch), whereas the habitat-generalist group was represented by 5238 individuals and 15 species (38.3% of the total catch) (Table 1). In 1995, the total catches of forest species and generalists were almost equal among the three treatments but open-habitat species were lacking (Table 1). However, the catches of open-habitat species and generalists increased greatly in the clear-cuts by 1997 (open-habitat species) and by 1998 (both groups). In contrast, the total catch of forest species decreased in the clear-cuts in 1998. Occasional open-habitat individuals were caught in the control stands during both 1997 and 1998.

In the pairwise Discriminant analyses using vegetation, carabid and wood-ant catches, the control and clear-cut, and thinned and clear-cut sites were similar in 1995 but the thinned stands differed from the control ones: the value of the Wilks-Lambda statistic was 0.54 and the related $F = 1.84$ and $p = 0.020$. In the jackknifed classification matrix, 60%–65% of these trapping sites could be classified into the treatments into which they were randomised. The PCA for vegetation, carabids and red wood ants indicated that the thinned stands had on average more *Sphagnum* mires, more sites rich in red wood ants and needle litter, and slightly less deciduous-tree admixture than the control and clear-cut sites (not shown). However, the basal areas of coniferous and deciduous trees were relatively similar among the treatments regarding median, mean, minimum and maximum values but the thinned stands contained on average a larger total volume of trees compared to the control and clear-cut stands, indicating that the dominant trees of the thinned stands were on average older than those of the other treatments. The above results indicate that any differences in abundance patterns between thinned and control or clear-cut stands may not solely be due to logging, but could also be due to the slightly different habitat quality among the treatments, although no treatment-specific clusters of sites were detected in the PCA for carabids only (not shown).

Table 2. The results of ANOVA with repeated measures. The analyses were performed at the species level for two forest species (*C. micropterus* and *N. biguttatus*) and one generalist (*P. oblongopunctatus*). The group-level analyses below were performed without the catches of these species. Time = the effect of study year (1997 and 1998), AREA = the eight study areas, TREAT = the three treatments tested, and COV95 refers to the data for 1995 before the treatments, which were used as a covariate in the ANOVA. The Tukey's post-hoc tests were performed for the pooled data 1997–1998 and without the covariate data. Statistically not significant differences but with $p < 0.07$ are given in parentheses. The test indicates which treatment types (control, thinned, or clear-cut) differed from the others. For example, "Clear > Contr, Thinn" indicates that clear-cuts housed larger catches than control or thinned stands (which were similar).

Species/Group	Factor	MS	df	SS	*F*	*p*	Post-hoc test
Carabids, total	Time	0.21	1	0.21	5.95	0.030	
	Time × TREAT	0.13	2	0.07	1.86	0.194	
	Time × AREA	1.10	7	0.16	4.47	0.010	
	Time × COV95	0.13	1	0.13	3.72	0.076	
	Error	0.46	13	0.04			
C. micropterus	Time	0.12	1	0.12	4.22	0.061	
	Time × TREAT	0.01	2	0.00	0.12	0.892	
	Time × AREA	0.96	7	0.14	4.92	0.007	
	Time × COV95	0.03	1	0.03	1.15	0.303	
	Error	0.36	13	0.03			
P. oblongopunctatus	Time	0.35	1	0.35	3.19	0.097	
	Time × TREAT	0.06	2	0.03	0.26	0.777	
	Time × AREA	1.12	7	0.16	1.46	0.263	
	Time × COV95	0.27	1	0.27	2.46	0.141	
	Error	1.43	13	0.11			
N. biguttatus	Time	0.02	1	0.02	0.30	0.595	
	Time × TREAT	0.02	2	0.01	0.20	0.824	
	Time × AREA	1.00	7	0.14	2.70	0.058	
	Time × COV95	0.00	1	0.00	0.08	0.783	
	Error	0.69	13	0.05			
Other generalists	Time	0.05	1	0.05	0.85	0.373	
	Time × TREAT	0.40	2	0.20	3.55	0.059	(Clear > Contr, Thinn)
	Time × AREA	1.05	7	0.15	2.64	0.062	
	Time × COV95	0.00	1	0.00	0.00	0.973	
	Error	0.73	13	0.06			
Other forest spp.	Time	0.19	1	0.19	2.69	0.125	
	Time × TREAT	0.11	2	0.05	0.75	0.491	
	Time × AREA	0.55	7	0.08	1.09	0.423	
	Time × COV95	0.13	1	0.13	1.86	0.196	
	Error	0.93	13	0.07			
Open-habitat spp.	Time	0.06	1	0.06	1.50	0.240	
	Time × TREAT	0.96	2	0.48	11.88	0.001	Clear > Contr, Thinn
	Time × AREA	0.79	7	0.11	2.80	0.048	
	Error	0.57	14	0.04			

