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Year-to-year variation in carabid beetle (Coleoptera, Carabidae) assemblages on the Åland Islands, south-west Finland

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Abstract

Aims (1) To investigate changes in structure of carabid assemblages between sites on the main island of Åland and five small nearby islands between 1982 and 1999. (2) To determine whether island differences observed in one year is mirrored in another one. (3) To examine changes in abundance levels of individual carabid species on these islands since 1982. (4) To compare the proportion of flightless species on the main island of Åland with those on the small islands.

Location Islands in the Baltic Sea, Finland; the main island of Åland (90,000 ha) and five small, nearby islands (8–29 ha).

Methods Carabid beetles were collected, using pitfall traps, during 4 years (1982, 1987, 1988 and 1999). Sampling took place in moist, spruce-dominated, lush forest patches.

Results Overall, 12,127 individuals representing forty-six carabid species were collected; forty-one species (8580 individuals) on the main island of Åland, and thirty-one species (3547 individuals) on the small islands. Carabid assemblage structure, measured using ordination techniques, was consistently and significantly different between the main island and the small island sites. Carabid assemblage structure and abundances of individual species did change significantly between years, possibly because of a combination of climatological and habitat changes in the Åland archipelago. The six most abundant species collected on the small islands, and the three most abundant species overall, were all short-winged. Furthermore, the small islands had a higher proportion and number of short-winged species compared with the main island of Åland.

Main conclusions Carabid assemblage structure was significantly different between the main island and the small islands in all years sampled, indicating that single-year studies are sufficient to demonstrate differences in carabid assemblages on Baltic islands. Small islands host a non-random proportion of species pools available on the main island of Åland and mainland Finland. It appears that dispersal to islands in the Baltic Sea is easy for carabid beetles of all wing forms, but that short-winged species are more successful colonizers.

Keywords

Baltic Sea islands, carabid beetles, dispersal ability, main island–small island comparison, year-to-year variation.

INTRODUCTION

Insect populations fluctuate between years, the changes in population sizes being often several orders of magnitude (Wolda, 1978, 1992; Den Boer, 1981). The mechanisms causing this pattern are not completely understood and many explanations have been proposed (Price, 1984). Furthermore, for many insect taxa, for instance carabid beetles, there are very few studies where sampling has continued over several years (Desender, 1996), making long-term studies particularly important in answering questions about year-to-year population dynamics, community dynamics and the importance of short-term conservation recommendations. Perhaps more importantly, long-term studies can distinguish gradual trends over time from short-term noisy fluctuations (Di Castri *et al.*, 1992).

In carabids, environmental conditions, such as weather, have been regarded as decisive for population fluctuations (Baars & Van Dijk, 1984a; Hengeveld, 1985). For instance, carabid larvae are very specific in their demands for suitable climatic conditions (Thiele, 1977). Thus, it may be expected that weather conditions varying between years affect carabid populations. Also, interspecific interactions, such as competition for food, are assumed to affect carabid populations (Lenski, 1982, 1984; Baars & Van Dijk, 1984b; Loreau, 1986), although interspecific competition has been considered to be of minor significance as compared with abiotic factors (Niemelä, 1993). Regardless of the causes of population fluctuations, the fact that populations vary between years make conclusions on the spatial distribution of species based on a 'snapshot' view from 1 year less reliable than data covering several years.

Islands are useful 'ecological laboratories' and many questions of ecology can be studied by comparing island faunas with those on the nearby mainland (Haila, 1990; Kotze *et al.*, 2000). Islands in the Baltic Sea are unique because inter-island distances are generally small, salinity is low (see Ås, 1984), and annual seasonality is pronounced (Järvinen & Ranta, 1987). Furthermore, there is a long history of research on many of these islands rendering them suitable for studies in population and community ecology and conservation (Niemelä *et al.*, 1985; Järvinen & Ranta, 1987; Ås *et al.*, 1997; Nieminen & Hanski, 1998; Saccheri *et al.*, 1998).

For example, in terms of carabid beetle wing form, islands off the coasts of Finland and Sweden host – contrary to expectation – a significantly higher proportion of short-winged or wingless carabid species compared with their nearest mainland provinces (Ås, 1984; Kotze *et al.*, 2000). Obviously, these short-winged species cannot fly from the mainland to the islands or between islands, but do get there in sufficient numbers to establish populations.

In this study we compared carabid samples taken with identical sampling design from the same sites on the main island of Åland and small, nearby islands in 4 years, spanning 17 years (1982, 1987, 1988 and 1999). The general observation in nature is that populations and assemblages are dynamic, and it is therefore expected that

the carabid assemblages here will change over 17 years. Specific questions asked are: (1) By what magnitude does the carabid assemblage change over the 17-year sampling period? (2) are differences observed between the main island and the small island carabid beetle assemblages in 1 year mirrored in the next, i.e. do the observed main island–small island distribution patterns of carabid species remain constant over the years? (3) following on from question 2, how reliable are the distribution patterns described on the basis of data from one year only, or in 1 year in general? (4) What are the proportions of flightless species vs. those able to fly on the islands compared with the main island of Åland?

