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Carabid beetles in fragments of coniferous forest

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We compared samples of carabid beetles (Coleoptera, Carabidae) from fifteen forest fragments in a suburban-agricultural setting with catches from a nearby large contiguous forest in Espoo, southern Finland. Forest fragments were relatively similar in vegetation and ranged in area from 0.5 to 21.5 ha. Samples were collected by pitfall traps from forest-fragment interior and edge and from the surrounding agro-urban environment. Abundance and species richness of carabids was lowest in the contiguous forest and highest in the fragment surroundings. Contiguous forest had none, large (9.6–21.5 ha) and medium-sized forest fragments (4.2–8.2 ha) a few, and small fragments (0.5–3.0 ha) several species typically found in the surrounding open habitats. High carabid diversity in the small fragments and in the surroundings was probably related to the higher vegetational diversity in such sites. High diversity of vegetation, in turn, was due to moderate human disturbance and effects of vegetation succession. Most of the abundant carabid species were non-randomly distributed among the habitat types. Some specialized forest carabids were caught exclusively in contiguous forest and only the most generalized forest species were obtained from small forest fragments. These results indicate that in order to preserve the integrity of forest arthropod faunas in urban areas it is essential to leave large, continuous forest tracts untouched to preserve specialist species and forest species assemblages.

1. Introduction

Fragmentation of continuous habitat, e.g. boreal forest, has two significant consequences for the biota. First, the total area of the habitat decreases, and second, the habitat that is left is broken up into isolated remnants (Saunders et al. 1991). Large areas fragmented by human activities have greatly changed natural landscapes (e.g. Burgess & Sharpe 1981, Harris 1984). For instance, in Espoo on the southern coast of Finland, forests were large and contiguous at the beginning of this century, but since the 1950's urbanization has split them into small and isolated fragments (Fig. 1). In the 1930's there were 25 different forest areas in southern Espoo. By the late 1970's the number of forest patches had increased to 603, but 85% of them were less than 5 ha (Wuorenrinne 1983). The ground vegetation had also changed, and was mostly worn and damaged in forest fragments of less than 2 ha (Wuorenrinne 1983). Further, the proportion of forest edge, or ecotones, has markedly increased.

Fig. 1. Reduction and fragmentation of forested area in southern Espoo between 1752 and 1976. Before 1872 fragmentation mainly due to agriculture and after 1872 to urbanization (maps reproduced with permission from H. Wuorenrinne).

A typical feature for habitat fragments is the high proportion of edge as compared to continuous area (e.g. Merriam & Wegner 1992). Ecotones function as a filter between different biotopes for movement of organisms and other particles (Forman & Moore 1992). Edges often have different species composition and abundance due to the 'edge effect' (Odum 1971, Morris & Webb 1987, Rusek 1992). Colonization is two-directional between fragments and the surrounding matrix through ecotones (Duelli 1990). Species from the fragments disperse to the surroundings and vice versa, and these two species groups may occur together in the edge. Which species prevail in the fragments depends on dispersal ability, habitat preference and species interactions.

The theory of island biogeography (MacArthur & Wilson 1967) has often been applied in studies of ecological processes in fragmented environments (Usher 1987). This is based on the assumption that immigration and extinction are similar processes both in biotope 'islands' and on true islands (Thomas et al. 1992). However, patchy terrestrial environments differ from real archipelagoes in that the intervening matrix is usually less hostile for dispersing individuals than is the water surrounding true islands (Forman & Godron 1981, Niemelä & Haila 1986, Webb 1989). Terrestrial habitat fragments are never completely isolated; paraphrasing Janzen (1983): 'No park is an island'.

In this paper we investigate the occurrence of carabids (Coleoptera, Carabidae) among forest fragments and in the adjacent urban-agricultural matrix. In particular, we focus on the effects of fragment area on carabid assemblages by comparing samples from different-size forest patches with a continuous forest of similar type. We examine characteristics of the assemblages, such as species richness and relative abundance, and study relationships between species occurrence and their characteristics, such as wing-length, body size and type of diapause.

2. Material and methods

2.1. Study area and sampling sites

We collected carabid beetles in two areas, namely in 15 forest islands in southern Espoo and in 10 sampling sites in a large contiguous forest area in northern Espoo (ca. 60°N, 25°E) (Fig. 2). The inter-patch distances in the south were 500 m – 5 km and the distance from the center of the study area in the south to the continuous forest was ca.

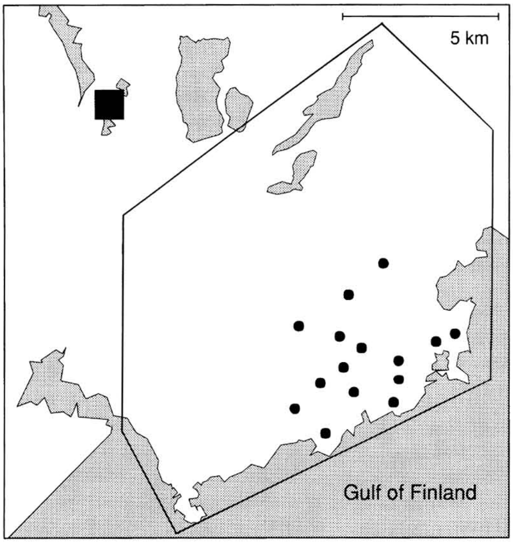

Fig. 2. Location of the sampling sites in Espoo. Contiguous forest area marked with square, forest islands with filled circles. The area of Fig. 1 is outlined.

