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Habitat occupancy of carabid beetles on small islands and the adjacent Åland mainland, SW Finland

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Carabid beetles (776 individuals from 33 species) were sampled with pitfall traps in five habitat types on small (8–29 ha) islands in the Åland archipelago (2.5–4 km off Main Åland), in the Baltic Sea (about 60°N, 20°E). Reference samples (1570 individuals from 32 species) were taken in three equivalent and two additional habitat types on the Åland mainland.

The occurrence of the species over the habitats was roughly similar on the islands and on the mainland. An ordination analysis showed that the carabid assemblages tend to be more similar within islands than between them. This can probably be attributed to the movement of individuals from one habitat patch to another, which tends to even out differences in species composition between patches. Due to the small size of the patches on the islands, most carabid species are able to cover the distances between neighbouring patches.

Only two of the thirteen abundant species were more numerous on the islands than on the mainland. Eight species were more abundant on the mainland, and three were equally abundant on the islands and on the mainland. The island-mainland distribution patterns were similar to those found in one habitat type only in a previous study. There are no obvious explanations for these patterns, but habitat effects, differences in dispersal ability and interspecific interactions are suggested.

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1. Introduction

Two factors are of crucial importance for the occurrence of carabid beetles on islands, compared with the mainland, in Baltic conditions: habitat availability on the islands and the colonization ability of the species. Most carabid species show clear preferences for broad habitat types such as, for example, forest vs. meadow (Lindroth 1985, 1986, Thiele 1977), but quantitative data of habitat occupancy are scarce. Furthermore, the mechanisms causing the abundance variation within a habitat patch and between similar patches at a local scale are still poorly understood (e.g. Luff 1986, Niemelä et al. 1986a). The pattern is further complicated as the local population in each habitat patch, in addition to its own dynamics, is also influenced by neighbouring patches — the mosaic (den Boer 1979, Wiens 1985). For instance, the movement of carabids between habitat patches affects species abundances in the local mosaic (e.g. Grüm 1965, 1971, Wallin 1985, 1986). Thus, the local habitat configuration may cause variation in carabid assemblages even among similar patches (den Boer 1968, 1970, 1981, Niemelä et al. 1985; see also Hansson 1977, Southwood 1977, Wiens 1976, 1985).

Dispersal ability is an important component of colonization, but the efficiency of flight and other means of dispersal in carabids are poorly known. Carabids with long hindwings are usually assumed to be able to fly and, thus, to be better dispersers than species with rudimentary wings (Lindroth 1949, den Boer 1977). Furthermore, it is difficult to estimate the importance of dispersal ability in the Baltic conditions, where distances between islands and the mainland are relatively short.

Table 1. Characterization of the study islands (F–J) and the study areas on the mainland (A and E). The habitats where samples were taken are marked with an asterisk. Species richness for the sample size of 100 individuals ($E(S)_{100}$ with ±$2SD$, standardized by rarefaction) is given for islands G–J.

	Islands					Mainland	
	Slätskär F	Äskskär G	Ärtskär H	Korsö I	Inre Korsö J	A	E
Vegetation area	12.3	4.8	2.9	19.8	18.2	29.5	28.5
Total area	19.9	7.8	14.6	28.7	26.2	30.0	30.0
Vegetation/total area, % total area	61.8	61.5	19.9	69.0	69.5	98.3	95.0
Distance to mainl., km	3.8	3.4	3.8	3.3	2.5		
Habitat type (ha)							
Rocky pine forest	2.9*	1.0*	1.5*	4.4*	8.2*	9.0*	5.0*
Young pine forest	–	–	–	–	–	2.4*	3.5*
Coniferous forest	4.8*	0.04*	0.7*	13.5*	8.5*	9.4	4.5
Mixed forest	–	–	–	–	–	5.2*	6.2*
Lush forest patch	0.01*	0.02*	0.01*	0.01*	0.01*	0.01*	0.01*
Alder belt/grove	2.7*	1.5*	0.5*	0.5*	0.9*	1.2	1.5
Shore	1.9*	0.7*	0.1*	1.2*	0.5*	–	–
Bog	–	–	0.1	–	–	–	–
Wooded meadow	–	1.5	–	–	–	–	–
Field	–	–	–	–	–	1.0	6.8
Human settlement	–	–	–	0.2	0.1	1.3	1.0
Carabid sample	99	264	107	190	116	390	523
Number of species	21	17	11	18	13	21	28
$E(S)_{100}$	21	11.8 ±2.9	10.7 ±1.0	15.1 ±2.5	12.3 ±1.6		