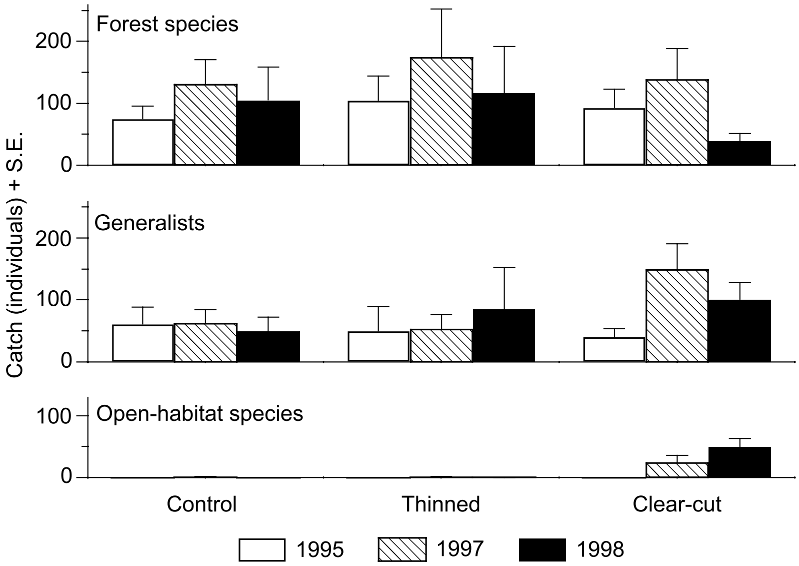

Fig. 1. The average catches of the three carabid groups in the control, thinned and clear-cut stands 1995, 1997 and 1998. For the statistical significances, *see* Table 1.

The catches of different species groups according to treatment

The open-habitat species catch indicated a highly significant preference for clear-cut sites and generalists showed the same preference, albeit statistically non-significantly (Table 2 and Fig. 1). Neither forest-species group nor any of the species that were analysed showed a treatment effect. The dominant species were always *C. micropterus* and *P. oblongopunctatus* (Table 1), regardless of the treatment or study year, comprising 52.5%–85.1% of the catch. After logging, *Agonum sexpunctatum* and *Amara lunicollis* were abundant in the clear-cuts, comprising 4.3% and 14.5% of the total catch in 1997 and 1998, respectively.

Effects of tree removal and site characteristics

The CA (Fig. 2) indicated clear effects of tree removal and remarkable site-to-site variation. The first two CA axes explained 13.0% and 10.5% of the variation in the carabid dataset. The most pronounced pattern in the analysis was that the clear-cut stand scores "moved" strongly toward the right (Fig. 2A–C). There was relatively much variation among the stand positions, reflecting year-to-year asynchronous variation of species' relative abundances and the effects of clear-cutting. The biplot scores of the species (Fig. 2D) formed three rather distinctive habitat-association groups of species, namely forest species and open-habitat species and a third cluster formed by *Agonum mannerheimii*, *Patrobus assimilis* and *Agonum fuliginosum*. The forest species formed an additional gradient from forest specialists (at the extreme left: *C. hortensis*, *C. caraboides* and *A. brunnea*) to canopy-closure generalists (e.g. *P. oblongopunctatus*, *P. niger*, *H. quadripunctatus* and *T. secalis*).

