

The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest

Jari Niemelä, Yrjö Haila, Eero Halme, Tapani Lahti, Timo Pajunen & Pekka Punttila

Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. 1988: The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. — *Ann. Zool. Fennici* 25:107–119.

Carabid beetles were sampled by using pitfall traps in 35 fragments of old coniferous taiga (area range 0.4–101 ha) and in managed forest in their immediate surroundings in southern Finland in 1984 and 1985. The pooled sample comprised 1986 individuals from 42 species. Species number, standardized by rarefaction, was greater in the forest surroundings than in the forest fragments, but the difference is due to great between-site variability in the surrounding areas. Marked differences in the composition of the carabid samples between the fragment interiors and their surroundings were mainly caused by species that are scarce or occasional in coniferous forests. Nine abundant forest generalists comprised about 90% of the pooled sample, and they were widely (although not uniformly) distributed over successional stages of forest. In order to detect possible area effects the pooled data sets of fragments larger than 30 ha and smaller than 5 ha were compared. No differences were detected in the species assemblage characteristics, and of the nine most abundant species seven were more abundant in the small fragments than in the large ones, and two species were equally abundant in the two fragment size classes. We discuss the significance of the results concerning the preservation of faunal diversity in coniferous taiga, using carabids as an example, and we support the maximization of habitat heterogeneity on the regional scale as an appropriate conservation strategy.

*J. Niemelä, Y. Haila, E. Halme, T. Pajunen & P. Punttila, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.
T. Lahti, Botanical Museum, University of Helsinki, Unioninkatu 44, SF-00170 Helsinki, Finland.*

1. Introduction

The proportion of forests older than 140 years is about 1% of the forest land in southern Finland (Yearbook of forest statistics 1984). The substitution of clear-cuts and managed forests for primeval taiga has presumably already caused changes in the composition of forest faunas. The changes are well documented for birds (e.g. Järvinen & Väisänen 1977, 1978), but data on other taxa, such as invertebrates are scarce (Huhta et al. 1986). Heliövaara & Väisänen (1984) suggested that specialized species of the decomposition system associated with decaying logs, and species with narrow microclimatic requirements, would be the most likely to have decreased in Finland. In Britain the decline in specialized species of this kind has already been recorded (Peterken 1985).

It is difficult to assess the realism of such estimates for northern European taiga, however. For instance, the microhabitat requirements of most taiga invertebrates are poorly known, and reliable evidence of faunal change is weak, due to the scarcity of adequate reference studies. Biström (1978, Coleoptera and Heteroptera) and Palmgren (1977, spiders) took quantitative samples from an undisturbed coniferous forest fragment of 40 hectares in southern Finland (about 61°N, 26°E), but took no quantitative samples in the surrounding managed forest (see also Palmgren & Biström 1979). From southern Finnish coniferous forests Huhta et al. (1967) give quantitative data on some invertebrate groups, but not specifically on carabids (for a summary of their studies see Huhta et al. 1986). Overall, the available data on the invertebrate faunas of primeval coniferous taiga are mainly

qualitative (e.g. Palm 1931, 1938, 1942, 1946, Kangas 1935, 1947, Forslund 1943), and comprise lists of species that are regarded as endangered because of the loss of primeval habitats (Mikkola 1979, Väisänen 1982).

To gain a realistic picture of long-term faunal changes in coniferous taiga old quantitative data sets are needed for comparison. For invertebrates, such data are lacking. Consequently, we have to base our conclusions on surveys conducted by either (1) monitoring changes in local faunas in forests that are undergoing changes, or (2) comparing the composition of present communities in primeval forests and their managed surroundings.

This study is part of a larger research project with the aim of studying the effect of modern forestry on the fauna and flora of the taiga. In addition to carabids, several other animal groups (ants, spiders, molluscs, birds) have been studied in the project (for birds see Haila et al. 1987). Carabids were chosen as one of the study groups because: (1) they can be quantitatively collected by pitfall-trapping, (2) they are usually regarded as typically occurring in open environments, but little quantitative information is available from coniferous taiga to support this assumption in our northern latitudes, and (3) the group is taxonomically well known.

In this paper, we summarize the results of a quantitative survey of carabid beetles (Coleoptera: Carabidae) in old coniferous forests and their human-modified surroundings in southern Finland. As continuous primeval forests have vanished from southern Finland, we collected our old forest samples from a series of forest fragments with an area range of 0.4 to 101 ha. This sampling design facilitates a comparison between small and large fragments. The study is focused on three problems: (1) How different are carabid communities in the fragments, compared with their surroundings?; (2) How different are the carabid assemblages in different sized forest fragments (i.e., is there a detectable area effect?); and (3) Can we identify carabid species that are endangered because of fragmentation of the southern Finnish coniferous taiga?

2. Material and methods

2.1. Study area

Our study area is situated in southern Finland, about 62°N, 24°E. The study area comprises three sampling areas — the

Seitseminen National Park (19 fragments of old forest), Hyytiälä region (14 fragments), and Helvetinjärvi National Park (2 fragments). The distances between the sampling areas range from about 25 to 80 km. Phytogeographically, Seitseminen is situated on the border between the middle boreal and southern boreal zone, and Hyytiälä and Helvetinjärvi belong to the southern boreal zone (Kalliola 1979). According to the classification widely used in the Soviet Union, our study area belongs to the middle and northern taiga (Ahti et al. 1968). The proportion of old forest (>140 years) is about 0.5% and the proportion of young forest (<60 years) is about 50% of the forest land in the study area, and forest land covers 70% of the total land area (Yearbook of forest statistics 1984). The dominating tree species in the forests are pine (50% of forest land) and spruce (40% of forest land). During the year of 1983, 2.5% of the forests were cut (of which, 0.4% were clear-cut) (Yearbook of forest statistics 1984). In most cases, the difference in habitat structure between fragments and their surroundings is very clear; a comparison of the forest structure of fragments and their surroundings in the same area is included in the ornithological survey of Haila et al. (1987).

2.2. Sampling design and methods

For the survey we selected 35 fragments of undisturbed coniferous taiga, with an area range of 0.4 to 101 ha, surrounded by economically managed forest. We took samples in the interior of each primeval forest fragment and in the surrounding managed forest, 100–200 m from the fragment edge. In 24 fragments we also took samples at the edge (10–20 m inside the actual edge), between the primeval forest fragments and the surrounding managed forest. Our samples are thus taken from three main categories of forest: *fragment interiors*, *fragment edges*, and *surroundings*.

The large fragments (>9 ha) comprise more heterogeneous forests than the small ones (<5 ha), but Haila et al. (1987) studied the pattern of habitat variation in some of the fragments included in our study and found it relatively uniform. We selected the sampling sites (a plot with a set of 15 or 30 traps) within each fragment so that they would represent as similar a *Myrtillus*-type forest as possible. However, the representativeness of our samples with respect to the carabid fauna of each fragment, as a whole, is much better in small than in large fragments.