In this work I study, on the basis of distributional data, the quantitative occurrence of carabids in five habitat types on small islands in the Åland archipelago. Reference samples were taken from Main Åland in three of the five habitat types studied on the islands and in two additional types. The study focuses on the following questions: (1) What is the distribution pattern of species in different habitat types? (2) Are there differences in the habitat occupancy of the species between islands and the mainland, and can they be attributed to the variation in local habitat configuration? (3) Are the island-mainland differences in carabid occurrence similar to those found in one type of habitat, on the same islands, in a previous study? Niemelä et al. (1985) compared the occurrence of carabids in similar habitat patches (lush forests) on the Åland mainland and on the five islands included in the present study. They found that some species (e.g. *Pterostichus niger*, *Cychrus caraboides*) were more abundant on the islands and some others (e.g. *Loricera pilicornis*, *Patrobus atrorufus*, *Pterostichus melanarius*) on the mainland.

2. Material and methods

2.1. Sampling sites

The study was carried out on the Åland Islands, located between SW Finland and Sweden in the Baltic Sea (about 60°N, 20°E). Phytogeographically Åland belongs to the hemiboreal zone (Ahti et al. 1968). The samples were taken on five islands (8–29 ha) in the archipelago near Mariehamn (2.5–4 km off Main Åland; islands F–J below, for the exact location of the islands see Niemelä et al. 1985, fig. 1). Island names, areas and distances to Main Åland are given in Table 1.

As the mainland reference I use samples taken on Main Åland, which comprises four large islands closely connected with each other (total area about 900 km^2). The sampling sites are located around study areas A and E in Niemelä et al. (1985; Fig. 1) and in four uniform coniferous forests on Main Åland (mainland coniferous forest) (Niemelä et al. 1986a).

I took samples in five main habitat types on the islands (shore, alder belt, rocky pine forest, coniferous forest, lush forest). The habitats form a gradient from the shores to the interiors of the islands. On Main Åland samples were taken in three habitats similar to the island counterparts (rocky pine forest, coniferous forest, lush forest). In addition, young coniferous forests and mixed forest patches were sampled on the mainland.

On Main Åland the habitats form a gradient from open, dry habitats to closed, moist ones. The lush forest patches are the same as in Niemelä et al. (1985).

I estimated the proportion of different habitat types on the islands and within a 30 hectare square around the mainland study areas A and E from aerial photographs (1:15500) (Table 1). All the four mainland coniferous forests are surrounded by at least about 200 ha of continuous forest. For more details on the mainland coniferous forests see Niemelä et al. (1986a).

The mainland study areas (A and E) differ from the islands by having a more continuous vegetation, larger areas under human activity and a greater variety of different habitat types. A substantial proportion of the islands is covered by bare bedrock, an unfavourable environment for carabids. Furthermore, among the islands there are considerable differences in the total area covered by vegetation and in habitat composition. A description of the habitat types with a list of the most abundant plant species is given in Appendix 1.

2.2. Vegetational similarity of the sites

The vegetation of the sampling sites was described by estimating the proportional cover of field layer and bottom layer plant species in five randomly selected 1 m^2 quadrates in each site. I use this quantitative floristic description to study the habitat similarity of the sites. The data were subjected to a detrended correspondence analysis (DCA; Gauch 1982) (ln-transformed data, mainland coniferous forests excluded). Wartenberg et al. (1987) criticized the DCA-method and discussed, for instance, problems with scaling and the curved structure of the ordination. As a conclusion they recommended a cautious interpretation of the ordination. I use the method here for comparing relative distances among the sites, not for strict hypothesis-testing (see also Birks 1987).

The first axis of the ordination (eigenvalue 0.67) identifies a gradient from shores and alder belts through moist forests to dry forests. Sites of similar habitat type are mostly located close to each other. The shores are characterized by plant species such as *Scirpus uniglumis, Sonchus sp., Poa annua, Angelica archangelica* and *Phalaris arundinacea*. The dry forests are characterized by species such as *Polypodium vulgare, Hieŕacium umbellatum, Empetrum nigrum, Viola uliginosum, Polytrichum commune* and *Cladonia rangiferina*. Two sites (coniferous forest and lush forest patch on island F) were outliers in the ordination, and are characterized by species scarce elsewhere (such as *Rubus saxatilis* and *Rhytidiadelphus sp*). The explanatory value of the second axis is lower (eigenvalue 0.28) and its significance is more difficult to interpret. The axis is determined by two sites: a mainland young pine forest at one end and the lush forest of island F at the other.