Carabid beetles (Coleoptera, Carabidae) were used as study object not only because of their apparent flight ability differences, but also because the group is both ecologically and taxonomically well known, and occurs abundantly on Baltic islands (Lindroth, 1985, 1986; Niemelä, 1992, 1996).

MATERIALS AND METHODS

Study area and carabid beetle sampling

Carabid beetles were collected on the Åland Islands in SW Finland (about 60°N, 20°E). Sampling was carried out in 4 years (1982, 1987, 1988 and 1999), in the same five moist, spruce-dominated lush forest patches on small (8–29 ha) islands (Slätskär, Åskskär, Ärtskär, Yttre Korsö and Inre Korsö), 2.5–3.8 km off the main island of Åland (area about 900 km²). Vegetation cover on these islands ranges between 20 and 70% of the island area (see Table 1 in Niemelä, 1988). Five patches of the same habitat type were studied on the main island of Åland. For more details on the location, vegetation and habitat structure of the sites, see Niemelä *et al.* (1985).

Mean yearly air temperature has increased slightly on Åland since 1970, more so during winter than summer months (Fig. 1). Yearly precipitation, however, has increased markedly since 1970 (Fig. 1).

Carabids were collected using fifteen pitfall traps (trap diameter 65 mm, volume 170 mm) per site. The fifteen traps were placed 4–5 m apart in three line transects of five traps each. A 50-mL ethylene or propylene-glycol : water mixture (1 : 1) was used to preserve beetles in the traps. In 1982 and 1987, carabids were sampled four times during each season with similar sampling effort (fifteen traps per site, 5–7 days per sampling period). The dates of the sampling periods were as follows: 22–27 May 1982 (20–27 May 1987), 24–29 June 1982 (24–30 June 1987), 22–27 July 1982 (28 July–3 August 1987), and 19–24 August 1982 (26 August–2 September 1987). Trapping was continuous in both 1988 and 1999 (fifteen traps per site), with sites being visited three times in each year. In 1988, sampling started on 23 May and ended on 28 August. In 1999, trapping started on 19 May and ended on 21 August.

Because of uneven sampling intensities between years, abundance values of each species were standardized to 100 trapping days as follows. For each carabid species, we

Table 1 Repeated measures analysis of variance (ANOVA) to test for differences in carabid standardized abundance and rarefied species richness between the main island of Åland and the small island sites (the between-groups factor) and between the 4 years sampled (the repeated-measures factor). The ability to fly (Flight) was entered as a covariate. Carabids were divided into those that have the potential of flight (macropterous and dimorphic species), and those that are flightless (brachypterous species)

Source of variation	d.f. effect	MS effect	d.f. error	MS error	F	P
Individuals (100 trapping days)						
Main–small	1	7.091	16	0.248	28.635	< 0.001
Flight	1	6.165	16	0.248	24.895	< 0.001
Year	3	0.326	48	0.041	7.895	< 0.001
Main–small × flight	1	1.032	16	0.248	4.166	0.058
Main–small × year	3	0.223	48	0.041	5.413	0.003
Flight × year	3	0.283	48	0.041	6.863	< 0.001
Main–small × flight × year	3	0.237	48	0.041	5.751	0.002
Species (rarefied, $n = 5$)						
Main–small	1	0.737	16	0.247	2.988	0.103
Flight	1	10.672	16	0.247	43.250	< 0.001
Year	3	0.282	48	0.214	1.316	0.280
Main–small × flight	1	1.026	16	0.247	4.158	0.058
Main–small × year	3	0.126	48	0.214	0.589	0.625
Flight × year	3	0.071	48	0.214	0.332	0.802
Main–small × flight × year	3	0.617	48	0.214	2.881	0.045

Main–small = Main island–small islands.

Standardized carabid abundance values (100 trapping days) were log-transformed to approximate normality. Rarefied species richness data ($n = 5$) were not transformed.

Pterostichus niger was classified as a flightless species (see Lindroth, 1986).

pooled the number of individuals collected at each site (fifteen traps), per year. Although trap number was similar between all sites, the periods over which sampling took place differed: twenty trapping days in 1982, twenty-six in 1987, ninety-seven in 1988 and ninety-four in 1999 (see above). Therefore, the site-specific abundance values were standardized to 100 trapping days in each year.

Figure 1 Main climatological indicators measured at Jomala (60°07' N 19°54' E), Åland, the closest meteorological station to the study sites (Meteorological Yearbook of Finland, 1968–99). Yearly precipitation, summer (T_{summer}), mean (T_{mean}) and winter (T_{winter}) mean air temperatures since 1970 are shown. Points represent moving average values (calculated from 5 years; i.e. the moving average value for 1970 was calculated using values from 1968–72, etc.).

Statistical analyses

To study changes in carabid assemblages across the years and reliability of 1 year's sampling we used three analyses. First, species richness on the small islands was compared with that on the main island by constructing species accumulation curves for both the main island and the small island sites. Sampling order was randomized 100 times to eliminate sampling error and heterogeneity among the units sampled, and the mean and standard deviation of the number of species collected, $S(n)$, was computed for each value of n between one and twenty (five main island or small island sites × 4 years) (Colwell & Coddington, 1994).

