Ann. Zool. Fennici 23:289–296. 1986

Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Åland Islands, SW Finland

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Niemelä, J. Haila, Y. Ranta, E. 1986: Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Åland Islands, SW Finland. — Ann. Zool. Fennici 23:289–296.

We studied the spatial occurrence of carabid beetles in four uniform forest areas on the Åland Islands, SW Finland. In each of the forest areas we took samples in five sampling sites with fifteen pitfall traps. The spatial dispersion of carabids was examined on both the community and the species level and in three spatial scales: (1) among the traps in each sampling site, (2) among the sampling sites within each forest area, and (3) among the forest areas. An ordination analysis did not reveal any systematic differences in the floristic characteristics among the sites.

Within the sampling sites, *Trechus secalis* showed an aggregated dispersion pattern in six out of 12 sites analyzed. The two other species analyzed (*Pterostichus melanarius, P. niger*) both differed from random dispersion in one site. Out of the six species studied only *T. secalis* showed an aggregated dispersion pattern among the sites in every forest area. A one-way analysis of variance indicated that none of the abundant species had an aggregated dispersion among the forest areas. In small spatial scales, aggregated dispersion pattern of forest carabids seems to be the rule, but the pattern has no obvious explanation in habitat variability.

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1. Introduction

The spatial dispersion of populations is often aggregated in natural habitats (Elliot 1977). Mathematical models have been developed to describe the aggregated dispersion pattern (e.g. Neyman 1939, Cole 1946, Thomas 1949, Pielou 1974, Hassell 1978), and the ecological significance of the pattern has been the focus of numerous studies (Krebs 1972).

A natural reason for non-random distribution of populations in space is habitat variation, and the habitat preferences of carabids have been the subject of many studies (e.g. Thiele & Kolbe 1962, Szyszko 1974, Thiele 1967). Forest carabid communities have been used as references for communities in other habitats such as urban areas or fields (e.g. Czechowski 1982, Neumann 1971, Thiele 1964, 1971). However, the aggregated dispersion pattern creates a methodological problem for such comparisons: How representative is a *local* sample for the community composition in the habitats as a whole? Most carabid species have clear preferences at the biotope ('macrohabitat') level (Thiele 1977), but little is known about the factors behind the aggregated dispersion pattern of carabids within a habitat (Greenslade 1964), or about their 'microsite' requirements (*sensu* Whittaker & Levin 1977) within habitats regarded as uniform by human standards. An analysis of the aggregated pattern is clearly relevant also for quantitative estimates of carabid communities within uniform habitats. In such studies we ought to know how large a sample has to be in order to be representative.

In this study we examine the spatial dispersion of carabid beetles in uniform coniferous, OMT-type forest areas on the Åland Islands, SW Finland. We sampled carabids in four areas that were as similar as possible to the human eye in their overall vegetation. We wanted to minimize the effect of habitat differences and to compare the spatial dispersion of the beetles among vegetationally similar areas. We analyzed the spatial dispersion of the carabid beetles both on the community and on the species level in three spatial scales: (1) among the traps in each sampling site, (2)

Table 1. Characteristics of the vegetation of the sampling sites (1−20) in the sampling areas (A−D). Proportions (%) of the eleven most abundant plant species are given as averages of the five randomly selected one m^2 squares. Plant species included in the correlation test (see p. 294) are marked with an asterisk.

	A					B					C					D				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Calluna vulgaris	—	—	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	27
*Deschampsia flexuosa**	8	12	—	12	—	8	6	5	9	5	8	2	1	8	4	13	6	7	—	3
*Dicranum majus**	10	2	2	6	3	4	11	10	2	18	10	8	12	1	12	—	—	2	1	—
Equisetum silvaticum	5	—	—	—	27	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
*Linnea borealis**	3	4	—	4	—	5	8	8	5	5	6	6	5	2	5	10	7	7	3	2
Lysimachia vulgaris	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	8	—
*Majanthemum bifolium**	6	10	—	8	—	2	4	6	5	4	6	10	5	10	9	12	7	4	3	—
*Pleurozium schreberi**	6	5	18	5	1	6	17	2	14	14	17	6	4	7	7	11	8	11	4	25
*Vaccinium myrtillus**	13	11	15	18	13	17	13	11	14	16	16	8	9	4	6	9	11	15	7	7
*V. vitis−idaea**	6	5	9	5	8	6	5	7	9	10	5	2	6	5	6	5	9	10	9	6
Sphagnum sp.	6	—	—	3	20	—	—	9	2	—	1	2	3	—	—	—	4	—	18	—
Total	63	49	63	61	72	48	64	60	60	72	69	44	45	37	50	60	52	56	53	70