The most important factor determining the location of the sites in the ordination seems to be their habitat type. The sites are clustered by their habitat type, and there seems to be no systematic island-mainland difference in their location.

2.3. Sampling method

I collected the carabids by using pitfall traps (Southwood 1978, Niemelä et al. 1986b). The traps (plastic cups, diameter 65 mm, volume 170 ml) were partially filled with water and detergent, and placed in grids of 15 traps (2–3 m apart) in each sampling site. To catch the species active in early summer and late summer I took the samples in periods of five days between 8–16 June and between 16–23 August, 1983. Pooled early summer and late summer samples give a realistic picture of local carabid assemblages in southern Finnish conditions (Niemelä et al. 1985, Niemelä et al. 1988b, Niemelä et al. in prep.). Sampling efforts are given in Table 2.

3. Results

3.1. Habitat occupancy of individual species

Most of the species show habitat preferences and these tend to be similar on the islands and on the mainland (Tables 2 and 3). There is much variation in the abundances of the species between the sites, however. Due to this variation, clear interpretations of the species' habitat occupancy are difficult, especially concerning the less abundant species. Thus, in the following, the habitat occupancy of only the most abundant species (sample size >20 individuals) is described.

Trechus secalis and *Carabus hortensis* were abundant in the two moist forest types. The former species was also numerous in young forests on the mainland, whereas the latter species was not found in these sites. The samples of *Pterostichus niger* were very similar on the islands and on the mainland in coniferous forests and lush forests, but considerably higher on the islands in rocky pine forests. Many species had a clear peak of abundance in the closed forests *(Agonum fuliginosum, Leistus terminatus, Loricera pilicornis, Patrobus assimilis, P. atrorufus, Pterostichus oblongopunctatus* and *P. melanarius)*. *Calathus micropterus* and *Cychrus caraboides* were quite evenly distributed over the three habitat types.

When samples from the other habitat types are added, a more detailed picture of the distribution patterns emerges. On the islands all the main habitat types were included and the results can be regarded as representing the relative abundances on the islands well. *P. niger* thrived in the open habitats on the islands, but was quite evenly distributed on the mainland. *Trechus secalis, Carabus hortensis, Calathus micropterus* and *Cychrus caraboides* were abundant in the forest sites. *Patrobus atrorufus, P. assimilis, Loricera pilicornis, Pterostichus oblongopunctatus* and *Leistus terminatus* were scarce in all habitat types on the islands, but abundant in the mainland forests. *Pterostichus melanarius* was not found in any habitat

Table 2. The carabid beetles caught in the sampling sites on the islands (Isl) and on the mainland (Ma). The thirteen most abundant species (total sample > 20 individuals) are given in the order of their sample size on the islands. Habitat type symbols: Sh=shore, Al=alder belt, Yo=young pine forest, Mi=mixed forest. Note the differences in sampling efforts between the habitat types.