In the CCA which was performed to study the relationship between carabids and environmental variables (Fig. 3), indications of effects of logging and site variation on carabid abundances were detected. The sum of all eigenvalues (total inertia) was 4.32. The eigenvalues of the first two axes were 0.37 and 0.15, explaining 45.6% and 18.2% of the species-environment relationship, respectively, and a total of 12% of the variation in the carabid dataset. The annual variation and the covariates (Area and Stand) explained 13% and 15% of the variance in the carabid dataset, respectively. Seven out of 26 environmental variables explained the carabid

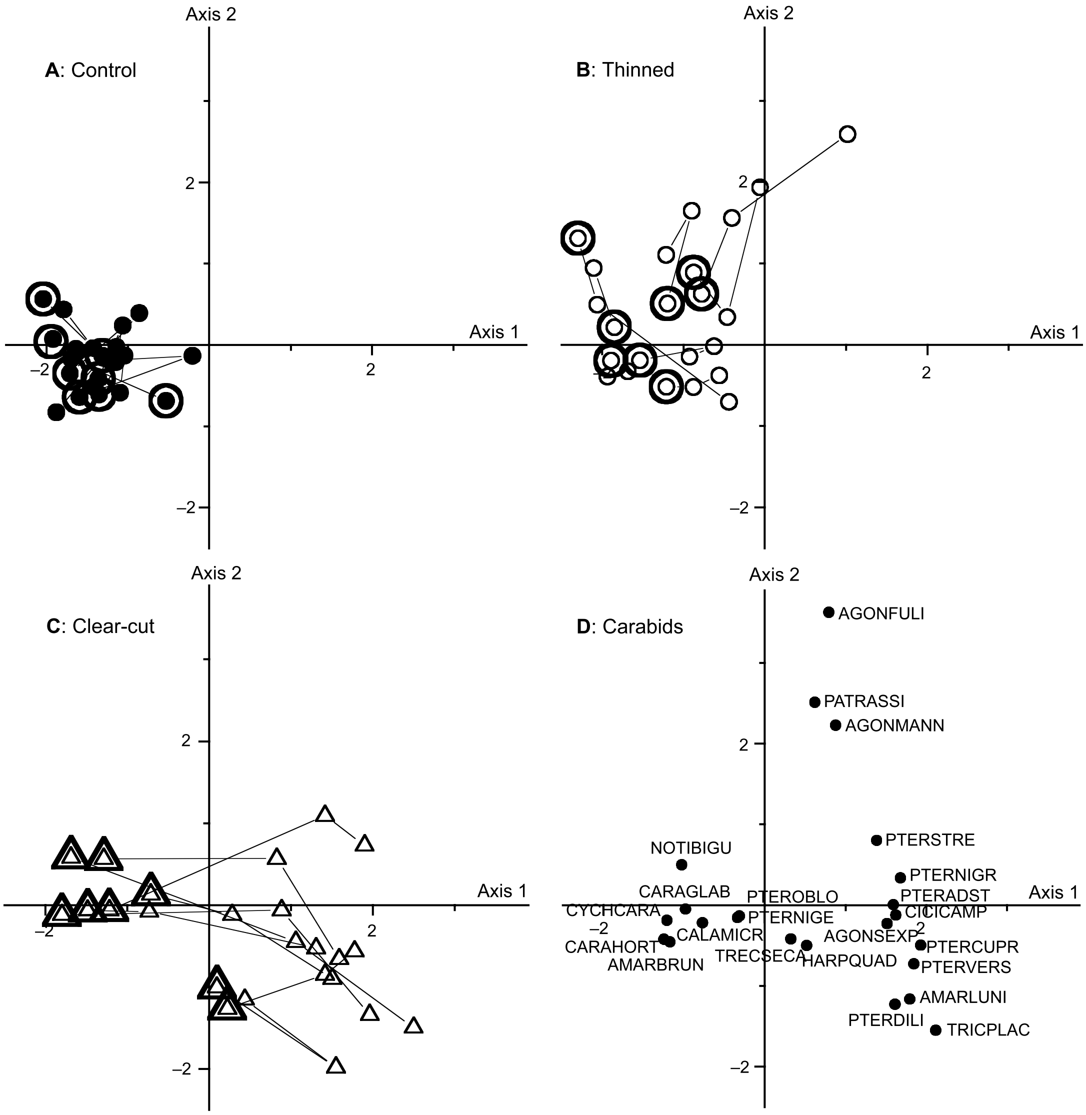

Fig. 2. CA biplot scores (**A**–**C**) for the sites with treatments separated (only stand averages presented), and (**D**) for the species during the study years. The axes show SD units. In panels **A**–**C**, only the average site scores of the stands are performed in order to simplify the figures and the scores of 1995 are presented with larger symbols, with the yearly scores of the same stands connected with a line.