Secondly, a nonmetric multidimensional scaling (NMDS) ordination, using a Bray–Curtis triangular similarity matrix was used to construct a two-dimensional map of carabid assemblage changes (carabid abundance standardized to 100 trapping days, see above) between the main island and the small islands, and between years (Clarke, 1993). The main advantage of using NMDS is that it displays rank similarities between samples, considered a biologically relevant definition of similarity between samples (Clarke, 1993). To test for differences in carabid assemblage-structure between the main island and the small island sites and between years, an analysis of similarity test (ANOSIM), was used. Analysis of similarity test is a nonparametric permutation procedure, and it uses the rank similarity matrix underlying the ordination of samples (Clarke & Green, 1988; Clarke, 1993). It is important to note that the ANOSIM was performed on *a priori* selected groups of samples, here the yearly main island and small island sites. This analysis was complemented by investigating the distribution patterns of

individual species between the main island and the small islands, and between the years sampled.

Thirdly, a repeated measures ANOVA was used to test for differences in carabid abundance (carabid abundance standardized to 100 trapping days, see above) and species richness between the main island and the small islands (between-group factor) and between years (repeated measures factor). Species richness values per site were adjusted using rarefaction, which is a statistical method for estimating the number of species expected in a random subsample (here five individuals) drawn from a larger sample (Simberloff, 1978; Magurran, 1988). Visual inspection of the data (using normal probability plots) suggested that the abundance data should be log-transformed to approach normality. Rarefied species richness data did not need to be transformed.

To test the effect of flight ability on the incidence of carabid species on the main island vs. on the small islands, and between years, flight ability was included in each of the two ANOVA models described above (abundance and species richness) as a covariate. Carabids were grouped into those with the potential of flight (hind wings constantly macrop-terous, or dimorphic species with individuals having either non-functional or functional hind wings), and flightless species (hind wings constantly brachypterous) [beetle characteristics obtained from Lindroth (1985, 1986)]. This design resulted in eighty sampling units per ANOVA test: carabid beetles collected at each site pooled into a capable of flight and flightless group, with forty sampling units per group (five main island sites $\times$ 4 years, plus five small island sites $\times$ 4 years).

RESULTS

Carabid assemblage structure changes

A total of 12,127 individuals representing forty-six carabid species were collected (Appendix 1). The three most abundant species accounted for 56.9% of the total catch. *Trechus secalis* was the numerically dominant species (24.8%), followed by *Patrobus atrofufus* (23.5%) and *Pterostichus niger* (8.6%). Nineteen carabid species were represented by less than ten individuals. Species accumulation curves for both the main island and small island sites indicate that most of the carabid species occurring in the sites were eventually collected, and that the main island sites accumulated species quicker than did the small islands (Fig. 2). Furthermore, the total number of species on the main island (forty-one species) was higher than on the small islands (thirty-one).

According to the NMDS analysis, there was a statistically significant separation between the main island and the small island sites in terms of carabid assemblages (Fig. 3). The main island–small island separation of the sites and their clustering according to location on the small islands or on the main island is to a great extent caused by the relatively high abundance of four of the fifteen species collected only on the main island (*Agonum livens*, *Carabus nemoralis*, *Leistus terminatus* and *P. melanarius*, see Appendix 1). On the contrary, the five species not collected on the main island

Figure 2 Species accumulation curves for main island and small island sites. Each point represents the mean of 100 randomizations of sample pooling order while the error bars are the corresponding standard deviations. The twenty points for the main island (or small island) curve represents the 'number of year-samples', i.e. 4 years $\times$ five sites.

were only represented in singletons on the small islands (Appendix 1). Furthermore, assemblage structure also changed significantly from 1982 to 1999 for both the main island and small island fauna (Fig. 3), but the separation of the main island–small island sites remained. Therefore, samples taken during 1 year only would correctly depict the difference between the main island–small island carabid assemblages.

To further explore the possible reasons for the marked differences between the main island and the small island assemblages, and between years, we plotted the distribution patterns of sixteen of the most abundant (standardized abundances) carabid species (Fig. 4). The species were selected on the basis of their abundance and distribution differences between the main island and small islands, and between years.

Some species have occurred only on the main island (Fig. 4, top row). *C. nemoralis*, a large (average body length = 23.9 mm), short-winged species was found for the first time in one of the main island sites in 1993 (Niemelä, pers. obs.) and only occurred on the main island of Åland in the 1999 samples. *Leistus terminatus* (6.9 mm, long-winged), *P. atrofufus* (8.6 mm, short-winged), *Clivina fossor* (6.0 mm, dimorphic) and *Loricera pilicornis* (7.1 mm, long-winged) occurred exclusively or predominantly on the main island, and have decreased in abundance since 1982. *Pterostichus melanarius* (14.7 mm, dimorphic) has not been captured on the small islands, but has been quite abundant on the main island, in particular in 1999. *Agonum livens* (8.9 mm, long-winged) is also confined to the main island. *Pterostichus oblongopunctatus* (10.9 mm, long-winged) has been collected from all the small islands, but is much less abundant there than on the main island.