	Rocky pine forest		Coniferous forest		Lush forest		Islands		Mainland		Islands total	Mainland total	Total
	Isl	Ma	Isl	Ma	Isl	Ma	Sh	Al	Yo	Mi			
Abundant species													
Pterostichus niger (Schall.)	108	16	22	81	16	7	125	64	19	8	335	131	466
Trechus secalis (Payk.)	2	0	35	202	61	80	4	11	60	30	113	372	485
Carabus hortensis L.	4	1	26	59	22	7	12	38	0	0	102	67	169
Calathus micropterus (Dft.)	6	17	19	50	4	5	5	14	9	4	48	85	133
Cychrus caraboides (L.)	2	3	5	22	11	1	1	11	0	0	30	26	56
Agonum fuliginosum (Pz.)	0	0	0	22	13	9	5	0	0	1	18	32	50
Patrobus atrorufus (Ström)	1	0	0	15	5	196	8	2	21	114	16	346	362
Loricera pilicornis (F.)	1	0	0	3	10	27	2	1	0	3	14	33	47
Carabus violaceus L.	6	4	0	13	1	0	0	2	4	4	9	25	34
Pterostichus oblongopunctatus (F.)	1	0	3	42	2	25	1	0	1	11	7	79	86
Patrobus assimilis Chaud.	0	0	0	5	2	14	0	0	0	1	2	20	22
Leistus terminatus (Hellw. in Pz.)	1	0	0	11	0	14	0	0	1	3	1	29	30
Pterostichus melanarius (Ill.)	0	3	0	112	0	9	0	0	96	36	0	256	256
Other species													
Agonum obscurum (Hbst.)	0	0	0	2	7	1	0	3	0	1	10	4	14
Amara brunnea (Gyll.)	1	3	0	1	1	0	0	0	0	1	2	5	7
A. communis (Pz.)	0	0	0	0	0	0	0	1	0	1	1	1	2
A. lunicollis Schiødte	0	0	0	0	0	0	0	0	3	0	0	3	3
Badister bullatus (Schrank)	0	0	0	0	0	0	1	1	0	0	2	0	2
Bembidion guttula (F.)	0	0	0	0	0	2	0	0	1	0	0	3	3
B. lampros (Hbst.)	0	0	0	0	0	0	1	0	0	0	1	0	1
B. obliquum Sturm	0	0	1	0	0	0	0	0	0	0	1	0	1
B. quadrimaculatum (L.)	0	0	1	0	0	0	3	0	0	0	4	0	4
Calathus melanocephalus (L.)	0	0	0	0	0	0	3	0	0	0	3	0	3
Clivina fossor (L.)	0	0	0	0	0	1	0	0	0	0	0	1	1
Dromius sigma (Rossi)	0	0	0	0	0	0	2	0	0	0	2	0	2
Dyschirius globosus (Hbst.)	0	1	0	1	1	0	12	0	0	0	13	2	15
Elaphrus cupreus Dft.	0	0	0	0	1	0	0	0	0	0	1	0	1
Harpalus quadripunctatus Dej.	0	0	0	1	0	1	0	2	2	3	2	7	9
H. rufipes (Deg.)	0	0	0	0	0	0	0	0	0	1	0	1	1
Leistus ferrugineus (L.)	2	5	1	4	0	0	1	2	2	1	6	12	18
Miscodera arctica (Payk.)	0	2	0	0	0	0	0	0	1	0	0	3	3
Nebria brevicollis (F.)	1	0	0	0	0	1	0	0	0	0	1	1	2
Notiophilus biguttatus (F.)	0	2	0	8	0	2	2	1	0	2	3	14	17
N. germinyi Fauv.	0	0	0	0	0	0	1	0	0	0	1	0	1
Olisthopus rotundatus (Payk.)	0	2	0	0	0	0	0	0	0	0	0	2	2
Pterostichus diligens (Sturm)	0	1	0	0	0	0	0	0	0	0	0	1	1
P. nigrita (Payk.)	0	0	0	3	7	0	1	3	0	0	11	3	14
P. strenuus (Pz.)	0	0	0	0	2	1	7	4	2	1	13	4	17
P. versicolor (Sturm)	1	0	0	0	0	0	0	0	0	0	1	0	1
Synuchus vivalis (Ill.)	0	0	0	0	0	1	0	0	0	0	0	1	1
Trechus discus (F.)	0	0	0	0	0	0	1	0	0	0	1	0	1
T. rubens (F.)	0	0	0	0	1	0	0	1	0	0	2	0	2
Trichocellus placidus (Gyll.)	0	0	0	0	0	0	0	0	0	1	0	1	1
Total	137	60	113	657	167	404	198	161	222	227	776	1570	2346
Number of species	14	13	9	20	18	20	21	17	14	20	33	32	43
Sampling effort (trap-days)	750	600	750	3000	675	300	750	750	300	300			

Table 3. The mean sample size (per sampling site) of the thirteen most abundant species in the three habitat types (with *SD*) studied both on the islands and on the mainland, and in the additional habitat types. Symbols: Isl=islands, Ma=mainland, sho=shore, ald=alder belt, yo=young pine forest, mix=mixed forest — =species was not found.