abundances significantly (Fig. 3). The variance inflation factor (VIF) values were all between 1.11 and 2.56, thus indicating that the variables in question correlated only weakly (if at all) with the others. Surprisingly, the abundance of red wood ants was not a significant variable, explaining only 3% of the variation of the species-environment relationship (VIF = 1.11). The most important variable alone, the amount of spruce trees, explained 33% of the species-environment relationship ($F = 30.47$, $p = 0.005$, VIF = 2.56), the gradient mostly indicating effects of the amount of trees on carabid catches. The optima of some forest species, e.g. *C. glabratus*, *C. hortensis*, *C. caraboides*, *C. micropterus*, *N. biguttatus* and *A. brunnea*, were in the same direction with spruce. Forest mosses explained 3% ($F = 3.40$, $p = 0.010$, VIF = 2.37) and their optima were close to that of spruce. The second important variable was *Sphagnum* ($F = 12.35$, $p = 0.005$, VIF = 1.23), which alone explained 13% of the variation and by and large the abundances of *A. mannerheimii*, *P. assimilis* and *A. fuliginosum*. All the open-habitat species were on the left side of the scatter. The optima of *Epilobium angustifolium*, grasses, *Rubus idaeus* and bare soil were in the same direction as those of open-habitat species, explaining a total of 19% of the species-environment relationship, their F- and p-values being 5.59 and 0.010, 5.18 and 0.005, 3.93 and 0.025, and 4.19 and 0.010, respectively, and VIF values between 1.31 and 1.70. Finally, between the forest and open-habitat species, there were four species — *T. secalis*, *H. quadripunctatus*, *P. oblongopunctatus* and *P. niger* — that can probably be considered canopy-closure generalists.

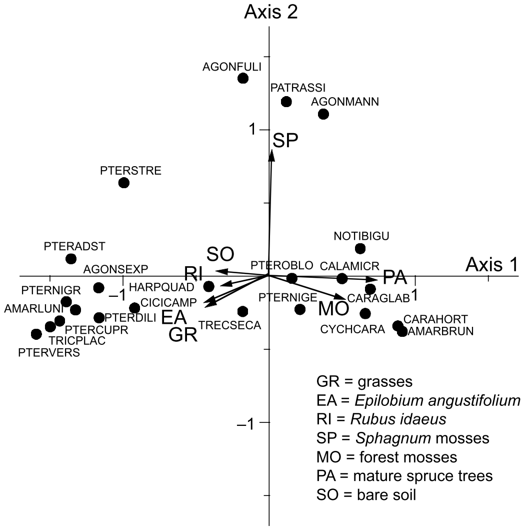

Fig. 3. CCA biplot for the carabid dataset and 7 most important environmental variables ($p < 0.05$). The optima on the variables are in the points of the arrows.

The importance of stand physiognomy

In the clear-cuts, the distance to the nearest mature stand varied between 45 and 60 m. Fig. 4 shows adjusted catches of forest-species and generalist groups along a mature-forest and an open-habitat gradient. The adjusted values for these species-group catches were calculated by equations n_{1997}/n_{1995} (for 1997) and n_{1998}/n_{1995} (for 1998) in order to rule out the variation among the before-treatment (1995) catches in the stands. The abundance of forest-species individuals seemed to increase with decreasing distance to the adjacent mature stand (Table 3A and Fig. 4A). The catches of generalist and open-habitat species showed no trend relative to the nearest mature stand. However, the distance to the nearest open habitat varied much more, between 50 and 245 m, and explained statistically significantly the abundance of generalists in the clear-cuts (Table 3B), though neither forest nor open-habitat species catches indicated a dependence on this gradient. The adjusted values for the generalist catches were plotted. Roughly, the catches were the larger the closer the adjacent open habitat was (Fig. 4B).

Increasing density of trees (tree individuals per hectare) was associated with a decrease in the abundance of generalists in the control and thinned stands (Table 3C and Fig. 5). Forest- and open-habitat species catches indicated no associations along this gradient, though the latter were scarce: zero in 1995, and a total of 20 in 1997–1998, when four control and five thinned stands were occupied.

