

INVERTEBRATE NUMBERS IN EDGES BETWEEN CLEAR-FELLINGS AND MATURE FORESTS IN NORTHERN FINLAND

PEKKA HELLE & JYRKI MUONA

Seloste

SELKÄRANGATTOMIEN RUNSAUSSUUTEISTA AVOHAKKUUALUEIDEN JA METSIEN
REUNA-ALUEILLA POHJOIS-SUOMESSA

Saapunut toimitukselle 15. 5. 1985

The abundance of main invertebrate groups was studied in clear-fellings, forests and in edges between them in northern Finland in June-August, 1983. Five trapping transects were used; one half (100 m) of each was in clear-felling and the other 100 m in the forest side. Each transect had 48 pitfall traps and 16 window traps on the ground and 4-6 window traps in bushes or trees.

Invertebrate groups *Homoptera*, *Diptera*, *Formicidae*, *Coleoptera* and *Gastropoda* were more abundant in forests than in clear cuts according to the pitfall data. In window traps the catches of all the main groups were larger in the forest side. Six out of the eight most important groups preferred the edge in pitfall data. *Formicidae*, Other *Hymenoptera*, *Arachnida* and *Gastropoda* were more numerous in edges than in interior habitats in both sides of the edge. In window trap material no consistent edge preference was found in clear-fellings, but in the forest side it was evident. *Coleoptera* and *Arachnida* preferred the edge on both sides of it in these data.

The variations in the catches of the invertebrate groups were studied by regression analyses. Independent variables used were the distance to the edge, the coverages of mosses, litter, mineral soil, grasses and sedges, herbs and the density of saplings. The analyses were run separately for clear-fellings and forests as well as for pitfall and window trap data. The percentage of variance explained in multiple regression analyses were highest for Other *Hymenoptera* (mean 60.1 %) and *Arachnida* (56.7) and lowest for *Coleoptera* (33.3) and *Homoptera* (19.6). As regards the explanation power of the independent variables the distance to the edge and the density of saplings clearly exceeded the others.

The results support the assumption that the often high breeding bird densities at forest edges may depend on high invertebrate density there. Several aspects concerning invertebrates as a food resource of birds and the representativeness of the methods used are discussed.

1. INTRODUCTION

Several studies have shown that breeding bird densities in habitat edges usually exceed densities in the interior parts of habitats (Oelke 1966, Hogstad 1967, Helle 1983, Tiainen et al. 1983, among others). This has been explained by the edge effect, according to which the number of animals (both specimens and species) is higher in transition

zones between two (or more) habitat types than in pure habitats (e.g. Odum 1971). The studies have concentrated on ecotones between open and forested habitats where the edge effect is presumably most pronounced. Abundant and diversified vegetation in habitat edges is the most probable reason for increased bird densities there, but other fac-

tors are involved, too (Helle 1984). Hansson (1983) suggests that trees at forest edges are often damaged by increased wind velocity and sun exposure and therefore have a rich insect fauna. The fragmentation of forests has created a large amount of open habitat/forest ecotones during the last few decades. The edge effect has been an important factor affecting breeding land bird populations in Finland in the latter half of the 20th century (e.g. Järvinen et al. 1977, Haila et al. 1980, Helle & Järvinen 1985).

The purpose of this study is to investigate whether there is an edge effect affecting invertebrate populations between clear-felled areas and mature forests in Northern Finland. Second, an attempt is made to explain the variation in invertebrate numbers by simple vegetation characteristics. With regard to the food resources of birds the results of this

study are only indirect, since the diet of even the most numerous bird species is relatively poorly known. Nearly all the passerines (which are overwhelmingly the most numerous birds in boreal forest), however, forage on invertebrates during the breeding season (e.g. v. Haartman et al. 1963–72), and the results give some general information on the amount of food available for birds in these habitats.

The Oulanka Biological Station of the University of Oulu in Kuusamo provided excellent working facilities for the study. We want to thank Maija Karjalainen, Katri Kärkkäinen, Mikko Mönkkönen, Jari Lampinen, Tellervo Patosalmi and Sirkka Savonmäki for helping in the field and laboratory work. Grants from the Emil Aaltonen Foundation (to PH) and the Finnish Cultural Foundation are gratefully acknowledged. Assoc. prof. Veikko Huhta kindly read the manuscript and made useful comments for its improvement.

2. STUDY AREA

The study area (appr. 5×10 km in size) is located in northern Kuusamo in and close to the Oulanka National Park (66°N, 29°E). It belongs to the biological province of Kuusamo (Ks). The fauna and flora of the area are rich and include in addition to ubiquitous species northern, eastern and southern elements. A prominent feature in the general scenery of the Kuusamo uplands compared to the adjacent areas is the abundance of spruce. The forests have been used by

man for a long time; the slash-and-burn cultivation as well as the burning of tar were common earlier. However, the effects of these practices were fairly insignificant, except locally. Since the 1950s modern forestry has drastically changed the area: large ploughed clear-fellings and sapling stands are frequent. More detailed descriptions on the study area can be found in Söyrinki et al. (1977) and Viramo (1979).

