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Carabid beetles on isolated Baltic islands and on the adjacent Åland mainland: variation in colonization success

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We collected carabid beetles (Coleoptera: Carabidae) with identical sampling effort in the main habitat types on three islands (area 29–93 ha, distance to the Åland mainland 4–20 km) in the Baltic Sea. The vegetation area on the islands decreases with increasing distance from the mainland. As the mainland reference we use samples taken from the Åland mainland (area about 900 km^2).

There was pronounced variation in the occurrence of individual carabid species between the islands and the mainland, and among the islands. Three of the 21 dominating species (59 species in total) were abundant on the mainland, but were not found on the islands. Eleven species were abundant on all three islands (successful colonists), and seven were found on one or two islands, but not on the other(s) ("mosaic distribution"). All of these seven species were found on the island closest to the mainland. Furthermore, the species number (standardized by sample size) was lowest on the most distant island. There is no clear relationship between the dispersal ability of the species and their island-mainland occurrence. The general habitat occupancy of the species seems to be an important factor determining their colonization success. Successful island colonists tend to be found in habitats common on the islands and species showing a "mosaic distribution" tend to occur in habitats scarce on the islands. The small area of vegetation and its patchy distribution on the two most distant islands, together with the stochasticity connected with dispersal over water for 10–20 km, is the most probable explanation for the uneven distribution of some carabid species among the three Baltic islands.

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1. Introduction

The colonization of islands includes two components — dispersal to islands and the persistence of populations established there (Simberloff 1981). Several factors affect the colonization success of individual species. For carabids, Ås (1984) regarded dispersal ability as the most important factor, whereas Enckell et al. (1987) stressed also the importance of the properties of the islands (especially habitat composition) for the colonization process. The demographic variables of the colonizing species have been regarded as crucial for the persistence of the species after reaching the island (e.g. MacArthur & Wilson 1967, Ebenhard 1987).

When distribution patterns are documented on the basis of quantitative data it is possible to distinguish between competing hypotheses explaining the distribution of island populations (Williamson 1981). Thus, Niemelä et al. (1985) concluded that the passive sampling hypothesis of Connor & McCoy (1979) is not valid for describing how carabid beetles colonize small islands that are only a few kilometers (2.5–4 km) off the coast of the Åland mainland. Carabid assemblages on the islands were not random samples from communities in similar habitats on the mainland. The differences might be attributed to island isolation, variation among species (e.g. for dispersal ability) and differences in habitat quality between the islands and the mainland.

In this paper, we continue our studies on the quantitative distribution of carabid beetles in Baltic archipelagoes (Niemelä 1988a, b, Niemelä et al. 1985, 1986, 1987). We extend the study to islands that are further off the mainland (4–20 km) and from each other but have, nevertheless, similar habitats. As the mainland reference we use samples taken from a large island complex (Main Åland, area about 900 km^2). As most carabid species show clear habitat preferences, island-mainland comparisons must be based on quantitative data from clearly defined habitat types to obtain useful information on colonization dynamics (Niemelä et al. 1985, 1987). Thus, we included all main habitat types found on the islands in the sampling scheme. The aims of this paper are: (1) to study the occurrence of carabid species on the three islands, compared with the mainland, and (2) to discuss the importance of habitat differences and increasing island isolation in determining carabid distribution.

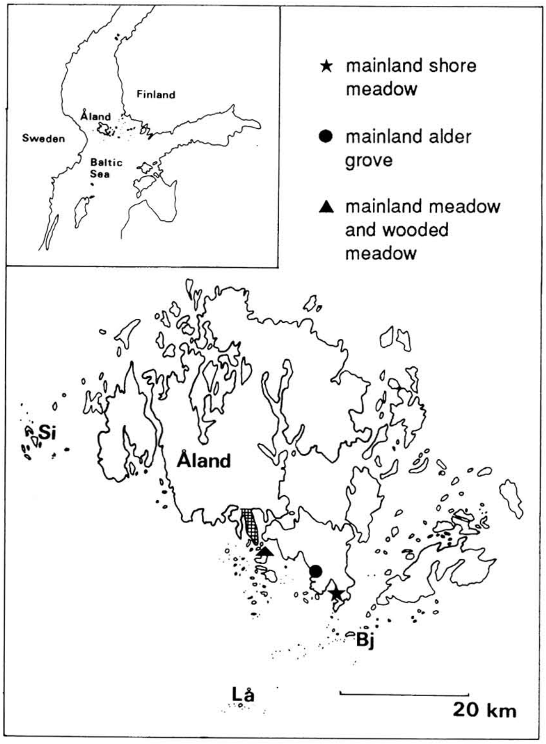

Fig. 1. The location of the study islands and the mainland reference habitats from R1. The town of Mariehamn is hatched. For more details see text.

2. Study area and methods

2.1. The archipelago

The three study islands — Björkör, Signilskär and Lågskär — belong to the Åland archipelago in the northern Baltic, about 60°N, 20°E (Fig. 1). As a reference area (hereafter called mainland) we use the main islands of Åland — a group of large islands closely connected with each other, with a total land area of about 900 km^2. The areas of the islands and their distances to Main Åland are given in Table 1.

A major part of the two most distant islands (Signilskär and Lågskär) is covered by bare bedrock, and vegetation areas (mostly meadow and scrub) are restricted to depressions among the cliffs. About one half of Björkör (closest to the mainland) is covered by almost continuous vegetation, and forest is the prevailing habitat type (Fig. 2). Palmgren (1917) and Hæggström (1985) described the flora of Björkör in detail.