Discussion

The main results of this short-term study can be summarised as follows:

1. Carabid species fell into three rather distinctive groups, supporting earlier studies concerning forest carabids. Some species were almost exclusively caught from open sites, while others formed a gradient from strict forest species to generalists, in relation to stand closeness. The third group consisted of three species occurring almost exclusively in spruce mires.
2. Site characteristics were important determinants of carabid assemblages. Carabid catches reflected vegetational variation, tree density and logging well.
3. Clear-cutting affected the forest species only

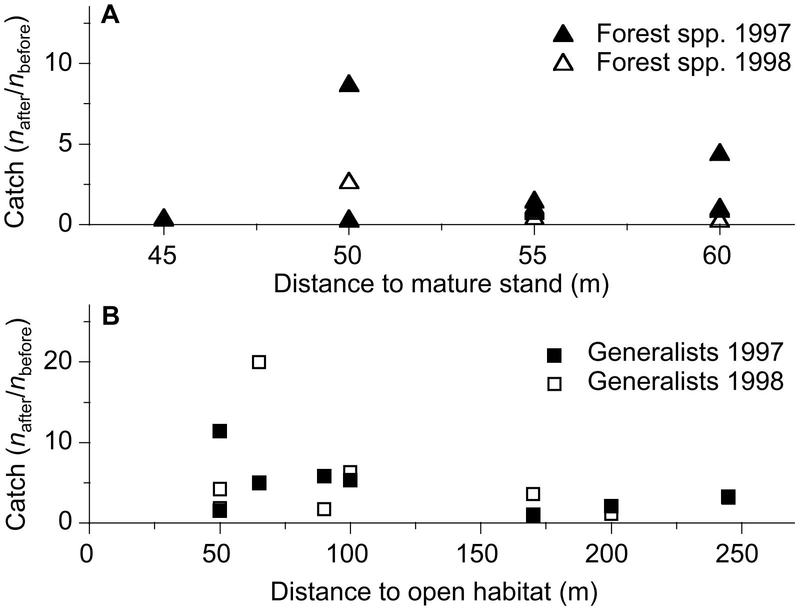

Fig. 4. The adjusted catches of (**A**) the forest-species group and (**B**) the generalist group in the eight clear-cut stands.

slightly, and generalists and open-habitat species benefitted from them. Consequently, clear-cuts hosted different assemblages as compared to uncut and thinned stands. Thinning (uneven age-structure of trees) maintained the forest-species assemblage rather well but generalist catches indicated that the tree density was an important determinant of the assemblage structure.

4. The quality of adjacent stands (distance to the nearest potential source habitat) affected the abundance of carabids. These results are discussed below in the contexts of habitat association of the species, the studied treatments and forest management.

Species-ecological groups in the spruce forests

The carabid assemblages of boreal spruce forests consist of a few abundant species, the rest of the species being scarce (Niemelä 1993). My results support Niemelä's (1993) results, since the two most abundant species always formed more than half of the catch in every treatment, irrespective of the study year. The most common species alone made up 34.7%–67.1%, while the third common species never reached 10% in abundance. As in Niemelä's (1993) study, the clear-cuts hosted more species than the closed (control and thinned) stands, which contrasts to the results of Jennings *et al.* (1986) and Atlegrim *et al.* (1997). However, the diversity pattern cannot be analysed by using diversity indices or e.g. rarefaction-standardised species richnesses, since indices do not separate different species (Magurran 1988) and differences in their catchability. The efficiency of pitfall trapping is highly dependent on the species in question (Desender & Maelfait 1986). Nevertheless, open-habitat species occurred almost exclusively in the clear-cuts and also the overall species richness increased there from 14 in 1995 to 35 in 1997 and 34 in 1998. As shown earlier, clear-cuts host much more individuals and species than do forests (e.g. Niemelä *et al.* 1993a, Spence *et al.* 1996, Butterfield 1997). The low species richness of forest-dwelling carabids can be explained by the environmental harshness, to which only a few species are adapted.