3. METHODS

3.1. Animal traps

Invertebrates moving on the surface of the ground were trapped with pitfall traps (Tretzel 1955, Thiele 1977). We used white plastic containers (500 cm³ by volume, the diameter of the opening 75 mm). About 5 cm liquid –

5:1 water-ethylene glycol plus a drop of detergent – was kept in the traps. The traps were dug into the ground so that the edge was just below the surface of the ground. The pitfall method has been questioned because the numbers of individuals caught does not depend only on animal density, but also on

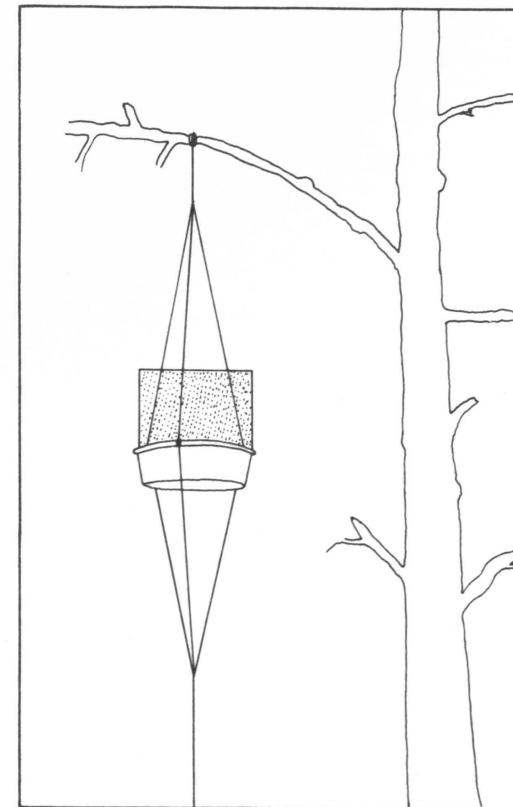


Fig. 1. The window trap used in the study. See text for its dimensions.

factors such as the activity of animals and the structure of the habitat (Adis 1979, Baars 1979, and references therein). Törmälä (1982) showed, however, that the method gives fairly reliable results for *Araneae*, *Auchenorrhyncha*, some *Coleoptera* (*Staphylinidae*) and some *Diptera*. We believe that the method is accurate enough for our purpose, as 1) the trapping was performed in different habitats at the same time, and 2) the comparisons are (mainly) restricted to clear-fellings and forests separately. A clear difference in the vegetation structure of these habitats may cause differences e.g. in the activity of species.

Window traps were used for trapping flying insects (e.g. Southwood 1978; see Fig. 1). The trap consisted of a plastic washbowl (400 mm in diameter, green in our study) and a 3 mm thick transparent acryl plate (370×350

mm in size) set in it. When used on the ground, the trap was placed into the vegetation on an even site. When used above the ground, in bushes or trees, the trap was fixed to the desired place and height with cords (see Fig. 1). The same liquid as in pitfall traps was used in the window traps (1–2 liters).

3.2. Trapping transects

Trapping was performed in five different clear-felling/mature forest edges. Transects were located in each area so that one half of the transect (100 m) was in the clear-felling (or sapling stand) and the other 100 m in the forest. The study sites were selected so that the variation in the forest type was as small as possible, which rendered the analyses on the effects of the age of the clear-felling on arthropod life more reliable. Four transects were in stands of *Empetrum-Myrtillus* type (A, B, D, E), one in a stand of *Ledum-Uliginosum* type (C; Table 1). The age of the clear-fellings on the open parts of the transects (A–E) were 25, 25, 8, 2 and 1 years, respectively. The age of the dominant trees was more than 100 years in the forest of every transect. For details on the characteristics of the forest types, see Söyrinki et al. (1977). All the habitat patches of the study were at least 25 ha in size.

48 pitfall traps were placed in each transect: six rows (four in each) to both clear-felling and forest. The distance between the traps in a row was 5 m, and the distance of the rows from the edge 5, 20, 40, 60, 80 and 100 m (Fig. 2). The location of the 16 window traps in each transect is depicted in Fig. 3. A pair of window traps consisted of two traps about 5 m apart from each other. One had its window parallel to the forest edge and the other perpendicular to the edge.

Window traps were also set in the bush layer and the canopy (heights 2.5 and 8 m, respectively). Each transect had four traps in its forest part: two in the shrub layer and two in the canopy, at distances of 20 m and 80 m from the forest edge. In clear-fellings transects A and B had two window traps in the shrub layer, located at the same distance from the edge as in forest side; transects C–E

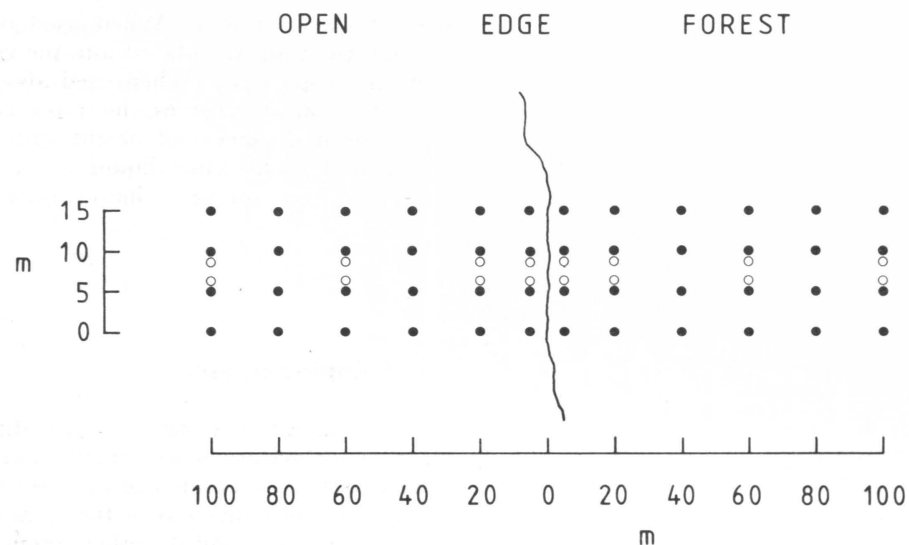


Fig. 2. A schematic picture of the trapping transect. ● pitfall trap, ○ window trap. Note that the scales on the two axes are not equal.

had not window traps above the ground in their open side.

