

Distribution of carabid beetles in four boreal archipelagoes

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The distribution of carabid beetles was studied in four archipelagoes near Stockholm and in southern Finland. The sample sizes (per sampling effort) varied considerably among the archipelagoes (0.3–2.4 individuals/trap-day). In all the four archipelagoes species number increases with island area.

There were distinct differences in the identities of the dominant species among the archipelagoes, but most of the species according to distribution maps occur on all mainland areas. Striking differences were also observed in the species distributions in similar habitats among the archipelagoes. The variation in species distribution patterns is probably due to subtle habitat variation (even between similar habitat types), to the differing area range of islands studied in the archipelagoes, and to stochastic population fluctuations. The habitat effects are mediated through two factors: (1) autecological requirements of individual species, and (2) dynamics of local populations.

It is suggested that population dynamic models which incorporate species characteristics, spatial and temporal variation in the environment, and interspecific interactions offer a promising approach for further studies.

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1. Introduction

The theory of island biogeography of MacArthur & Wilson (1967) has greatly inspired research on ecological processes in insular environments. The influence of the theory has contradictory features, however. It was originally greeted as a theoretical revolution in biogeography (Simberloff 1974), but later criticism began to accumulate and toward the late 1970s some basic concepts of the theory were challenged (e.g., Lynch & Johnson 1974, Simberloff 1976, Gilbert 1980). A problem is that the theory deals with qualitative presence – absence data, but data on population numbers often give a different and more realistic view of island colonization (Haila & Järvinen 1981, Haila et al. 1983, Williamson 1983, Niemelä et al. 1985).

Today, with hindsight we may conclude that the equilibrium theory has lasting significance as a re-

search programme that directs attention to dynamic aspects of insular ecology (Haila & Järvinen 1982, Haila 1986). Archipelagoes remain interesting subjects for ecological study, whatever the fate of particular theories. The challenge is to formulate more realistic hypotheses about insular processes.

In this paper we study distribution patterns of carabid beetles in four archipelagoes in southern Fennoscandia. We are primarily interested in the occurrence of individual species in these archipelagoes. The pools of potential colonists, defined on the basis of distribution maps (Lindroth 1945b), are practically identical for the Baltic archipelagoes, and the pool is only slightly different from the others for Lake Saimaa. We are interested in questions such as: Is the set of successful colonists identical in these four archipelagoes? What is the significance of habitat differences for colonization patterns?