All of our study islands have had permanent human habitation until recent decades. For instance, Björkör had about 40 inhabitants in the beginning of the 20th century (Palmgren 1917). Human influence has left clear traces on the vegetation of the islands. All three islands have meadows that were used for grazing a few decades ago. Björkör is still used for sheep grazing in the summertime. Nowadays, permanent settlement has vanished from the islands. Bird ringing stations (temporarily occupied) are located on Lågskär and Signilskär, where a summer cottage is also situated (see Fig. 2).

Table 1. Characterization of the islands included in the study. Habitats where samples were not collected are indicated with an asterisk.

	Björkör	Signilskär	Lågskär
Area, ha	37	93	29
Distance to the mainland, km	4	10	20
Vegetation area, ha	19.3	14.9	7.8
(% of total area)	(52)	(16)	(27)
Habitat composition, ha			
Alder grove	5.2	2.0	0.5
Meadow	0.9	3.4	1.0
Scrub	3.0	5.9	5.0
Coniferous forest	0.2	1.9	0.2
Abandoned field	0.2	–	0.2
Shore meadow	–	0.1	0.8
Deciduous forest	9.8[1]	–	–
Birch forest	–	0.4	–
Bog	–	1.2*	0.05*

[1] Includes the wooded meadow (0.5 ha).

2.2. Island habitats

For the sampling we defined, separately, six major habitat types that can be easily distinguished on the islands. Verbal habitat descriptions were made on each island during the sam-

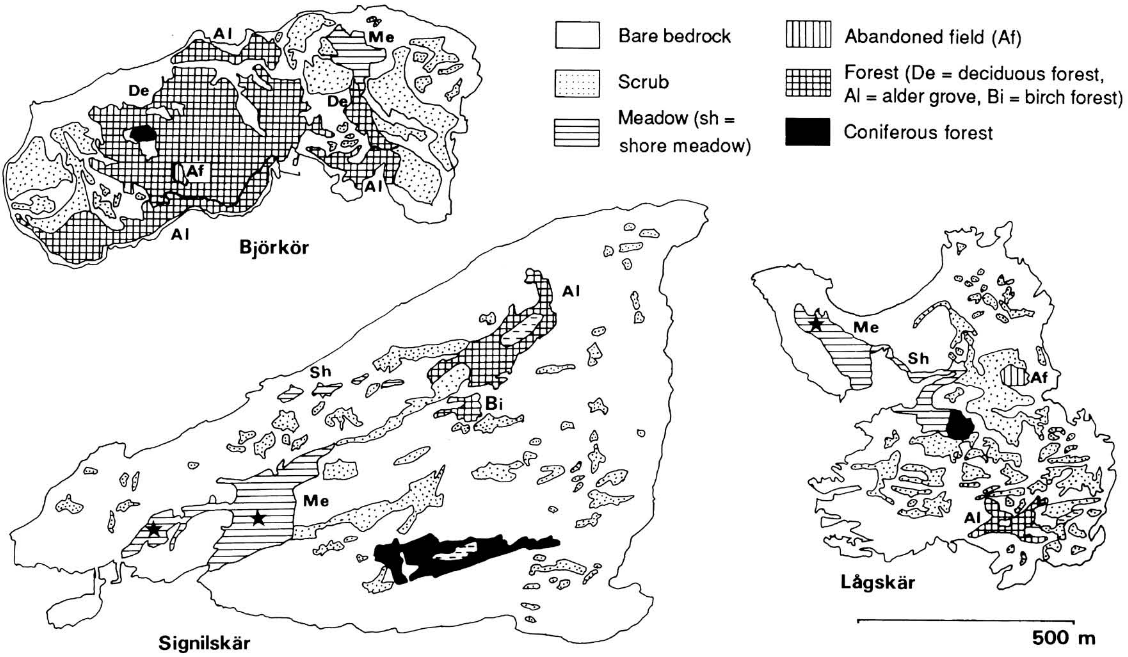

Fig. 2. A schematic illustration of the three study islands with the distribution of different habitat types. ★ = bird ringing station (Signilskär and Lågskär) and the summer cottage (Signilskär).

pling to ensure that the habitats were comparable with each other. Estimates of the habitat composition of the islands (based on aerial photographs, 1:5000), as well as our sampling scheme relative to different habitats, are included in Table 1. In the following, we briefly describe the habitats. They are arranged from dry, open habitats to humid, closed ones.

Scrub habitat is a mosaic of juniper bushes (*Juniperus communis*) and dry, grass-covered patches with *Festuca ovina* and *Deschampsia flexuosa* as abundant species, similar on every island. Also *Hypericum maculatum*, *Galium verum*, *Filipendula vulgaris* and *Rubus idaeus* were found. The ground is covered mainly by lichens and mosses. On Lågskär and Signilskär the habitat lacks trees, but on Björkör a few birches (*Betula pendula*) and rowans (*Sorbus aucuparia*) grow among junipers.

Meadows are dry and exposed sites, similar on every island. There is, however, some variation in the dominant plant species (*Elymus repens*, Lågskär; *Calamagrostis epigejos*, Björkör; and *Alopecurus pratensis* and *E. repens*, Signilskär). Other abundant species are *G. verum*, *Achillea millefolium*, *Anthriscus sylvestris* and *Potentilla erecta*. The Björkör site had been mowed.