The main sampling method was pitfall-trapping (Hertz 1927, Barber 1931, Westerberg 1977, Southwood 1978). The traps (plastic cups, diameter 65 mm and volume 170 ml) were placed in a grid in each sampling site, 3–4 m from each other. 104 sampling sites were included in the study. In 1984 we took samples at 72 sampling sites (24 forest fragments, 24 edges and 24 surroundings). Fifteen traps (in a 3 × 5 grid) were in operation for five days in two sampling periods (between 3–10 June and 19–26 August 1984). In 1985 we collected at 62 sampling sites, 30 of these being the same sites as in the previous year (10 fragments, 10 edges, 10 surroundings). In addition, we selected 16 small (<5 ha) fragments with surroundings for the study. Due to the low numbers of carabids in the samples in 1984, the sampling effort was increased in 1985: 30 traps (in a 5 × 6 grid) were in operation at each sampling site for 21 days (between 3–26 June) plus 15 days (between 5–21 August). The

sampling effort at each site was 150 'trap-days' in 1984, and 1080 'trap-days' in 1985. The carabids were identified by EH and JN with the key of Lindroth (1961, 1985, 1986).

The pooled data of two periods give an adequate picture of both the composition of the carabid assemblages and species abundances for comparisons. This is indicated by the results of an extensive sampling scheme conducted during the whole growing season in northern Häme in 1985 (Niemelä et al. 1988, Niemelä et al. in prep.) and by data from the Åland Islands (Niemelä et al. 1985).

As a methodological test of the efficiency of pitfall sampling we collected invertebrates in nine forest fragment interiors (ten sampling sites) and nine surroundings by sieving, hand-picking and sweep-netting in July 1985 (but edges were not included in this study). About 20–30 dead trees (either snags or decaying logs) and stumps were selected for the hand-picking in the fragments. We sought invertebrates under the bark and, by digging, in the soft parts of the decaying wood. Dead trees within an area of about 2–3 ha in the large fragments, and practically the whole of the small fragments were investigated. The sampling procedure was similar in all sampling sites. In the surrounding managed forest the number of suitable objects for hand-picking was usually considerably lower due to the removal of dead trees, snags, decaying logs etc., and practically all objects of this kind were investigated within an area of 2–3 hectares.

For sieving, we collected 96 samples, 0.25 m² each, with a total area of about 24 m². About 300 sweeps were made by PP, using a sweep-net, in the field layer of the sampling sites.

In particular, we wanted to find out whether such species that cannot be caught by using pitfall traps could be found by directing the manual collecting effort to specific microsites, such as decaying logs, old tree stumps and snags. The results are presented in section 3.3.

2.3. Habitat structure

Habitat descriptions, made by TL, include the floristic composition of the vegetation and the structure of the tree layer. In three surroundings no habitat description was made. The variables estimated were: the Cajanderian forest site type, dominating tree species, canopy cover (in %), and the mean height of the trees and basal area (the total diameter of trees measured at the height of 1.3 m, in m²/ha). The structure of the tree layer was estimated in an area of 0.1 hectares around each sampling site. Mean height, canopy cover and basal area characterize the tree stands at the sites and give indirect information about the light conditions on the ground. The field layer and bottom layer vegetation of each sampling site was analyzed by estimating the proportional cover of the plant species in a 100 m² circle, in the middle of the pitfall-grid.

2.4. Habitat groups

In order to compare the structure of carabid samples in the primeval forests and different types of surrounding managed forest, we formed five habitat groups according to the habitat structure of the sites. The grouping of the sites was based on the habitat description described in sect. 2.3. Only the representative

sites were included in the grouping. For instance, edges were excluded from the groups because of their inherent heterogeneity, and because carabid communities on the edges may be influenced by individuals moving from the surroundings to the interiors, and vice versa (Levenson 1981, Harris 1984). A total of 60 sampling sites were included in the following habitat groups: (1) Moist, spruce-dominated primeval forests (mostly >120 yrs, canopy cover 80% and height 20 m, basal area 29 m²/ha); (2) Dry, mainly pine-dominated primeval forests (>100 yrs, canopy cover 80% and height 18 m, basal area 24 m²/ha); (3) Managed mature forests (60–100 yrs, canopy cover 65% and height 17 m, basal area 18 m²/ha); (4) Old mixed plantations (20–60 yrs, canopy cover 62% and height 11 m, basal area 8 m²/ha); and (5) Young plantations, mainly pine (<20 yrs, canopy cover 30% and height 6 m, basal area 7 m²/ha). The number of sampling sites in each habitat group are given in Table 2.

3. Results

3.1. Distribution patterns

Our pooled sample comprised 422 carabids from 22 species in 1984, and 1564 carabids from 40 species in 1985. The complete data are presented in Table 1. The number of carabids in the pooled sample (1984+1985) was 0.025 individuals/trap-day. Due to the increased sampling effort, the sample sizes were higher in 1985, but the relative abundances of different species in the samples remained stable; a detailed between-year comparison is included in Sect. 3.4.

Calathus micropterus was by far the most abundant species (37% of the pooled sample). The proportion of the second species (*Pterostichus oblongopunctatus*) was 13%. The nine most abundant species (>2% of the sample) comprise 89% of the sample (Table 1).

In the following, we investigate the distribution of carabids relative to the forest structure in our study area, using two complementary approaches, namely, (1) In an ordination space made on the basis of the habitat descriptions of individual sites; and (2) in the five habitat groups described in Sect. 2.4 above; and (3) at the fragment edges, compared with their interiors and surroundings.

Distribution over the sites

Using the 1985 data, we made an ordination of the sampling sites according to their vegetation characteristics using detrended correspondence analysis (Gauch 1982). The variables included in the analysis were: the proportional cover of the 15 most abundant plant species (log transformed) and five tree stand characteristics (canopy cover, mean height, basal

Table 1. The total carabid sample in sampling sites studied only in 1984, in sites studied both in 1984 and 1985, and in sites studied only in 1985 (F=fragment interior, E=fragment edge, S=surrounding managed forest). Nomenclature follows Lindroth (1985, 1986).