I have shown from the multivariate analyses that carabids can be divided into forest species, those preferring open habitats and spruce-mire species. The forest species formed a gradient from forest specialists to canopy-closure generalists, as proposed in earlier studies (e.g. Niemelä *et al.* 1988, 1993a, Bortmann 1996). Open-habitat and forest-species assemblages are different, many of their representatives being seldom caught from the same sites, although the two dominant species seemed always to be *C. micropterus* and *P. oblongopunctatus*. However, Koivula *et al.* (2001) showed that the dominant species may change 5–10 years after logging. Lenski (1982) showed that clear-cutting may increase within-genus component of species diversity, leading to a decrease in the numerical dominance of one species over the others. The increase of open-habitat and generalist species, at the expense of some forest species, may also explain much of the assemblage-level alterations

Table 3. ANCOVA results for the species-group catches of (A) clear-cuts in relation to distance to nearest mature stand, (B) clear-cuts in relation to distance to nearest open habitat, and (C) control and thinned stands in relation to the amount of trees (tree individuals per hectare). DIST = distance to source habitat, TREES = trees retained in the stand (n ha^{-1}). For the other factor terms, *see* Table 2.

Measure/group	Factor	SS	df	MS	*F*	*p*
A: Catches in clear-cuts in relation to distance to mature-forest edge						
Forest spp.	Time	0.19	1	0.19	21.05	0.006
	Time × DIST	0.24	1	0.24	26.73	0.004
	Time × COV95	0.01	1	0.01	0.97	
	Error	0.04	5	0.01		
Generalists	Time	0.01	1	0.19	0.25	0.642
	Time × DIST	0.11	1	0.24	3.09	0.139
	Time × COV95	0.16	1	0.01	4.48	0.088
	Error	0.18	5	0.01		
Open-hab. spp.	Time	0.03	1	0.03	0.35	0.577
	Time × DIST	0.17	1	0.17	1.98	0.209
	Error	0.50	6	0.08		
B: Catches in clear-cuts in relation to distance to open habitat						
Forest spp.	Time	0.01	1	0.01	0.23	0.651
	Time × DIST	0.09	1	0.09	2.37	0.184
	Time × COV95	0.06	1	0.06	1.44	0.285
	Error	0.19	5	0.04		
Generalists	Time	0.21	1	0.21	16.01	0.010
	Time × DIST	0.22	1	0.22	17.09	0.009
	Time × COV95	0.54	1	0.54	41.70	0.001
	Error	0.06	5	0.01		
Open-hab. spp.	Time	0.29	1	0.29	2.61	0.157
	Time × DIST	0.00	1	0.00	0.00	0.964
	Error	0.67	6	0.11		
C: Catches in control and thinned stands in relation to tree amount						
Forest spp.	Time	0.09	1	0.09	6.37	0.045
	Time × AREA	0.77	7	0.11	7.56	0.013
	Time × TREAT	0.03	1	0.03	2.38	0.174
	Time × TREES	0.03	1	0.03	2.19	0.190
	Error	0.09	6	0.01		
Generalists	Time	0.47	1	0.47	13.64	0.010
	Time × AREA	1.07	7	0.15	4.42	0.045
	Time × TREAT	0.05	1	0.05	1.34	0.291
	Time × TREES	0.58	1	0.58	16.83	0.006
	Error	0.21	6	0.03		
Open-hab. spp.	Time	0.03	1	0.03	0.46	0.521
	Time × AREA	0.34	7	0.05	0.84	0.593
	Time × TREAT	0.04	1	0.04	0.61	0.463
	Time × TREES	0.01	1	0.01	0.21	0.665
	Error	0.35	6	0.06		