among sampling sites within each of the four sampling areas, and (3) among the sampling areas within the uniform forest habitat. We also studied the relationship between vegetation characteristics and carabid abundance.

2. Material and methods

2.1. Study area

The study was made on the Åland Islands, situated in the northern Baltic between SW Finland and Sweden (about 60°N, 20°E). The study area is on the main island of Åland, which actually comprises two large islands separated by a narrow (10 m) channel. The total area of Main Åland is about 970 km^2.

We selected four sampling areas (indicated as A, B, C and D) from the largest and most uniform forest areas that we could find on the topographic maps. Continuous forest covers about 625 ha in sampling area A, 222 ha in B, 388 ha in C, and 175 ha in D. The forests are mainly spruce-dominated, belonging to the Oxalis-Myrtillus type in the Finnish forest site type classification. Distances from the sampling areas to habitats under intensive human influence such as fields, villages and main roads range from 0.5 km (B) to 1.5 km (A). The distances between the sampling areas range from 10 km to 27 km.

In each of the four sampling areas we selected five separate sampling sites with distances of 100−150 m. The field layer and ground layer vegetation of the sampling sites in five randomly placed 1 m^2 grids was examined by visually estimating proportional coverages of the plant species (Table 1).

2.2 Sampling procedure

The carabids were sampled by pitfall traps (Southwood 1978). Plastic cups, 65 mm in diameter and 170 ml in volume, were half filled with a solution of water and detergent. Sampling was done twice during the season in periods of five days: 8−16 June and 16−23 August 1983. Fifteen traps were placed in a grid of 3×5 traps (Niemelä et al. 1985) in each sampling site, making the total number of traps 75 at each sampling area. The distance between the pitfall traps in the grid was 2−3 m. The sampling procedure was similar in each sampling area and in both sampling periods, but the exact location of the traps was different in the two periods.

To analyze the spatial dispersion of single species among the traps within each site, and among the sites within each sampling area, we calculated the agreement of the dispersion with the Poisson series. The test is based on the equality of the variance and mean in the Poisson series:

$$I = s^2/\bar{x},$$

where I = index of dispersion, s^2 = variance and $\bar{x}$ = mean (Elliot 1977:40−44). Index values close to one indicate an agreement with the Poisson series, i.e., random dispersion. The agreement of the index with the Poisson series was tested with a χ^2-test ($df = n-1$):

$$\chi^2 = I(n-1),$$

where n=number of sampling units (Elliot 1977:40−44). Index values significantly greater than one (i.e., $s^2 > \bar{x}$) indicate aggregated dispersion. The power of the test is naturally dependent on sample size. For instance, if only one individual is found in a set of fifteen traps, the pattern of necessity agrees with the Poisson series. Consequently, we included in the analysis only the most abundant species (in the analysis among the traps we included species with five or more individuals, and among the sites species with 42 or more individuals).

We also examined the dispersion pattern among all the 20 sites by the one-way analysis of variance in order to test whether the variance among the sites was greater than within the sites (original data square-root transformed). Dispersion among the sampling areas was examined using the one-way analysis of variance on the basis of the pooled samples of each sampling site.

Table 2. Number of carabid beetles sampled in sampling sites 1 – 20 in sampling areas A – D (sampling periods pooled). P indicates number of sampling sites where a species was sampled. The expected species number (with *SD*) is calculated with rarefaction to 40 individuals. Nomenclature follows Silfverberg (1979).