Some species occurred both on the main island and on the small islands in more or less equal numbers. These include

Figure 3 Non-metric multidimensional scaling ordination illustrating the separation between the main island and the small island sites, and between years. Each sampling year is connected with a line. Stress values, analysis of similarity (ANOSIM) r -statistic and P values are also given. (A–E) (open circles) are the five sites sampled on the main island of Åland. (F–J) (closed triangles) are the five small island sites sampled [see Fig. 1 in Niemelä *et al.* (1985)], 82 = 1982, 87 = 1987, 88 = 1988, 99 = 1999.

A. fuliginosum, *P. nigrita*, *Calathus micropterus*, *A. obscurum* and *Trechus secalis*.

Carabus hortensis (24.8 mm, short-winged), *P. niger* (17.5 mm, macropterous, but wings are probably not functionary; Lindroth, 1986) and *Cychrus caraboides* (16.3 mm, short-winged) were abundantly captured on the small islands in all 4 years sampled. Of particular interest here is that the last six species in Fig. 4 (those that are abundant on the small islands), are either short-winged or with non-functionary wings, and therefore have not been able to colonize these islands by flight.

Carabid abundance, species richness and flight ability changes

Flight ability had a significant effect on the incidence of carabid beetles in the Åland archipelago (Table 1; Fig. 5). Overall, significantly more individuals were captured on the main island of Åland, compared with the small islands. Also, significantly more flightless individuals were captured on both the main island and the small islands, compared with individuals capable of flight (Fig. 5a, b). In terms of rarefied species richness, there was no detectable significant difference between the main island and the small islands or between years (Table 1), although total number of species collected was higher on the main island compared with the small islands (Fig. 2).

Flight ability did have a significant effect on species occurrence on the islands. Although there were more species capable of flight on both the main island of Åland and the small islands (compared with the number of flightless species), there were more flightless species on the small islands than on the main island of Åland (Table 1; Fig. 5c, d). This result supports previous findings that small islands

sample a higher proportion of flightless carabid species compared with the nearby mainland species pools (Ås, 1984; Kotze *et al.*, 2000).

In absolute numbers, 33% (ten of thirty) of the species collected on the small islands were short-winged, compared with 30% (twelve of forty) on the main island of Åland. Although this difference is not large, it is considerably higher than the proportion of short-winged species in the closest Finnish mainland province [12%, 24/195; see Lindroth (1985, 1986)]. In other words, 63% (twenty of thirty-two) of the species capable of flight, were collected on the small islands, while 83% (ten of twelve) of the flightless species collected, were collected on the small islands.

This result seems surprising as only 1.8% (18/996) of the carabid individuals, and 3.4% (three of eighty-seven) of the carabid species collected in sea drift on islands in the Eastern Gulf of Finland National Park between 1996 and 2000, were short-winged (Karjalainen, 2000) (Table 2).

DISCUSSION

Year-to-year variation

Both the main island of Åland and small island fauna changed between 1982 and 1999, but the distinction between the main island–small island fauna remained. Thus, it is possible to predict differences in carabid assemblage structure between the main island and the small islands based on 1 year of observation. This kind of ability to predict the pattern in ecological systems depends on the relationship between spatial and temporal scales of variation (Wiens, 1989). For example, studies conducted over a long time at fine spatial scales have low predictive powers, while studies conducted over larger spatial scales have higher

Figure 4 Standardized (100 trapping days) abundances of sixteen of the most abundant carabid species collected. The first ten panels represent species predominantly collected on the main island of Åland, while the last three panels represent species predominantly collected on the small islands. Note that the scales of the y-axes differ. Per year mean values and standard errors were calculated from five values – either the five main island or the five small island sites.

predictability. Our study showed that it is possible to predict carabid differences at the assemblage level, i.e. in each of the 4 years sampled the main island fauna was significantly different from the small island fauna. As expected, at the finer level of populations among small island or main island sites, this was not possible as abundance levels of individual species changed considerably between years.

The year-to-year variation in carabid assemblages may be caused by weather conditions. It has been suggested that macro-climatological factors are important in regulating carabid populations (Hengeveld, 1985; Desender, 1996), but it appears that climate alone is not responsible for the changes in the abundances of individual species on Åland. For example, three of the most abundant carabid species collected on the main island, *P. atrorufus*, *L. pilicornis* and

L. terminatus are associated with wet conditions (Lindroth, 1985, 1986), but have decreased markedly in numbers since 1982. Yet, conditions have become wetter on the Åland islands since 1970.

Forestry may be more important in influencing carabid numbers on the main island of Åland. For example, forestry is responsible for the draining of moist areas and clearcuts (Esseen *et al.*, 1997). This 'drying up' of habitat may be responsible for the decline in numbers of wet-habitat species (see above), the increase in numbers of dry-habitat species (*C. nemoralis* and *P. oblongopunctatus*), and the increase in numbers of species associated with disturbed, human environments (*P. melanarius*, *Trechus secalis* and *P. niger*). Indeed, forestry activity has been recorded in three of the five main island sites investigated.