Trapping was started at the end of May, 1983, and the traps were emptied at intervals of 3–4 weeks. The results presented here are based on the first three catches (trapping season 28. 5.–20. 8.). The invertebrates were identified to the following taxonomic groups: *Heteroptera*, *Homoptera*, *Nematocera*, *Other Diptera*, *Symphyta*, *Apocrita*, *Formicidae*, *Myrmicidae*, *Other Hymenoptera*, *Lepidoptera*, *Coleoptera*, *Arachnida*, *Gastropoda* (and others, including also all the larvae). The animals were classified into three size classes according to their body length: <2, 2–6 and >6 mm.

3.3. Vegetation analyses

Vegetation analyses were made in an area of 1 m² around each pitfall trap. The coverage of mosses, lichens, litter and mineral soil was estimated in the ground layer, and those of dwarf shrubs, grasses and sedges as well as herbs in the field layer. General features of the tree and shrub layers were recorded at the mid-points of each pitfall trap row using the principles of Söyrinki et al. (1977).

4. RESULTS

4.1. Vegetation of the transects

The tree stands (A–E) closely resemble each other; this is true of the understorey vegetation as well. In the ground layer of the mature stands, mosses covered on the aver-

age 87 %, lichens 21 %, litter 11 % and mineral soil 1 %. *Pleurozium schreberi* dominated the ground layer in transects A and B, *Hylocomium splendens* in transect C; the species were equally abundant in transects D and E. In the field layer, the coverage of dwarf

shrubs amounted to 50 %, those of grasses and sedges to 5 and herbs to 1 %. *Vaccinium vitis-idaea* was the dominant species in all the transects except transect E, where *V. uliginosum* was the most abundant species.

The vegetation of the open parts of the transects varied more than in forest parts. Short descriptions are given.

Transect A: Height of stand about 4 m. The proportion of pine and spruce was 3:1. The hardwood brush was removed some five years earlier. The abundance of dwarf shrubs was lower and grasses greater than in the mature forest.

Transect B: No planting or thinning after clear-felling. The stand reaching the height of 5 m was dominated by deciduous saplings. The ground layer did not differ from the forest part, but dwarf shrubs were sparse and grasses as well as herbs abundant.

Transect C: A slight preparation of the ground after clear-felling. Stocked with pine seedlings in 1977. Scattered *Betula* seedlings occurred in addition to the pine. About one fourth of the ground was without vegetation. The coverages of grasses and herbs exceeded those in the forest part of the transect.

Transect D: The ground was ploughed during the study period, for which reason the vegetation description is based only on estimates. Before the ploughing, the understorey vegetation was similar to that in the forest part. After the treatment, the vegetation is comparable to the open part of transect E.

Transect E: Heavy ploughing has increased the area without vegetation to 50 %. Planted with pine in the beginning of the study period. In early summer there was plenty of water in the ditches, by the end of the summer most of them dried up.

4.2. Invertebrate catches

4.2.1. Pitfall traps

The average numbers of the specimens of the main invertebrate groups obtained by pitfall trapping as a function of the distance to forest edge are presented in Fig. 3. The results reveal large variation among the dis-

tance classes. *Formicidae*, the group *Other Hymenoptera*, *Arachnida* and *Gastropoda* showed a slight edge preference in open habitats, the opposite was true of *Nematocera* and *Other Diptera*; *Homoptera* and *Coleoptera* showed no trend. In forest parts of the transects *Other Diptera* and *Arachnida* clearly preferred edges. The numbers of *Formicidae* and *Coleoptera* varied considerably without a trend. The other taxa showed a peak at the distance of 20–60 m from forest edge.

The average number of individuals caught in edge and interior parts of clear-cuttings as well as forests are shown in Table 1. The edge includes the trap rows closer than 50 m to the edge, and interior the trap rows further than 50 m away from the edge. In the open side the edge was preferred by six taxa and avoided by two. A similar result was found in forest. Four groups – *Formicidae*, *Other Hymenoptera*, *Arachnida* and *Gastropoda* – preferred edges on both sides of the forest edge.

No regular pattern can be found with regard to the variation in average catch of the invertebrate groups between edges and interior. The variation was higher in open land than in forest in *Homoptera*, *Formicidae*, *Arachnida* and *Gastropoda*, whereas it was larger in the forest than in the open side in *Nematocera*, *Other Diptera*, *Other Hymenoptera* and *Coleoptera*.

4.2.2. Window traps on the ground

The average numbers of the specimens of the main invertebrate groups per a pair of window traps at different distance from the forest edge are presented in Fig. 3. The window traps did not catch flying insects only but other invertebrates as well (*Arachnida*, *Gastropoda*). In the open habitat, edge preference was found in *Formicidae*, *Coleoptera* and *Arachnida*; *Nematocera* showed the opposite response. In the other groups the variation was large without any clear trend. In the forest side, *Homoptera*, *Nematocera* and *Other Diptera* as well as *Coleoptera* preferred edges. Patterns in *Formicidae*, *Arachnida* and *Gastropoda* were trendless.