	Rocky pine forest		Coniferous forest		Lush forest		Islands		Mainland	
	Isl	Ma	Isl	Ma	Isl	Ma	sho	ald	yo	mix
Pterostichus niger	21.6±21.5	4.0±4.8	4.4±5.5	4.1±4.7	3.2±4.4	3.5±5.0	25.0±13.2	12.8±13.1	9.5±10.6	4.0±2.8
Trechus secalis	0.4±0.5	—	7.0±7.9	10.1±11.9	12.2±16.7	40.0±25.5	0.8±1.1	2.2±2.0	30.0±38.2	15.0±5.7
Carabus hortensis	0.8±0.8	0.3±0.5	5.2±3.3	3.0±2.4	4.4±6.3	3.5±3.5	2.4±2.3	7.6±9.1	—	—
Calathus micropterus	1.2±1.8	4.3±3.2	3.8±2.8	2.5±2.6	0.8±1.1	2.5±3.5	1.0±1.7	2.8±5.2	4.5±0.7	2.0±2.8
Cychrus caraboides	0.4±0.5	0.8±1.0	1.0±1.0	1.1±1.3	2.2±3.8	0.5±0.7	0.2±0.4	2.2±3.3	—	—
Agonum fuliginosum	—	—	—	1.1±4.5	2.6±1.5	4.5±0.7	1.0±1.7	—	—	0.5±0.7
Patrobus atrorufus	0.2±0.4	—	—	0.8±2.2	2.8±1.9	98.0±41.0	1.6±3.0	0.4±0.5	10.5±14.8	57.0±48.1
Loricera pilicornis	0.2±0.4	—	—	0.2±0.5	2.0±1.6	13.5±0.7	0.8±1.1	0.2±0.4	—	1.5±2.1
Carabus violaceus	1.2±1.8	1.0±0.0	—	0.7±1.0	0.2±0.4	—	—	0.4±0.5	2.0±1.4	2.0±2.8
Pterostichus oblongopunctatus	0.2±0.4	—	0.8±1.3	2.1±3.4	0.4±0.9	12.5±14.9	0.2±0.4	—	0.5±0.7	5.5±6.4
Patrobus assimilis	—	—	—	0.3±0.6	0.4±0.9	7.0±4.2	—	—	—	0.5±0.7
Leistus terminatus	0.2±0.4	—	—	0.6±0.9	—	7.0±9.9	—	—	0.5±0.7	1.5±0.7
Pterostichus melanarius	—	0.8±1.0	—	5.6±10.1	—	14.0±9.9	—	—	48.0±59.4	18.0±17.0

type on the islands, but was caught in all types on the mainland.

3.2. Island-mainland distribution of individual species

Twenty-two out of the 43 species occur both on the mainland and on the islands, but there are clear differences in the island-mainland abundance among the species. The thirteen abundant species (sample size >20 individuals) can be divided into three distribution types according to their sample sizes on the islands, as compared with the mainland (Table 4):

(a) Two species were more abundant on the islands than on the mainland (*Carabus hortensis, Pterostichus niger*).

(b) Eight species were more abundant on the mainland than on the islands (*Calathus micropterus, Leistus terminatus, Loricera pilicornis, Patrobus assimilis, P. atrorufus, Pterostichus melanarius, P. oblongopunctatus, Trechus secalis*).

(c) Three species occurred in comparable numbers on the islands and on the mainland (*Agonum fuliginosum, Carabus violaceus, Cychrus caraboides*).

The variation in sample sizes among islands and the mainland study areas is considerable (Table 2), leading to large deviations from the mean (Table 4). In most cases, these deviations make the clear numerical differences in the mean sample sizes between the islands and the mainland less convincing.

Table 4. The mean sample size (with *SD*) of the thirteen most abundant species (per island and mainland study area, all habitats pooled) on the islands and on the mainland. *Pterostichus melanarius* was not found on the islands.

	Islands	Mainland
Abundant on islands		
Carabus hortensis	20.4±18.9	7.0±5.9
Pterostichus niger	67.0±38.4	29.1±7.7
Abundant on mainland		
Calathus micropterus	9.6±10.9	20.0±2.3
Leistus terminatus	0.2±0.4	9.6±8.3
Loricera pilicornis	2.8±2.3	15.2±1.2
Patrobus assimilis	0.4±0.9	7.8±3.6
P. atrorufus	3.2±5.5	166.3±21.0
Pterostichus melanarius	—	77.6±66.5
P. oblongopunctatus	1.4±3.1	20.6±9.6
Trechus secalis	22.6±17.8	95.1±4.0
Abundant on islands and mainland		
Agonum fuliginosum	3.6±1.8	6.1±2.7
Cychrus caraboides	6.0±7.9	3.1±0.3
Carabus violaceus	1.8±2.5	6.7±4.0

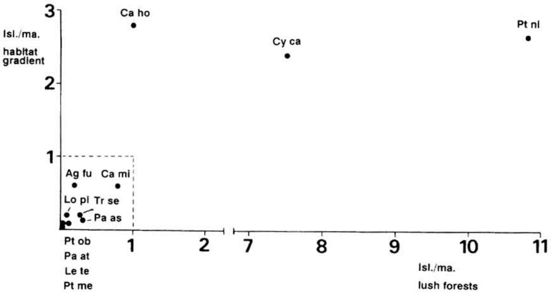

Fig. 1. The relation between the island and mainland samples (island sample/mainland sample) in lush forests (*x*-axis) and the present study (habitat gradient, *y*-axis). The interrupted lines indicate the the ratio of 1 (the species is equally abundant on the islands and the mainland). Species abbreviations: Ag fu = *Agonum fuliginosum*, Ca mi = *Calathus micropterus*, Ca ho = *Carabus hortensis*, Cy ca = *Cychrus caraboides*, Le te = *Leistus terminatus*, Lo pi = *Loricera pilicornis*, Pa as = *Patrobus*