Figure 5 Yearly standardized carabid abundance on the main island of Åland (a) and the small islands (b), and yearly rarefied carabid species richness on the main island of Åland (c) and the small islands (d). Carabid beetles were divided into those capable of flight (macropterous and dimorphic) and flightless species (brachypterous). The figure represents the three-way interactions in Table 1.

Table 2 Carabid beetles collected in sea drift in the Eastern Gulf of Finland National Park, from 1996 to 2000 (Karjalainen, 2000). Species are divided into a macropterous group (first sixty-five species), dimorphic group (next seventeen species), unknown wing-form group (two species), and a brachypterous group (last three species)

Species	<i>n</i>
<i>Acupalpus flavicollis</i> (Sturm 1825) ^{14, 16}	2
<i>A. meridianus</i> (L. 1761) ^{2, 9, 12, 14, 16}	8
<i>A. parvulus</i> (Sturm 1825) ^{2, 4, 9, 12, 13, 14, 15, 16}	20
<i>Agonum piceum</i> (L. 1758) ^{14, 16}	3
<i>A. sexpunctatum</i> (L. 1758) ^{9, 14}	3
<i>A. thoreyi</i> Dejean 1828 ^{9, 13, 14, 15, 18}	7
<i>Amara aenea</i> (Degeer 1774) ^{4, 13, 14}	4
<i>A. apricaria</i> (Paykull 1790) ³	1
<i>A. aulica</i> (Panzer 1797) ¹⁴	1
<i>A. bifrons</i> (Gyllenhal 1810) ¹⁴	1
<i>A. brunnea</i> (Gyllenhal 1810) ^{4, 15, 19}	3
<i>A. communis</i> (Panzer 1797) ^{2, 9, 12, 13, 14, 16}	11
<i>A. famelica</i> Zimmermann 1832 ^{2, 12, 14, 16}	6
<i>A. familiaris</i> (Duftschmid 1812) ^{2, 3, 4, 12, 14, 16}	19
<i>A. fulva</i> (Müller 1776) ^{3, 9, 12, 13, 16}	6
<i>A. ingenua</i> (Duftschmid 1812) ¹²	1
<i>A. lunicollis</i> Schiödte 1837 ^{2, 4, 9, 13, 14, 16}	21
<i>A. majuscula</i> (Chaudoir 1850) ^{3, 8, 9, 12, 13}	7
<i>A. nitida</i> Sturm 1825 ^{2, 12, 14}	5
<i>A. ovata</i> (F. 1792) ³	1
<i>A. plebeja</i> (Gyllenhal 1810) ^{2, 3, 9, 14, 16}	6
<i>A. praetermissa</i> (Sahlberg 1827) ⁴	2
<i>A. similata</i> (Gyllenhal 1810) ^{2, 14}	3
<i>A. tibialis</i> (Paykull 1798) ^{2, 14}	2
<i>Anchomenus dorsalis</i> (Pontoppidan 1763) ^{12, 13}	7
<i>Anisodactylus binotatus</i> (F. 1787) ¹⁵	1
<i>Asaphidion pallipes</i> (Duftschmid 1812) ¹²	1
<i>Badister bullatus</i> (Schränk 1798) ²	1
<i>B. dilatatus</i> (Chaudoir 1837) ¹⁴	1
<i>B. peltatus</i> (Panzer 1797) ^{14, 15}	2
<i>Bembidion articulatum</i> (Panzer 1796) ¹⁶	1
<i>B. bruxellense</i> Wesmähl 1835 ^{4, 16}	2
<i>B. deletum</i> (Audinet-Serville 1821) ^{12, 13, 14}	3
<i>B. doris</i> (Panzer 1797) ^{4, 9, 12, 13, 14, 16}	56
<i>B. obliquum</i> Sturm 1825 ^{9, 12, 14, 16}	11
<i>B. pygmaeum</i> (F. 1792) ⁹	1
<i>B. quadrimaculatum</i> (L. 1761) ^{2, 4, 9, 12, 13, 14, 16}	149
<i>B. saxatile</i> Gyllenhal 1827 ^{2, 4, 9, 13, 16}	9
<i>Dromius fenestratus</i> (F. 1794) ²	1
<i>D. schneideri</i> Crotch 1871 ¹³	1
<i>D. quadraticollis</i> Morawitz 1862 ^{2, 9, 14, 16}	4
<i>Dyschirius aeneus</i> (Dejean 1825) ^{4, 13, 14, 16}	7
<i>Elaphrus riparius</i> (L. 1758) ³	1
<i>Harpalus affinis</i> (Schränk 1781) ^{2, 3, 4, 12, 13, 14, 16}	16
<i>H. laevipes</i> (Zetterstedt 1829) ^{2, 3, 12, 13, 14, 15, 16}	18
<i>H. latus</i> (L. 1758) ¹⁴	1
<i>H. rubripes</i> (Duftschmid 1812) ^{3, 9, 12, 16}	6
<i>H. rufipes</i> (Degeer 1774) ^{3, 4, 12}	3
<i>Lebia chlorocephala</i> (Hoffmann 1803) ^{9, 13, 16}	3
<i>Loricera pilicornis</i> (F. 1775) ^{13, 14, 16}	14
<i>Microlestes minutulus</i> (Goeze 1777) ¹⁴	1
<i>Ophonus nitidulus</i> (Stephens 1828) ³	1
<i>O. rufibarbis</i> (F. 1792) ^{2, 9}	3
<i>Panagaeus cruxmajor</i> (L. 1758) ^{2, 23}	3