10 km. All the forests sampled belonged to the *Myrtillus*- or *Oxalis-Myrtillus* forest-site type (Cajander 1949). The forest fragments were divided into three size-classes, five fragments in each: small (0.5–3.0 ha), medium (4.2–8.2 ha) and large (9.6–21.5 ha). The surroundings included various open habitats such as lawns, cultivated fields and abandoned fields. We took samples in the interiors, the edges (except in the small forest fragments) and the surroundings of each forest island.

The field and ground layer vegetation was described in five randomly selected 1 m^2 squares at each site. The most dominant herb species were *Vaccinium myrtillus, Deschampsia flexuosa, Melampyrum pratense* and mosses *Pleurozium schreberi* and *Polytrichum* spp. The dominant trees were *Picea abies, Pinus sylvestris* and *Betula pubescens* (Appendix 1).

2.2. Sampling procedure and statistical treatments

To collect the beetles we used pitfall trapping (Southwood 1978, Niemelä et al. 1985, 1986). The traps were transparent plastic jars (170 ml, diameter 67 mm) filled to one third with water, NaOH and detergent. Fifteen traps (ca. 5 m apart) were placed in each sampling site in three rows, five traps per row. Traps were in operation for five days in the early season (3–10 June, 1983) and five days in late season (1–7 August, 1983). This trapping procedure is sufficient for the purpose of this study. For instance, Niemelä et al. (1990), in comparing ten-day sampling periods with the pooled whole season sample, found that the set of dominant species in the shorter sampling periods and in the whole season sample was similar. Also the species rank order among the different samples was similar. However, they cautioned against unwarranted conclusions based on material collected during short sampling periods.

To control the effect of catch size on species richness, we used the rarefaction method (Simberloff 1978, James & Rathbun 1981) for comparing numbers of species. This method estimates number of species for random subsamples out of a larger sample. Plant and carabid samples were separately subjected to detrended correspondence analysis (DCA, Gaugh 1982) to study their compositional similarity. The method has been widely used in studies of the relationship between carabid distribution and environmental characteristics (e.g. Niemelä et al. 1985, Eyre & Rushton 1989, Eyre & Luff 1990, Eyre et al. 1989, 1990, Rushton et al. 1990, Holmes et al. 1993). However, Wartenberg et al. (1987) criticized the method and recommended a cautious interpretation of the ordination. We use the method in an exploratory fashion for comparing relative distances among sites, not for strict hypothesis-testing (see Birks 1987). When studying clustering of carabid assemblages in the ordination analyses and species occurrence among forest types we used Kruskal-Wallis non-parametric ANOVA and Tukey-type *a posteriori* tests in subsequent multiple comparisons from the BMDP3S statistics package (Dixon 1990).

3. Results

3.1. Vegetation cover of the fragments

In our DCA-ordination of the vegetation of the sampling sites (Fig. 3), the first axis of the ordi-

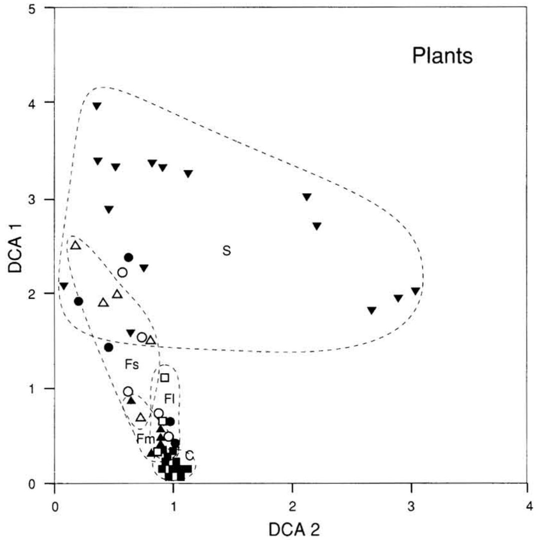

Fig. 3. Location of the sampling sites by DCA-ordination (1st and 2nd axes) according to plant cover. Eigenvalue of first axis, 0.48 and second axis, 0.32. Symbols: contiguous forest (C), large forest fragments (Fl), ▲ medium-size forest fragments (Fm), △ small forest fragments (Fs), ▼ fragment surroundings (S), ● edges of large forest fragments (Fel), ○ edges of medium-size fragments (Fem).

nation identified a gradient from field vegetation to forest vegetation. Sampling sites from the different forest fragment size-classes formed, by and large, separate clusters. However, sites from the surroundings were scattered due to great variation in their floristic composition. The second axis was determined by variation among the sampling sites located in the surroundings. In summary, the vegetation was fairly similar in contiguous forest and in larger forest fragments but the smallest forest patches, all the edges and patch-surroundings varied considerably.

Table 1. Number of species and individuals per site and number of sampling sites by habitat type. C = contiguous forest, Fl = large forest fragments, Fm = medium-sized forest fragments, Fs = small forest fragments, Fe = edge, S = surroundings.