The island-mainland distribution patterns are quite similar to those found in a previous study, in the lush forest patches alone (Niemelä et al. 1985) (Fig. 1). Of the twelve species abundant in both the lush forests alone and the present study, (*Carabus violaceus* was very scarce in the former study) only *C. hortensis* showed a different pattern between the two data sets. The species was more abundant on the islands in the present study, but found in equal numbers both on the islands and on the mainland in lush forest patches. The proportion of *P. niger* on the islands was remarkably high in both data sets (about 40%). Note, however, that the sample sizes of some species (*Agonum fuliginosum, Cychrus caraboides, Leistus terminatus*) were numerically quite low, weakening the power of the comparison.

3.3. Carabid assemblages in the sites

I examined the composition of the carabid assemblages in the sites using DCA (ln-transformed data, mainland coniferous forest was excluded). Most of the sites are located roughly along a gradient from open habitats (rocky pine forests and shores) to closed habitats (e.g. lush forests and mixed forests) identified by the first axis. Abundant carabid species in the closed sites are *Patrobus assimilis, P. atrorufus, Pterostichus oblongopunctatus, P. melanarius* and *Leistus terminatus*. Species characterizing the open sites are usually scarce (e.g. *Olisthopus rotundatus, Pterostichus diligens, Notiophilus germinyi*). The second axis is difficult to interpret as it is determined by an outlier (mainland rocky pine forest).

The gradient from open to closed habitats in the carabid data is less clear than in the vegetation ordination. Also the explanatory power of the axes are lower than in the vegetation ordination (eigenvalue of the first axis is 0.39 and of the second axis 0.29). Furthermore, the sites of each island tend to form a cluster. To test this pattern I calculated the mean Euclidian distance between all 10 pairs, between five sampling sites, on each of the islands and mainland study areas. The observed mean distance was then compared with the mean Euclidian distance calculated for five randomly drawn sites from the total of 35 sites included in the ordination. The result of 1000 random draws is shown in the following tabulation:

	Observed distance	Percent observed > random
Island F	1099	5.3
Island G	554	0.0
Island H	1119	6.6
Island I	798	0.1
Island J	732	0.0
Mainland, A	1176	11.7
Mainland, E	1685	84.0

On three islands (G, I, J) the observed distance between the sampling sites is shorter than the random

Table 5. The samples of the abundant species on the five islands (F–J). Sampling effort and the value of the *G*-test for island occurrence are given. Statistical significance: *** $P<0.001$, ns $P>0.05$, $df=4$ in all cases.

	F	G	H	I	J	*G*-test
Pterostichus niger	16	119	79	47	74	101.1***
Trechus secalis	30	30	0	44	9	70.9***
Carabus hortensis	17	52	1	18	14	65.5***
Calathus micropterus	5	10	0	28	5	44.8***
Cychrus caraboides	1	20	4	3	2	31.4***
Agonum fuliginosum	2	6	5	2	3	3.7 ns
Patrobus atrorufus	0	1	0	13	2	29.7***
Sampling effort (trap-days)	750	750	675	750	750	

one (on 0.05 level), but on two islands (F, H) and in both mainland areas the location of the sites do not differ from random. The result suggests that the carabid assemblages on each island are more similar to each other than on the mainland.

3.4. Variation between islands

Considerable variation was observed in species abundances both between similar habitats on the individual islands (Table 3) and among the different islands (Table 4). Of the seven abundant species (>2% of the island sample) *Agonum fuliginosum* was the only one occurring in equal numbers on every island (*G*-test, sampling effort was used as the expected ratio) (Table 5). The remaining six species showed a clear deviation from an even distribution. Three of them (*Carabus hortensis, Cychrus caraboides* and *Pterostichus niger*) were most numerous on island G, and three species (*Calathus micropterus, Trechus secalis* and *Patrobus atrorufus*) on island I. On island H most of the species were very scarce or absent. Also, the species richness was lowest on island H (differences in sample size eliminated by rarefaction, Simberloff 1978), but it did not differ statistically from the species richness of islands G and J (Table 1).

