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The effect of isolation on the occurrence of farmland carabids in a fragmented landscape

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The effect of isolation by forest on carabid beetle communities was studied in small patches of farmland in Southern Finland. We divided the studied patches into three categories by isolation and area of farmland in their surroundings. Less individuals and species were caught in small and isolated patches than in non-isolated ones of similar size. The positive correlation between species number in the patch and farmland area in the surrounding matrix was significant in buffers larger than 1 000 m. The proportions of scarce, medium and abundant species in local communities did not depend on isolation. Short-winged open land species were found both in isolated and non-isolated patches. Winged morphs of the dimorphic species *Pterostichus melanarius* (Ill.) were found in isolated patches in a somewhat greater frequency than in non-isolated fields. Though dispersal by air is possibly the most important way of colonization, we do not exclude the possibility that especially brachypterous individuals may have dispersed anthropocorously, or actively along narrow road verges. On the other hand, the populations may be relicts from times when the forests were more open.

1. Introduction

Finnish farmland is a very patchy and fragmented environment in the matrix of boreal forest. The patch size of farmland varies from less than one hectare to several hundreds of hectares, and the connectedness varies from total isolation to a network in which corridors of varying width, length and form link patches to each other. In the southern half of Finland, the proportion of farmland of the total land area varies from about one third in the southernmost rural districts to 12% in central Finnish rural districts (Yearbook of farm statistics 1992).

Various approaches can be applied in the study of communities in patchy environments. One is community-oriented stemming from the theory of island biogeography (MacArthur & Wilson 1967), which has been used in true island situations (Niemelä *et al.* 1985), and, for instance, forest fragments in human-managed environments (e.g. Halme & Niemelä 1993), Dutch polders (Den Boer 1970, Ranta & Ås 1982), and heathlands in Britain (Webb 1989). Another approach is based on the theory of metapopulation dynamics which focuses on colonization and extinction processes of local populations in a network of habitat patches (e.g. Gilpin & Hanski 1991, Hanski 1994). Random factors and the history of the system studied are also important when explaining observed occupancy patterns (e.g. Haila 1983).

In heterogenous environments, patches are often considered to be internally homogenous and surrounded by a matrix of non-habitat. In real world, however, this kind of situations are rare. For instance, small farmland patches can be rather homogenous since only one crop type is grown, but larger patches usually consist of a greater number of fields growing different crops. With crop rotations, the fields become temporally heterogeneous. For animal species, the quality of the matrix can also differ in varying extent in various parts of the landscape.

In this paper we concentrate on studying the effect of isolation on carabid communities. We used GIS-assisted methods to measure isolation, one of the most important factors in all approaches mentioned above, and its dependence on the spatial scales of the environment. We studied carabid beetles communities in small patches of farmland isolated in various degrees from large patches, the supposed source areas.

Four landscape ecological factors can be expected to affect the carabid communities of small farmland patches. Two of them characterize the patch itself: (i) the size and (ii) the habitat type of the patch. The other two characterize the surroundings of the patches: (iii) the distance from supposed source areas, and (iv) the habitat composition of the matrix landscape. In this paper, we are interested in the latter two factors, and therefore have ruled out the first two factors in our sampling design.

We asked what kind of carabid communities inhabit small and isolated patches of farmland in Southern Finland and whether the communities were impoverished in comparison to small non-isolated or large patches? We expected to find that (i) the community would be impoverished in terms of species number in the isolated patches in comparison to

Table 1. Characteristics of the study sites selected. The abbreviations used to characterize soil types are: CT = Carex-peat, vf = very fine sand, grain size 0.02–0.002 mm, f = fine 0.2–0.02 mm, c = coarse 2.0–0.2 mm and g = gravel 60–2 mm. Isolation categories are: SIP = small isolated field, SNIP = small non-isolated field and LARGE = the field studied was a part of a large farmland area.