Table 2 continued

Species	<i>n</i>
<i>Perigona nigriceps</i> (Dejean 1831) ¹²	1
<i>Platynus livens</i> (Gyllenhal 1810) ^{3, 12, 16}	7
<i>Porotachys bisulcatus</i> (Nicolai 1822) ¹²	1
<i>Pterostichus cupreus</i> (L. 1758) ^{2, 14}	9
<i>P. crenatus</i> (Duftschmid 1812) ^{2, 3, 9, 12, 13, 14, 16}	16
<i>P. niger</i> (Schaller 1783) ¹⁴	1
<i>P. oblongopunctatus</i> (F. 1787) ^{13, 16}	3
<i>P. rhaeticus</i> (Heer 1837) ^{4, 14, 16}	7
<i>P. versicolor</i> (Sturm 1824) ^{3, 5, 9, 12, 13, 15, 16}	15
<i>Stenolophus mixtus</i> (Herbst 1784) ^{2, 3, 12, 14, 16}	8
<i>Trichocellus placidus</i> (Gyllenhal 1827) ^{9, 12, 14, 16}	35
<i>Agonum fuliginosum</i> (Panzer 1809) ^{2, 12, 14, 16}	12
<i>Bembidion gilvipes</i> Sturm 1825 ¹⁴	1
<i>B. guttula</i> (F. 1792) ^{2, 3, 4, 12, 13, 14, 16}	273
<i>B. lampros</i> (Herbst 1784) ^{4, 9, 12, 13, 14, 16}	15
<i>B. properans</i> (Stephens 1828) ¹⁴	2
<i>B. transperans</i> (Geblers 1829) ^{4, 9, 12, 13, 14, 16}	10
<i>Bradycellus caucasicus</i> (Chaudoir 1846) ¹²	3
<i>Calathus erratus</i> (Sahlberg 1827) ³	1
<i>C. melanocephalus</i> (L. 1758) ^{2, 3, 9, 13, 14, 16}	8
<i>Carabus clathratus</i> L. 1761 ⁴	1
<i>Clivina fossor</i> (L. 1758) ^{2, 7, 9, 13, 14, 16}	12
<i>Notiophilus biguttatus</i> (F. 1779) ^{9, 13}	3
<i>N. palustris</i> (Duftschmid 1812) ¹⁶	1
<i>Pterostichus diligens</i> (Sturm 1824) ^{7, 14}	2
<i>P. minor</i> (Gyllenhal 1827) ^{2, 3, 9, 12, 13, 14, 16}	15
<i>P. strenuus</i> (Panzer 1797) ^{2, 3, 4, 5, 7, 9, 12, 13, 14, 16}	37
<i>Syntomus truncatellus</i> (L. 1761) ^{3, 9, 12, 14}	6
? <i>Harpalus brachypus</i> (Dejean) ⁹	1
? <i>Nebria rufescens</i> (Strøm 1768) ¹³	1
<i>Dyschirius globosus</i> (Herbst 1784) ^{2, 9, 12, 13, 14}	15
<i>Leistus ferrugineus</i> (L. 1758) ⁹	1
<i>Stomis pumicatus</i> (Panzer 1796) ¹²	2

Island abbreviations: 2-Mustaviiri, 3-Pitkäviiri, 4-Ristisaari, 5-Vaihkäri, 7-Vähä Eteläkari, 8-Eteläkari, 9-Kilpisaari, 12-Koivu-luoto, 13-Rääntiö, 14-Ulkotammio, 15-Varis, 16-Lanskeri, 17-Majakartti, 18-Kivikartti, 19-Suuri-Pisi, 23-Huovari.

Main island–small island comparisons

Carabid fauna differed significantly between the main island and small island sites. First, although there was no statistically significant difference in rarefied species richness between the main and small islands (see also Niemelä *et al.*, 1985), in terms of absolute numbers more species were collected on the main island (forty-one species) compared with the small islands (thirty-one species). The non-significant difference in rarefied species richness is because of the lower abundances on the small islands, indicating that the relationship between abundance and species richness was quite similar on the main island and on the small islands. Secondly, many of the abundant species showed distinct preference for either the main island or the small island sites, which was reflected in that the main and small island sites were significantly different in terms of carabid assemblage structure.