Shore meadows, quite similar to each other, are found on Signilskär and Lågskär. Abundant plant species are *Potentilla palustre*, *Lythrum salicaria*, *Carex spp.*, *Eriophorum sp.* and *Peucedanum palustre*. Some juniper bushes grow randomly in both sites.

Abandoned fields are found on Lågskär and Björkör, although with somewhat different vegetation. On Lågskär the field layer is dominated by grasses (*Phalaris arundinacea* and *C. epigejos*). Also *Epilobium angustifolium*, *Urtica dioica* and *R. idaeus* are abundant. The Björkör field is covered by 5 m-high saplings (*Alnus glutinosa*, *B. pendula* and *Salix sp.*), with *Rubus idaeus*, *R. caesius*, *Geum urbanum*, *Filipendula ulmaria* and *Deschampsia caespitosa* being abundant in the field layer.

Wooded meadow is found on Björkör on a site where hazelnut (*Corylus avellana*) was planted in the 1920s or 1930s (Danielsson 1972, Hæggström pers. comm., see also Palmgren 1917). The field layer is dominated by herbs such as *R. idaeus*, *R. caesius*, *G. urbanum* and *Geranium silvaticum*. Other species found are *Maianthemum bifolium*, *F. ulmaria* and *Anemone nemorosa* (see also Palmgren 1917 and Hæggström 1985).

Coniferous forests cover only small patches on the islands. Both pine (*Pinus silvestris*) and spruce (*Picea abies*) are found. On Signilskär and Björkör a substantial proportion of birch is included in the forest stands. The Lågskär forest was planted in the 1930s (T. Johansson, pers. comm.). Abundant species in the field layer include *Vaccinium myrtillus* (Björkör), *U. dioica*, *E. angustifolium* and *R. idaeus* (Lågskär), and *Cornus suecica*, *Melampyrum pratense*, *Maianthemum bifolium* and *V. myrtillus* (Signilskär).

Birch forest grows in a moist depression on Signilskär. Other trees found are rowan, juniper and pine. Abundant species in the field layer are *Vaccinium vitis-idaea*, *Empetrum nigrum*, *M. pratense*, *Poa nemoralis* and *Melica nutans*.

Alder groves are moist and shaded alder (*Alnus glutinosa*) stands, similar on every island. Other abundant trees are birch and rowan. The field layer is dominated by dense herb vegetation, the most abundant species being *R. idaeus* and *F. ulmaria*. Also *U. dioica*, *Potentilla palustre* and *Lysimachia vulgaris* are found. In early summer there were pools of standing water at the sites.

2.3. Mainland references

It is impossible to find identical habitat configurations on the Åland mainland where habitats cover larger, more continuous areas than on the islands. For instance, scrub is a widespread habitat type on the islands, but scarce on the mainland. On the mainland we identified direct references for four island habitat types (meadow, shore meadow, wooded meadow, alder grove, called reference R1 below), and we use our data from previous studies from Åland as additional references (R2–R7). These data sets give a rough picture of the abundances of carabid species in a variety of habitats on the Åland mainland and small islands in the Åland archipelago. The reference data sets are presented in Appendix 1.

The four mainland reference habitats (R1) were structurally similar to their island counterparts, but there was some variation in plant species composition. The mainland meadow was dominated by *Phleum pratense* and *Filipendula vulgaris*, and *Trifolium pratense, Heracleum sphondylium* and *Taraxacum vulgare* were abundant. The mainland shore meadow was dominated by *Juncus filiformis*, and the wooded meadow by *G. silvaticum, Rubus saxatilis* and *Geum rivale*. The reference meadow and wooded meadow were located on a large island (Nåtö, area about 200 ha, see Palmgren 1917, Hæggström 1983) close to the Åland mainland.

2.4. Sampling procedure

We used pitfall traps (Southwood 1978) to collect the carabids. The traps (diameter 65 mm, volume 170 ml) were partially filled with water and detergent (NaOH). Thirty traps were placed in a grid (usually 5 × 6 traps) at each sampling site on the islands and the mainland references (R1). To get a representative sample of species active in spring and of those active in autumn, samples were taken in periods of five days in early summer (19–26 May) and late summer (4–13 August 1986) (mainland wooded meadow was similarly sampled in May and August 1985). Pooled early and late summer samples give a similar picture of the local carabid assemblages to that which a continuous sampling throughout the season would give (Niemelä et al. 1988). A similar sampling procedure was used in the additional mainland reference studies (R2–R7), but sampling effort differed (see Appendix 1).

3. Colonization success of individual species

It would be difficult to estimate the colonization success of individual species on the basis of mere presence-absence data, because a species' "presence" may be due to transient individuals and this would, therefore, be a weak estimator of colonization success. We selected only the abundant species for a numerical comparison of their island-mainland distribution. The species can be roughly divided into three classes using their abundances on the islands, compared with the mainland, as a criterion (Table 2):

(1) Three species (*Clivina fossor, Pterostichus melanarius* and *P. versicolor*) were abundant on the mainland (> 1% of the mainland sample), but were not found on the islands (except one individual of *P. versicolor* on Signilskär) (Table 2 and Appendix 2). Both *Pterostichus* species were abundant also in the mainland references R2, R3, R5, R6 and R7; the total mainland sample of *P. melanarius* was 796 individuals and that of *P. versicolor* was 663 individuals. However, both species were absent from islands included in the references (except one individual of *P. versicolor* in R5). Also *C. fossor* was more abundant on the mainland (20 individuals) than on islands (2 individuals) in references R3, R5, R6 and R7.