	1984 only			1984 and 1985						1985 only		Total
	F	E	S	F			E			S	F	
Abundant species												
<i>Calathus micropterus</i> (Dft.)	43	38	31	35	92	9	62	19	113	180	111	733
<i>Pterostichus oblongopunctatus</i> (F.)	4	14	3	11	57	4	19	12	22	49	53	248
<i>Notiophilus biguttatus</i> (F.)	6	5	3	7	38	8	36	11	20	57	18	209
<i>Carabus hortensis</i> L.	3	6	6	6	20	3	8	4	26	48	15	145
<i>C. glabratus</i> Payk.	6	4	3	6	7	7	9	10	10	15	17	94
<i>Cychrus caraboides</i> (L.)	2	4	2	5	25	2	7	3	8	22	11	91
<i>Amara brunnea</i> (Gyll.)	2	2	3	4	39	1	16	0	7	11	4	89
<i>Trechus secalis</i> (Payk.)	0	0	4	0	1	1	0	2	14	21	46	89
<i>Leistus terminatus</i> (Hellw. in Pz.)	6	0	1	3	10	4	10	3	6	25	5	73
Other species												
<i>Agonum ericeti</i> (Pz.)	0	0	0	0	0	0	0	0	0	0	9	9
<i>A. fuliginosum</i> (Pz.)	0	10	1	0	0	2	0	0	1	0	2	16
<i>A. livens</i> (Gyll.)	0	0	1	0	0	0	0	0	0	0	0	1
<i>A. mannerheimii</i> (Dej.)	0	0	0	0	4	0	0	0	4	0	0	8
<i>Amara familiaris</i> (Dft.)	0	0	0	0	0	0	0	0	0	0	1	1
<i>A. lunicollis</i> Schjødt	0	0	0	0	0	0	0	0	0	0	7	7
<i>Bembidion gilvipes</i> Sturm	0	0	0	0	0	0	0	0	0	0	2	2
<i>Bradycellus caucasicus</i> (Chaud.)	0	0	0	0	0	0	0	0	0	0	1	1
<i>Calathus melanocephalus</i> (L.)	0	0	0	0	0	0	0	0	3	0	0	3
<i>Carabus nitens</i> F.	0	0	0	0	0	0	0	0	0	1	1	2
<i>C. violaceus</i> L.	0	0	0	0	0	0	0	0	0	0	1	1
<i>Cicindela sylvatica</i> L.	0	0	0	0	0	0	0	1	9	0	0	10
<i>Cymindis vaporariorum</i> (L.)	0	0	0	0	0	0	0	0	1	0	2	3
<i>Dromius agilis</i> (F.)	0	0	0	0	0	1	1	0	0	0	1	3
<i>Dyschirius globosus</i> (Hbst.)	0	1	0	1	0	0	0	0	0	0	0	2
<i>Harpalus quadripunctatus</i> Dej.	0	0	0	0	0	0	0	0	0	4	7	11
<i>Harpalus</i> sp.	0	0	0	0	0	0	0	0	0	0	1	1
<i>Leistus ferrugineus</i> (L.)	0	0	0	0	0	0	0	0	0	1	1	2
<i>Loricera pilicornis</i> (F.)	0	0	1	0	0	0	0	0	3	0	4	8
<i>Miscodera arctica</i> (Payk.)	0	0	0	0	0	0	0	1	1	0	12	14
<i>Notiophilus aestuans</i> Mtsch.	0	0	0	0	0	0	0	0	1	0	1	2
<i>N. germyi</i> Fauv.	0	1	0	0	1	0	0	1	8	0	0	11
<i>N. palustris</i> (Dft.)	0	0	0	0	0	0	0	0	0	1	10	11
<i>N. reitteri</i> Spaeth	0	0	0	0	1	0	0	0	0	4	7	12
<i>Patrobus assimilis</i> Chaud.	0	0	0	0	0	0	0	0	0	0	1	1
<i>P. atrorufus</i> (Ström)	0	1	0	0	1	0	0	0	0	0	0	2
<i>Pterostichus adstrictus</i> Eschtz.	0	0	0	0	0	0	0	0	0	0	23	23
<i>P. cupreus</i> (L.)	0	0	0	0	0	0	0	0	0	2	1	3
<i>P. diligens</i> (Sturm)	0	0	5	0	0	0	2	0	1	1	3	12
<i>P. niger</i> (Schall.)	0	0	3	0	0	0	0	0	0	0	10	13
<i>P. nigrita</i> (Payk.)	0	0	6	1	0	0	0	0	0	0	1	8
<i>P. strenuus</i> (Pz.)	0	0	0	0	0	0	0	3	0	0	5	8
<i>Synuchus vivalis</i> (Ill.)	0	0	0	0	0	0	0	0	1	0	3	4
Total	72	86	73	79	296	42	170	70	259	442	397	1986
Number of species	8	11	15	10	13	11	10	12	20	16	35	42
Number of sampling sites	14	14	14	10	10	10	10	10	10	16	16	

area, forest site type, dominating tree species). The first axis of the ordination (eigenvalue 0.14) identifies a weak gradient from dry pine plantations to moist, shady forests. Indicator plant species for the dry end of the gradient are *Calluna vulgaris* and *Deschampsia*

flexuosa, and the moist end is characterized by *Dicranum majus*, *D. scoparium* and *Vaccinium myrtillus*.

We made another ordination of the sites according to the carabid samples, using the same cara-

Table 2. Carabid samples from the five habitat groups, (for the groups see sect. 2.4). The G-test is included for the nine most abundant species. Statistical significance: *** $P < 0.001$, ** $0.001 < P < 0.01$, * $P < 0.05$, ns = nonsignificant $p > 0.05$.

	Primeval forests		Managed forests	Plantations		G
	moist	dry		old	young	
Abundant species						
<i>Calathus micropterus</i>	203	91	161	29	48	68.1 ***
<i>Pterostichus oblongopunctatus</i>	101	18	54	9	23	56.2 ***
<i>Notiophilus biguttatus</i>	73	29	37	1	3	66.5 ***
<i>Carabus hortensis</i>	68	6	43	0	2	101.5 ***
<i>Carabus glabratus</i>	22	9	22	1	15	8.6 ns
<i>Cychrus caraboides</i>	41	8	16	1	6	29.4 ***
<i>Amara brunnea</i>	30	16	9	0	2	28.7 ***
<i>Trechus secalis</i>	11	11	4	15	30	51.5 ***
<i>Leistus terminatus</i>	31	4	8	1	3	29.1 ***
Other species						
<i>Agonum fuliginosum</i>	0	0	2	0	0	
<i>A. mannerheimii</i>	7	0	1	0	0	
<i>Amara familiaris</i>	0	0	0	0	1	
<i>A. lunicollis</i>	0	0	0	0	7	
<i>Bembidion gilvipes</i>	0	0	0	0	2	
<i>Bradycellus caucasicus</i>	0	0	0	0	1	
<i>Calathus melanocephalus</i>	0	0	0	0	3	
<i>Carabus nitens</i>	0	0	1	0	1	
<i>C. violaceus</i>	0	0	0	0	1	
<i>Cicindela sylvatica</i>	0	0	0	0	10	
<i>Cymindis vaporariorum</i>	0	0	0	0	3	
<i>Dromius agilis</i>	0	0	1	0	0	
<i>Dyschirius globosus</i>	1	0	0	0	0	
<i>Harpalus quadripunctatus</i>	1	3	0	0	7	
<i>Harpalus sp.</i>	0	0	0	0	1	
<i>Leistus ferrugineus</i>	0	1	0	0	1	
<i>Loricera pilicornis</i>	0	0	8	0	0	
<i>Miscodera arctica</i>	0	0	1	0	13	
<i>Notiophilus aestuans</i>	0	0	0	0	2	
<i>N. germnyi</i>	1	0	0	0	9	
<i>N. palustris</i>	0	1	1	0	9	
<i>N. reitteri</i>	5	0	7	0	0	
<i>Patrobus assimilis</i>	0	0	1	0	0	
<i>P. atrorufus</i>	1	0	0	0	0	
<i>Pterostichus adstrictus</i>	0	0	0	0	23	
<i>P. cupreus</i>	0	2	0	0	1	
<i>P. diligens</i>	0	0	1	2	1	
<i>P. niger</i>	1	0	3	0	7	
<i>P. strenuus</i>	0	0	0	4	4	
<i>Synuchus vivalis</i>	0	0	0	0	4	
Total	597	199	381	63	243	
Number of species	16	13	20	9	31	
Expected ratio (trap-days)	20 880	16 290	17 040	4 230	14 010	
Number of sampling sites	19	14	12	3	12	