Area *per se* is likely to account for the differences in species richness between the islands (Niemelä *et al.*, 1985). The main island of Åland is about 90,000 ha in size and supports a diverse number of habitats compared with the small islands (8–29 ha) sampled. Although sampling was only carried out in moist, spruce-dominated lush forest patches on both the main and small islands [thereby excluding the habitat diversity hypothesis for increased species richness, see Ås *et al.* (1997)], main island sites were in close proximity to many different habitat types from where tourist and dispersing species penetrate the study sites accidentally (Niemelä, 1988; Desender, 1996). This is evident from the high proportion (32%, thirteen of forty-one) of species collected at the main island sites during one of the 4 years only (Appendix 1). Although the percentage for single year incidences on the small islands was the same (32%, ten of thirty-one), all of these ten species had the potential for flight, i.e. were either macropterous or dimorphic, while four of the thirteen main island species were brachypterous (*C. glabratus*, *C. nemoralis*, *C. violaceus* and *C. fuscipes*). This result suggests that tourist species of all dispersal abilities occasionally occur in main island forest sites, while most tourists to the small islands are capable of flight.

Apart from the obvious size difference between the main island of Åland and the small islands, human land use, in particular forestry, may also be responsible for differences seen in carabid assemblage structure between these islands. Forestry is practised on the main island, but not on the small islands, and combined with the low degree of other human disturbances on the small islands may at least in part explain why *C. hortensis*, *P. niger* and *Cychnus caraboides* are common on these islands. As these species do not possess functional flight apparatuses, they are considered to be poor dispersers, but at the same time relatively good survivors (Turin & Den Boer, 1988). Island and mainland fauna are also expected to be quite different because of a unique combination of climatic, geological and topographical factors on the islands (Ås *et al.*, 1997).

Colonization success

Carabid species of smaller body size and long wings are more successful in colonizing Dutch polder islands (Ranta & Ås, 1982). On the contrary, in our study the small islands had a higher proportion and number of short-winged species compared with the main island of Åland, and many of the abundant species on the small islands, apart from being short-winged, are also large (see also Niemelä *et al.*, 1985). A similar pattern has been found for other studies on islands in the Baltic Sea (Ås, 1984; Niemelä *et al.*, 1988; Kotze *et al.*, 2000).

Although the wing-form patterns of this study are in agreement with those of Ås (1984) and Kotze *et al.* (2000), our study eliminates an important confounding aspect present in these studies. Both previous studies tested for differences in proportions of wing form between islands and the closest mainland province. This comparison is problematic because not only were the mainland fauna collected over

many more years compared with the island samples, but also because the mainland sites consist of many more habitat types than the island sites sampled. For example, very few streams occur on Baltic islands, excluding many *Bembidion* species. This riparian genus of long-winged or wing dimorphic species, is the largest carabid genus in Fennoscandia (Lindroth, 1985, 1986), and their absence in island samples may seriously influence this wing-form comparison.

Our study compared carabid beetles in similar habitat types between the main island of Åland and the small islands, thereby eliminating the confounding effects of habitat diversity introduced by comparing small islands with a mainland. Although absolute proportions of short-winged species were quite similar between the main island and the small islands (30 and 33%, respectively), small islands were characterized by more short-winged species, compared to the main island, and that these short-winged species were abundant on the small islands (Figs 4 and 5).

The obvious questions are how these short-winged species disperse to small islands in the Baltic Sea, and why they appear to be more successful than long-winged species, once on these islands. It appears that for most taxa, island colonization is quite easy because of short inter-island distances in the Baltic (Järvinen & Ranta, 1987) and because salinity is low (Ås, 1984). Carabids can survive up to 5 days in brackish water without adverse effects on fertility (Palmén, 1944) during which time they can drift up to 10 km (Ås, 1984). Short-winged carabids can therefore easily reach most islands in the Baltic Sea. Once on these islands, short-winged species seem more successful in establishing viable populations, probably because they (1) do not use energy for developing wing muscles and wings, and therefore have more resources available for immediate reproduction (Ås, 1984; Lövei & Sunderland, 1996), (2) use less energy getting to the islands (drifting vs. flying), and (3) stand a lower risk of being repeatedly blown off of the islands (Ås, 1984).

The argument presented above seems reasonable, but needs systematic, empirical investigation, in particular (1) do carabid individuals survive drifting from island to island, and what is the volume of drift-beetles reaching island shores, (2) what is the proportion of winged to wingless species in drift material, (3) are short-winged species at an advantage when colonizing new habitat? To answer points (1) and (2) Karjalainen (2000) collected drift carabids on island shores in the Eastern Gulf of Finland National Park. He found that very few carabid individuals (1.8%) and species (3.4%) collected were short-winged. These findings suggest that very few short-winged carabids reach these islands, but that those who do are successful in establishing populations (point '3' above).

Here is clearly potential for further research (see also Niemelä *et al.*, 1985). For example, it has been suggested that short-winged species, being poorly dispersing species, are slow immigrants, but at the same time relatively good survivors, good competitors for resources and have short pre-oviposition periods, leading to greater egg production at the onset of reproductive life (Ås, 1984; Turin & Den

Boer, 1988; Spence, 1989; Roff, 1990; Roff & Fairbairn, 1991; Spence & Andersen, 1994). Alternatively, it is also known that certain carabid beetles, and other insects, capable of flight are able to re-absorb their flight muscles after dispersal and before reproduction, potentially increasing their colonization success (Robertson, 1998; Desender, 2000), and that some long-winged carabid females produce more eggs and over a longer period of time (Aukema, 1991).