	C	Fl	Fm	Fs	Fe	S
Species	16	19	15	25	32	54
Beetles/site	44	39	54	81	76	115
Sampling sites	10	5	5	5	10	15

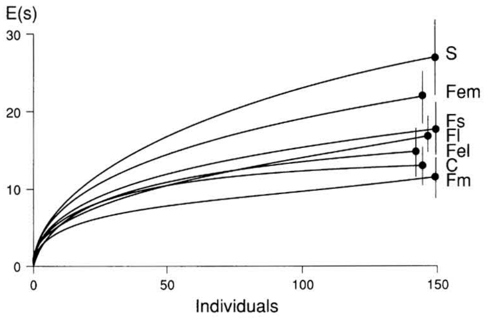

Fig. 4. Species richness *E*(*s*) standardized by rarefaction to 150 individuals (*N*). Symbols: C = contiguous forest area, Fl = large forest fragments, Fel = edges of large forest fragments, Fm = medium-size forest fragments, Fem = edges of medium-size forest fragments, Fs = small forest fragments, S = surroundings.

3.2. Carabid assemblages in the forest fragments

Total carabid abundance was lowest in the contiguous forest and in the large fragments (Table 1, Appendix 2). Beetle catches increased as the size of the fragment decreased, and the surroundings yielded the highest numbers. Carabid species richness was significantly higher in the patch-surroundings than in the forest fragments (Table 1, Fig. 4). However, rarefaction estimates of species richness in small fragments, large fragments and contiguous forest did not differ significantly from each other.

We then compared the estimated species richness in individual sites in the surroundings and in the contiguous forest. The expected number of species in the contiguous forest sites did not differ from those in the surroundings (*t*-test, $t = 1.35$, $P = 0.19$ for 30 individuals, and $t = 0.90$, $P = 0.38$ for 40 individuals), indicating that the high species richness in the pooled sample from the surroundings was mainly a consequence of high variability between sampling sites. The high variability in the assemblages in the surroundings was also reflected in the pairwise comparisons using the Czekanowski percentage similarity index. Samples from contiguous forest were most similar with each other, whereas samples from surroundings were least similar to each other (Table 2).

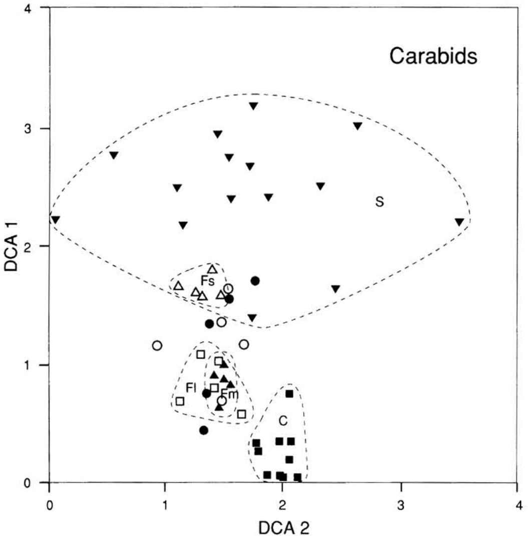

Fig. 5. Location of sampling sites by DCA-ordination (1st and 2nd axes) according to carabid samples. Eigenvalue of the first axis, 0.49 and second axis, 0.18. Symbols as in Fig. 3.

We made a DCA-ordination based on the carabid samples of the sites (Fig. 5). The first axis of the ordination (eigenvalue 0.49) identified a gradient from the fragment surroundings to the contiguous forest. Sites from different fragment size classes formed separate clusters (Kruskal-Wallis AOV, $H = 42.50$, $P < 0.001$). An *a posteriori* multiple comparison revealed that the location of contiguous forest sites along the first axis differed from that of small forest fragments ($Z = 3.38$, $P < 0.05$) and from that of surroundings ($Z = 6.09$, $P < 0.05$), and large and medium sized forest fragments differed from surroundings ($Z = 3.41$, $P < 0.05$ and $Z = 3.12$, $P < 0.05$). Edges were scattered across the ordination. The second axis of the ordination (eigenvalue 0.18) described differences between the samples from the surroundings but did not permit a clear biological interpretation (Fig. 5). The correlation between the first axes of the carabid ordination and vegetation ordination was statistically significant (Spearman rank correlation, $r_s = 0.82$, $P < 0.001$) indicating that carabids and plants react similarly to some common environmental variables. In conclusion, it appears that, based on the DCA-analysis, two types of carabid assemblages can be distinguished: (1) assemblages in the surroundings and small fragments, and (2) assemblages in the larger fragments and in the continuous forest.