bid/site matrix as in the first ordination. The first axis of the ordination (eigenvalue 0.36) represents a similar moisture gradient as in the vegetation ordination. Indicator carabid species for the dry sites are *Bembidion gilvipes*, *Miscodera arctica*, *Cymindis vapo-*

rriorum and *Pterostichus adstrictus*, and species typical for the old forests are *Amara brunnea* and *Agonum mannerheimii*. We calculated the Spearman rank correlation between vegetation and carabid DCA-scores (1st axes) to study whether variation in

the general composition of carabid assemblages correlates with variation in habitat structure in the sites. The correlation is statistically significant ($r_s=0.430$, $0.001 < P < 0.01$, $n=57$).

The low sample sizes preclude direct comparisons between the original habitat variables and samples of single carabid species in individual sites. Instead, we studied the correlation between the carabid DCA-score and the original value of each habitat variable in each site (the five tree variables and the proportion of the three most abundant plant species). The rank correlation is statistically significant between carabid DCA-scores and canopy cover ($r_s=0.623$, $P<0.001$, $n=57$), mean height of trees ($r_s=0.496$, $P<0.001$, $n=57$), basal area ($r_s=0.559$, $P<0.001$, $n=57$) and the proportion of *Vaccinium myrtillus* ($r_s=0.300$, $P<0.05$, $n=57$). There is no correlation between carabid DCA-scores and the occurrence of *V. vitis-idaea* or *Pleurozium schreberi* in the sites.

Overall habitat composition (characterized by the structure of tree stands) seems to be related to the composition of carabid assemblages over the sites, whereas abundance of single plant species is less important.

Distribution in the habitat groups

We used the pooled carabid data of the five habitat groups (Sect. 2.4) in further comparisons. Because of the low densities of carabids in our study area (0.025 individuals/trap-day) this is the only option.

The dispersion of individual species among the five habitat groups is shown in Table 2. The nine most abundant species were included in the comparison. Using the *G*-test, we compared observed distributions with expectations derived from sampling efforts; the results are included in Table 2. They indicate that eight of the nine species are not uniformly dispersed over the habitat groups, but show some preferences.

The abundance patterns of the nine species are presented in Fig. 1. The species can be divided into three groups: (1) Species abundant in primeval and managed forests (*Amara brunnea*, *Cychrus caraboides*, *Leistus terminatus*, *Notiophilus biguttatus*, *Pterostichus oblongopunctatus*, *Carabus hortensis*, *Calathus micropterus*); (2) species equally abundant in all habitat groups (*Carabus glabratus*); and (3) species abundant in young plantations (*Trechus secalis*). There is variation among the species of the first group, however. The main pattern seems to be that population numbers are high in moist primeval forests and managed forests, and lower in dry

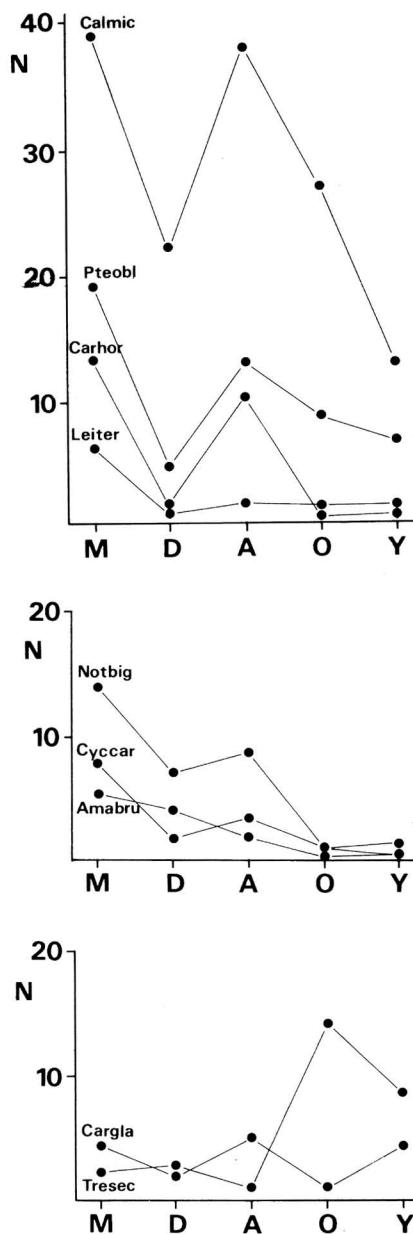
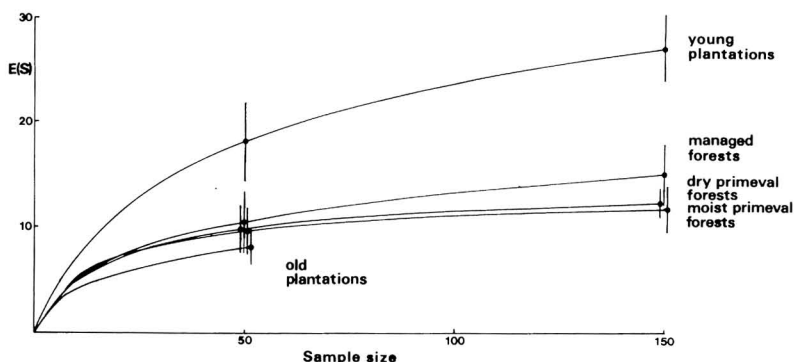


Fig. 1. The occurrence of the nine most abundant carabid species in the habitat groups (M = moist primeval forests, D = dry primeval forests, A = managed forests, O = old plantations, Y = young plantations). The number of individuals (N) is standardized to 4000 trap-days in each habitat group. Species codes are: Calmic = *Calathus micropterus*, Pteobl = *Pterostichus oblongopunctatus*, Carhor = *Carabus hortensis*, Leiter = *Leistus terminatus*, Notbig = *Notiophilus biguttatus*, Cyccar = *Cychrus caraboides*, Amabru = *Amara brunnea*, Cargla = *Carabus glabratus*, Tresec = *Trechus secalis*.