I compared the structure of the island carabid assemblages by calculating the Czekanowski-Sørensen-Renkonen index of percentage similarity (see e.g. Wolda 1981) for pairs of islands:

$$PS = \Sigma \min(p_{ji}, p_{ki}),$$

where p_{ji} = the proportion of species i in sample j.

Table 6. The value of the Czekanowski-Sørensen index of percentage similarity (in %) among the islands (F–J).

	F	G	H	I
G	63			
H	38	41		
I	59	58	41	
J	59	61	47	69

The lowest similarities are between island H and the other islands (38–47%) (Table 6). The lowest value, between islands H and F (38%), is at least partly due to a great difference in species number (21 vs. 11). The similarities between the other four islands range from 58 to 69%.

4. Discussion

4.1. Habitat spectrum and island colonization

Habitat diversity is widely used to explain the often found positive correlation between species richness and island area (see e.g. McGuinness 1984). It is obvious that species, such as carabids, with clear preferences for habitat types are unable to colonize an island lacking the particular habitat required. To estimate the suitability of island habitats for carabids one needs to know, in addition to the habitat spectrum on the island, the habitat requirements of the species. For most carabid species the broad habitat distribution patterns are known, but data on population numbers in different habitats are scarce. Furthermore, the factors causing the within and between habitat occupancy are not known in detail.

The scarcity of suitable habitats is the most obvious explanation for the absence of forest species such as *Trechus secalis* and *Calathus micropterus* from island H in this study. Also the scarcity of *Patrobus atrorufus* on the study islands may be attributed to the lack of suitable habitats or to subtle habitat variation between the islands and the mainland. The species occurs mainly in deciduous forests and in human modified habitats (Lindroth 1985), which are scarce on the study islands (see Table 1). Dispersal should not be a limiting factor as the species was one of the most abundant ones on more distant islands (4–20 km off Main Åland), where human influence has been considerable (Niemelä et al. 1988a). It is more difficult to explain the scarcity of *Pterostichus oblongopunctatus* on islands in terms of habitat effects. The species is a forest generalist (Lindroth 1986), and forests are of several hectares on most of the islands. Interestingly, the species was found only on one island (I), but it was widely distributed there (caught in four sampling sites out of five).

The lowest species number was on island H, where the proportion of vegetation was the smallest (20%) and consists largely of barren pine forest, the remaining patches being all under 1 ha in area and separated from each other by bare rocks. On all other islands the proportion of the vegetation area was higher (60–70%). On island G, the smallest in total area, species richness was comparable with that of the larger islands, and the sample size was clearly higher than on the other islands. The high species richness and sample size are probably due to the high proportion of luxurious habitats on the island (see also Nilsson et al. 1985). The impoverishment of island H and the richness of island G were true also for the lush forest patches, but the differences were smaller (Niemelä et al. 1985).

The availability of suitable habitats is not the only explanation for the species' island-mainland distribution in my data. An example of this is the absence of *Pterostichus melanarius* from the islands. The species occurred in all habitat types on the mainland, three of which have direct counterparts on the islands. Moreover, its dispersal ability should be sufficient as it is dimorphic and the long winged individuals are able to fly (Haeck 1971, den Boer 1977, Lindroth 1986). *P. melanarius* has been absent from islands in other studies conducted in the Åland Islands as well, although it has been frequently found on the mainland (Niemelä 1988, Niemelä et al. 1985, 1988a). An explanation for the pattern could be that competition exists between *P. melanarius* and *P. niger*. The species are of overlapping size and their life history characteristics are relatively similar (Lindroth 1986, Thiele 1969, 1977, Wallin 1986). As abundant and widely distributed on the islands, *P. niger* may be able to keep *P. melanarius* from colonizing the islands, but testing this assumption requires experimental studies (see also Safriel & Ritte 1980).

To conclude, all the study islands are roughly at the same distance (2.5–4 km) from the Main Åland, but there are differences in area and habitat composition among them (see Table 1). These factors, together with the chance effects associated with colonization, may cause variation in carabid occurrence among the islands (Niemelä et al. 1987; see also Haila et al. 1982). Species with a good dispersal ability are often regarded as superior colonizers (e.g. Simberloff 1981). Unfortunately, dispersal ability of carabid species is poorly studied (see e.g. Ås 1984, Niemelä et al. 1985). The lack of detailed information on the scale of the species' habitat occupancy, together with variation in dispersal ability, makes the distribution of carabids on islands rather difficult to predict on the basis of mainland occurrence.