Table 2. Number of sampling sites (*n*), mean value of the Czekanowski percentage similarity and its range for carabid catches from sampling sites by habitat type.

	n	mean	range
Contiguous forest	10	79	50–93
Large forest fragments	5	30	12–47
Medium-size forest fragments	5	51	21–75
Small forest fragment	5	50	29–76
Edges of large forest fragm.	5	27	6–50
Edges of medium forest fragm.	5	24	5–52
Surroundings	15	20	0–65

3.3. Species characteristics and occurrence among habitat types

The 15 abundant carabid species (>50 individuals of each captured) can be divided into four distributional types based on the Kruskal-Wallis ANOVA and the subsequent pairwise comparisons between habitat types (Table 3 and Table 4):

a) *Trechus secalis* was the only habitat generalist that occurred in equal numbers in all habitat types.

b) Five species were widely distributed in forested habitats but were scarcer in the surroundings. *Pterostichus niger* was classified as a forest generalist, although it had a bizarre distribution, being numerous in the contiguous forest and in the surroundings but scarce in the other habitat types. None of these five species was restricted to the contiguous forest but the scarcer *Carabus glabratus, C. violaceus, Cychrus caraboides* and *Pterostichus nigrita,* were almost entirely confined to the contiguous forest (Appendix 2).

c) Four species were more abundant in the small forest fragments and surroundings than in the larger forest fragments.

d) Five species were more numerous in the surroundings than in the forested habitats. They were all found in low numbers in the small forest fragments but were virtually absent from the larger fragments (Appendix 2).

Although the distribution of *Loricera pilicornis* and *Patrobus atrorufus* did not differ from random distribution in the ANOVA (Table 3), they were assigned to the distributional groups above because the lack of statistical significance was mainly due to low catches in some habitat types. None of the abundant species was consistently most numerous in the edges.

Table 3. Pairs of habitat types with significantly different catches of the 15 abundant carabid species based on a Tukey-type multiple comparison following a Kruskal-Wallis non-parametric ANOVA. Habitat type with higher catch given first. Habitat abbreviations: C = contiguous forest, Fl = large forest fragments, Fm = medium-sized forest fragments, Fs = small forest fragments, Fe = edge, S = surroundings. Statistical significance: ° $P < 0.10$, * $P < 0.05$.

Species	Habitat pairs
Pterostichus niger	C – Fl *
	C – Fm *
	C – Fs °
	C – Fe *
	C – S *
Pterostichus oblongopunctatus	Fm – S *
	Fs – S *
	Fe – S °
Amara brunnea	Fl – S *
	Fm – S *
	Fs – S *
	Fe – S *
Calathus micropterus	C – S *
	Fl – S *
	Fm – S *
Carabus hortensis	C – Fs *
	C – S *
Leistus terminatus	Fs – C *
	Fs – Fl *
Carabus nemoralis	Fs – C *
	S – C *
	Fs – Fl °
	S – Fm *
Pterostichus melanarius	Fs – C *
	S – C *
	S – Fm *
Amara aulica	S – C *
	S – Fe *
Amara communis	S – C *
	S – Fm *
	S – Fe *
Harpalus rufipes	S – C *
	S – Fe °
Bembidion lampros	S – C *
	S – Fe *
Patrobus atrorufus	–
Loricera pilicornis	–
Trechus secalis	–

The 'invasion' of forest by open-habitat species increased as the size of the fragment decreased. Of the 23 species classified as strict inhabitants of open, grassy environments by Lindroth (1985, 1986), 8 were found also in the small fragments, 1 in the medium-size ones, and 2 in the large fragments. None of these species was found in the contiguous forest (Table 4, Appendix 2).

Table 4. Catches of the 15 most abundant carabid beetles per site classified into four distributional types based on the Kruskal-Wallis ANOVA and subsequent multiple comparisons. Species of open habitat in last rows classified according to Lindroth (1985, 1986): *Amara* spp. (except *A. brunnea*), *Bembidion* spp., *Clivina fossor, Harpalus* spp. (except *quadripunctatus*), *Pterostichus cupreus, P. vernalis, P. versicolor, Calathus melanocephalus, Anisodactylus binotatus*. C = Contiguous forest, Fl = large fragments, Fm = medium fragments, Fs = small fragments, Fe = edge, S = surroundings, – = species not caught.

Carabid species	C	Fl	Fm	Fs	Fe	S
Habitat generalist						
Trechus secalis	7	6	13	21	16	14
Forest generalists						
Pt. oblongopunctatus	4	7	12	11	11	2
Pt. niger	10	0	0	1	0	13
Amara brunnea	1	10	13	10	9	1
Calathus micropterus	8	7	6	5	5	0
Carabus hortensis	5	3	5	1	2	0
Abundant in small fragments and surroundings						
Leistus terminatus	0	–	0	5	2	1
Carabus nemoralis	–	0	–	5	2	4
Pt. melanarius	–	0	–	14	12	31
Patrobus atrorufus	0	–	1	1	4	5
Species of open habitat						
Amara aulica	–	0	0	1	–	6
A. communis	–	0	–	1	0	6
Harpalus rufipes	–	–	–	0	0	7
Bembidion lampros	–	–	–	0	–	3
Loricera pilicornis	0	0	0	0	1	3
No. of open–habitat species	0	2	1	8	7	23
Ind. of open habitat spp.	0	2	1	21	12	530
Proportion (%) of total catch	0	1.0	0.4	5.2	1.8	14.3