(2) Six species were abundant on all three islands (found on all islands and comprising ≥1% of the pooled sample of each island ; *Calathus fuscipes, C. melanocephalus, Patrobus atrorufus, Pterostichus niger, P. nigrita* and *Trechus secalis*). Another five species (*Agonum fuliginosum, Amara communis, Dyschirius globosus, Loricera pilicornis* and *Pterostichus strenuus*) were found on all three islands, although in small numbers on some of them. We consider these eleven species as being successful colonists.

To describe the general abundance of the eleven species on the Åland mainland we give their abundances in the additional mainland references in Table 3. However, the sample sizes in Table 3 should be considered as indicative only, due to differences in sampling design. *Calathus fuscipes* and *C. melanocephalus* are relatively scarce in the mainland reference data (Tables 2 and 3). They are mainly restricted to R1 and to the mainland field sample (R2, 15 and 155 individuals, respectively, in a total sample of 3837 individuals). *Patrobus atrorufus* and *Trechus secalis* were found in comparable abundances on the islands and on the mainland. *Pterostichus niger* and *P. nigrita* tend to be more abundant on the islands than on the mainland. *P. nigrita* was abundant in shore habitats in reference R3.

Of the five less abundant successful colonists, *Agonum fuliginosum* and *Dyschirius globosus* were abundant on large and small islands in Vargskär (R7). *Loricera pilicornis* was abundant in the mainland shores (R3) and lush forests (R6). *Amara communis* was abundant in the field sample (R2), whereas *Pterostichus strenuus* was quite scarce in all references.

Table 2. Classification of the abundant species, and their sample sizes on the three islands and on the mainland (standardized by the mainland sampling effort, 1200 trap-days). Wing length (Lindroth 1949, 1985, 1986): M = macropterous, (M) = macr. but no flight observations, D = dimorphic, B = brachypterous). Dispersal power (den Boer 1977): L = low dispersal power, H = high, U = uncertain). Habitat preferences according to Lindroth 1985, 1986.

	Björk-ör	Signil-skär	Låg-skär	Main-land	Wing length	Dispersal power	Habitat preference
Abundant on the mainland							
Clivina fossor	0	0	0	12	D	H	euryt., grassy, humid habs.
Pterostichus melanarius	0	0	0	145	D	U	eurytopic in open hab. } cultiv.
P. versicolor	0	1	0	37	(M)	L	open, dry habitats } soil
Successful colonists							
Agonum fuliginosum	11	5	13	8	D	H	moist forests
Amara communis	3	19	5	5	M	H	eurytopic in open hab.
Calathus fuscipes	61	29	283	4	B	L	euryt. in dry, open hab.
C. melanocephalus	17	85	61	11	D	L	open, dry (e.g. meadows)
Dyschirius globosus	15	39	3	4	B	L	euryt. in humid, open hab.
Loricera pilicornis	15	3	3	15	M	H	euryt. in humid forests
Patrobus atrorufus	83	61	63	192	B	L	humid, deciduous forests
Pterostichus niger	161	65	165	37	(M)	L	eurytopic in forests
P. nigrita	17	40	25	10	M	H	wet, humus-rich habitats
P. strenuus	5	19	11	23	D	H	deciduous forests
Trechus secalis	197	67	94	33	B	L	moist, shaded, humus-rich habitats
Mosaic distribution							
Agonum obscurum	26	0	14	2	D	L	deciduous forests
Amara brunnea	31	2	0	1	(M)	H	shady hab. (open forest)
Calathus micropterus	45	7	0	3	B	L	moderately dry forests
Carabus hortensis	91	0	1	1	B	–	deciduous-mixed forests
Cychrus caraboides	35	0	3	3	B	L	moist, deciduous forests
Nebria brevicollis	33	0	1	3	M	U	euryt. in deciduous forests
Pterostichus oblongopunctatus	88	59	0	13	(M)	L	eurytopic in forests

Table 3. Pooled sample of the eleven successful colonists on the three study islands, compared with the sample in our mainland reference data sets (for the symbols see text and Appendix 1). The sample sizes are standardized to 500 trap-days. + indicates that the standardized sample size was <1, and – that the species was not caught.

	Islands	R1	R2	R3	R4	R5	R6	R7
Agonum fuliginosum	4	13	4	4	4	11	11	102
Amara communis	4	2	20	2	+	+	–	1
Calathus fuscipes	52	2	1	–	–	–	–	3
C. melanocephalus	23	5	10	1	–	–	–	5
Dyschirius globosus	8	2	3	5	+	1	–	27
Loricera pilicornis	3	8	2	27	1	11	47	6
Patrobus atrorufus	29	80	6	31	3	115	199	1
Pterostichus niger	54	15	9	15	14	44	3	38
P. nigrita	11	4	1	19	1	1	9	6
P. strenuus	5	10	10	3	–	1	2	5
Trechus secalis	50	14	49	16	34	124	12	253

(3) Seven species show a "mosaic distribution", being abundant on one or two of the islands (>1% of the pooled island sample), but not caught on the other(s) (*Agonum obscurum, Amara brunnea, Calathus micropterus, Carabus hortensis, Cychrus caraboides, Nebria brevicollis* and *Pterostichus oblongopunctatus*) (Table 2). It is practically impossible to get clear records of "absence" of carabid beetles on islands as large as 30 ha. However, the samples of most species are large in some of the data sets, and we regard the zero records as indicating either absence or very low population numbers.