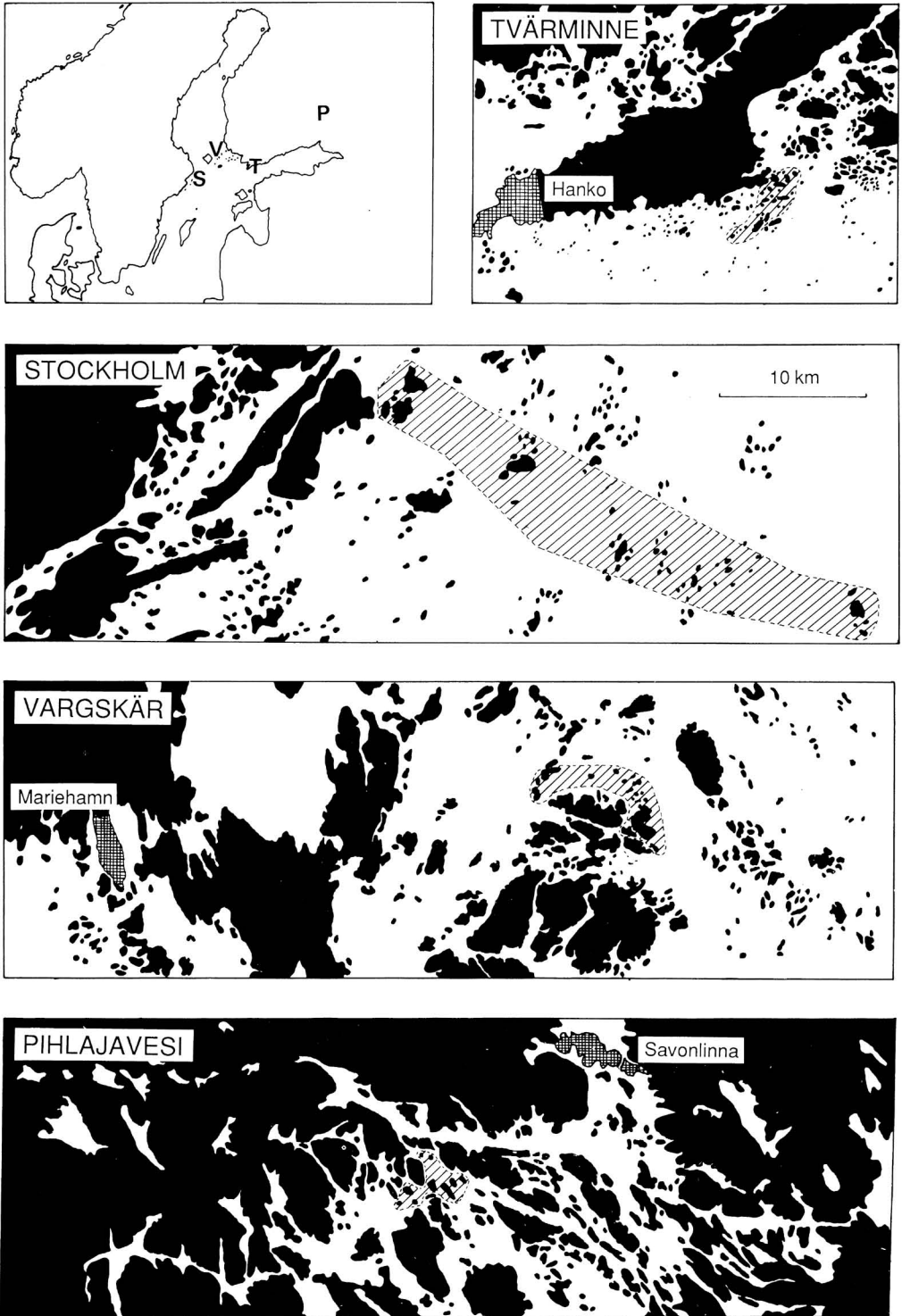


Fig. 1. Location of the four archipelagos in Fennoscandia (S=Stockholm archipelago, V=Vargskär, T=Tvärminne, P=Pihlajavesi) and the study islands (within the hatched area) in the archipelagos (black areas indicate land and cross-hatching the towns). All maps are drawn to the same scale.

2. Material and methods

2.1. The archipelagoes

The four archipelagoes studied are all located in the southern part of Fennoscandia (Fig. 1). The archipelagoes of Stockholm, Vargskär and Tvärminne belong to the hemiboreal, and Pihlajavesi to the southern boreal, phytogeographical zone (Ahti et al. 1968). The regional species richness of carabids varies in the study area from 150 to 200 (Lindroth 1949). Three of our study archipelagoes lie in the Baltic Sea (Stockholm, Vargskär, Tvärminne), while Pihlajavesi is part of a large fresh water lake complex, that of Lake Saimaa. Thus, relative to the mainland the three Baltic archipelagoes lie offshore, while mainland surrounds the Pihlajavesi archipelago. The area range of the islands is somewhat larger in Stockholm (12 islands, 0.4–160 ha), and Vargskär (13 islands, 0.5–58 ha) than in Tvärminne (16 islands, 0.03–8.7 ha) and Pihlajavesi (13 islands, 0.2–38 ha) islands. In Table 1 we give a list of the habitat types found in the four archipelagoes and indicate island by island which habitats were sampled. Most of the habitats had obvious counterparts in several study areas, whereas a few of them were found in only one area. Our study areas are briefly characterised below (Table 1).

The Stockholm archipelago lies off the Swedish coast in the Baltic Sea (about 59°N, 19°E). The 12 islands selected form a 40 km transect off the mainland in the vicinity of the town of Norrtälje. The islands are characterized by deciduous forests, meadows and dry *Calluna vulgaris* dominated moors. Pure coniferous forests are rare and were not sampled. A clear zonation of the island vegetation goes as follows: The largest islands close to the mainland are covered by deciduous and coniferous forests. Further off the forested area decreases and islands become covered by moor vegetation (*Calluna* and *Empetrum* being characterizing species of the field layer). In the outermost archipelago deciduous forests on the islands diminish to small woodlots; bare rocks, heather moor and juniper shrubs characterize the island vegetation (see Ås 1984 for more details).

The Vargskär archipelago (about 60°N, 20°E) lies 10–15 km east of the main island of Åland, between SW Finland and Sweden. Luxuriant habitats (mixed forests, deciduous forests and meadows) dominate, but barren habitats (*Cladonia* and *Vaccinium* type forests) were also sampled. The largest islands are covered by deciduous and coniferous forests. Luxuriant habitats are common on islands of larger than five hectares. Island area and habitat diversity correlate positively, although area alone is not a good indicator of the number of habitats on the Vargskär islands. Isolation among islands is minimal. A detailed description of the Vargskär archipelago is given by Haila (1983; see also Palmgren 1950).

The Tvärminne archipelago (about 60°N, 23°E) is located at the easternmost corner of Hanko peninsula, which forms the SW tip of the Finnish mainland. Habitat diversity and luxuriance correlate positively with island size. The smallest islands are composed of bare rock with patches of mosses and grasses, and larger islands harbour small woodlots of pine. Human influence on the islands is minimal. Luther (1961) and Silfverberg (1968) describe the islands in detail. Several skerries with small patches of different habitat types were sampled. The general appearance of habitats is more barren than in the other Baltic archipelagoes.

The Pihlajavesi archipelago (about 62°N, 29°E) is situated in the northwestern part of Lake Pihlajavesi (area about 340 km²) about 20 km southwest of the town of Savonlinna. The archipelago is rich in islands (about 4000) ranging from a few acres to several square kilometres. Distances between islands are short. A general feature everywhere in the archipelago is the abundance of bare bedrock. Pine forest (on large islands also birch forest) is the dominant habitat type in elevated parts of the islands. Lush patches occur mostly on the largest islands. Where shores are not rocky, the islands are fringed by narrow (1–5 m) strips of scree, sometimes also by gravel or sandy beaches, but rarely by shore meadows. Non-rocky shores prevail on large islands. A detailed description of the area will be published elsewhere (Tiainen, in prep.).

2.2. Sampling procedure

As carabid species have varying habitat preferences, our sampling was designed to cover the main habitat types in the archipelagoes. Habitat categories were defined so that they would be comparable.