Field and isolation category	Study year	Habitat type	Soil type	Area	Farmland area (ha) within a buffer zone of 400 m	1 000 m	1 600 m
SIP 1	93 & 95	fallow	CT	4.3	4.8	4.8	4.8
SIP 2	93 & 95	fallow	c	0.9	3.1	3.1	6.0
SIP 3	93 & 95	fallow	c	0.2	0.2	0.2	0.6
SIP 4	93 & 95	fallow	f	2.9	2.9	4.8	7.0
SIP 5	93 & 95	fallow	c	0.3	0.5	0.5	6.2
SIP 6	95	fallow	c	0.9	1.9	4.3	4.8
SIP 7	95	fallow	g	0.4	1.0	1.0	1.0
SNIP 1	93	ley	f	2.5	2.9	20.2	75.1
SNIP 2	93	ley	vf	2.0	4.1	34.1	92.3
SNIP 3	93	ley	f	0.3	8.5	68.3	145.9
SNIP 4	93	ley	g	1.6	13.5	75.3	200.0
SNIP 5	93	ley	vf	0.6	17.0	81.3	232.1
SNIP 6	95	fallow	CT	1.7	2.3	11.0	26.4
SNIP 7	95	fallow	f	3.4	3.4	11.9	32.2
SNIP 8	95	fallow	c	1.1	2.0	17.1	35.5
SNIP 9	95	fallow	c	0.1	2.0	17.2	55.5
SNIP 10	95	fallow	f	1.4	1.8	35.9	179.8
LARGE 1	93	ley	f	0.4	14.9	68.7	197.2
LARGE 2	93	fallow	f	2.3	18.0	142.0	251.0
LARGE 3	93	ley	f	1.6	21.0	93.0	202.0
LARGE 4	93	fallow	f	4.0	23.1	123.3	225.2
LARGE 5	93	fallow	f	1.1	40.5	179.7	359.9

similar non-isolated ones, (ii) that the species of the isolated patches should possess a high dispersal capacity, that brachypterous species should be absent there, and (iii) that the probability of an open land species to have colonized a small patch would depend on its abundance in the regional species pool.

2. Study area and sampling design

Our study was conducted in the surroundings of Lammi Biological Station (61°03′N, 25°03′E) between the zones where farmland area decreases from a third to 12% of total land area.

In the summers of 1993 and of 1995, we selected 22 sampling sites, five of which were studied in both years (Table 1). The surrounding matrix around the studied farmland patches was pure coniferous and coniferous-deciduous mixed forest. Each of the fields studied was presumed to be a set-aside growing hay and grass, but in six fields the selection failed as they were harvested for silage in 1993.

In 1993, sampling was done in 15 fields divided into three isolation groups: five Small Isolated Patches (SIPs, 4–7 km from large farmland patches), five Small Non-Isolated Patches (SNIPs, distance less than 0.5 km to large farmland patches), and five fields situated in large patches of farmland (LARGE). In 1995, we studied seven SIPs and five SNIPs.

The mean areas of fields in the three isolation groups did not differ significantly from each other (Table 2). The area of farmland in the matrix was quantified by creating buffer zones around each of the patches studied at every 200 meters starting at the centroid of each patch. The isolation groups clearly differed in relation to total farmland area within the buffer zones. Within the 400 m and 1 000 m buffers the mean area of farmland in LARGE patches was significantly larger than in other isolation groups, but in large buffers (1 600 m) all the groups differed from each other (Table 2). However, the farmland area inside the buffers varied considerably between non-isolated patches (Fig. 1).

Sampling was done with pitfall traps (170 ml plastic jars, diameter 70 mm, filled up to one third with a dilution of ethyleneglycol, water and detergent). In 1993, a set of 16 pitfall traps was placed in a grid of 4 × 4 traps about three meters from each other in each of the fields for four two-week periods between 28 May–31 August. In 1995, beetles were trapped continuously during ten weeks in five two-week periods from the beginning of June to mid-August. Each set consisted of 25 pitfall traps arranged in a grid of 5 × 5 traps.