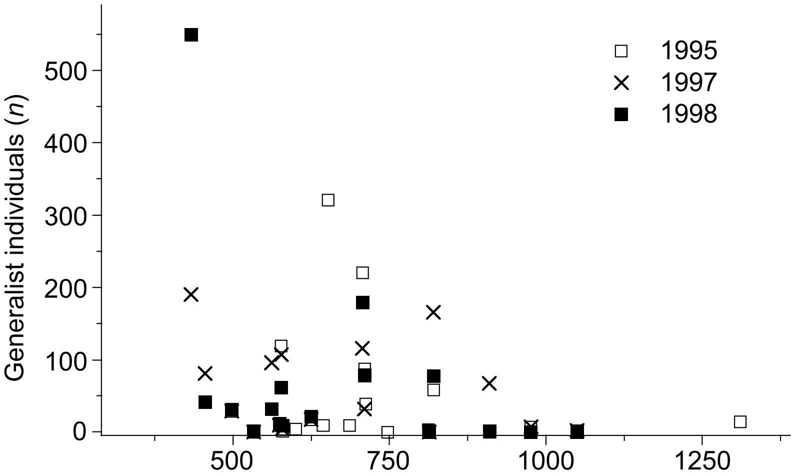

Fig. 5. The generalist group catches along the tree density gradient in the control and thinned stands 1995, 1997 and 1998.

(Spence *et al.* 1996, Butterfield 1997, Koivula *et al.* 2001). For example, in Canadian jack pine (*Pinus banksiana*) forests, *Amara* and *Harpalus* species were almost exclusively caught in clear-cut sites (Beaudry *et al.* 1997) and in this study *A. sexpunctatum* and *A. lunicollis* were among the five most abundant species in the clear-cuts.

Variation in habitat structure may explain assemblage-level differences between forest patches (Niemelä *et al.* 1988). Certain forest species are associated with spruce mires: *A. mannerheimii*, *A. fuliginosum* and *P. assimilis*. The latter two may not demand canopy cover, as indicated in earlier studies (Halme & Niemelä 1992, Kinnunen 1999, Koivula *et al.* 2001), but mires are more common in mature stands than in clear-cuts or in young plantations. Some species — *C. hortensis*, *C. caraboides* and *A. brunnea* — are associated with mesic within-stand sites, although they may be caught from a wider variety of forest sites than the mire species (Lindroth 1985, 1986, Niemelä *et al.* 1992). Furthermore, e.g. *C. micropterus*, *N. biguttatus* and *Leistus terminatus* probably have even wider tolerance to environmental conditions and are associated with sites with much litter (Niemelä *et al.* 1992, Koivula *et al.* 1999, 2001). Potentially the most sensitive species to habitat alteration are poor dispersers with strict microhabitat demands (den Boer 1990a, 1990b, de Vries & den Boer 1990), thus likely to be found from the mire-species group and possibly also from the species preferring mesic sites.

Carabids in thinned and clear-cut stands

Thinning affected carabids only slightly and lower tree density benefited the generalists. Rather similar results were reached by Atlegrim *et al.* (1997), who found no effects of thinning on carabid assemblages in Swedish spruce forests. It seems that the retained trees shelter the ground well, or the carabid assemblages may respond to the logging more slowly than the time scale of this study. However, thinning may decrease the abundance of beetles which are dependent on deciduous trees (Økland 1995). Since this may result from thinning practices which reduce 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, Koivula *et al.* 1999), along with other components that may help sensitive species to persist in the managed landscape (Lindenmeyer & Franklin 1997). Maintenance of heterogeneous stands is also important since, for example, many bird species (e.g. Capercaillie *Tetrao urogallus*) require different habitats at different phases of their life cycles (Law & Dickman 1998). Such stands also host more microhabitat types, thus enabling more carabid species to occur there, as is indicated by the present results. Apart from studies with other taxa, comparisons among sites with different densities of retained trees to detect threshold conditions for species' presence/absence patterns may be fruitful in further studies concerning thinning.

Some forest species were associated with uncut sites in the multivariate analyses, which probably indicates that they suffer from clear-cutting. The time scale, however, was probably too short to detect clear declines. For instance, Szyszko (1990) showed that forest-carabid abundances decreased strongly three years after clear-cutting in Polish pine forests. Some studied forest-dwelling carabids (e.g. *C. micropterus*, *C. hortensis* and *C. caraboides*) decreased in the clear-cuts (Butterfield 1997, Abildsnes & Tømmerås 2000, Koivula *et al.* 2001, and M. Koivula unpubl.) and some species can be completely missing from these sites (Langor *et al.* 1994, Spence *et al.* 1996) but the disappearance may take place after a time lag. In Canada, the effects of cuttings on carabid assemblages were modest during the first season after logging (Niemelä *et al.* 1993b) and the present results support this view. However, the similarity between two-year-old sites and nearby uncut stands was only 25% in the Canadian study, some mature-forest species had disappeared and no indications of many of these species' recovery was detected even 27 years after logging (Niemelä *et al.* 1993b). Niemelä *et al.* (1993a) and Langor *et al.* (1994) concluded that it takes longer than 25–30 years for the original assemblages to recover and Desender *et al.* (1999) showed that, if the soil is strongly altered, the recovery of some old-forest carabid populations may take hundreds of years.