	A						B						C						D							
	1	2	3	4	5	A	6	7	8	9	10	B	11	12	13	14	15	C	16	17	18	19	20	D	Total	P
Trechus secalis	0	16	0	48	12	76	8	2	10	20	7	47	0	8	8	4	1	21	21	28	3	1	5	58	202	17
Pterostichus melanarius	1	46	5	4	3	59	11	6	4	3	3	27	1	0	0	2	0	3	0	2	13	5	3	23	112	16
P. niger	3	2	18	11	2	36	9	4	6	3	8	30	0	1	0	1	0	2	7	5	0	1	0	13	81	15
Carabus hortensis	5	6	0	4	1	16	7	3	3	8	4	25	1	6	2	0	1	10	1	3	3	0	1	8	59	17
Calathus micropterus	2	2	5	3	0	12	12	3	4	3	2	24	2	2	1	2	1	8	2	2	0	0	2	6	50	17
P. oblongopunctatus	0	2	1	0	5	8	7	0	3	3	14	27	0	0	0	0	1	1	1	2	0	2	1	6	42	12
Agonum fuliginosum	0	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	22	3
A. obscurum	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Amara brunnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
C. violaceus	1	0	4	1	0	6	0	0	1	0	1	2	1	0	0	1	0	2	0	2	0	0	1	3	13	9
Cychrus caraboides	0	2	1	0	0	3	3	0	0	1	2	6	0	0	0	0	0	0	2	4	3	3	1	13	22	10
Dyschirius globosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Harpalus quadripunctatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Leistus ferrugineus	1	0	2	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3
L. terminatus	1	2	0	0	0	3	1	0	0	0	0	1	0	0	0	0	1	1	0	1	2	3	0	6	11	7
Loricera pilicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	3	3	2
Notiophilus biguttatus	1	1	0	0	1	3	0	1	0	0	1	2	0	0	0	0	1	1	1	1	0	0	0	2	8	8
Patrobus assimilis	0	0	0	0	1	1	0	0	2	0	0	2	0	0	1	0	0	1	0	0	0	1	0	1	5	4
P. atrorufus	0	0	0	0	1	1	10	0	2	1	0	13	0	0	0	0	0	0	0	0	1	0	0	1	15	5
P. nigrita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	1
Sample size	15	79	36	72	48	250	68	19	35	42	42	206	5	17	12	10	7	51	35	51	26	23	15	150	657	
Species number: observed	4	9	7	7	10	15	9	6	9	8	9	12	4	4	4	5	7	11	7	11	7	11	8	17	20	
expected	9.6±1.4						8.9±1.0						9.8±0.9						11.4±1.5							

2.3 Plant cover

The characteristic field layer dominants of the OMT-forest type, *Vaccinium myrtillus* and *V. vitis-idaea* were found in all sampling sites in roughly equal percentages. Another vegetation characteristic common to the sites is the great coverage of *Majanthemum bifolium* and the scarcity of *Oxalis acetosella*. Some important indicator plant species were characteristic only for some of the sampling sites. For instance, *Calluna vulgaris* was found in only two sampling sites, but was abundant in these sites, indicating the relative dryness of the sites (Table 1).

We made an ordination of the vegetation of the sampling sites by the detrended correspondence analysis (DCA) (Gauch 1982). Sampling sites in the four sampling areas do not form clusters separated from each other in the ordination (Fig. 1). There are, however, some outliers in the ordination, characterized by relatively scarce indicator species (Table 1). Two of the outlier sites (3, 5) are in study area A and three (18, 19, 20) in study area D. The first axis of the ordination most likely indicates differences in the soil moisture of the sampling sites, characterized by plant species such as *Calluna vulgaris* at the dry end of the axis and *Lysimachia vulgaris* and *Sphanum* sp. at the wet end.