Carabids were sampled by pitfall-traps (Southwood 1978). The basic sampling unit was a set of nine plastic jars (65 mm in diameter, 170 ml in volume) placed in a grid of 3x3 traps, the distance between neighbouring traps being about 5 m. The exact location of the traps was adapted to the configuration of the rocks and boulders at the sampling sites. The traps were one-third filled with diluted (approx. 50%) ethylene glycol and detergent. One set of nine traps was placed in each main habitat type on each island (Table 1). Thus, depending on the habitat spectrum, the number of pitfall traps per island varied from 9 to 54. The islands were sampled through five days in the first half of July in 1980.

3. Results

3.1. General

Our combined sample from all the four archipelagoes consists of 6507 carabids belonging to 59 species (for details see Table 2). The sample sizes are not directly comparable because somewhat different numbers and types of habitats were studied in the archipelagoes. The number of carabids/trap-day can be used as a rough measure of carabid beetle density in the different archipelagoes. The figures are 0.5, 2.4, 0.3 and 0.5 carabids/trap-day in Stockholm, Vargskär, Tvärminne and Pihlajavesi, respectively.

We examined the relationship between sample size and species number with the rarefaction technique (Simberloff 1978, James & Rathbun 1981). Fig. 2. graphs the expected species numbers against

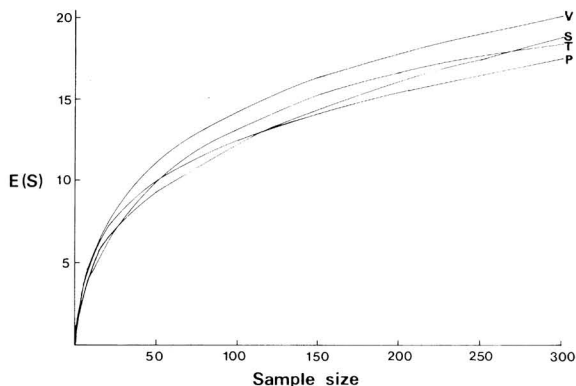


Fig. 2. Sample-size standardized regional species richness in the four archipelagoes. (S = Stockholm archipelago, V = Vargskär, T = Tvärminne, P = Pihlajavesi).

sample size (as the Tvärminne sample contains 357 specimens, rarefaction curves are calculated up to 300 individuals only). The Vargskär sample differs consistently from the others in having a higher species richness throughout the sample size range.

On the island level our data show the generally found positive correlation between island area and species number. The following equations describe the relationship between log area and log species richness in the four archipelagoes:

Stockholm	$\log S = 0.426 + 0.308(SD=0.092)\log A, r=0.694$
Vargskär	$\log S = 0.848 + 0.326(SD=0.059)\log A, r=0.857$
Tvärminne	$\log S = 0.528 + 0.291(SD=0.076)\log A, r=0.690$
Pihlajavesi	$\log S = 0.683 + 0.241(SD=0.099)\log A, r=0.483$

The slopes of the regression equations do not differ significantly from each other (analysis of covariance, $F=0.35, P=0.792$), but the intercepts of the regression lines do differ ($F=9.25, P<0.001$). The difference is due to the Vargskär data (if excluded, no significant difference between the three data sets remains). The positive correlation between island area and species number is partly due to our sampling design: the number of traps was higher on large islands than on small ones because of the greater habitat diversity of the former. Both the number of beetles caught and the number of species included in the samples correlate positively with the number of traps used (Spearman rank correlations in all archipelagoes significant at least at 0.05 level), and positive correlations also emerge between sample sizes and species numbers in the four data sets (all rank correlations significant at 0.01 level). Because of the sampling design the effect of habitat diversity on the results cannot be eliminated.

3.2. Habitat distribution of individual species

We examined the habitat affinity of individual species in each archipelago by comparing the observed numbers of individuals in the main habitats (Table 2) with the G -test against the expectations derived from the number of trapping days. Only the most abundant species were included in the examination. For this comparison we formed new habitat groups that roughly represent a range from forests to shores and skerries. The habitat distributions are shown in Figs. 3A–3D. The G -test shows a statisti-