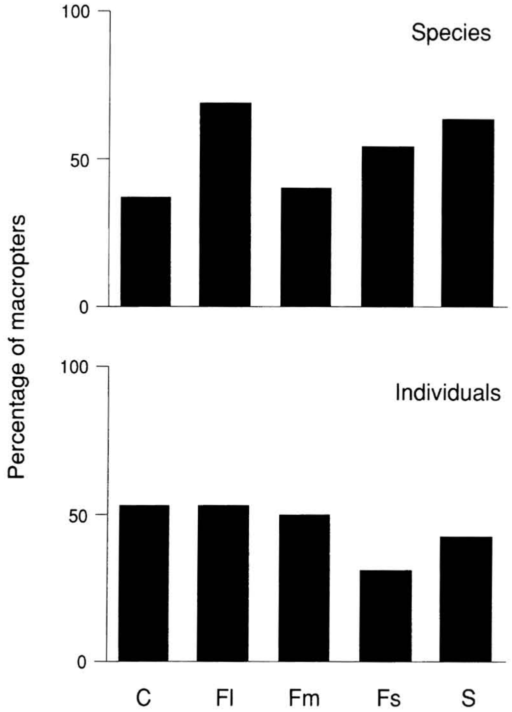

Fig. 6. Proportion of macropterous species and individuals by habitat type. For abbreviations see Fig. 3.

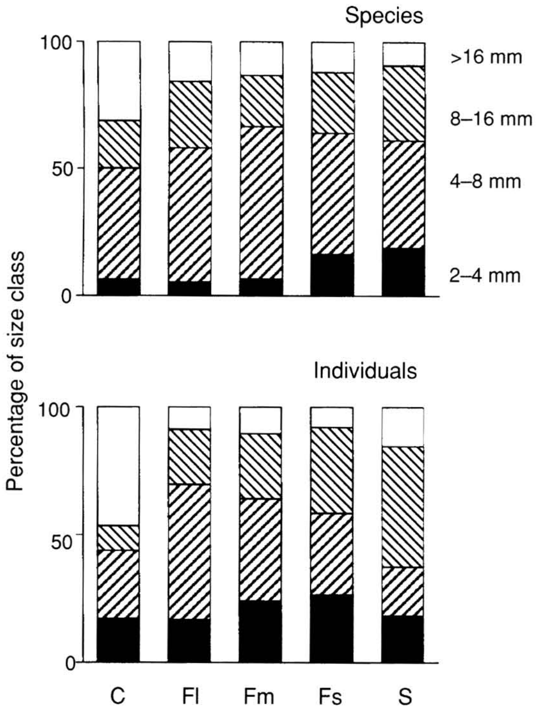

Fig. 7. Proportion of carabid species and individuals in four body-size classes. For abbreviations see Fig. 3.

We compared the proportions of macropterous and brachypterous species and individuals in different fragment-size classes. The dimorphic species were included in the short-winged or long-winged group according to their wing-length in the present material. A total of 789 individuals (of them, 652 *Pterostichus melanarius*) belonged to six dimorphic species. The proportion of macropterous species varied greatly from the low of 37% in the contiguous forest to the high of 63% in the surroundings, but the differences between habitat types were not statistically significant ($G^2 = 5.40$, $P < 0.1$) (Fig. 6).

The proportion of long-winged individuals decreased along the gradient from the contiguous forest to the surroundings. There were significantly more short-winged individuals in the small fragments and in the surroundings than in the contiguous forest ($G^2 = 37.15$, $P < 0.001$ and $G^2 = 21.68$, $P < 0.001$, respectively). However, the statistical significance was due to only one species, *Pterostichus melanarius,* which, although dimorphic, was almost exclusively short-winged in our data.

We divided the carabid species into four body-size classes (Fig. 7). The proportion of species in the second smallest size-class (4–8 mm) was highest in all fragment-size classes. In samples from small forest fragments and surroundings, the number of large species (>16 mm) was low, whereas as in the contiguous forest the number of large species was higher. Thus, forest species were on average slightly larger than field species, but the difference was not statistically significant ($G^2 = 8.71$, $P > 0.1$).

The body-size distribution of individuals differed among the fragment-size classes ($G^2 = 504.68$, $P < 0.001$). As in species, large (>16 mm) individuals were more abundant in the contiguous forest than in the forest fragments or surroundings.

The distribution of adult- and larval-hibernators among species and individuals is shown in

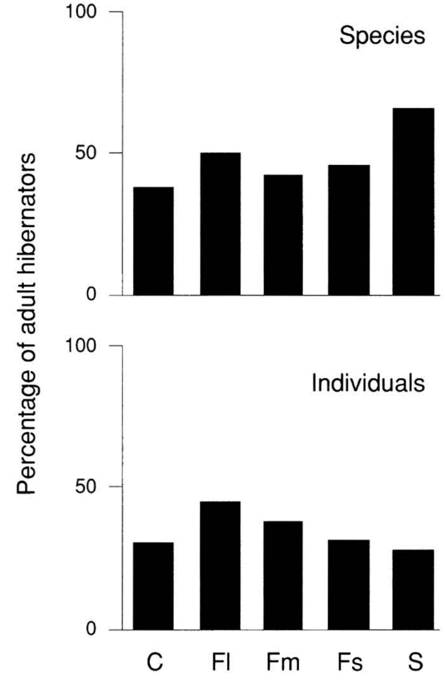

Fig. 8. Proportion of adult hibernators by habitat type. For abbreviations see Fig. 3.