The average numbers of specimens of the groups (per a window trap) for habitat edge

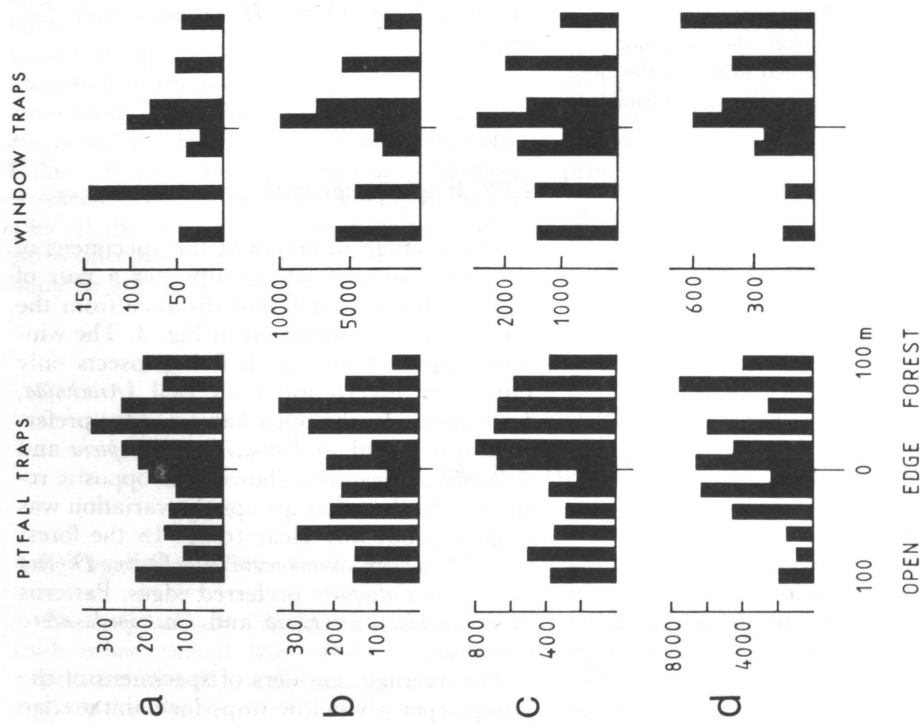


Fig. 3. Average number of specimens caught in the main invertebrate groups per a row of pitfall traps (at distances of 5, 20, 40, 60, 80 and 100 m from the forest edge) and per a pair of window traps (at distances of 5, 20, 60 and 100 m from the forest edge). Data from the five transects pooled; see text for details. a) *Homoptera*, b) *Nematocera*, c) *Formicidae*, d) *Other Diptera*, e) *Other Hymenoptera*, f) *Coleoptera*, g) *Arachnida*, h) *Gastropoda*.

Table 1. Average catch (no. of specimens) and range (min-max) of main invertebrate groups per a row of pitfall traps in open habitat and forest edges and interiors of the transects. Significant differences between the means (\bar{x}) of the adjacent columns are shown by asterisks, also for open vs. forested habitats as a whole (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	Open		Forest		Open vs. forest
	>50 m from edge	<50 m from edge	>50 m from edge	<50 m from edge	
<i>Homoptera</i> \bar{x}	3.3	2.7	5.3	3.7	*
range	1-11	1-5	0-15	0-13	
<i>Nematocera</i>	39.9 ***	30.7 ***	38.8	38.4	
	4-168	6-100	10-174	4-231	
<i>Other Diptera</i>	81.1 **	59.2 ***	145 *	109	***
	18-329	14-141	35-395	16-384	
<i>Formicidae</i>	291 ***	635 ***	1151 **	930	***
	2-952	37-3703	65-3770	49-3819	
<i>Other Hymenoptera</i>	45.6 **	52.9 *	44.2 ***	24.4	**
	17-95	9-141	11-133	2-53	
<i>Coleoptera</i>	116 ***	132 ***	268	274	***
	32-193	58-251	105-558	43-786	
<i>Arachnida</i>	155 ***	208	217 ***	129	*
	51-307	72-411	127-370	86-182	
<i>Gastropoda</i>	6.4 *	10.6 ***	24.5	23.3	***
	0-23	3-21	2-93	4-56	

and interior are shown in Table 2. In the open side four taxa preferred interiors, three habitat edge. In the forest in turn, six taxa showed edge preference, two edge avoidance. *Coleoptera* and *Arachnida* were the only groups preferring edge on both sides of the edge. In all the taxa, the catches were larger in the forest edge than in the open habitat edge. As in pitfall data, no consistent differences were found in the variation in catches between edge and interior.

4.2.3. Window traps above the ground

Comparisons of specimens caught from window traps above the ground concentrate on the two most numerous taxa, *Diptera* and *Coleoptera*. Traps in the bush layer of forest caught about 5 times more *Diptera* than traps

on the ground level, and their catch also exceeded that of the canopy traps (Table 5). The number of *Diptera* caught was significantly higher in the habitat interior than in the habitat edge in the bush layer and in the canopy and in both habitats.

For *Coleoptera*, the catches in the bush layer traps in the open and forest sides of the transects did not differ significantly from each other. The average catch in the bush layer traps (open and forest combined) exceeded that of the canopy traps (see Tables 2 and 3). Edge and interior habitats did not differ significantly in the catches of the bush layer and canopy traps.

The values obtained from window traps above the ground and especially from canopy traps should be taken as minimum figures. During hard winds the traps swung a lot, and part of the catch was presumably lost. A decrease in the amount of liquid in the traps

Table 2. Average catch (no. of specimens) and range (min-max) of main invertebrate groups per a pair of window traps in open habitat and forest edges and interiors of the transects. For explanations see Table 1.