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Appendix I Carabids captured on the main island of Åland and adjacent islands in 1982, 1987, 1988 and 1999

Species	Body size	Wing form	Main island sites				Small island sites			
			1982	1987	1988	1999	1982	1987	1988	1999
<i>Agonum fuliginosum</i> (Panzer 1809)	6.5	d	34	70	296	89	6	45	41	13
<i>A. gracile</i> Sturm 1824	6.6	m	12				6			
<i>A. livens</i> (Gyllenhal 1810)†	8.9	m	13	4	24	32				
<i>A. obscurum</i> (Herbst 1784)	5.7	B		3	68	156	2	30	43	49
<i>A. thoreyi</i> Dejean 1828*	6.9	m					1			
<i>Agonum</i> species†					1					
<i>Amara brunnea</i> (Gyllenhal 1810)	5.9	m	1	2	17	3	3	2	15	9
<i>A. communis</i> (Panzer 1797)	6.4	m				2			3	1
<i>Amara</i> species*									1	
<i>Badister bullatus</i> (Schränk 1798)*	5.6	m						1	1	
<i>Bembidion guttula</i> (F. 1792)†	3.1	d	1	3	2	1				
<i>B. lampros</i> (Herbst 1784)†	3.6	d				1				
<i>Calathus fuscipes</i> (Goeze 1777)†	12.0	B				1				
<i>C. melanocephalus</i> (L. 1758)†	7.3	d		1	1					
<i>C. micropterus</i> (Duftschmid 1812)	7.6	B	10	48	261	99	8	58	241	41
<i>Carabus glabratus</i> Paykull 1790	25.7	B			2			1	5	
<i>C. hortensis</i> L. 1758	24.8	B	21	4	21	33	21	29	77	101
<i>C. nemoralis</i> Müller 1764†	23.9	B				48				
<i>C. violaceus</i> L. 1758	24.5	B				8	2			23
<i>Clivina fossor</i> (L. 1758)	6.0	d	7	1	12	5			1	
<i>Cychrus caraboides</i> (L. 1758)	16.3	B	4	1	15	13	30	21	102	67
<i>Elaphrus cupreus</i> Duftschmid 1812	8.7	m	1		5				1	
<i>E. riparius</i> (L. 1758)	7.2	m		1				2		
<i>Harpalus latus</i> (L. 1758)†	9.5	m		1						
<i>H. quadripunctatus</i> Dejean 1829	10.7	m	2	3	8	19		1	2	
<i>Leistus terminatus</i> (Hellwig 1793)†	6.9	m	15	13	24	12				
<i>Loricera pilicornis</i> (F. 1775)	7.1	m	142	117	84	37	21	21	4	2
<i>Notiophilus aquaticus</i> (L., 1758)†	5.2	d		1						
<i>N. biguttatus</i> (F. 1779)	5.5	d	3	10	29	9		5	5	4
<i>N. palustris</i> (Duftschmid 1812)†	5.5	d			1					
<i>Patrobis assimilis</i> Chaudoir 1844	8.9	B	33	3	3	15	10		1	
<i>P. atrorufus</i> (Ström 1768)	8.6	B	597	280	1604	329	2	9	30	4
<i>Pterostichus cupreus</i> (L. 1758)*	12.1	m								1
<i>P. diligens</i> (Sturm 1824)	6.0	d			2	18		3		
<i>P. melanarius</i> (Illiger 1798)†	14.7	d	37	10	44	590				
<i>P. minor</i> (Gyllenhal 1827)*	7.7	d						4		
<i>P. niger</i> (Schaller 1783)	17.5	m§	9	8	35	279	97	43	347	220
<i>P. nigrita</i> (Paykull 1790)	10.6	m	28	21	51	232	19	28	14	9
<i>P. oblongopunctatus</i> (F. 1787)	10.9	m	50	61	223	344	2	1	17	6
<i>P. strenuus</i> (Panzer 1797)	6.6	d	7	19	29	42	1	9	16	7
<i>Synuchus vivalis</i> (Illiger 1798)†	7.1	d			1	1				
<i>Trechus quadristriatus</i> (Schränk 1791)†	3.7	m			15					
<i>T. rivularis</i> (Gyllenhal 1810)†	4.6	d	1	3		9				
<i>T. rubens</i> (F. 1792)	5.7	m			1	9		1		
<i>T. secalis</i> (Paykull 1790)	3.7	B	37	127	646	726	10	206	616	641
<i>Trichocellus placidus</i> (Gyllenhal 1827)	4.7	m	4	2	2	5	4			1
Total number of individuals			1069	817	3527	3167	245	520	1583	1199
Total number of species			24	27	31	31	18	21	22	18

†Species collected on the main island of Åland only.

*Species collected on the small islands only.

§Although *Pterostichus niger* is classified as having long wings (macropterous), they are probably non functional (see Lindroth, 1986).