Fig. 8. The proportion of species hibernating as larvae was 34% in the surroundings, nearly 50% in the forest fragments and edges, and 62% in the contiguous forest. The difference between the proportions in the contiguous forest and surroundings was statistically significant ($G^2 = 4.01$, $P < 0.05$), but the other habitats did not differ from each other. In each fragment size-class, the number of individuals hibernating as larvae was greater than those hibernating as adults, but differences between the fragment types were not consistent.

4. Discussion

Three main conclusions arise from this study:

1) composition of carabid assemblages varied greatly among the habitat types,
2) strict forest specialists were found only in the contiguous forest, and 'invasion' of species from the surroundings increased as fragment-size decreased, and
3) there were small differences in the characteristics of species occupying the different habitat types.

We will discuss these observations below.

4.1. Structure of carabid assemblages in the fragment size-classes

Both carabid catches and species richness were lower in the contiguous forest than in the small forest fragments and in the surroundings. This observation of higher carabid diversity in open habitats as compared to closed coniferous forest is in accordance with other studies from southern Finland (e.g. Niemelä & Halme 1992). Our results corroborate that earlier conclusion that coniferous boreal forest, as a rule, harbours less diverse carabid fauna than do adjacent open habitats. The higher carabid diversity in the open habitats was not due to higher 'point' or alpha diversity but to higher beta-level diversity. At single sampling sites alpha diversity was similar in the surroundings and in the contiguous forest, but pooling of several sites from the open habitat increased the overall carabid diversity of that habitat type. This increase did not occur in the contiguous forest where the assemblages in different individual sites were fairly similar.

The high carabid diversity in the open habitat of the surroundings is probably attributable to the generally higher 'biological productivity' and small-scale habitat diversity of open and moderately human-modified habitats as compared to closed coniferous forest (Flårgård 1984; also see Owen & Owen 1975, Frankie & Ehler 1978). As predators, carabids are not strictly associated with food plants, but high 'biological productivity' and habitat diversity may increase numbers of invertebrate herbivores, i.e. carabid prey, and thus indirectly affect carabid abundance.

4.2. Invasion of forest fragments from the surroundings

Carabid assemblages in the forest fragments surrounded by cultural habitats contained elements of the field fauna as well. The proportion of field fauna increased as the size of the fragments decreased, and small fragments (< 3 ha) did not support pure forest carabid assemblages but had mixtures of forest species and open habitat species. The plant cover showed a similar gradient. Similar results were reported by Webb & Hopkins (1984) from fragmented heathland in the UK, where species richness of plants and beetles increased with decreasing area or increasing isolation of the heathland patches. This pattern was to a great extent explained by increasing invasion of species into the patches from the surroundings as patch-size decreased (Webb & Hopkins 1984, Hopkins & Webb 1984, Webb et al. 1984, Webb 1989). Similarly, small (<10 ha) and heavily grazed fragments support few forest birds and more farmland birds (Loyn 1987). In general, forest fragmentation affected specialized forest-interior birds adversely, whereas edge-species were favoured (Lynch 1987). In our study, the original plant cover in the small fragments had been replaced by more tolerant plants, often grasses and other herbaceous plants. These vegetational changes together with the drier microclimate (Thiele & Weiss 1976, Flårgård 1984) favour field carabids in the small forest patches. The same patterns have been detected also in other studies (Turcec 1966, Ranney et al. 1981).

In addition to direct human disturbance, vegetation in the small forest fragments may have changed through the effects of increasing proportion of edge. In fragments of only a few hectares most of the area is affected by physical conditions of the edge, e.g. increased light and wind (Merriam & Wegner 1992). Levenson (1981) estimated that in the deciduous forest zone of the eastern United States, the critical minimum fragment size at which interior vegetation is still differentiated from edge vegetation is 4 ha. Fragments in our smallest size class were <3 ha. Thus, applying Levenson's estimate to our study indicates that all forest in the small fragments is actually edge habitat, i.e. 'deteriorated' forest habitat. These edge habitats may harbour specialized species assemblages that do not survive in the forest interior but from which occasional individuals in the larger fragments may wander deeper into the 'true' forest. However, in our study the edges did not have distinct assemblages of either plants or carabids but resembled the surroundings. For instance, only three carabid species, represented by a total of four individuals, were found exclusively in the edges. But many carabid species found in the surroundings occurred also in the edges and were able to migrate to the interiors of the small fragments and perhaps maintain viable populations in that changed forest habitat. However, whether the invasion of the small fragments by carabid species from the surroundings was due to habitat effects increasing the probability of survival in the fragment or to the small size of the fragment leading to a high number of occasional invaders cannot be determined with the present material.

4.3. Species characteristics and distribution among fragments

Of the four species virtually restricted to the contiguous forest, three (*Carabus glabratus*, *C. violaceus*, *Cychrus caraboides*) were short-winged and large (>16 mm). However, according to Lindroth (1985, 1986) they inhabit a variety of forest habitats, and could probably be found in the forest fragments. For these wingless and relatively scarce species, the isolation of the forest fragments may have been the main reason for their absence from the largest fragments, although the fragment habitat appears to be suitable for them (see also Hopkins & Webb 1984). If these species disappear from the fragment, it may be difficult for them to disperse there again, passing through unsuitable habitats (de Vries & den Boer 1990, Niemelä et al. 1993a, b).