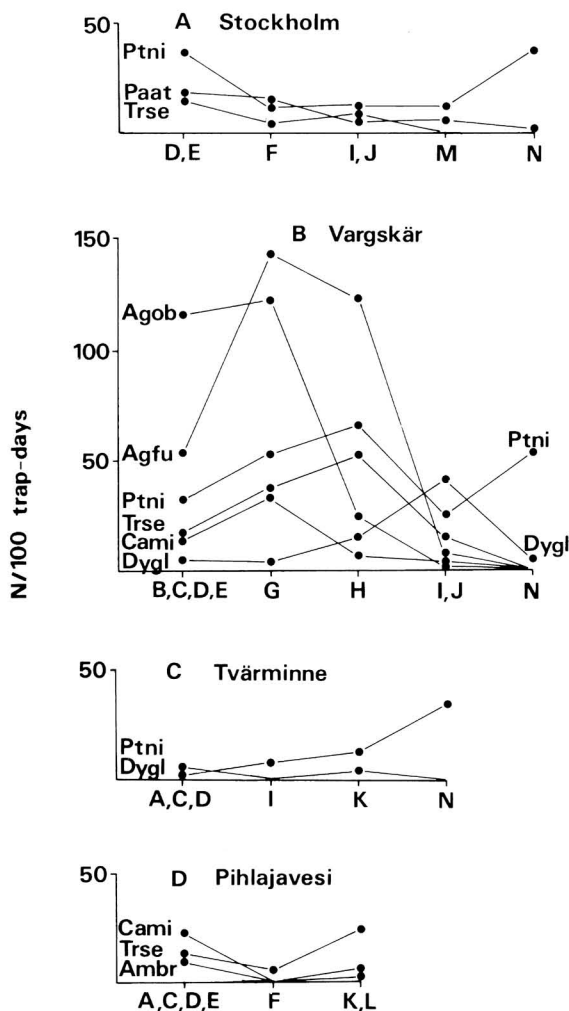


Fig. 3. Habitat distribution of the most abundant carabid species in the archipelagoes. Symbols for carabid species: Agob = *Agonum obscurum*, Agfu = *A. fuliginosum*, Ambr = *Amara brunnea*, Cami = *Calathus micropterus*, Dygl = *Dyschirius globosus*, Paat = *Patrobus atrorufus*, Ptnti = *Pterostichus niger*, Trse = *Trechus secalis*. For the habitat symbols see Table 1.

Table 2A. The number of carabid beetles in the habitats in the Stockholm archipelago. For the habitat symbols see Table 1.

Habitat:	D	E	F	I	J	M	N	Total
<i>Agonum fuliginosum</i>	0	0	4	0	1	0	0	5
<i>A. obscurum</i>	0	0	2	0	0	1	0	3
<i>Amara apricaria</i>	0	0	0	1	0	0	0	1
<i>A. aulica</i>	0	0	0	1	0	0	0	1
<i>A. communis</i>	0	0	0	1	0	0	0	1
<i>Badister bullatus</i>	0	0	0	1	0	0	0	1
<i>Bembidion guttula</i>	0	0	0	0	1	0	0	1
<i>B. quadrimaculatum</i>	0	0	0	0	1	0	0	1
<i>Calathus fuscipes</i>	0	0	0	5	0	0	0	5
<i>C. melanocephalus</i>	0	4	0	20	0	4	40	67
<i>C. micropterus</i>	0	4	1	0	0	2	1	8
<i>Carabus hortensis</i>	0	3	1	0	0	0	0	4
<i>C. violaceus</i>	0	17	2	6	3	11	1	41
<i>Cychnus caraboides</i>	0	8	1	0	1	0	0	10
<i>Dyschirius globosus</i>	0	3	0	0	7	4	2	16
<i>Loricera pilicornis</i>	0	0	0	0	20	1	0	21
<i>Nebria brevicollis</i>	0	1	0	0	0	0	0	1
<i>Notiophilus biguttatus</i>	0	2	0	0	0	0	0	2
<i>N. germyni</i>	0	2	0	0	0	0	0	2
<i>Patrobus atrorufus</i>	1	60	28	8	30	22	1	150
<i>Pterostichus diligens</i>	0	0	1	0	0	0	0	1
<i>P. minor</i>	0	0	0	0	1	0	0	1
<i>P. niger</i>	0	116	23	38	31	40	53	301
<i>P. nigrita</i>	0	0	0	1	0	0	0	1
<i>P. oblongopunctatus</i>	0	1	0	0	0	0	0	1
<i>P. strenuus</i>	0	0	0	0	1	0	0	1
<i>Trechus discus</i>	0	0	0	0	0	0	1	1
<i>T. secalis</i>	2	55	8	43	8	0	0	116
Total	3	276	71	125	105	85	99	764
Number of species	2	13	10	11	12	9	7	28
Number of trap-days	45	270	180	270	180	360	135	1440

cally significant difference from expectations for every species in every archipelago; i.e., the species are not uniformly distributed over the habitats. It is remarkable, however, that the majority of species were found in almost all habitat groups. Below we discuss the distributions archipelago by archipelago.

Stockholm archipelago. *P. niger*, the most abundant species, has peak abundance in forests and skerries. The species was found on only one skerry, however. *T. secalis* has peak abundance in forests, while *P. atrorufus* has the highest abundances in forest and marsh groves (Fig. 3A).

Vargskär. The most abundant species, *Agonum obscurum*, prefers lush forests and alder groves (Fig. 3B, Table 2B). *A. fuliginosum* has its peak of occurrence in alder groves and grove meadows. *P. niger* occurred in 39 of the 42 sampling sites, and in all of

the nine habitat types examined. It had its peak occurrence in grove meadows, but was abundant also in alder groves and on small skerries. On small skerries it was by far the most abundant species. *T. secalis* is another species with a wide habitat amplitude, but it was absent from the skerries. *D. globosus* was abundant in meadows but rare in forests. Several species (*L. pilicornis*, *P. atrorufus*, *P. assimilis*, *P. diligens*) were absent from open habitats (Table 2B). Population densities of carabid beetles were highest (4.6 individuals/trap-day) in alder groves and lowest on the skerries (0.8).

Tvärminne. *D. globosus* (over 50% of the total sample) had its peak abundance on small skerries, where it comprised 85% of the carabids sampled. It also occurred in other open habitats (shores and meadows), but was almost absent from forests. *Ca-*

Table 2B. The number of carabid beetles in the habitats in the Vargskär archipelago. For the habitat symbols see Table 1.