All the seven species were numerous on Björkör (nearest to the mainland), but were not caught either on Signilskär or Lågskär (or both). Note that different species are absent from Signilskär and Lågskär.

There is great variation in the occurrence of these seven species in our additional references. On small

Table 4. The species number (with standard deviation) standardized to 50 individuals in each habitat type, and in the combined samples from island and mainland meadows and alder groves. In the pooled sample from each island (entire island) the sample is standardized to 800 individuals. Observed species numbers are marked with an asterisk (sample size about 50 individuals, see Appendix 2). Mainland coniferous forest is reference sample R4.

	Scrub	Meadow	Shore meadow	Wooded meadow	Coniferous forest	Alder grove	Entire island
Björkör	11.6±1.0	10.1±1.1	–	13.7±1.6	10.6±1.1	12.1±1.4	27.4±1.3
Signilskär	11.6±1.0	10.0±1.5	13*	–	9.5±1.3	11.0±1.4	31.8±0.4
Lågskär	3.9±0.9	1.9±0.6	7*	–	10.0±1.4	7.5±1.2	18.9±0.9
Mainland	–	10.9±1.5	15*	10.8±2.0	11.4±1.5	15.3±1.6	–
Mainland +							
Björkör		12.6±1.8				16.3±1.8	
Signilskär		12.7±1.8				15.9±1.8	
Lågskär		7.7±1.4				11.7±1.7	

islands in the Mariehamn archipelago (R3, R5, R6) *Agonum obscurum* was scarce (17 individuals from a sample of 1360 individuals), but on small islands in Vargskär (R7) it was the most abundant species (1239 from a sample of 4612 individuals). *Calathus micropterus, Carabus hortensis* and *Cychrus caraboides* were considerably more abundant on islands than on the mainland, and *Pterostichus oblongopunctatus* was more abundant on the mainland in our references studies (R3, R5, R6 and R7). *Amara brunnea* was scarce in all references. *Nebria brevicollis* is restricted in Finland to the Åland Islands. The species prefers deciduous forests (Lindroth 1985), but was found in the additional mainland references only twice (two individuals).

Another four species (*Amara lunicollis, Carabus violaceus, Notiophilus aquaticus* and *Pterostichus diligens*, see Appendix 2) were abundant on Signilskär and scarce on the other(s). As the samples are small, however, it is not possible to assess how reliable the patterns are.

4. Species richness and diversity

We studied variation in carabid species richness among sampling sites using rarefaction (Simberloff 1978). The analysis was done by comparing species richness in similar habitats from the islands and the mainland. We used the samples from: (1) the three habitats sampled on all islands and on the mainland (meadows and alder groves R1, and coniferous forests R4, see Appendix 2), (2) the two habitats (shore meadow and wooded meadow) that were found on some of the islands and on the mainland, and (3) the scrubs that were sampled on all the three islands (Table 4). The main pattern in the comparisons is that Lågskär sites (the most distant island) have lower species richness than similar habitats on the other islands and the mainland (except in coniferous forest). This conclusion holds true also for the pooled island data. Moreover, Björkör and Signilskär have similar species richness in all habitat types studied.

Rarefaction technique was also used to estimate how much species richness increases in pairwise combinations of the samples, compared with the original ones; the two structurally most similar habitats (meadows, alder groves) sampled on all islands and the mainland are included. The relations of Björkör and Signilskär habitat samples to their mainland counterparts are similar, whereas Lågskär samples are impoverished (Table 4).

The compositional similarity of the samples from individual sites was studied using detrended correspondence analysis (ln-transformed data) (Gauch 1982). 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. We use the method here in exploratory fashion for comparing relative distances among the sites, not for strict hypothesis-testing (see also Birks 1987).

The first axis of the ordination (eigenvalue 0.37) identifies a weak gradient from dry, open sites to

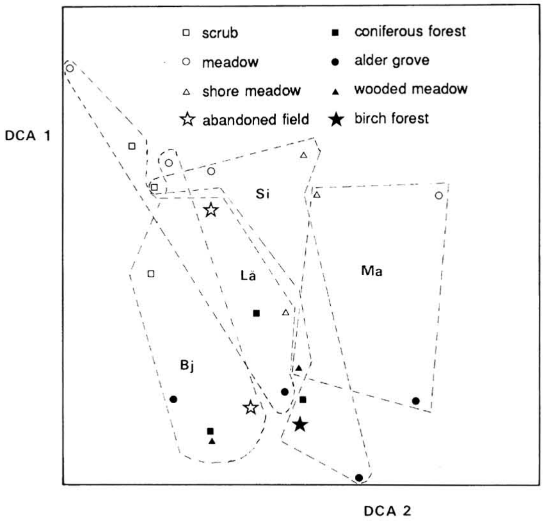

Fig. 3. The location of the sampling sites in the DCA-ordination (first and second axis). The habitats of each island (Bj, Si, Lå) and the mainland (Ma) are within an interrupted line.

closed, moist ones (Fig. 3). The dry end of the gradient comprises mainly scrubs and meadows, and the characteristic carabid species include *Calathus fuscipes, C. melanocephalus, Amara tibialis, A. ovata* and *Notiophilus aquaticus*. The moist end of the ordination consists mainly of coniferous forests and alder groves, characterized by carabid species such as *Agonum fuliginosum, A. obscurum, Loricera pilicornis, Patrobus atrorufus* and *Pterostichus nigrita*. The mainland habitats were located close to their counterparts on the islands, with one exception — the mainland meadow — due to the absence of *Pterostichus melanarius* and *P. versicolor* from the islands.