	Open		Forest		Open vs. forest
	>50 m from edge	<50 m from edge	<50 m from edge	>50 m from edge	
<i>Homoptera</i> \bar{x}	18.9	6.0	17.3	10.2	
range	0-116	0-15	1-65	1-29	
<i>Nematocera</i>	943	593	1714	819	***
	331-1926	132-1814	210-6001	94-1764	
Other <i>Diptera</i>	287	253	427	303	***
	111-499	143-581	184-1327	69-1033	
<i>Formicidae</i>	32.7	50.4	107	108	***
	0-80	4-97	5-196	3-405	
Other <i>Hymenoptera</i>	38.8	34.7	52.0	42.7	***
	5-152	11-73	13-143	12-73	
<i>Coleoptera</i>	67.1	90.3	141	82.8	***
	10-132	32-241	21-444	20-201	
<i>Arachnida</i>	17.3	24.2	50.8	46.1	***
	1-71	3-56	10-105	14-83	
<i>Gastropoda</i>	1.3	1.3	3.2	4.0	**
	0-4	0-5	0-11	0-16	

Table 3. Average catch (no. of specimens) of *Diptera* and *Coleoptera* per a window trap in the bush layer and the canopy.

	Bush layer				Canopy Forest	
	Open Exterior	Open Edge	Forest Edge	Forest Interior	Edge	Interior
<i>Diptera</i>	670	384	2179	2907	1052	1186
<i>Coleoptera</i>	16.5	20.5	15.8	18.6	9.0	6.2
No. of traps	2	2	5	5	5	5

Table 4. Percentage distribution of *Diptera* and *Coleoptera* into three size classes (body length <2, 2-6, >6 mm) and their medians in window traps at different sites. Relative values 1, 2 and 3 are used for the size classes in calculation of the medians.

	<i>Diptera</i>				<i>Coleoptera</i>			
	<2	2-6	>6	Md.	<2	2-6	>6	Md.
Open								
Ground	18	77	5	1.92	1	54	45	2.42
Bush layer	11	82	7	1.98	0	31	69	2.78
Forest								
Ground	12	84	0	1.95	0	63	37	2.30
Bush layer	22	75	3	1.87	0	74	26	2.18
Canopy	30	67	3	1.80	0	37	63	2.71

Table 5. Percentages of *Diptera* and *Coleoptera* caught in window traps having the window parallel to forest edge and traps with the window perpendicular to forest edge. See Table 1 for the symbols of statistical significance.

	Open		Forest	
	>50 m from edge	<50 m from edge	<50 m from edge	>50 m from edge
<i>Diptera</i>				
window parallel to the edge	37.8	48.0	45.2	45.7
window perpendicular to the edge	62.2	52.0	54.8	54.3
significance	***	**	***	***
<i>Coleoptera</i>				
window parallel to the edge	34.6	49.9	53.4	47.6
window perpendicular to the edge	65.4	51.0	46.6	52.4
significance	***	ns	***	ns

might support this assumption. However, it was observed that evaporation was often stronger in the traps above the ground than in the traps on the ground.

4.3. Size of specimens

We deal here with *Diptera* and *Coleoptera* because their size variation is large and the data base broad enough. In calculation of the size of a mean specimen relative values 1, 2 and 3 were used for the size classes distinguished (see Sect. 3.2.). The 'largest' dipteras were caught from the bush layer of clear-fellings and the 'smallest' ones from the canopy of forest (Table 4). The variation among the different sites had no clear trends; in the forest side the mean size, however, tended to decrease from the ground upwards.

For *Coleoptera* the results were somewhat different (Table 4). The mean size of specimens was larger in clear-fellings than in the forest and in the open habitat larger in the bush layer than on the ground. In the forest, the mean size of specimens increased from the ground towards the canopy.

4.4. Flight direction

Since every pair of window traps had the window parallel to the edge in one trap and perpendicular in the other, the results can be used for studying the flight directions of invertebrates. We deal with the most numerous flying insects, *Diptera* and *Coleoptera*.

The traps with window perpendicular to the edge trapped significantly more *Diptera* than the other traps. The same pattern was observed in all the four main 'habitats': open exterior, open edge, forest edge and forest interior (Table 5). The results for *Coleoptera* were mainly the same. In exterior clear-felling and forest interior the perpendicular traps got more specimens than the parallel traps. In open habitat edge the difference was small, and in forest edge the figures were significantly the opposite (see Table 5).

There was nothing in the location of the window traps which could produce patterns observed. The differences in 'perpendicular' and 'parallel' traps are probably attributable to wind directions prevailing in clear-felling and forest edges (see e.g. Odin 1974), but we do not have any data on them in our study area.

5. DISCUSSION

5.1. Effects of forest succession

The present data can be used for studying the effects of the age of stand on invertebrate numbers only partly, because the open habitats do not differ only with respect to their age but also with regard silvicultural treatments. The data include five different stages of forest succession: mature forest, and four clear-felled areas of different age. In order to diminish the effects of ecotones in the analysis, only the data from habitat interiors were used (transect parts further than 50 m from the edge).

Fig. 4. shows the relative abundance of the four main invertebrate taxa in relation to the age of stand. The two youngest phases (D and E) are pooled. The patterns revealed by pitfall and window trap data are rather dissimilar, which might, however, be explained by differences in species composition in each taxon. A common feature in these two data sets is that all the groups have decreased after clear-felling (at the age of 1–2 years) except Other *Hymenoptera* in pitfall data (mainly *Apidae*) which showed a continuous increase after clear-felling. An increase is also seen in *Arachnida*. After the decrease *Diptera* reached the level of mature forest by the age of 25 years after felling. *Formicidae* decreased during the whole period. The numbers of *Coleoptera* were variable but a slight decreasing trend was evident.

In window trap data Other *Hymenoptera* exceeded shortly after felling the level present in mature forest. *Diptera* decreased during the whole period. All the other groups showed a clear trend towards the density in old forest.