Habitat:	B	C	D	E	G	H	I	J	N	Total
<i>Agonum fuliginosum</i>	0	82	245	103	262	341	0	33	0	1066
<i>A. livens</i>	0	0	2	0	0	0	0	0	0	2
<i>A. obscurum</i>	4	20	662	259	222	63	1	8	0	1239
<i>A. viduum</i>	0	1	0	5	0	0	0	0	0	6
<i>Amara brunnea</i>	0	0	0	0	0	1	0	0	0	1
<i>A. communis</i>	1	0	0	0	0	0	0	1	0	2
<i>Badister bullatus</i>	0	0	0	0	0	3	0	0	0	3
<i>Bembidion doris</i>	0	4	0	1	2	0	0	1	0	8
<i>B. guttula</i>	0	1	2	0	0	3	0	6	0	12
<i>B. mannerheimi</i>	0	0	0	0	3	2	3	9	0	17
<i>B. minimum</i>	0	0	0	0	0	0	0	1	0	1
<i>Bradycellus caucasicus</i>	0	0	1	0	0	0	0	0	0	1
<i>Calathus melanocephalus</i>	2	0	6	0	1	0	1	3	9	22
<i>C. micropterus</i>	22	23	60	14	61	16	0	15	3	214
<i>Carabus hortensis</i>	2	18	6	29	5	29	9	14	1	113
<i>Clivina fossor</i>	0	0	0	0	0	1	0	0	0	1
<i>Cychrus caraboides</i>	0	3	15	1	8	11	2	3	5	48
<i>Dromius sigma</i>	0	0	0	0	0	0	0	0	1	1
<i>Dyschirius globosus</i>	0	6	13	5	7	41	48	153	7	280
<i>Elaphrus cupreus</i>	0	0	0	1	0	0	0	0	0	1
<i>E. uliginosus</i>	0	0	0	0	0	1	0	0	0	1
<i>Harpalus latus</i>	0	0	0	1	0	0	0	0	0	1
<i>H. quadripunctatus</i>	1	2	0	0	1	0	0	0	0	4
<i>Leistus ferrugineus</i>	1	0	1	0	1	1	0	4	3	11
<i>L. terminatus</i>	0	0	0	0	0	44	0	0	0	44
<i>Loricera pilicornis</i>	0	2	74	14	11	9	0	8	0	118
<i>Miscodera arctica</i>	1	0	0	0	0	0	0	0	0	1
<i>Notiophilus aquaticus</i>	0	0	0	0	0	0	1	0	0	1
<i>N. germiny</i>	0	0	0	0	1	0	0	0	0	1
<i>N. palustris</i>	0	0	1	0	0	0	0	0	0	1
<i>Patrobus assimilis</i>	1	2	4	5	16	3	0	1	0	32
<i>P. atrorufus</i>	1	1	8	18	43	11	0	0	0	82
<i>Pterostichus diligens</i>	3	3	45	2	7	1	0	3	0	64
<i>P. minor</i>	0	0	2	0	1	0	0	0	0	3
<i>P. niger</i>	6	43	168	33	93	181	29	91	70	714
<i>P. nigrita</i>	0	3	7	3	1	1	0	2	0	17
<i>P. oblongopunctatus</i>	1	3	0	0	1	0	0	1	0	6
<i>P. strenuus</i>	0	1	1	3	2	14	0	7	1	29
<i>P. vernalis</i>	0	0	1	0	0	0	0	3	0	6
<i>Synuchus vivalis</i>	0	0	0	0	0	0	0	0	1	1
<i>Trechus secalis</i>	18	30	63	21	71	140	14	78	0	435
<i>Trichocellus placidus</i>	0	0	0	0	2	0	0	0	0	2
Total	64	248	1387	518	822	917	108	447	101	4612
Number of species	14	19	22	18	23	22	9	22	10	42
Number of trap-days	90	225	360	135	180	270	90	450	135	1935

latus micropterus was most abundant in forests. *P. niger* occurred in all habitats, while *P. diligens* was found almost exclusively on small skerries (Table 2C, Fig. 3C).

Pihlajavesi. *T. secalis* (33% of carabids sampled) was most abundant on the shores, while *C. micropterus* and *A. brunnea* were most abundant in the forests (Table 2D, Fig. 3D).

3.3. Regional comparison

The most obvious impression gained from the data in Tables 2A–2D and Figs. 3A–3D is that there are major differences between the regions. Total abundances of carabids (individuals/trap-day) vary, and this is true of the occurrence of single species as well. The most striking difference is the scarcity of

Table 2C. The number of carabid beetles in the habitats in the Tvärminne archipelago. For the habitat symbols see Table 1.