Dispersal ability is one of the most important factors affecting the dispersion of species in a fragmented landscape, and flying ability improves the possibility of dispersal (den Boer 1977). For instance, most of the species found in recently emerged habitats such as Dutch polders are capable of flying (Ranta & Ås 1982). Other determinats of species occurrence are habitat preference and the number of suitable habitats, their isolation, and species interactions (Gillerfors 1966, Niemelä 1988a, b, Niemelä et al. 1985, 1988). For instance, dispersal ability together with habitat availability in relation to habitat requirements determines the presence or absence of species on the islands in the Baltic Sea (Gillerfors 1966, Niemelä 1988a, b). Gillerfors (1966) stated that the importance of flight is not clear in Baltic conditions, where distances between the mainland and the islands are often short. Niemelä et al.(1988) found, however, that poor dispersers (usually forest denizens) were not able to reach the distant islands in numbers high enough to establish breeding populations in the small patches of suitable habitat. In our terrestrial study area, distances between the forest fragments were shorter, but the isolation effect could still restrict colonization by the poorest dispersers. In conclusion, fragment size together with habitat composition and isolation, plus species characteristics seemed satisfactorily to explain the distribution of forest carabids in our study area.

4.4. Implications for landscape management

Our study demonstrated that as the size of the forest fragment decreased, the resemblance of its carabid fauna to the surrounding human-modified habitat increased. Species abundant in the surroundings were commonly found in the forest fragments, but the strictest forest species occurred only in the contiguous forest. Not even the largest forest fragments of ca. 20 hectares supported populations of the forest species *Carabus glabratus, C. violaceus* and *Cychrus caraboides.* These observations have implications for the management of landscapes in the face of the increasing forest fragmentation caused by urbanization. First, large fragments of forest must be left undisturbed to maintain populations of forest species. Although forest generalists occurred even in the smallest fragments, possible long-term effects of such a habitat change on their survival cannot be evaluated from these data. Further, the invasion of the smaller forest fragments by species from the surroundings may in the long run threaten the survival of forest species through interspecific competition (Hopkins & Webb 1984, Loyn 1987). Second, the absence of forest specialists from even the large fragments implies that large, continuous and natural forest areas must be left untouched for the future survival of these species (Hopkins & Webb 1984). The specialized forest species require habitats that are not found in the modified environments of the forest fragments. Also, because such species often have a limited dispersal ability, fragmentation and isolation makes it increasingly difficult for them to find a suitable habitat. The survival of specialist carabids has been found to be reduced if suitable habitat patches become too isolated (de Vries & den Boer 1990). The three forest specialists, *Carabus glabratus, C. violaceus* and *Cychrus caraboides,* are all flightless, which probably makes them poor dispersers and decreases their possibilities of moving between forest patches even if suitable habitat may be present in some patches.

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Appendix 1. Average plant cover of 5 randomly selected 1 m^2 squares in each sampling site by habitat type. Minimum value, 1. C = Contiguous forest, Fl = large fragments, Fm = medium fragments, Fs = small fragments, S = surroundings.

Plant species	C	Fl	Fm	Fs	S
Ground layer					
Achillea millefolium	–	–	1	–	7
Aegopodium podagraria	–	–	–	3	4
Alopecurus pratensis	–	–	–	–	4
Angelica sylvestris	–	–	–	3	4
Artemisia vulgaris	–	–	–	–	2
Calamagrostis arundinacea	5	–	–	–	–
Calamagrostis epigejos	–	–	–	3	–
Calamagrostis sp.	–	–	3	16	–
Calluna vulgaris	2	7	4	–	–
Cirsium arvense	–	–	–	–	3
Convallaria majalis	–	–	–	7	–
Deschampsia flexuosa	9	12	10	10	4
Deschampsia caespitosa	–	–	6	–	8
Elymus repens	–	–	–	–	2
Epilobium angustifolium	–	–	–	2	–
Equisetum pratense	–	–	–	6	–
Equisetum sylvaticum	–	–	–	–	3
Festuca pratensis	–	–	–	–	5
Festuca rubra	–	–	–	–	5
Fragaria vesca	–	–	–	2	–
Galium boreale	–	–	–	7	–
Gymnocarpium dryopteris	–	1	–	–	–
Hypericum maculatum	–	–	–	–	1
Juncus filiformis	–	–	–	–	1
Lathyrus pratensis	–	–	–	–	4
Linnea borealis	3	–	3	–	–
Luzula pilosa	1	2	2	–	–
Maianthemum bifolium	2	3	11	2	–
Melampyrum pratense	4	2	10	2	–
Melampyrum silvaticum	–	3	–	–	–
Myosotis arvense	–	–	–	–	1
Oxalis acetosella	–	3	5	–	–
Phleum pratense	–	–	–	–	8
Poa annua	–	–	–	–	2
Poa pratensis	–	–	–	3	–
Poa sp.	–	–	–	9	2
Poaceae sp.	–	8	17	–	15
Pteridium aquilinum	2	–	2	4	–
Rubus idaeus	–	–	1	3	2
Rubus saxatilis	–	–	3	–	–
Stellaria graminea	–	–	–	–	2
Taraxacum officinale	–	–	–	–	5
Trientalis europaea	–	–	3	–	–
Trifolium media	–	–	–	1	–
Trifolium pratense	–	–	–	–	2
Trifolium repens	–	–	–	–	3
Tripleurospermum inodorum	–	–	–	–	3
Tussilago farfara	–	–	–	–	1
Vaccinium myrtillus	32	22	16	3	–
Vaccinium vitis–idae	8	11	–	–	–
Veronica chamaedrys	–	–	–	3	–
Vicia cracca	–	–	–	1	5
Bottom layer					
Polytrichum sp.	26	12	3	–	–
Pleurozium schreberi	8	7	–	–	–
Sphagnum sp.	3	–	3	–	–
Dicranum sp.	3	2	–	–	–
Ptilium crista–castrensis	1	–	–	–	–
Musci sp.	–	7	1	1	2
Litter					
Mould	31	29	31	33	33
Leaf litter	28	18	24	19	6
Needle litter	18	48	15	3	–
Peat	1	–	–	–	–
Clay	–	–	–	–	5