A heavy ploughing after clear-felling is presumably the reason for the general decrease in arthropod densities. The effects of clear-felling (and also prescribed burning) are usually not so detrimental; in fact, most groups benefit from these measures (Huhta et al. 1967 and references therein). Huhta (1971, 1976) found out that in Northern Finland *Coleoptera* increases whereas *Araneae* and *Diptera* larvae decrease during the first thirteen years after clear-felling.

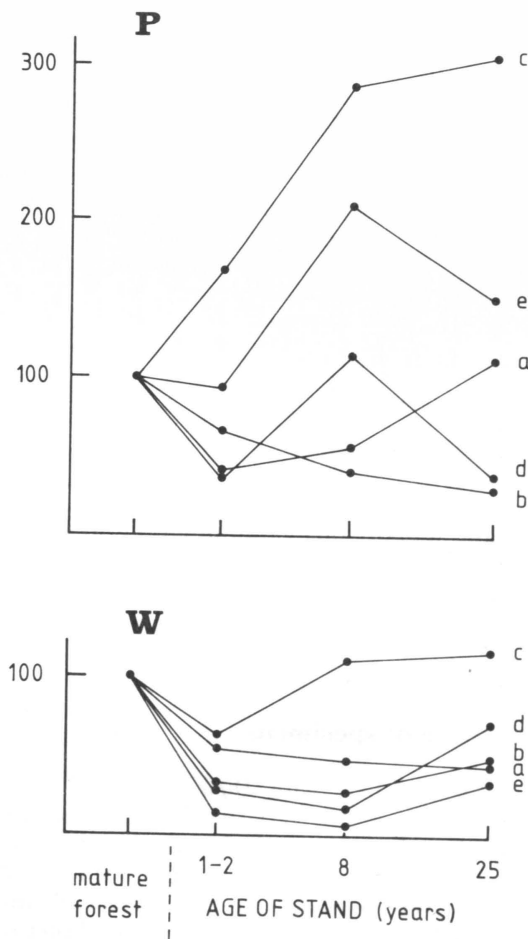


Fig. 4. Relative abundances of the most important invertebrate groups in relation to the age of stand in the data. Relative abundance in mature forest = 100; see text for further explanation. P = pitfall data, W = window trap data. a *Diptera*, b *Formicidae*, c Other *Hymenoptera*, d *Coleoptera*, e *Arachnida*.

5.2. Invertebrate numbers and vegetation characteristics

Multiple regression analyses were run in order to assess how the vegetation characteristics measured in the field explain the variation in invertebrate numbers. The analyses were made separately for clear-fellings and forests as well as for pitfall and window trap data. Eight independent variables were used for open habitat data, six for forest data (see Table 6).

The correlations between the vegetation variables are shown in Table 6. Seven out of the 28 correlations in clear-felling data are significant; the corresponding proportion in forest data amounts to 2/15. The proportion of significant correlations of all the correlations between the invertebrate groups and vegetation features varies by habitat and trapping method. In clear-felling data it exceeds that of forest data and in pitfall data that of window trap data.

The variation among the variance explained in the regression models is large

(Table 7). In general, the variables used best explained the variation in the numbers of Other *Hymenoptera* and *Arachnida* while the poorest results are obtained for *Coleoptera* and *Homoptera* (Table 7).

The power of explanation in the regression models is clearly higher in clear-fellings than in forests. This is probably due to lesser environmental heterogeneity in open habitats as compared to multilayered forest habitat. As regards the explanation power of the individual variables two are above the others. Sapling density has 18 significant correlations out of altogether 24 (main taxa, habitats and trapping methods pooled; all positive, the higher the density the larger the catch), and the distance to the edge has 17 significant correlations (all negative, the further the edge the smaller the catch).

5.3. Relations to bird studies

Especially in the forest side the edge preference by invertebrates was clear, which confirms the assumption that high bird density at forest edges could be due to high invertebrate density there. The distance to the forest edge and sapling density were among the best vegetation variables in explaining the variation in invertebrate numbers. Helle (1983) showed that sapling density (or the strength

Table 6. Correlations between the vegetation features studied in the trapping transects. Explanation for the variables: DIS – distance from the forest edge, MOS – coverage of mosses, LIT – coverage of litter, MIN – coverage of mineral soil, DWA – coverage of dwarf shrubs, GRA – coverage of grasses and sedges, HER – coverage of herbs, SAP – sapling density. The critical r value for $p < 0.05$ is 0.361.

Clear-fellings	
DIS	
MOS	-.162 MOS
LIT	-.253 -.172 LIT
MIN	.094 -.664 -.191 MIN
DWA	-.096 .529 -.073 -.551 DWA
GRA	-.246 .249 .350 -.558 .255 GRA
HER	.104 .065 -.121 -.197 .124 .477 HER
SAP	-.130 .802 -.126 -.654 .513 .354 .356
Forests	
DIS	
MOS	.096 MOS
LIT	-.043 -.489 LIT
DWA	.076 -.049 .324 DWA
GRA	-.109 -.344 .168 .170 GRA
SAP	-.197 .435 .095 .200 -.103

Table 7. Total percentages of variance explained in multiple regression analyses for the main invertebrate groups in the main habitats in pitfall and window trap data. For the independent variables see Table 6. Statistically significant figures are shown, symbols as in Table 1.