Habitat:	A	C	D	G	I	K	N	Total
<i>Amara brunnea</i>	0	0	3	0	0	0	0	3
<i>A. communis</i>	0	0	0	0	0	2	3	5
<i>Bembidion bipunctatum</i>	0	0	0	0	0	0	3	3
<i>B. obliquum</i>	1	0	0	0	0	0	0	1
<i>B. quadrimaculatum</i>	0	0	0	0	1	1	1	3
<i>Calathus fuscipes</i>	0	0	0	0	6	0	0	6
<i>C. melanocephalus</i>	0	0	0	0	1	0	0	1
<i>C. micropterus</i>	5	2	17	3	3	0	0	30
<i>Carabus hortensis</i>	0	0	0	7	3	0	0	10
<i>Cychrus caraboides</i>	0	0	2	0	0	0	0	2
<i>Dyschirius globosus</i>	8	0	0	0	6	21	156	191
<i>Harpalus latus</i>	0	0	0	0	1	1	0	2
<i>H. quadripunctatus</i>	0	0	0	1	1	1	0	3
<i>Pterostichus diligens</i>	0	0	1	0	0	0	18	19
<i>P. niger</i>	14	2	25	4	1	13	1	60
<i>P. vernalis</i>	0	0	0	0	0	0	1	1
<i>Syntomus truncatellus</i>	0	0	0	0	6	0	0	6
<i>Synuchus vivalis</i>	0	0	0	0	2	0	0	2
<i>Trechus secalis</i>	0	0	3	0	2	4	0	9
Total	28	4	51	15	33	43	183	357
Number of species	4	2	6	4	12	7	7	19
Number of trap-days	360	90	225	45	90	180	450	1440

A. obscurum and *A. fuliginosum* in Stockholm, Tvärminne and Pihlajavesi, whereas these were by far the most dominant species in Vargskär (50% of the pooled sample)! According to Lindroth (1945a), both species prefer moist deciduous forests, and such habitats were included in our sampling in each of the archipelagoes. *A. fuliginosum* occurs throughout Fennoscandia, but *A. obscurum* in Finland has its distributional limit at 63°N, which may explain its absence from Pihlajavesi.

Four other species were dominant (>5% of the total sample) in one archipelago but scarce in all the others, viz. *Agonum viduum* and *A. brunnea*, abundant in Pihlajavesi, and *Calathus melanocephalus* and *Carabus violaceus*, abundant in Stockholm. In Pihlajavesi the former of the two dominated in shore habitats, and the latter in forests. *C. melanocephalus* was found in deciduous forests and meadows in Stockholm. Again these differences have no obvious relationship with the known distributions of the species as they occur throughout Fennoscandia (Lindroth 1945b).

It is impossible to directly compare the pooled data sets from the archipelagoes because of the great differences in the overall habitat compositions (Table 1). A more realistic comparison can be made among

samples from similar habitats. For such comparisons we formed three groups of habitats that are represented in the different archipelagoes: (1) Pine-dominated forests (A, B and C in Table 1); (2) Mixed and deciduous forests (D and E); and (3) Skerries smaller than about 1 ha where we assume micro-scale habitat differences to be of relatively small significance because of the extremity of the general conditions. The comparisons are shown in Tables 3 and 4 for all species abundant (>2% of the sample) in the habitat samples of at least two of the archipelagoes.

Table 3 shows that the between-archipelago trends in the occurrence of abundant species are similar in pine-dominated and deciduous forests. Fig. 4 shows the abundances of these species in all forested habitats of the four archipelagoes (individuals/100 trap-days). The differences between the regions are striking and, furthermore, the patterns are very variable from species to species. Three of the seven species (*C. micropterus*, *C. caraboides* and *T. secalis*) were found in the island forests of every archipelago, but in varying abundances. The other species were abundant in some of the archipelagoes, but scarce in the others.

The differences among archipelagoes are even more pronounced in the carabid communities of small

Table 2D. The number of carabid beetles in the Pihlajavesi archipelago. For the habitat symbols see Table 1.

Habitat:	A	C	D	E	F	G	K	L	N	Total
<i>Agonum sexpunctatum</i>	0	0	0	0	0	0	0	1	0	1
<i>A. viduum</i>	0	0	0	4	0	4	75	5	1	89
<i>Amara brunnea</i>	3	30	5	43	0	0	8	7	3	99
<i>A. communis</i>	0	0	0	0	0	0	4	0	0	4
<i>Bembidion quadrimaculatum</i>	0	0	0	0	0	0	0	1	0	1
<i>Calathus micropterus</i>	2	89	34	42	0	18	1	1	0	187
<i>Carabus glabratus</i>	0	7	8	5	1	3	1	0	0	25
<i>C. hortensis</i>	0	1	17	7	0	4	0	0	0	29
<i>Cychrus caraboides</i>	0	3	8	7	1	0	4	1	0	24
<i>Dyschirius globosus</i>	5	0	0	0	0	0	2	7	6	20
<i>D. thoracicus</i>	0	0	0	0	0	0	0	1	0	1
<i>Nebria gyllenhali</i>	0	0	1	0	0	1	2	8	0	12
<i>Notiophilus biguttatus</i>	0	0	0	1	0	0	0	0	0	1
<i>N. palustris</i>	0	1	0	1	0	0	0	0	0	2
<i>Patrobus atrorufus</i>	0	0	0	1	0	0	0	0	0	1
<i>Pterostichus melanarius</i>	0	0	0	3	0	0	0	0	0	3
<i>P. minor</i>	0	0	1	0	0	0	0	0	0	1
<i>P. nigrita</i>	0	0	0	0	0	0	1	0	0	1
<i>P. strenuus</i>	0	0	0	0	0	0	0	0	2	2
<i>P. vernalis</i>	0	0	0	0	0	0	2	0	0	2
<i>P. versicolor</i>	0	0	0	0	0	0	2	0	0	2
<i>Synuchus vivalis</i>	1	3	0	0	0	0	5	0	1	10
<i>Trechus secalis</i>	0	16	19	59	18	11	119	14	1	257
Total	11	150	93	173	20	41	226	46	14	774
Number of species	4	8	8	11	3	6	13	10	6	23
Number of trap-days	90	405	90	180	45	45	360	135	135	1485

Table 3. The number of individuals of the seven most abundant forest carabid species (caught in at least two archipelagoes) in the pine dominated forests (Pi; habitat types A, B, C in Table 1) and in deciduous forests (De; D, E) of the four archipelagoes.