To test whether there are systematic differences in the vegetational composition of the sites among the four sampling areas we calculated the Euclidian distances between the five sampling sites in each sampling area on the basis of the DCA-ordination (axes I and II). The observed distances were then compared with the Euclidian distance between five sites drawn randomly from the 20 sampling sites. The observed distance among the sites in sampling area A is 130 (randomly drawn distance < observed 995 times out of 1000), in B 40 (211), in C 29 (69), and in D 114 (961). The distances between five randomly drawn sites are not significantly longer than the distances observed within the sampling areas, i.e. there are no systematic differences among the four sampling areas. On the other hand, in sampling areas A and D the observed distances are significantly longer than the random ones due to the vegetationally deviating sites (Fig. 1, Table 1).

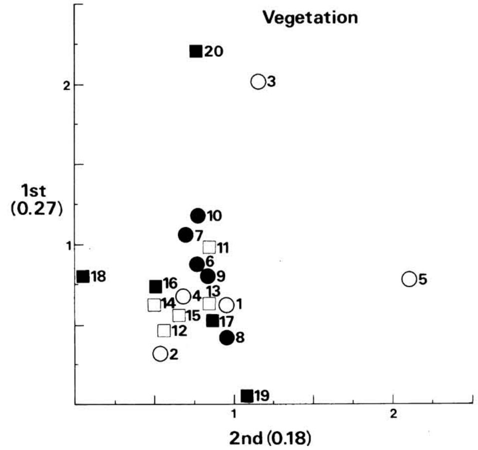

Fig. 1. The sampling sites (1 – 20) of the sampling areas (A = o, B = ●, C = □, D = ■) plotted on the 1st and 2nd axis of detrended correspondence analysis according to their plant cover. The eigenvalues of the axes are shown in parentheses.

3. Results

3.1. Dispersion of single species

The total number of carabid beetles in the samples from the four forest areas was 657 individuals belonging to 20 species (Table 2). The most abundant species was *Trechus secalis* (31 % of the pooled sample) and the second in terms of abundance was *Pterostichus melanarius* (17 %). *P. niger* comprised about 12 % of the pooled sample, while the proportions of the remaining species fell below 10 %. *Calathus micropterus* and *Carabus hortensis* were scarce, but evenly distributed, occurring in 17 of the 20 sites.

Within the sampling sites

The lowest spatial level of the analysis comprises the spatial dispersion among the traps within each of the 20 sampling sites. We investigated the three most abundant species (*Trechus secalis, Pterostichus melanarius, P. niger*) in sites where the sample size was five or more individuals. Because the exact location of the traps differed between the two sampling periods, calculations were made separately for both periods. *T. secalis* shows an aggregated dispersion pattern (Table 3) within six of the 12 sampling sites examined. The dispersion of *P. melanarius* and *P. niger* differed from random in one site out of five and four sites, respectively.

The difference between *T. secalis* on the one hand and *P. melanarius* and *P. niger* on the other hand is presumably due to differences in abundances. Naturally, the χ^2 value and sample size are positively correlated (Elliot 1977; Table 3). The dispersion of the three species within the outlier sites in the vegetation ordination (3, 5, 18, 19, 20, Fig. 1) does not seem to differ from the dispersion pattern in other sites. We also compared the dispersion of *Agonum fuliginosum* in site 5 (20 individuals) with the Poisson series; it agrees with random ($\chi^2 = 13.78$, NS, $df = 14$).

Table 3. Agreement with the Poisson series (tested by χ^2) of the three most abundant species in the sampling sites (1–20) with five or more individuals in the sampling areas A–D. Period of analysis (I,II) and number of individuals (in brackets) are given. Levels of statistical significance: NS not significant $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

		Trechus secalis (II)	*Pterostichus melanarius* (I)	*P. niger* (I)
A	1			
	2	36.5 (16)***	21.6 (34) NS	
	3		10.2 (5) NS	20.3 (18) NS
	4	35.7 (48)**		16.9 (10) NS
	5	23.0 (12) NS		
B	6	18.2 (8) NS	20.0 (10) NS	10.8 (8) NS
	7		28.0 (5)*	
	8	29.0 (10)*		
	9	56.6 (20)***		
	10	25.2 (7)*		33.7 (7)**
C	11			
	12	22.0 (8) NS		
	13	10.8 (8) NS		
	14			
	15			
D	16	36.8 (21)***		
	17	14.8 (28) NS		
	18		22.0 (5) NS	
	19			
	20	22.0 (5) NS		

Within the sampling areas

We included the six most abundant species in the investigation at the intermediate spatial level. The analysis is based on the pooled samples of both sampling periods (Table 2). *T. secalis* showed an aggregated dispersion within every sampling area, in the other species the pattern is variable (Table 4).