The second axis (0.23) of the ordination is more difficult to interpret, but it seems to represent a gradient from the mainland sites to the sites on the most distant island (Lågskär).

Although the carabid assemblages seem to be primarily influenced by habitat, the sites of each island and the mainland tend to form clusters in Fig. 3. We tested this pattern by calculating Euclidian distances in the DCA-ordination (I and II axes) between the six sites within each island and the four sites on the mainland on the basis of their location. The observed distances were then compared with distances between the same number of pairs of sites (six sites on the islands and four on the mainland) drawn randomly from the 22 sampling sites. The result of 1000 random draws is summarized in the following tabulation:

	Observed distance	Percent observed > random distance
Björkör	881	0.2
Signilskär	1339	22.4
Lågskär	1196	7.0
Mainland	1150	5.4

The observed distances are shorter (at 0.10 level) than the random ones on Björkör, Lågskär and on the mainland. The result indicates that the carabid assemblages are more similar to each other than random within these two islands and the mainland (see also Enckell et al. 1987).

5. Discussion

5.1. Colonization propensity of carabid beetles

Our data give a "snapshot" view of the distribution of carabid beetles on the three islands in one summer. Long-term data are needed for conclusions on the colonization dynamics of the species. However, the proportion of islands with a local population gives a rough estimate of the colonization ability of different species. Our data show clear differences among the species according to this criterion. No less than seven of the 21 abundant species occur in rather high numbers on Björkör, but occasionally — or in low numbers — on the two other islands ("mosaic distribution"). Another three species were not caught on the islands although they were abundant in comparable habitats on the mainland. The probable explanation for the distribution patterns differ from species to species and more detailed work is required to reveal the mechanisms, but in the following we discuss some alternatives on the basis of our data.

(1) Dispersal ability is clearly an important factor affecting colonization (e.g. Simberloff 1981, Enckell et al. 1987). For instance, Ranta & Ås (1982) found out that long-winged carabid species (probably good disperses) are more successful in colonizing Dutch polders than short-winged species. However, there is no clear relationship with our results (Table 2) and the wing length or dispersal ability of the species given in literature (Lindroth 1945, 1949, 1985, 1986, den Boer 1977). For instance, *Clivina fcssor* has a high flying

activity and often occurs in sea drifts (Lindroth 1985), but the species was not found on the islands in our study.

Palmén (1944) and Lindroth (1949) proposed that anemohydrochoric dispersal is the most important way of dispersal of carabids to islands in the Baltic (see also Gillerfors 1966, Thiele 1977, Ås 1984). Twenty-six of the 44 species we found on our study islands had been found in sea drift (Palmén 1944). Of our successful colonists, *Calathus fuscipes, Patrobus atrorufus, Pterostichus niger* and *Trechus secalis* were not listed by Palmén (1944). Note that three of these species are short-winged.

(2) Abundance in the source area might affect the probability of reaching islands. However, the abundant species in the mainland references (*Clivina fossor, Loricera pilicornis, Patrobus atrorufus, Pterostichus melanarius, P. niger, P. oblongopunctatus, P. strenuus, P. versicolor* and *Trechus secalis*) have highly variable colonization success. Hence, it seems that we cannot directly predict the colonization success of the species on the basis of mainland abundance. Moreover, Niemelä et al. (1985) found that several species abundant on the Åland mainland were scarce, or were not caught at all, on small islands close to the mainland. Ranta & Ås (1982) concluded that mainland abundances could not alone explain the colonization success of carabids on Dutch polders.

(3) Habitat preference may be important for the establishment of a population on an island. We assume that species abundant on the mainland in habitats widespread also on the islands have a greater possibility of establishing a population on the islands than species living in habitats scarce on the islands. Furthermore, founding a population on an island is presumably easier for a habitat generalist than for a habitat specialist (Williams 1969).

However, it seems difficult to explain the distribution of the species in our data by mere habitat preferences. The habitat preferences and mainland distribution of the species in the three distributional groups described in sect. 3 (abundant on the mainland, successful colonists, "mosaic distribution") are quite similar. For instance, *Pterostichus niger, P. melanarius* and *P. versicolor* occurred in several habitats on the mainland, but on the islands only *P. niger* was widespread and numerous, the other two species being absent. *P. melanarius* and *P. versicolor* have been numerous on the mainland in other studies as well, but on the islands, *P. versicolor* has been scarce and *P. melanarius* has been completely absent (studies given in Appendix 1).

The species showing a "mosaic distribution" are predominantly forest species, which may contribute to their absence from some of the islands. Gillerfors (1966) did not find some forest carabids (e.g. *Calathus micropterus, Carabus hortensis, C. violaceus* and *Pterostichus oblongopunctatus*) on islands with no forests.