Fig. 2. Expected species number ($E(S)$), estimated by rarefaction, in the habitat groups as a function of their sample size (vertical lines indicate $\pm 2SD$).



primeval forests (e.g. *Carabus hortensis*, *Calathus micropterus*). All of the abundant species occur over a wide range of successional forest stages — none of them were missing from any habitat group.

The species numbers of the pooled samples were compared, using rarefaction (Simberloff 1978, James & Rathbun 1981). The resulting rarefaction curves are shown in Fig. 2. Species richness is highest in the pooled sample from young plantations, while the samples from the other habitat groups are similar to each other.

To study whether the high species number in young plantations is due to richness at individual sampling sites, or to heterogeneity among the sites, we compared the observed species number in young plantations with an expectation derived from the pooled sample of the large fragment interiors (1985 data, Fig. 3). In two of the 12 sites the species number was significantly higher, and in one site it was lower than expected. In the two sites with higher species number we caught individuals of scarce species that are denizens of open grasslands (Lindroth 1945, 1985; e.g. *Amara lunicollis*, *Bembidion gilvipes*). Overall, the comparison indicates that the high species number in the pooled sample from young plantations is mainly due to variation among the sites, rather than to high species number in individual sites.

In comparing the composition of the pooled samples of the five habitat groups (Table 2) we used the Czekanowski-Sørensen index of percentage similarity (log transformed data), following the advice of Wolda (1981) and Pesenko (1982):

$$PS = \sum \min(p_{ij}, p_{ik}),$$

where p_{ij} , p_{ik} is the proportion of the species i in samples j and k .

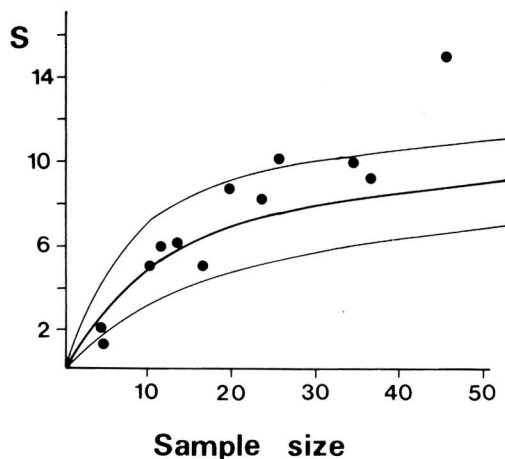


Fig. 3. The observed species number in young plantations, compared with rarefaction expectation from the pooled data of ten fragment interiors in the 1985 data (fragments >12 ha, the rarefaction curve with $\pm 2SD$).

Pesenko (1982:161–163) gives a formula, based on the t -test, for estimating confidence limits for the index:

$$PS \pm t_{st} \sqrt{\sum \min(m_{ij}^2, m_{ik}^2)},$$

where t_{st} = t value corresponding to significance level st , $m_{ij} = \sqrt{p_{ij}(1-p_{ij})/N_j}$, and N_j = the total number of individuals in sample j .

The comparison is shown in Table 3. Primeval forests and managed forests are similar to each other concerning their carabid assemblages, while both types of plantations differed more from the other groups.

Table 3. Comparison of the carabid assemblages in the five habitat groups using the Czekanowski-Sørensen index of percentage similarity (I). The value of the t -test (t) is given. Statistical significance as in Table 2.

	Moist primeval forest	Dry primeval forest	Managed forests	Old plantations
Dry primeval forests	$I=0.770$ $t=1.62$ ns $df=12$			
Managed forests	$I=0.767$ $t=1.770$ ns $df=15$	$I=0.704$ $t=2.292^*$ $df=12$		
Old plantations	$I=0.494$ $t=3.597^{**}$ $df=8$	$I=0.553$ $t=2.857^*$ $d=8$	$I=0.482$ $t=3.673^{**}$ $df=8$	
Young plantations	$I=0.408$ $t=6.712^{***}$ $df=15$	$I=0.471$ $t=5.612^{***}$ $df=12$	$I=0.451$ $t=5.850^{***}$ $df=19$	$I=0.380$ $t=6.424^{***}$ $df=8$

Fragment edges

We used the 1985 data for comparing species assemblages at the fragment edges with those in fragment interiors and surroundings (Table 1). Because of small sample sizes from individual sites it is necessary to use pooled data. In general community characteristics edges were similar to fragment interiors: Species richness, standardized by rarefaction, was similar (expectation for a sample of 170 individuals from the interiors is 11.2 species, $SD=1.0$), and percentage similarity is 0.822 ($t=1.084$, $df=9$, ns). Some individual species favouring moist primeval forests (see Fig. 3) were less abundant at the edges than in the interiors (e.g. *Amara brunnea*). The similarity between edges and interiors is presumably due to their habitat similarity. Species richness in the pooled data set from the surroundings is greater than in the data from the edges.

3.2. Effect of fragment area

It is impossible to use our data directly for a comparison of carabid communities in individual different-sized fragments because the sampled areas in the fragments were not related according to their size. However, it is possible to use pooled data for a comparison between small and large fragments. Our

Table 4. Carabid samples from the two fragment size classes — small (<5 ha) and large (>30 ha). The value of the G -test is given. Statistical significance as in Table 2.

	Small	Large	G
<i>Calathus micropterus</i>	202	89	32.8 ***
<i>Pterostichus oblongopunctatus</i>	46	11	19.1 ***
<i>Notiophilus biguttatus</i>	59	29	7.2 **
<i>Carabus hortensis</i>	51	0	64.3 ***
<i>C. glabratus</i>	17	9	1.6 ns
<i>Cychrus caraboides</i>	20	6	6.3 *
<i>Amara brunnea</i>	13	20	2.4 ns
<i>Trechus secalis</i>	20	0	24.8 ***
<i>Leistus terminatus</i>	27	2	22.5 ***
Total	455	166	
Expected ratio (trap-days)	16 950	15 090	

samples were collected in the same habitat type, and micro-scale habitat variation is averaged out in pooled data sets. If communities in this habitat were more diversified in the large fragments than in the small ones, this would be reflected in the pooled samples by a greater species richness in the large fragments.

For such a comparison, we divided the fragments into two size classes, namely, large, >30 ha (11 fragments) and small, <5 ha (20 fragments). The difference in standardized species number is not statistically significant (expected species number for 150 individuals: large fragments 10.5 ($SD=0.59$), small fragments 12.1 ($SD=1.08$)).

We then compared the occurrence of the nine most abundant species in the size classes using the G -test (see Table 4). In calculating the expected numbers we used the ratios of sampling efforts. Seven of the nine species were more abundant in the small, than in the large fragments (*Calathus micropterus*, *Carabus hortensis*, *Cychrus caraboides*, *Leistus terminatus*, *Notiophilus biguttatus*, *Pterostichus oblongopunctatus* and *Trechus secalis*); *Amara brunnea* and *Carabus glabratus* showed no significant difference between the size classes.