We also analyzed the dispersion of *T. secalis, P. melanarius* and *P. niger* within each sampling area by one-way analysis of variance. For *T. secalis* the variation between the sampling sites is significantly greater than within the sites in sampling area A ($F_{4,70} = 10.52$, $p<0.001$), in C ($F_{4,70} = 2.84$, $p<0.05$), and in D ($F_{4,70} = 7.61$, $p<0.001$), for *P. melanarius* in A ($F_{4,70} = 15.70$, $p<0.001$), and for *P. niger* in A ($F_{4,70} = 6.26$, $p<0.001$). In sampling area A the variance between the sampling sites was significantly greater than within the sites for all three species, while the reverse holds true in sampling area B. In the other two study areas the pattern is more variable.

The abundance of carabids might correlate with differences in the vegetation characteristics of the sampling sites. We checked whether the abundances of *T. secalis, P. melanarius* and *P. niger* differed in the outlier sites in the vegetation ordination (3, 5, 18, 19, 20) (Fig. 1)

Table 4. Agreement with the Poisson series (χ^2) of the six most abundant species among the sampling sites within the sampling areas A–D. Sample sizes (periods pooled) are given in brackets. Statistical significance as in Table 3.

	A	B	C	D
Calathus micropterus	5.5 (12) NS	14.0 (24)**	0.8 (8) NS	4.0 (6) NS
Carabus hortensis	8.4 (16) NS	4.4 (25) NS	11.0 (10)*	4.5 (8) NS
Pterostichus melanarius	124.8 (59)***	8.4 (27) NS	5.2 (3) NS	22.0 (23)***
P. niger	28.0 (36)***	4.4 (30) NS	3.0 (2) NS	16.0 (13)**
P. oblongopunctatus	10.8 (8)*	21.6 (27)***	4.0 (1) NS	2.4 (6) NS
Trechus secalis	102.0 (76)***	18.8 (47)***	13.6 (21)**	50.8 (58)***

from the abundances in the other sites. In site 3, *P. niger* is most abundant in study area A, in site 18 the abundance of *P. melanarius* is highest in area D, and in site 19 the abundance of *T. secalis* is lowest in area D. However, this variation does not seem to be greater than the variation in species abundances at the other sites (see Table 2).

Among the sampling areas

We analyzed the large scale spatial dispersion (among the four sampling areas) by the one-way analysis of variance. The variance between the study areas is not significantly greater than the variance within the areas for any of the six most abundant species (data in Table 2).

3.2 Community structure

To study the structure of entire carabid communities in the sampling sites, we ordinated the data with the DCA (Fig. 2). The sampling sites are more dispersed than in the vegetation ordination. Of the four outliers, three (5, 18, 19) are the same as in the vegetation ordination (Fig. 1 and 2). They are characterized by species that were scarce in our study area: Sampling site 5 by *Agonum fuliginosum* (20 individuals of the total of 22 caught), site 18 by *Loricera pilicornis* (one individual of the total three caught), while site 19 is the only one where *Dyschirius globosus* and *P. nigrita* were caught. In addition to these, sampling site 15, comprising seven individuals of seven species, is an outlier in the carabid ordination.

To check whether there are systematic differences in the carabid community structure of the sampling sites among the four sampling areas we calculated the Euclidian distances between the five sites in each sampling area on the basis of the DCA ordination (I and II axes). The observed distance was then compared with the Euclidian distance between five sites drawn randomly from the 20 sampling sites. The observed distance among the sampling sites in sampling area A is 96 (randomly drawn distance < observed 666 times out of 1000), in B 26 (1), in C 95 (653), and in D 92 (608). The random distances tend to be shorter than the observed distances in all but one study area (B), indicating that the sampling sites of study area B form a distinct group.