The relative importance of dispersal ability and habitat availability in Baltic conditions has been discussed by Gillerfors (1966) and Ås (1984). Ås (1984) regarded the abundance of short-winged carabid individuals on islands close to the mainland, and their scarcity on more distant islands, as evidence for the importance of dispersal ability for colonization. Gillerfors (1966), however, considered that the high proportion of short-winged beetles on islands is due to habitat composition: the proportion of short-winged species was high also on the mainland in habitat types dominant on the islands (generally dry, treeless habitats). Thus, Gillerfors (1966) concluded that the occurrence of individual species in the archipelago was mainly determined by the habitat composition of the islands. Haeck et al. (1980) concluded that both dispersal ability and the habitat preference of the species are important in determining the colonization success on Dutch polders.

(4) Colonization by human transportation may be an important mechanism for species of cultural habitats. Our data include no species that are entirely restricted to cultural habitats and depend on human activities for colonization. However, several of the successful colonists (*Patrobus atrorufus, Calathus fuscipes* and *C. melanocephalus*) favour cultural habitats, and human influence has increased their colonization propensity, at least through habitat modification (see also Enckell et al. 1987). On the other hand, also the three abundant species not found on the islands are favoured by human activity.

5.2. How distant an island is isolated?

Our study islands differ from each other and from the mainland in their degree of isolation, but also the habitat composition varies with increasing isolation. Björkör is the most luxuriant of our study islands, with considerably larger patches of continuous vegetation than Signilskär or Lågskär. The decreasing area of vegetation, with increasing isolation, makes it difficult to determine whether the absence of a particular species from some of the islands is due to the scarcity of immigrants as a result of isolation (because of poor dispersal ability) or due to the failure of establishing a population (e.g. due to the lack of a suitable habitat).

One may presume, however, that the differences between the islands in terms of occurrence of individual carabid species indicate a gradient of increasing isolation. Most of the species found on the islands were included in the species list of Björkör, which is nearest to the mainland and has the largest vegetation area. The DCA-ordination showed that the carabid samples on Björkör were more similar to each other than random. This pattern may be due to the relatively continuous and luxurious habitat composition of the island, enhancing the movement of carabids between the sampling sites. Furthermore, the habitat composition of Björkör and the mainland are so similar that habitat variation cannot explain the absence of *Pterostichus melanarius*, *P. versicolor* and *C. fossor* from Björkör.

Habitats studied on the two most distant islands (Signilskär and Lågskär) are so similar that habitat differences can hardly be the only explanation for the variation in carabid assemblages between these two islands, although habitat patches and the total area of vegetation are smaller on Lågskär. We assume that the habitat patches on Lågskär and Signilskär are large enough to fulfill the minimum requirements of the seven species not found there, because all these species were found on small islands in the Mariehamn archipelago (R5) or on small islands (<7 ha) in the Vargskär archipelago (R7).

We suggest that both habitat effects and island isolation determine the distribution patterns of the species. The small area of the habitats and their patchy distribution on distant islands, combined with the stochasticity of dispersal over water, may lead to a total failure to establish populations on the islands (*Pterostichus melanarius*, *P. versicolor* and *Clivina fossor*) or to a "mosaic distribution" of the species.

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Appendix 1. Some characteristics of the data sets used as a reference for the island samples.

	Location	Sampling year	Habitat type	Sampling effort (trap-days)	Sample size	Species number	Reference
R1	Main Åland	1986	alder grove	300	see Appendix 2.		
	Main Åland	1986	meadow	300	see Appendix 2.		
	Main Åland	1986	shore meadow	300	see Appendix 2.		
	Main Åland	1985	wooded meadow	300	see Appendix 2.		
R2	Main Åland	1985	51 fields/meadows	7650	3837	75	Niemelä et al. in prep.
R3	Main Åland	1984	shore, alder belt	3375	1414	58	Niemelä 1988b
	Four islands[1] (8–29 ha)	1984	shore, alder belt	1800	341	24	
R4	Main Åland	1983	coniferous forest	3000	657	20	Niemelä et al. 1986
R5	Main Åland	1983	five habitat types	1500	913	31	Niemelä 1988a
	Five islands[1] (8–29 ha)	1983	five habitat types	3000	776	33	
R6	Main Åland	1982	lush forest patches	1500	1069	25	Niemelä et al. 1985
	Five islands[1] (8–29 ha)	1982	lush forest patches	1500	245	18	
R7	Vargskär, five large islands (2–6 km^2)	1980	six habitat types	900	1182	42	Niemelä et al. 1987
	Vargskär, 13 small islands (49–0.5 ha)	1980	nine habitat types	1890	4612	42	

[1] The islands are the same in R3 (four out of the five), R5 and R6.

Appendix 2. Carabid beetles caught at the sampling sites on the islands and on the mainland. Symbols: Bj = Björkör, Si = Signilskär, Lå = Lågskär. Nomenclature follows Lindroth (1985, 1986).