A plausible explanation for this difference is variation in habitat structure. Forests in small fragments may be more open and light than in the large ones. For instance, in the tropics, fragments of rainforest smaller than 10 ha differ considerably from larger ones in air humidity and temperature (Lovejoy et al. 1986, see also Wilcove et al. 1986).

Table 5. Carabids sampled by sieving (Si) and hand-picking (H) in ten sampling sites in forest fragments and in nine surroundings (large and small fragments are pooled). Pitfall samples from the same sites (interiors and surroundings are pooled) are given in the last column.

	Fragment interiors		Surroundings		Total Si+H	Pit-fall
	Si	H	Si	H		
<i>Agonum fuliginosum</i>	0	1	0	0	1	1
<i>Amara brunnea</i>	2	0	0	0	2	22
<i>Bradycellus caucasicus</i>	0	0	1	0	1	0
<i>Calathus micropterus</i>	14	4	13	0	31	125
<i>Cicindela sylvatica</i>	0	1	0	0	1	9
<i>Cychrus caraboides</i>	1	0	1	0	2	9
<i>Notiophilus biguttatus</i>	1	3	1	0	5	18
<i>Patrobus assimilis</i>	0	0	1	0	1	0
<i>Pterostichus diligens</i>	0	0	4	0	4	1
<i>P. oblongopunctatus</i>	0	3	1	2	6	38
Total	18	12	22	2	54	223
Number of species	4	5	7	1	10	8
Density (ind./m ²)	1.4	1.8	1.6			

3.3. Hand-picking and sieving

By hand-picking and sieving we found 54 carabids from 10 species (with a sampling effort of about 350 working-hours!) (Table 5). No carabids were found in the sweep-netting samples. The densities of carabids, calculated on the basis of the sieving samples, vary greatly between sites (0–12 individuals/m²). The mean density of carabids in the interiors of the fragments was about 1.4 individuals/m², and in the surroundings about 1.8 individuals/m². These figures are only suggestive because of small sample sizes.

Samples from sieving and hand-picking did not include a single species that was not caught using pitfall traps (all sites pooled). The relative abundances of species caught by using pitfall-traps, and by sieving and hand-picking in the same sites were similar (Czekanowski-Sørensen index: $I=0.854$, $t=2.073$, ns, $df=7$; data in Table 5). The samples are small, but the result increases our confidence in pitfall-trapping as a quantitative sampling method for carabids. However, we have missed a few arboreal carabid species found by hand-picking in coniferous old forest by Palm (1946), in mid-Sweden, and Biström (1978) in southern Finland.

Table 6. The proportion (%) of the nine most abundant carabid species in the pooled samples in 1984 and 1985 at the same sites.

	1984	1985
Equal proportions in the two years		
<i>Calathus micropterus</i>	33	37
<i>Notiophilus biguttatus</i>	14	13
<i>Pterostichus oblongopunctatus</i>	14	13
<i>Carabus hortensis</i>	7	7
<i>Cychrus caraboides</i>	6	5
<i>Leistus terminatus</i>	5	4
<i>Trechus secalis</i>	2	2
Different proportions in the two years		
<i>Amara brunnea</i>	3	8
<i>Carabus glabratus</i>	13	4
Total proportion of the nine species	97	93

3.4. Comparison between the years

We compared our samples from the same sites in 1984 and 1985 as a methodological check of year-to-year differences (data in Table 1). The following conclusions emerge:

First, the distributions of total sample sizes over the three sampling site categories (fragment interiors, edges and surroundings) are similar in the two years (G-test: $G=0.187$, $df=2$, ns).

Second, there is no significant difference in species richness in the pooled data sets of the two years (expected species number for 191 individuals in the 1985 data: 15.7, $SD=1.6$; observed species number in 1984 was 17).

Third, the composition of the samples is relatively similar (Czekanowski-Sørensen index of percentage similarity: $I=0.748$, $t=2.029$, $df=16$, ns).

Fourth, the proportions of the most abundant species were quite similar in the two years (Table 6), with small differences only in *Amara brunnea* and *Carabus glabratus*.

To conclude, no differences were detected in the overall structure and species composition of the pooled samples of the two years (but possible fluctuations of local populations at individual sampling sites are masked by the pooling of the data). The similarity of the samples is even more interesting as the sampling efforts differed between the years (150 trap-days/site in 1984 and 1080 trap-days/site in 1985); this indicates that even a relatively small sampling effort can give a reliable picture of local carabid

communities in Finnish coniferous forest (Niemelä et al. 1986a, b). The inter-year similarity of the samples increases confidence in our results: they are not only a one-year phenomenon.

4. Discussion

The effect of silviculture on the insect fauna of primeval forest is usually looked upon as disastrous (e.g. Ehnström 1979, 1981, Bråkenhielm 1982). Our results on carabid beetles in southern Finnish taiga disagree with these predictions. Taiga carabids, being mostly generalized above-ground predators ("zoophagous epigeobiontic species"; Sharova 1981), seem to be relatively unspecialized in their requirements concerning different forest types (see also Šustek 1981). A few species (e.g. *Agonum mannerheimii*) have distinct microhabitat preferences, however. Their future in the boreal taiga is threatened by intensive modern forestry (Niemelä et al. 1987).

Such specific micro-sites in the primeval taiga as snags, stumps, old trees, and detritus may be the only suitable habitat for many insect species. For the majority of carabids their significance is negligible. The low productivity of plants (probably leading to scarcity of food for carabids) in old coniferous forest and the unspecialized way of living, of the carabids residing there, are the probable reasons for the uniformity of the species assemblages in our forest areas.

We found two carabid species that occurred only in old forests, and 20 species that occurred exclusively in managed forests or plantations. A lower species number in primeval forests, compared with 'disturbed' forests, was also reported by Middleton & Merriam (1985) from Canada. They compared the faunas in a 50 ha area of virgin forest and in a managed forest: all of the taxa occurring in the virgin forest were found in the managed forest as well. The number of invertebrate taxa was similar in the virgin forest and in the 'disturbed' forest, but only ten taxa were studied (Middleton & Merriam 1985).

The carabid species in our data are the same as those reported by other authors in coniferous Fennoscandian taiga. Biström (1978) caught seven carabid species by using pitfall traps in a primeval forest of 40 ha in southern Finland. We caught all of these species in the old forests. Collecting by hand, from dead trees, Biström (1978) found two tree-living species (*Tachys nanus* (Gyll.), *Dromius fenestratus* (F.)) that we did not catch at all. Palm (1946) collected five carabid species from spruce trunks in an old (>200 yrs)

coniferous forest in Sweden. Our data from the interiors of the fragments include all, but one, of these species (*T. nanus*).

Both our own methodological comparisons (Sect. 3.3 and 3.4) and faunistic reference data, thus, suggest that our samples be representative of the carabid assemblages of southern boreal coniferous taiga. The results indicate that changes in the forest structure do not have drastic effects on the carabid fauna at the community level — actually, species richness is highest in recently thinned areas. A few particular species are impeded, however. The challenge for conservation is to identify such species, and to plan efficient management measures.