	Clear-fellings		Forests	
	pit-fall	window trap	pit-fall	window trap
<i>Homoptera</i>	12.1	31.1	16.4	18.8
<i>Diptera</i>	82.8***	26.4	31.6	40.6
<i>Formicidae</i>	35.0	83.2*	40.0	17.5
Other <i>Hymenoptera</i>	66.1**	54.7	66.9**	52.7
<i>Coleoptera</i>	25.1	49.1	20.1	40.6
<i>Arachnida</i>	70.4**	58.2	71.7***	26.5

of bush layer) was the best variable in predicting the breeding bird density in forest edges. That study and also Helle (1984) suggest that the strength of bush layer depends on the age of the edge: in young edges (recently created by clear-felling) it is sparse and in older ones well-developed. Combining the present data and earlier bird studies forest edges A and B can be considered 'good' bird edges (density clearly higher than in the forest interior) and C, D and E 'poor' bird edges (density equal or lower than in the forest interior; see Helle 1983). When the invertebrate numbers of these two edge types are compared, no consistent difference can be found. In pitfall data five taxa out of eight are in agreement, three against the pattern found in bird density; the figures are four vs. four in window trap data. In the bush layer and canopy the result is against the expectation.

The food availability for air feeding birds is presumably best covered in this study. The food resources of birds foraging on the ground

6. FINAL REMARKS

Finally, we want to pay attention to four points. First, our data originate from one summer only. Although the season was rather normal as regards the weather conditions, there may be year-to-year variation in the phenomenon assessed. Second, the results obtained support the idea that forest edges harbor a rich invertebrate fauna. More detailed analyses, however, fail (comparison between 'good' and 'poor' bird edges). It should be remembered that in this study we are working on a very general level dealing with broad animal taxa, the importance of which for birds are not exactly known.

We have assumed that the edge width does not exceed 100 m. In most bird studies the edge breadth has been supposed to be 50 m or less, but very little is known of it (e.g. Gates & Mosher 1981). The simplest way to determine the breadth of the edge effect is to

are imperfectly studied here, because pitfall data include e.g. only few *Oligochaeta*, which are important for many of these birds (e.g. v. Haartman et al. 1963–72). The food availability in the bush layer and canopy is also only partly covered here. Insect larvae are very important for many bird species, and these occurred poorly in our traps.

The importance of the diversity of vegetation on bird life has been documented in several studies since MacArthur & MacArthur (1961). The properties of vegetation are obviously not the basic factor, but the amount of invertebrates found in it (e.g. Nilsson 1979, Robinson & Holmes 1984, and references therein). Relating the amount of food available to parameters of bird communities such as total density or species diversity or densities of different feeding ecological groups is now immature. More advanced trapping techniques and more thorough information on the diets of individual bird species are needed.

gather data from a very long transect, but this approach creates a problem, as the longer the transect is the more probably it includes several vegetation types.

We used several vegetation characteristics in explaining the variation in invertebrate numbers. An important environmental variable affecting invertebrate life is the microclimate of a site or habitat (see e.g. Szujeci 1966, Huhta et al. 1967, Thiele 1977, and references therein), and it should preferably be included. According to some scattered observations the mean temperatures in clear-fellings and forests were nearly equal, whereas the daily variation in temperature (min-max) was about 2.5 °C wider in open than in forest habitat (see also Leikola 1975). It is probable, however, that vegetation (which is studied here) reflects the microclimate of a site – at least in some extent.

REFERENCES

- Adis, J. 1979. Problems in interpreting arthropod sampling with pitfall traps. *Zool Anz.* 202: 177–184.
- Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia (Berl.)* 41: 25–46.
- Gates, J. E. & Mosher, J. A. 1981. A functional approach to estimating habitat edge width for birds. – *Am. Midl. Nat.* 105: 189–192.
- v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuori, R. 1963–72. Pohjolan linnut värikuvain 1–12. Otava, Helsinki.
- Haila, Y., Järvinen, O. & Väisänen, R. A. 1980. Effects of changing forest structure on long-term trends in bird populations in SW Finland. *Ornis Scand.* 11: 12–22.
- Hansson, L. 1983. Bird numbers across edges between mature conifer forest and clearcuts in Central Sweden – *Ornis Scand.* 14: 97–103.
- Helle, P. 1983. Bird communities in open ground – climax forest edges in Northeastern Finland. *Oulanka Reports* 3: 39–46.
- 1984. Effects of habitat area on breeding bird communities in Northeastern Finland. *Ann. Zool. Fennici* 21: 421–425.
- 1985. Effects of forest regeneration on the structure of bird communities in Northern Finland. – *Holarctic Ecology* 8 (in press).
- & Järvinen, O. 1985. Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 43 (in press).
- Hogstad, O. 1967. The edge effect on species and population density of some passerine birds. *Nytt Magasin Zool.* 14: 40–43.
- Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. *Ann. Zool. Fennici* 8: 483–542.
- 1976. Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. *Ann. Zool. Fennici* 13: 63–80.
- , Karppinen, E., Nurminen, M. & Valpas, A. 1967. Effects of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. *Ann. Zool. Fennici* 4: 87–143.
- Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977. Metsien rakenteen muutoksen vaikutus pesimälinnustoomme viimeisten 30 vuoden aikana. Summary: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. *Silva Fenn.* 11: 284–294.
- Leikola, M. 1975. Verhopuuston vaikutus metsikön lämpöoloihin Pohjois-Suomessa. Summary: The influence of the nurse crop on stand temperature conditions in northern Finland. *Commun. Inst. For. Fenn.* 85: 1–33.
- MacArthur, R. H. & MacArthur, J. W. 1961. On bird species diversity. *Ecology* 42: 594–598.
- Nilsson, S. G. 1979. Density and species richness of some forest bird communities in South Sweden. *Oikos* 33: 392–401.
- Odin, H. 1974. Några meteorologiska förändringar vid hyggesupptagning. Summary: Some meteorological effects of clear felling. *Sveriges Skogsvårdsförb. Tidskr.* 72: 60–65.
- Odum, E. P. 1971. *Fundamentals of ecology.* 3rd ed. Philadelphia, Saunders.
- Oelke, N. 1966. 35 years of breeding bird census work in Europe. *Audubon Field Notes* 20: 635–642.
- Robinson, S. K. & Holmes, R. T. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *The Auk* 101: 672–684.
- Southwood, T. R. E. 1978. *Ecological methods with particular reference to the study of insect populations* 2nd ed. London.
- Söyrinki, N., Salmela, R. & Suvanto, J. 1977. Oulangan kansallispuiston metsä- ja suokasvillisuus. Summary: The forest and mire vegetation of the Oulanka National Park, Northern Finland. *Acta For. Fenn.* 154: 1–150.
- Szujeci, A. 1966. Zależność między wilgotnością wierzchniej warstwy gleb lesnych a rozmieszczeniem kusakowatych (Staphylinidae, Col.) na przykładzie nadlesnictwa szeroki bor w puszczy piskiej. *Folia Forest. Polon.* 12, Ser. A.
- Thiele, H. U. 1977. *Carabid beetles in their environments.* Berlin, Springer.
- Tiainen, J., Vickholm, M., Pakkala, T., Piironen, J. & Virolainen, E. 1983. Impact of the amount of edges and habitat diversity on the breeding bird community in southern Finnish forests. *Proc. VIII Int. Conf. Bird Census Work.*
- Törmälä, T. 1982. Evaluation of five methods of sampling field layer arthropods, particularly the leafhopper community, in grassland. *Ann. Ent. Fenn.* 48: 1–16.
- Tretzel, E. 1955. Technik und Bedeutung des Fallenfanges für ökologische Untersuchungen. *Zool. Anz.* 155: 276–287.
- Viramo, J. (ed.) 1979. *Kuusamon alueen luonnosta. Summary: Studies on the natural environment of the Kuusamo district, Northeastern Finland.* *Oulanka Reports* 1: 1–236.