Appendix 2. Catches of carabid species by habitat type. Abundant species given in order of decreasing catch by forest habitat and less abundant ones in alphabetical order. C = Contiguous forest, Fl = large fragments, Fm = medium fragments, Fs = small fragments, Fe = edge, S = surroundings, T = total.

Carabid species	C	Fl	Fm	Fs	Fe	S	T
Abundant species							
Trechus secalis	74	32	64	104	156	207	637
Pt. oblongopunctatus	40	37	61	55	107	31	331
Pt. niger	99	2	1	3	2	192	299
Amara brunnea	14	51	65	51	85	16	282
Calathus micropterus	76	37	32	23	49	6	223
Carabus hortensis	47	13	27	3	23	4	117
Leistus terminatus	1	0	3	25	15	12	56
Carabus nemoralis	0	2	0	26	17	64	109
Pt. melanarius	0	1	0	70	121	460	652
Amara aulica	0	1	1	4	0	87	93
A. communis	0	1	0	3	2	83	89
Harpalus rufipes	0	0	0	1	1	98	100
Bembidion lampros	0	0	0	1	0	49	50
Patrobus atrorufus	1	0	6	4	35	68	114
Loricera pilicornis	3	1	1	1	11	49	66
Less abundant species							
Agonum assimile	0	0	0	0	5	13	18
A. fuliginosum	3	0	0	0	7	6	16
A. obscurum	0	0	1	0	6	0	7
A. sexpunctatum	0	0	0	0	0	1	1
Amara bifrons	0	0	0	1	2	43	46
A. eyrynota	0	0	0	0	0	3	3
A. lunicollis	0	0	0	0	2	6	8
A. montivaga	0	0	0	0	0	3	3
A. nitida	0	0	0	0	0	7	7
A. ovata	0	0	0	0	0	3	3
Anisodactylus binotatus	0	0	0	0	0	2	2
Badister bullatus	0	0	0	0	1	0	1
Bembidion gilvipes	0	0	0	0	0	33	33
B. guttula	0	0	0	0	0	6	6
B. properans	0	0	0	0	0	3	3
B. quadrimaculatum	0	0	0	1	0	2	3
Bradycellus caucasicus	0	0	0	0	0	1	1
Calathus erratus	0	2	0	0	0	3	5
C. melanocephalus	0	0	0	7	4	27	38
Carabus glabratus	28	0	0	0	0	0	28
C. granulatus	0	0	0	0	0	2	2
C. violaceus	6	0	0	0	0	0	6
Clivina fossor	0	0	0	0	0	7	7
Cycrus caraboides	23	0	0	0	3	1	27
Dicheirotrichus rufithorax	0	0	0	0	0	2	2
Dromius schneideri	0	1	0	0	0	0	1
Dyschirius globosus	0	0	0	0	0	6	6
Harpalus luteicornis	0	0	0	3	0	4	7
H. quadripunctatus	0	1	0	1	1	3	6
H. rufibarbis	0	0	0	0	0	22	22
Leistus ferrugineus	17	4	1	4	6	3	35
Metabletus truncatellus	0	0	0	1	0	1	2
Notiophilus aquaticus	0	0	0	0	1	0	1
N. biguttatus	3	4	4	4	5	3	23
N. palustris	0	0	0	0	2	0	2
Patrobus assimilis	0	0	0	0	1	1	2
Pterostichus cupreus	0	0	0	0	1	32	33
P. diligens	0	1	0	0	0	0	1
P. nigrita	2	0	0	0	0	0	2
P. strenuus	0	0	1	6	7	6	20
P. vernalis	0	0	0	0	1	2	3
P. versicolor	0	0	0	0	0	2	2
Stomis pumicatus	0	0	0	0	0	2	2
Synuchus vivalis	0	2	0	3	2	18	25
Trechus discus	0	0	0	0	0	3	3
T. micros	0	0	0	0	0	5	5
T. quadristriatus	0	0	0	0	0	3	3
T. rubens	0	1	0	0	0	0	1
Trichocellus placidus	0	0	1	0	3	4	8
Total	437	194	269	405	684	1720	3709