4.1. Population dynamics in primeval forests

Regional populations of animals consist of relatively isolated local populations even in continuous habitats, and a patchy distribution is presumably a prevailing pattern for scarce species (e.g. Levins 1968, Wiens 1976, Hanski 1985). However, very little is known about the immigration and emigration rates between local populations. Most of the species in our data are poor flyers (Lindroth 1949). Immigration rates of such species are probably low, and the distances covered by one individual rather short (some hundreds of meters). Thus, independent fluctuation of local populations ('interaction groups', den Boer 1977, 1979, 1981) might provide an explanation for the heterogenous occurrence of carabids in the sites.

According to den Boer (1981, 1985), local carabid populations frequently become extinct. Species that are critical from the point of conservation might thus be divided into small local populations, with restricted exchange of individuals among them. We suggested above that some scarce taiga carabids have this status in southern Finland.

4.2. Scarce species of old taiga

Two of the species included in our samples — *Agonum mannerheimii* and *Notiophilus reitteri* — occur in moist, spruce dominated forests (Lindroth 1945, 1961, 1985) and are among entomologists recognized as scarce residents of old coniferous forests. We caught *A. mannerheimii* at three sites, and *Notiophilus reitteri* similarly at three sites, none of the sites being the same.

Our data suggest that these two species, particularly *A. mannerheimii* — the scarcer of the two — are influenced negatively by modern forest management. The local populations of *A. mannerheimii* reside in our study area in moist spruce mires, and their distribution seems to be very restricted. It is probable that the destruction of suitable habitats, and increasing isolation among the remaining habitat patches, threaten its future survival (see Niemelä et al. 1987).

4.3. Conservation of taiga carabids

If we use species richness as a criterion, primeval coniferous forest is no more a valuable habitat for carabid beetles than managed forest. Species richness at individual sampling sites (alfa-diversity in the terminology of Wolda, 1983) was stable over the whole range of successional forest stages (Figs. 2 and 3). In young plantations, variation among sites (beta-diversity) was high, but it was mainly due to relatively scarce species of open habitats. A higher proportion of species of open grasslands in clear-cut areas, compared with the adjacent pine forest, was found also by Šustek (1981), in Czechoslovakia, and by Szyszko (1986), in Poland. Young forests are more heterogeneous landscape mosaics than old ones,

which increases variation in population distributions over the sites (Wiens et al. 1985).

Merriam & Middleton (1985) recommended maximization of habitat diversity on a regional scale as a strategy for conservation (see also Pickett & Thompson 1978, Boecklen 1986). In a forest landscape this would be achieved by a mosaic of forest patches including primeval, intermediate and young stages (Harris 1984, Middleton & Merriam 1985). This would also clarify the confusion that exists between the concepts 'primeval forest' and 'natural forest'. The term 'natural' covers all stages of forest succession (plantations excepted), whereas the term 'primeval' refers to the climax stage.

Our results support this suggestion, as regards carabid beetles in the southern taiga. Most of the species are habitat generalists, but a few of them require old forests of a particular type. A habitat mosaic approach at the regional scale seems to be a good conservation goal.

Acknowledgements. Our thanks are due to Kari Heliövaara, Olli Järvinen and Esa Ranta for comments on this paper. We thank Tiina Mattila for help in the field work. The study was financed by the Academy of Finland; grants from the Finnish Cultural Foundation and Oskar Öflunds Stiftelse to JN are gratefully acknowledged.

References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5:169–211.
- Barber, H. S. 1931: Traps for cave inhabiting insects. — *Journ. Elisha Mitchell Science Soc.* 46:259–266.
- Biström, O. 1978: Coleoptera and Heteroptera in a natural forest in Mäntymäki (southern Finland). — *Notulae Entomol.* 58:95–100.
- Boecklen, W. J. 1986: Effects of habitat heterogeneity on the species-area relationship of forest birds. — *J. Biogeography* 13:59–68.
- Bråkenhielm, S. (ed.) 1982: Urskogar, inventering av urskogssartade områden i Sverige (in Swedish with English summary). — *Statens Naturvårdsverk PM 1507*:1–107.
- den Boer, P. J. 1977: Dispersal power and survival. Carabids in a cultivated countryside. — *Misc. Papers Landb. Hogeschool Wageningen* 14.
- 1979: The significance of dispersal power for the survival of species, with special reference to the carabid beetles in a cultivated countryside. — *Fortschr. Zool.* 25:79–94.
- 1981: On the survival of populations in a heterogeneous and variable environment. — *Oecologia (Berl.)* 50:39–53.
- 1985: Fluctuations of density and survival of carabid populations. — *Oecologia (Berl.)* 67:322–330.
- Ehnström, B. 1979: Vård av den lägre faunan i skogsbruket. — In: Ahlén, I., Boström, B., Ehnström, B. & Pettersson, B. (eds.), *Faunavård i skogsbruket*: 31–39. Skogstyrelsen, Jönköping.
- 1981: Skogens hotade småkryp. — *Sveriges Natur* 72: 73–77.
- Forslund, K.-H. 1943: Studier över det lägre djurlivet i Nordsvensk skogsmark. — *Meddelanden från Statens Skogsförsöksanstalt*, häfte 34, nr. 1.
- Gauch, H. H. Jr. 1982: Multivariate analysis in community ecology. — 298 pp. Cambridge University Press, Cambridge.
- Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga in southern Finland. — *Ornis Fennica* 64:90–106.
- Hanski, I. 1985: Single-species spatial dynamics may contribute to long-term rarity and commonness. — *Ecology* 66: 335–343.
- Harris, L. D. 1984: The fragmented forest: island biogeographic theory and the preservation of biotic diversity. — 211 pp. University of Chicago Press.