Total of 30 references

SELOSTE

SELKÄRANGATTOMIEN RUNSAUSSUHTEISTA AVOHAKKUUALUEIDEN JA METSIEN REUNA-ALUEILLA POHJOIS-SUOMESSA

Selkärangattomien eläinten runsautta tutkittiin avohakkuualoilla, metsissä ja näiden reunoissa Pohjois-Suomessa kesä-elokuussa 1983. Eläimiä pyydettiin kohtisuoraan metsänreunojen poikki kulkevilla linjoilla, jotka ulottuivat 100 m reunasta kumpaankin suuntaan. Kullakin linjalla oli maassa 48 kuoppapyydystä ja 16 ikkunaloukkua sekä puu/pensaskerrossa 4–6 ikkunaloukkua. Saalis määritettiin pääsääntöisesti lahkon tarkkuudella.

Kuoppapyydöksissä hyönteisryhmät yhtäläissiipiset (*Homoptera*), kaksisiipiaiset (*Diptera*), muurahaiset (*Formicidae*) ja kovakuoriaiset (*Coleoptera*) sekä etanat ja kotilot (*Gastropoda*) olivat metsässä runsaimpia, hyönteisistä muut pistiäiset (*Hymenoptera*) kuin muurahaiset ja varsinaiset hämähäkkieläimet (*Arachnida*) puolestaan hakkuualoilla. Maanpinnan ikkunapyydöksissä kaikki ryhmät olivat metsässä runsaimpia kuin hakkuualalla. Kuoppa-aineistossa kahdeksasta tärkeimmästä ryhmästä kuusi esiintyi runsaimpana metsänreunassa. Muurahaiset, muut pistiäiset, hämähäkit sekä etanat ja kotilot suosivat reunaa sekä hakkuualan että metsän puolella. Ikkunaloukkuaineistossa reunansuosintaa ei havaittu hakkuualan puolella, mutta metsän puolella se oli selvä. Biotoopista riippumatta kovakuoriaiset ja hämähäkit olivat reunoissa runsaimpia kuin kauempana hakkuualalla tai metsässä.

Eläinryhmien runsauseroja eri pyyntipaikoilla tutkittiin regressioanalyysin avulla. Selittävinä muuttujina olivat etäisyys metsänreunasta, sammalten, karikkeen, mineraalimaan, varpujen, heinien ja sarojen sekä ruohovartisten kasvien peittävyys ja taimikon tiheys. Analyysi tehtiin erikseen avohakkuualoille ja metsille sekä kuoppapyydys- ja ikkunaloukkuaineistoille. Muutujat selittivät parhaiten ryhmien muut pistiäiset (keskim. 60.1 %) ja hämähäkit (56.7) runsauseroja ja kehnoimmin ryhmien kovakuoriaiset (33.3) ja yhtäläissiipiset (19.6) runsauseroja. Kokonaisselityssaste oli avohakkuualojen aineistossa korkeampi kuin metsästä kerättyssä aineistossa (49.6 vs. 37.0 %) ja pitfallaineistossa korkeampi kuin ikkunaloukkuaineistossa (44.9 vs. 41.7 %). Käytetyistä muuttujista parhaiten eläinryhmien runsauseroja selittivät etäisyys metsänreunasta ja taimikon tiheys.

Tulokset tukevat olettamusta, että lintujen yleensä korkea pesimäaikainen tiheys metsänreunoissa olisi osaltaan seurausta ravinnon suuremmasta runsaudesta siellä. Tutkimuksessa tarkastellaan, miten hyvin työssä käytetyillä menetelmillä voidaan arvioida linnuille tarjolla olevan ravinnon määrää.