	Stock- holm Pi/De	Varg- skär Pi/De	Tvär- minne Pi/De	Pihlaja- vesi Pi/De
<i>Amara brunnea</i>	-/ 0	0/ 0	0/ 3	33/ 48
<i>Calathus micropterus</i>	-/ 4	45/ 74	7/ 17	91/ 76
<i>Carabus hortensis</i>	-/ 3	20/ 35	0/ 0	1/ 24
<i>Cychrus caraboides</i>	-/ 8	3/ 16	0/ 2	3/ 15
<i>Patrobus atrorufus</i>	-/ 61	2/ 26	0/ 0	0/ 1
<i>Pterostichus niger</i>	-/ 116	49/ 201	16/ 25	0/ 0
<i>Trechus secalis</i>	-/ 57	48/ 84	0/ 3	16/ 78

Table 4. The number of individuals/100 trap-days of the six species caught on the skerries of at least two archipelagoes.

	Stock- holm	Varg- skär	Tvär- minne	Pihlaja- vesi
<i>Calathus melanocephalus</i>	29.6	6.7	0	0
<i>Calathus micropterus</i>	0.7	2.2	0	0
<i>Dyschirius globosus</i>	1.5	5.2	34.7	4.4
<i>Pterostichus niger</i>	39.2	51.8	0.2	0
<i>P. strenuus</i>	0	0.7	0	1.5
<i>Synuchus vivalis</i>	0	0.7	0	0.7

skerries. The total number of species included in the four data sets is 21, but 15 of them were found in only one archipelago in very low numbers (*P. diligens*, however, comprised 10% of the sample in Tvärminne). Three species (*C. micropterus*, *Pteros-*

tichus strenuus and *Synuchus vivalis*) were represented by stray individuals in the data sets of two archipelagoes (Table 4). *D. globosus* was the only species found in the skerries of every archipelago. In Tvärminne the species was found on every skerry. Two other species were abundant in at least two archipelagoes (*C. melanocephalus* and *Pterostichus niger*).

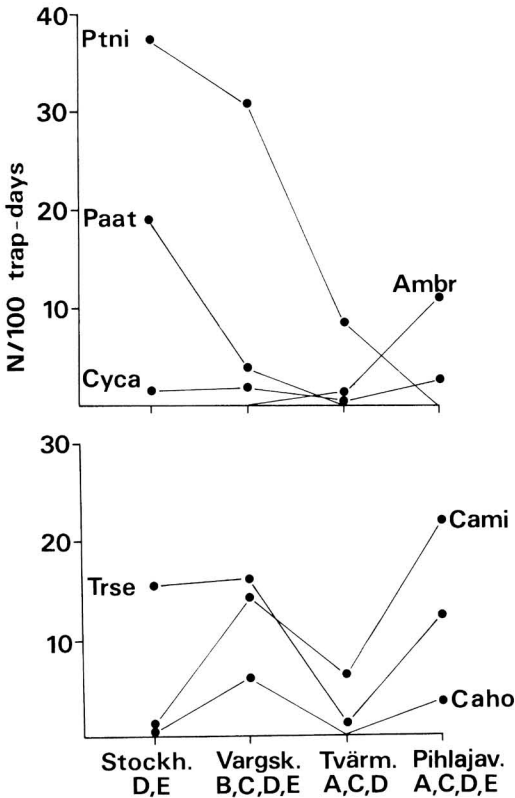


Fig. 4. Occurrence of the most abundant forest carabid species (sampled in at least two archipelagoes) in the pooled forest data in the archipelagoes. Symbols for carabid species as in Fig. 3. and habitat symbols as in Table 1.

4. Discussion

4.1. Geographic ranges

An obvious hypothesis to explain the great differences in the colonization pattern in our study archipelagoes would be to attribute them to differences in species distributions. As we have no quantitative data from the mainland areas, we examined the mainland occurrence of the species by inspecting the distribution maps in Fennoscandia, compiled by Lindroth (1945b). The maps are based on point observations, the density of which varies greatly in different parts of Fennoscandia. Consequently, we had to use somewhat variable criteria in judging whether our archipelagoes belong to the distribution range of a particular species. For the three Baltic archipelagoes we checked the presence of the species in the nearby mainland areas (Uppland coast in Sweden, the main island of Åland, and Hankoniemi peninsula in SW Finland, respectively). For Pihlajavesi we checked

the presence of the species in the regions surrounding the lake. Our total data include 59 species. All of these occur in the mainland areas close to Stockholm and the Vargskär archipelago, one (*Nebria brevicollis*), and three (*Bembidion minimum*, *Calathus fuscipes*, *Nebria brevicollis*) are absent from the Tvärminne and Pihlajavesi region, respectively. Two species (*A. obscurum*, *Pterostichus melanarius*) have the northern limit of their distribution at about 63°N (Lindroth 1945a). Abundances of the species presumably differ among the four mainland areas, but the result suggests that the differences in the occurrence of most of the species among the archipelagoes cannot be explained by their geographical distribution alone.