- Heliövaara, K. & Väisänen, R. 1984: Effects of modern forestry on northwestern European forest invertebrates: a synthesis. — *Acta Forestalia Fennica* 189:1–32.
- Hertz, M. 1927: Huomioita petokuoiraisten olinpaikoista. — *Luonnon Ystävä* 31:218–222.
- Huhta, V., Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I., Sulander, M. & Vilkkama, P. 1986: Soil fauna of Finnish coniferous forests. — *Ann. Zool. Fennici* 23:345–360.
- Huhta, V., Karppinen, E., Nurminen, M. & Valpas, A. 1967: Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. — *Ann. Zool. Fennici* 4:87–143.
- James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — *Auk* 98:785–800.
- Järvinen, O. & Väisänen, R. 1977: Recent quantitative changes in the populations of Finnish land birds. — *Polish Ecol. Stud.* 3(4):177–188.
- 1978: Long-term population changes in the most abundant south Finnish forest birds during the past 50 years. — *J. Ornithol.* 119:441–449.
- Kalliola, R. 1979: Pohjolan luonnonmaantieteellinen aluejako (in Finnish with English summary). — *Terra* 91:95–107.
- Kangas, E. 1935: Siikakankaan maakiitäjäisfaunasta. — *Ann. Entomol. Fenn.* 1:63–64.
- 1947: Kovakuoriaisfaunamme erikoisuuksia luonnon-suojelun kannalta. — *Suomen Luonto* 6:45–55.
- Levenson, J. B. 1981: Woodlots as biogeographic islands in southeastern Wisconsin. — In: Burgess, R. L. & Sharpe, D. M. (eds.), *Forest island dynamics in man-dominated landscapes*: 13–39. Springer Verlag, Berlin.
- Levins, R. 1968: Evolution in changing environments. — 120 pp. Princeton Univ. Press, Princeton.
- Lindroth, C. H. 1945: Die Fennoskandischen Carabidae. I. — *Göteborgs Kungl. Vetensk. Handl.* B4(1):1–710.
- 1949: Die Fennoskandischen Carabidae. III. — *Göteborgs Kungl. Vetensk. Handl.* B4(3):1–911.
- 1961: Svensk Insektafauna 9, Coleoptera, Fam. Carabidae. — *Entomologiska Föreningen i Stockholm*: 1–209.
- 1985: The Carabidae (Coleoptera) of Fennoscandia and Denmark. — *Fauna Entomol. Scand.* 15, part 1:1–225.
- 1986: The Carabidae (Coleoptera) of Fennoscandia and Denmark. — *Fauna Entomol. Scand.* 15, part 2:233–497.
- Lovejoy, T. E., Bierregaard, R. O. Jr., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown, K. S. Jr., Powell, A. H., Powell, G. V. N., Schubart, H. O. R. & Hays, M. B. 1986: Edge and other effects of isolation on Amazon forest fragments. — In: Soulé, M. E. (ed.), *Conservation biology, the science of scarcity and diversity*: 257–285. Sinauer Associates, Massachusetts.
- Middleton, J. & Merriam, G. 1985: The rationale for conservation: problems from a virgin forest. — *Biol. Conserv.* 33:133–145.
- Mikkola, K. 1979: Vanishing and declining species of Finnish Lepidoptera. — *Notulae Entomol.* 59:1–9.
- Niemelä, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P. & Tukia, H. 1987: Habitat preferences and conservation status of *Agonum mannerheimii* Dej. in Häme, southern Finland. — *Notulae Entomol.* 67:175–179.
- 1988: The annual activity cycle of carabid beetles in the southern Finnish taiga. — *Ann. Zool. Fennici* (submitted).
- Niemelä, J., Haila, Y. & Ranta, E. 1986a: Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Åland islands, SW Finland. — *Ann. Zool. Fennici* 23:289–296.
- Niemelä, J., Halme, E., Pajunen, T. & Haila, Y. 1986b: Sampling spiders and carabid beetles by pitfall traps: the effect of increased sampling effort. — *Ann. Entomol. Fennici* 52:109–111.
- Niemelä, J., Ranta, E. & Haila, Y. 1985: Carabid beetles in lush forest patches on the Åland Islands, south-west Finland: an island-mainland comparison. — *J. Biogeography* 12:109–120.
- Palm, T. 1931: Om coleopterfaunan i Ombergstrakten. — *Entomol. Tidskr.* 52:13–79.
- 1938: Några skalbaggslokaler från Norrlands sydgräns. — *Entomol. Tidskr.* 59:112–122.
- 1942: Coleopterfaunan vid nedre Dalälven. — *Entomol. Tidskr.* 63:1–59.
- 1946: Coleopterfaunan i jämtländsk lavgranskog. I. Träd- och trädsvampfaunan. — *Entomol. Tidskr.* 67:109–139.
- Palmgren, P. 1977: Studies on spider populations in Mäntylharju, Finland. — *Comment. Biol.* 87:1–44.
- Palmgren, P. & Biström, O. 1979: Populations of Aranea (Arachnoidea) and Staphylinidae (Coleoptera) on the floor of a primeval forest in Mäntylharju, southern Finland. — *Ann. Zool. Fennici* 16:177–182.
- Pesenko, Yu. A. 1982: Printsipy i metody kolichestvennogo analiza v faunisticheskikh issledovaniyah. — 287 pp. Izd-vo Nauka, Moskva.
- Peterken, G. 1985: Woodland conservation and management (paperback). — 328 pp. Chapman and Hall, London.
- Pickett, S. T. A. & Thompson, J. N. 1978: Patch dynamics and the design of nature reserves. — *Biol. Conserv.* 13:27–37.
- Sharova, I. H. 1981: Zhiznennye formy zhuzhelits, Coleoptera, Carabidae. — 360 pp. Izd-vo Nauka, Moskva.
- Simberloff, D. S. 1978: Use of rarefaction and related methods in ecology. — In: Dickson, K. L., Garins, J. Jr. & Livingston, R. J. (eds.), *Biological data in water pollution assessment: Quantitative and statistical analysis*. Am. Soc. for Testing and Materials, STP 652:150–165.
- Southwood, T. R. E. 1978: Ecological methods. 2nd. edition. — 524 pp. Chapman & Hall, London.
- Šustek, Z. 1981: Influence of clear cutting on ground beetles (Coleoptera, Carabidae) in a pine forest. — *Communicationes Instituti Forestalis Cechoslovaniae* 12:243–254.
- Szyzsko, J. 1986: Dynamics of population size and development of the carabid fauna in pine stands of poor sandy soils (facts and suppositions). — In: den Boer, P. J., Luff, M. L., Mossakowski, D. & Weber, F. (eds.), *Carabid beetles, their adaptations and dynamics*: 331–341. Gustav Fischer, Stuttgart.
- Väisänen, R. 1982: Vanishing and vulnerable Diptera of Finland. — *Notulae Entomol.* 62:111–121.
- Westerberg, D. 1977: Utvärdering av fallfällemetoden vid inventering av fält- och markskiktets lägre fauna (in Swedish with English summary). — *Statens Naturvårdsverk PM* 844, Våna Rapport 5.

- Wiens, J. 1976: Population responses to patchy environments. — *Ann. Rev. Ecol. Syst.* 7:81–120.
- Wiens, J., Crawford, C. S., & Gosz, J. R. 1985: Boundary dynamics: a conceptual framework for studying landscape ecosystems. — *Oikos* 45:421–427.
- Wilcove, D. S., McLellan, C. H. & Dobson, A. P. 1986: Habitat fragmentation in the temperate zone. — In: Soulé, M. E. (ed.), *Conservation biology, the science of scarcity and diversity*: 237–256. Sinauer Associates, Massachusetts.
- Wolda, H. 1981: Similarity indices, sample size and diversity. — *Oecologia (Berl.)* 50:296–302.
- 1983: Diversity, diversity indices and tropical cockroaches. — *Oecologia (Berl.)* 58:290–298.
- Yearbook of forest statistics 1984: — *Folia Forestalia* 620.

Received 3.III.1987

Printed 23.IX.1988