Carabids in the managed landscape

The (re-)colonisation success of individuals, and population maintenance in patchy environments, depends on the species' dispersal abilities (Burkey 1989, den Boer 1990a, Taylor *et al.* 1993) and landscape structure (Dunning *et al.* 1992), and also on the degree of habitat preference. Dispersal of taxa can potentially be enhanced by the retention of tree cover for connectivity within managed landscapes (Lindenmeyer & Franklin 1997). In the clear-cuts, the forest-carabid abundance along the mature-forest distance gradient, although being very short, provided some evidence for edge effect reaching from the adjacent forest to the clear-cut, supporting similar results reached by Koivula *et al.* (2001). Shading effect of large trees reach the clear-cuts from the uncut forests, more effectively if the site is close to a mature stand. The shelter of adjacent stands may enable forest species to survive in small clear-cuts. If some of these species, such as *A. mannerheimii*, *C. hortensis* and *C. caraboides*, cannot live in the central parts of larger clear-cuts than the present ones, they may also not be able to recolonise the regenerating stands over a critical distance between suitable habitats (Riecken & Raths 1996). Even more pronounced effects of logging were detected in a forest-clearcut edge study with bark beetles in Finland (Peltonen *et al.* 1997). In that study, some species were scarce in or absent from the forest edges up to 30–50 m into the forest interior. In contrast, open-habitat species were commonly found even in the most isolated clear-cuts (over 200 m to the nearest open habitat) and generalists were significantly more abundant the closer the nearest open habitat was. Similarly, Kinnunen *et al.* (1996) observed that flightless open-habitat species had successfully colonised small and isolated field patches. These species may thus disperse from small subpopulations of naturally or anthropogenically created forest gaps or, perhaps more likely in the case of open-habitat species, disperse by flying (Kinnunen *et al.* 1996) or by foot along roadsides (Vermeulen 1995, and M. Koivula unpubl.).

Management implications

The importance of ecological forestry planning is not just to maintain old-growth forests but also to prevent the gradual decrease of the overall forest biodiversity at the within-stand, regional and national scales. A Swedish study showed that with forestry planning on an ecological basis, approximately 3%–10% of the harvesting potential is lost (Holgén & Lind 1994). Since the level of woody material removed yearly from the forests will probably remain constant in the near future, applying thinning and other “ecological” methods widely expands the total land area that has to be managed in order to achieve the same economical benefit as before.

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Appendix. Microenvironmental factors gathered from the adjacent surroundings of the trap groups. Quality: *n* = individuals counted, % = percentage cover estimated.

Factor	Area (radius, m)	Quality
Bottom layer		
Sphagnum mosses	2	%
Polytrichum mosses	2	%
Dicranum, *Pleurozium* etc. mosses	2	%
Needle litter	2	%
Leaf litter	2	%
Needle and leaf litter	2	%
Stumps	2	%
Logging residue	2	%
Visible sand layer	2	%
Aggregated humus and sand	2	%
Formica ant nests	2	%, *n*
Rocks and stones	2	%
Field layer		
Spruce, saplings	2	%
Birch, saplings	2	%
Pine, saplings	2	%
Rowan, saplings	2	%
Deciduous bushes	2	%
Juniperus communis	2	%
Poaceae (grasses)	2	%
Vaccinium dwarf shrubs	2	%
Equisetum spp.	2	%
Pteridium aquilinum	2	%
Dryopteridaceae and Polypodiaceae	2	%
Epilobium angustifolium	2	%
Rubus idaeus	2	%
Filipendula ulmaria	2	%
Oxalis acetocella	2	%
Trees h > 5.0 m		
Spruce	10	*n*
Pine	10	*n*
Birches	10	*n*
Aspen	10	*n*
Other spp.	10	*n*
Dead standing trees	10	*n*
Dead lying trees	2	%, *n*