We then compared the relation between sample size and species numbers in the four sampling areas by the rarefaction method (Simberloff 1978, James & Rathbun 1981). No statistically significant differences were found (Table 2).

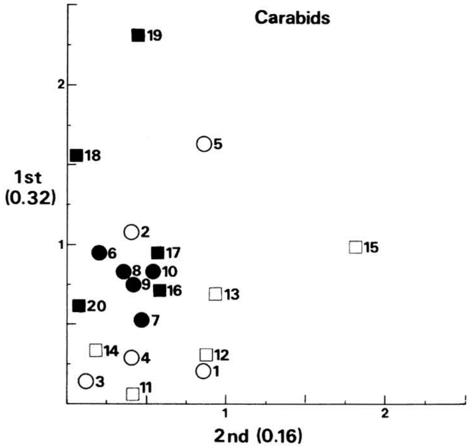

Fig. 2. The sampling sites (1–20) of the sampling areas (A= o, B= ●, C= □, D= ■) plotted on the 1st and 2nd axes of detrended correspondence analysis according to their carabid communities. The eigenvalues of the axes are shown in parentheses.

3.3 The influence of habitat differences

Vegetational composition presumably reflects environmental factors that are important for carabids. To test whether the variation in the structure of carabid communities can be explained by the floristic differences among the sites, we calculated the Spearman rank correlation between the vegetation and carabid DCA scores of the sites (Fig. 1 and 2). No correlation was found: $r_s = -0.329$, $df = 18$ (between the first axes of the ordinations), $r_s = 0.103$, $df = 18$ (between the second axes). We also calculated the Spearman rank correlation between the seven most abundant plant species (for the species see Table 1) and the sample size of *T. secalis, P. melanarius* and *P. niger* in the sampling sites. Two out of 21 correlations were statistically significant at the 0.05 level (*P. melanarius* vs. *Majanthemum bifolium* and *P. niger* vs. *Vaccinium myrtillus*) but this low number of significant correlations can be due to the great number of comparisons. The vegetation descriptions were made on the level of sampling sites which makes it impossible to estimate the effect of vegetation on the dispersion of carabids among the traps within individual sampling sites.

The spatial dispersion of carabids may also reflect the dispersion of their food items. Since most carabid species are predatory, we calculated the number of springtails, mites, earthworms, molluscs and different insect larvae in the traps to compare the dispersion of carabids and their potential food. A positive correlation was only found between the number of carabids and springtails at the level of sampling sites (Fig. 3). We also compared the sample sizes of springtails and *T. secalis* in the traps in one randomly selected sampling area (B) by Spearman rank correlation. The correlation is not statistically significant (at 0.05 level) in any of the five sampling sites, although the springtails showed an aggregated dispersion in every sampling site within study area B.

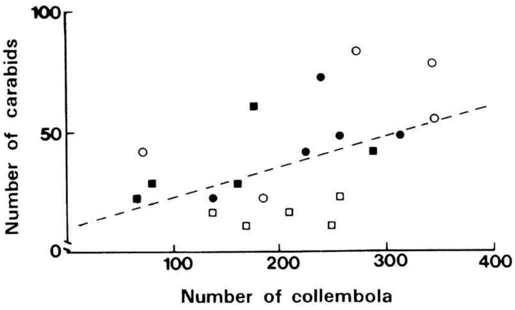

Fig. 3. Number of carabids as a function of number of collembola in the sampling sites in the sampling areas (A=○, B=●, C=□, D=■) with regression line ($r^2 = 0.262$, $p < 0.05$) drawn.

4. Discussion

The aggregated dispersion of carabids seems to be a prevailing pattern in our study area in the two lowest spatial scales, i.e., among the traps within sampling sites and among sampling sites within sampling areas. At the level of the sampling areas, however, differences in abundances tend to even out; i.e. average densities are fairly uniform in the regional scale. Habitat characteristics do not offer any obvious explanations for the aggregated dispersion pattern, except in some specific cases (e.g., the concentration of *Agonum fuliginosum* in the moist sampling site 5). It is obvious that the aggregated dispersion pattern of forest carabids is important both methodologically and in the population dynamics of individual species.