4.2. Habitat effects

Another, more plausible, explanation to the varying patterns in our study archipelagoes would be to attribute them to habitat differences. Although our study archipelagoes belong, by and large, to the same biogeographic zone, the habitats are certainly not identical. Their variation can be characterized at three different levels: (1) The counterpart habitats may be different from each other in their structural characteristics. This is certainly true of Pihlajavesi islands compared with the Baltic archipelagoes, but the Baltic ones may differ from each other as well. (2) The area range of islands studied is somewhat different between the regions. In particular, islands in Tvärminne were smaller than islands in the other areas. Consequently, our samples measure colonization success in different parts of island gradients, which possibly correlates with habitat characteristics as well. (3) The proportions of different habitat types vary on the regional scale among the study regions. For instance, lush deciduous habitats are characteristic of large Vargskär islands in the immediate vicinity of our study islands (Palmgren 1950, Haila 1983), but such habitats are far scarcer in the other Baltic archipelagoes and they are lacking from Pihlajavesi, where forests are relatively barren. We presume that the abundance of *Agonum fuliginosum* and *A. obscurum* in Vargskär can be attributed to the high proportion of lush deciduous habitats in the archipelago on the regional scale. Both species are characterized by Lindroth (1945a) as favouring moist deciduous forests, and such habitats make up about 20% of the area of large Vargskär islands (Haila & Järvinen 1983). The abundance of *P. atrorufus*, characterized

as an anthropocoric species by Lindroth (1945a), in various habitats in the Stockholm archipelago might be due to the relatively intensive human influence there.

If "diffusion" (Pielou 1979) from neighbouring favourable habitats to less favourable ones is important in carabids (as suggested by Niemelä et al. 1985), differences in regional habitat proportions would influence the compositions of island communities. We interpret the high abundance of *A. fuliginosum* in Vargskär pine forests as a result of "diffusion" from optimal deciduous to less optimal pine habitats. The species made up 33% of the total sample from Vargskär pine forests (habitat C in Table 2B; 0.4 individuals/trap-day), but it only occurs sporadically in the coniferous forests of the mainland of Åland (Niemelä et al. 1986), and its proportion of the total community of spruce-dominated marsh groves on Åland is 3% (0.01 individuals/trap-day) (Niemelä et al. 1985). The latter habitat, in particular, is definitely more luxuriant than the pine forests of Vargskär.

Differences in habitat composition on the regional scale presumably influence less abundant species as well (e.g., lush habitats of Vargskär might explain the high species richness observed there, see Fig. 2), but sufficiently detailed knowledge on the environmental requirements of carabid beetles is lacking. For the same reason it is difficult to infer what is the significance of structural differences in counterpart habitats for the varying colonization patterns. We hazard a guess that subtle habitat differences explain the great abundance of *D. globosus* on small skerries in Tvärminne. It is a species of moist habitats close to waterbodies (Lindroth 1945a, 1985), and the low and exposed skerries of Tvärminne might be more favourable for it than narrow strips of shore habitats on the larger forested islands in the other archipelagoes (see also Gillerfors 1966). *A. viduum* could be another example of the effect of subtle habitat differences between the archipelagoes. In Pihlajavesi the species was abundant in the shore habitats (especially gravel shores), which were more common there than in the other archipelagoes. According to Lindroth (1986), *A. viduum* prefers shore habitats.

4.3. Concluding remarks

To conclude, we assume that habitat differences among the archipelagoes are important for the occurrence of carabids and that the habitat effects are mediated through two factors: (1) Detailed autecological

requirements of individual species, and (2) dynamics of local populations in patches of favourable habitats, bordering on a variety of other habitat types. The second factor emphasizes the role of history and chance in insular colonization. A great number of the differences observed among the carabid communities in our study archipelagoes have no obvious explanation. For instance, from autecological information alone it would be very difficult to predict the distribution of *P. diligens*, another ubiquitous species of moist habitats (Lindroth 1945a), in our archipelagoes (see Table 2). It was abundant in Tvärminne, but restricted to small skerries, and found in Vargskär in mixed forests but absent from small skerries, absent from Pihlajavesi, and one individual was caught in Stockholm (see also Gillerfors 1966). The absence of *P. niger* from Pihlajavesi in another inexplicable enigma.

Being distributional, our data do not give any basis for concluding whether interspecific competition plays a role in the colonization of islands by carabids. Some of the patterns might be caused by a combination of priority effects and competition (e.g., differences in the identities of *Agonum* and *Amara* species in the four archipelagoes; and the distribution of *P. niger* vs. *P. melanarius* see Niemelä et al. 1985), but experimental data on the exact mechanism of the presumed interactions are needed.

Finally, our data show that there are perplexingly great differences in the distribution patterns of carabids in our four study archipelagoes, and no obvious explanations for these differences are at hand. We regard chance population fluctuations as a plausible mechanism behind these differences, combined with differences in the habitat preferences of the species. The explanation is *ad hoc*, but it agrees with theoretical models on population dynamics in heterogeneous, fluctuating environments (Levins 1969, Slatkin 1974, Levin 1976, 1978, Hanski 1983). In principle the explanation is also testable, but only on the basis of quantitative data covering longer periods. Our results once more underline the necessity for collecting quantitative data in studies on island distribution patterns.

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