	Scrub			Meadow				Shore meadow			Aband. field		Wooded meadow		Coniferous forest			Birch forest	Alder grove				Total			
	Bj	Si	Lå	Bj	Si	Lå	Ma	Si	Lå	Ma	Bj	Lå	Bj	Ma	Bj	Si	Lå	Si	Bj	Si	Lå	Ma	Bj	Si	Lå	Ma
Abundant on mainland																										
Clivina fossor (L.)	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	6	0	0	0	12
Pterostichus melanarius (Ill.)	0	0	0	0	0	0	60	0	0	0	0	0	0	82	0	0	0	0	0	0	0	3	0	0	0	145
P. versicolor (Sturm)	0	0	0	0	0	0	29	1	0	3	0	0	0	1	0	0	0	0	0	0	0	4	0	1	0	37
Successful colonists																										
Agonum fuliginosum (Pz.)	0	0	0	0	0	0	0	0	3	1	5	1	1	1	7	1	4	1	3	5	11	6	16	7	19	8
Amara communis (Pz.)	0	8	0	3	3	0	1	9	1	3	0	6	0	1	0	6	1	2	2	0	0	0	5	28	8	5
Calathus fuscipes (Gz.)	32	23	125	39	18	269	1	2	0	0	1	24	2	3	0	0	5	0	17	0	1	0	91	43	424	4
C. melanocephalus (L.)	1	4	39	18	123	6	8	0	0	0	2	19	2	3	2	0	26	0	1	0	2	0	26	127	92	11
Dyschirius globosus (Hbst.)	9	4	0	3	50	0	0	4	5	4	9	0	0	0	0	0	0	0	2	0	0	0	23	58	5	4
Loricera pilicornis (F.)	0	0	0	0	0	0	1	0	0	0	20	0	3	1	0	3	1	0	0	2	3	13	23	5	4	15
Patrobus atrorufus (Ström)	0	7	0	1	6	0	0	0	1	0	74	1	19	156	12	16	4	38	18	25	89	36	124	92	95	192
Pterostichus niger (Schall.)	11	6	6	4	23	1	15	6	28	9	81	45	64	13	36	20	14	37	45	6	154	0	241	98	248	37
P. nigrita (Payk.)	0	0	0	0	1	0	0	8	5	1	11	0	4	1	4	31	7	9	6	11	26	8	25	60	38	10
P. strenuus (Pz.)	0	17	0	0	5	0	0	3	0	7	2	16	0	6	4	2	0	1	1	0	0	10	7	28	16	23
Trechus secalis (Payk.)	9	2	0	6	72	0	8	0	2	12	152	64	30	7	55	24	66	3	43	0	9	6	295	101	141	33
Mosaic distribution																										
Agonum obscurum (Hbst.)	0	0	0	0	0	0	0	0	0	0	11	0	1	1	17	0	0	0	10	0	21	1	39	0	21	2
Amara brunnea (Gyll.)	0	0	0	0	0	0	0	0	0	0	6	0	23	1	2	3	0	0	16	0	0	0	47	3	0	1
Calathus micropterus (Dft.)	3	0	0	0	1	0	0	0	0	0	3	0	7	3	30	2	0	4	24	3	0	0	67	10	0	3
Carabus hortensis L.	9	0	0	0	0	0	0	0	0	0	8	0	7	1	45	0	1	0	68	0	0	0	137	0	1	1
Cychrus caraboides (L.)	2	0	2	1	0	0	0	0	0	0	5	0	10	1	19	0	1	0	16	0	1	2	53	0	4	3
Nebria brevicollis (F.)	0	0	0	0	0	0	0	0	0	0	7	0	43	3	0	0	1	0	0	0	0	0	50	0	1	3
Pterost. oblongopunctatus (F.)	4	1	0	0	0	0	0	0	0	0	13	0	13	10	39	56	0	18	63	13	0	3	132	88	0	13
Rare species																										
Agonum viduum (Pz.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
A. sexpunctatum (L.)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Amara apricaria (Payk.)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
A. aulica (Pz.)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
A. bifrons (Gyll.)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
A. lunicollis Schiødte	0	0	0	1	6	0	1	7	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	13	0	4
A. ovata (F.)	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
A. tibialis (Payk.)	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0
Badister bullatus (Schrank)	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	2	0	2
Bembidion lampros (Hbst.)	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	3
B. guttula (F.)	0	0	0	2	0	0	0	0	0	1	4	0	1	2	0	0	0	0	1	0	0	1	8	0	0	4
B. quadrimaculatum (L.)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Blethisa multipunctata (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Carabus violaceus L.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	12	0	2	0	0	0	14	0	1
Elaphrus cupreus Dft.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
E. uliginosus F.	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Harpalus affinis (Schrk.)	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
H. latus (L.)	2	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	2	1	2
H. luteicornis (Dft.)	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
H. quadripunctatus Dej.	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3	1	0	3
H. rufibarbis (F.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	5	0
H. rufipes (Deg.)	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Harpalus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Leistus ferrugineus (L.)	2	0	1	0	1	0	0	0	0	0	0	1	2	0	1	0	1	0	2	0	5	0	7	1	8	0
L. terminatus (Hellw. in Pz.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Notiophilus aquaticus (L.)	0	3	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0
N. biguttatus (F.)	0	0	0	1	0	0	0	0	0	0	1	0	2	6	0	0	0	0	0	0	0	0	4	0	0	6
N. germinyi Fauv.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Olisthopus rotundatus (Payk.)	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Oodes helopioides (F.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Pterostichus cupreus (L.)	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
P. diligens (Sturm)	0	0	1	0	3	0	0	2	0	1	0	0	0	0	0	3	0	0	0	1	1	2	0	9	2	3
P. minor (Gyll.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	12	0	2	2	12
P. vernalis (Pz.)	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Syntomus truncatellus (L.)	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Synuchus vivalis (Ill.)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Trechus discus (F.)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
T. rivularis (Gyll.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0
Total	90	79	174	81	332	276	144	46	45	51	416	178	236	316	273	168	138	125	341	74	324	120	1437	824	1135	631
Number of species	13	13	6	12	19	3	17	13	7	15	20	10	20	28	14	13	15	10	19	12	13	21	30	32	20	45

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