There are several potential explanations for the within-habitat aggregation of organisms. Reproductive behaviour may lead to aggregation of adults, or of the offspring (due to clustering of eggs laid by the females) (Cole 1946). Prey dispersion may also be the reason for aggregation of predators. Bryan & Wratten (1984) confirmed experimentally this effect on carabids that use aphids as prey in a cereal field. The numbers of springtails and carabids correlate positively at the level of sampling sites in our study area, which suggests that carabids and springtails react in a similar way to some environmental factors. However, it is difficult to assess the significance of the correlation as we do not know the exact food requirements of the carabid species occurring in our study area.

Individuals may also prefer a certain microclimate within a habitat, which would lead to aggregations at the most favourable sites (Cole 1946). Organisms might also show a tendency to aggregate due to behavioural interactions without any apparent influence of abiotic environmental factors (Cole 1946, Elliot 1977). Reise & Weideman (1975) showed that aggregations of *Pterostichus oblongopunctatus* changed from trap to trap in three successive nights without any clear connection to environmental differences.

Another approach for interpreting the spatial dispersion of populations among the sampling sites would be by the concept of the 'interaction group' (den Boer 1977, 1981). Den Boer (1977:23) defined an 'interaction group' as "a group of individuals living in places with spatial dimensions that do not substantially exceed the distances normally covered by the individuals in the relevant patterns of activity during their lifetime". The densities of different 'interaction groups' may fluctuate independently of each other even in a relatively homogenous area (den Boer 1981). If samples are taken from independently fluctuating 'interaction groups' the sample sizes may differ considerably, but as the samples from several 'interaction groups' are pooled the variation in the population level as a whole tends to even out (den Boer 1981). The fluctuations of independent 'interaction groups' are presumably due to differences in reactions to the spatial heterogeneity of the sampling sites, and to demographic stochasticity (den Boer 1981).

It would be important to know whether our samples represent different 'interaction groups'. The distance covered by a carabid during its lifetime depends on its size (Thiele 1977). Den Boer (1981) reported that most of the individuals of a *Pterostichus*-species slightly smaller than *P. melanarius* covered less than 200 metres during their lifetime. As the distances between the sampling sites within our sampling areas were 100—150 metres, we cannot be sure that we have sampled different *P. melanarius* and *P. niger* 'interaction groups'. For *T. secalis* the samples have presumably been taken from different 'interaction groups', as the distance covered by an individual of the species is probably considerably under 100 metres. Den Boer (1981) reported that the majority of individuals of *Calathus melanocephalus* (size 6—8.8 mm, Lindroth 1961) covered less than 80 metres during their lifetime; the size of *T. secalis* is 3.5—4 mm (Lindroth 1961). Thus, the differences in abundances of *T. secalis* among sampling sites in our study could be explained by the effect of independently fluctuating 'interaction groups'. When the samples from different sampling sites are pooled within each sampling area, the differences tend to level off.

However, we only have a one-year snapshot of the abundances of populations in different sampling sites, and in subsequent snapshots details of the picture would presumably be different (Andrewartha & Birch 1984). Den Boer (1981) showed that the size of the same 'interaction group' varies a lot between subsequent years. The 'interaction group'-approach does not, however, explain the aggregated dispersion pattern of carabids in the lowest spatial scale, among the traps within individual sampling sites.

To conclude, there is variation in the local abundances of carabids in our vegetationally uniform sampling habitat. The aggregated dispersion pattern of individual species makes it difficult to predict the composition of local carabid assemblages on the basis of habitat composition alone.

Acknowledgements. Our thanks are due to Olli Järvinen, Sara Tjossem and Kari Vepsäläinen for valuable comments on an earlier draft of this paper. The study was financed by the Academy of Finland; a grant from the Emil Aaltonen foundation to JN is gratefully acknowledged.

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Received 13.V.1985, revised 27.I.1986
Printed 30.IX.1986