4.2. Movement of carabids between habitat patches

To estimate the importance of carabid movement between patches in a local habitat mosaic and to study the habitat preferences of carabids in detail, quantitative population level studies are clearly needed (see also Andersen 1969, Birks 1987). In my study the habitat composition differed slightly between the mainland and the islands, but abundant species showed roughly similar habitat occupancy on the islands as on the mainland. It is noteworthy, however, that many species were caught in a wider variety of habitat types on the islands than on the mainland. Some species numerous in humid habitats (*Loricera pilicornis, Patrobus atrorufus, Trechus secalis*) were not found in mainland rocky pine forests, but occurred in low numbers in equally dry habitat types on the islands. Furthermore, *Carabus hortensis* and *Cychrus caraboides* occur in all habitat types on the islands, but were not found in two types on the mainland (young pine forest and mixed forest). This movement or spread of individuals from the preferred habitat type (habitat where sample sizes are highest) to marginal ones leads to a wider habitat occurrence of the species on the islands. The high within-island similarities of carabid assemblages and also the low explanatory power of the DCA-ordination reflect this pattern.

Also the higher proportion of abundant and widely distributed species on the islands increases the similarity of the carabid assemblages within the islands. On the islands five species occurred in all habitat types and made up 81% of the sample, whereas on the mainland three species occurred in all habitat types and made up 30% of the sample.

On the basis of the distributional data only some suggestions to explain the above pattern can be given. The wider habitat occupancy on the islands may be due to the small area of the islands, as well as the habitat patches. In such a fine-grained environment (Wiens 1976) carabids can presumably move easily between habitat patches. On the mainland, on the other hand, habitat patches are usually larger and the movement of individuals from one patch to another may be slower (see also Niemelä et al. 1985). Thus, the occurrence of carabid species in a mosaic of habitat patches seems to largely depend on the habitat composition and the size of the patches.

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Appendix 1. Description of the habitat types on the islands and on the mainland with the most abundant plant species given (abbreviation after the plant name indicates the study area/island where the species was abundant).

	General description	Tree layer	Field and bottom layer
Islands			
Shores	treeless, sand or gravel stone	–	*Phalaris arundinacea, Potentilla anserina, Centaurea jacea, Stachys palustris, Hippophaë rhamnoides, Plantago maritima*
Alder belt	toward the interior from the shore	*Alnus glutinosa, Prunus padus* (F, G), *Sorbus aucuparia* (I, J), *Picea abies* (I, J)	*Convallaria majalis* (F, G), *Filipendula ulmaria* (F, G, J), *Lysimachia vulgaris* (H), *Deschampsia flexuosa* (I), *Lycopodium selago* (J), *P. arundinacea* (J)
Rocky pine forest	dry forest patches in depressions among the cliffs	*Pinus silvestris* (G, H, I), *P. abies (F, J),*	*Calluna vulgaris, D. flexuosa, Empetrum nigrum, Vaccinium vitis-idaea, Cladonia rangiferina, Pleurozium schreberi*
Coniferous forest	located in the interior of the islands	*P. abies*	*Vaccinium myrtillus* (F, H, I), *D. flexuosa* (G, J)
Lush forest	moist, *P. abies*-dominated luxurious patches (details in Niemelä et al. 1985).	*P. abies, Betula sp., A. glutinosa, S. aucuparia*	*Rubus saxatilis* (F), *Maianthemum bifolium* (F), *Hepatica nobilis* (G), *V. vitis-idaea* (H), *Poa sp.* (H), *V. myrtillus* (I), *F. ulmaria* (J)
Mainland			
Rocky pine forest	as rocky pine forest on the islands	as rocky pine forest on the islands	as rocky pine forest on the islands
Coniferous forest	MT- or the somewhat more lush OMT-type (details in Niemelä et al. 1986a)	*P. abies*	*V. myrtillus, V., vitis-idaea, M. bifolium, D. flexuosa, Linnea borealis, C. vulgaris*
Lush forest	as island lush forest	as island lush forest	*Oxalis acetosella, F. ulmaria, Rubus idaeus, Anemone nemorosa, M. bifolium*

	General description	Tree layer	Field and bottom layer
Young pine forest	planted pine, about 5 m high	*P. silvestris*	*D. flexuosa, Agrostis tenuis, Melica nutans, M. bifolium, Pteridium aquilinium, M. bifolium, Trientalis europaea*
Mixed forest	coniferous and deciduous trees	*P. abies, Betula sp.*	*F. ulmaria, O. acetosella, Equisetum silvaticum, Ranunculus cassubicus*

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