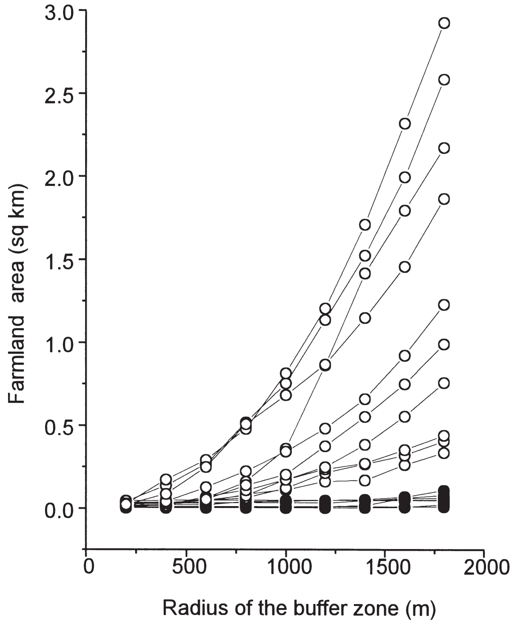

Fig.1. Farmland area inside the different sized buffer zones in each patch studied in 1995. Small isolated patches (SIPs) are indicated by solid circles and small non-isolated patches (SNIPs) by open circles.

3. Results

3.1. Carabid catch and species richness

During the two seasons, 6 773 individuals belonging to 67 carabid species were caught, 47 in SIPs, 56 in SNIPs and 65 in LARGEs, with the sample sizes

Table 2. Mean area (ha) and standard deviations of fields studied and farmland within three buffer zones around the study sites. No statistical difference was found between the patch sizes. SIPs, SNIPs and LARGEs differed from each other when farmland area inside the buffers was measured (One-way ANOVA).

	SIP		SNIP		LARGE		ANOVA	
	Mean	*S.D.*	Mean	*S.D.*	Mean	*S.D.*	*P*	*F*
Area	1.40	1.60	1.60	1.00	1.90	1.40	0.82	0.20
Area within								
400 m	2.03	1.66	5.78	5.46	23.50	0.99	0.0000	20.7
1 000 m	2.51	1.94	32.33	24.10	121	43.00	0.0000	32.1
1 600m	4.34	2.54	93.63	66.10	247	66.60	0.0000	29.5

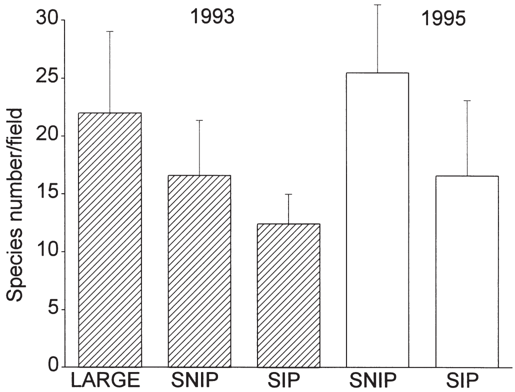

Fig. 2. Mean species number per patch and standard deviations in small isolated (SIP), small non-isolated patches (SNIPs) and fields in large patches of farmland (LARGE).

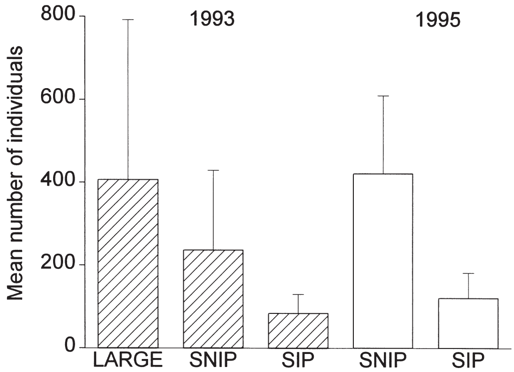

Fig. 3. Mean number of individuals per patch and standard deviations in small isolated patches (SIPs), small non-isolated patches (SNIPs) and fields in large patches of farmland (LARGE).

of 1 270, 3 473 and 2 030 individuals, respectively. In 1993, 3 631 individuals were caught with an effort of 868 trapping days. In 1995, the effort was doubled, being 1 750 trapping days, but the total catch was only 3 142. Most of the species caught may be considered as open land species (Lindroth 1985, 1986, Kinnunen & Tukia 1995). Some species found in our samples may inhabit both forest and open land and thus are more generalistic in their habitat choice.

In 1993 the number of species observed (S_{obs}) and individuals caught (N) were lower in small and isolated patches than in either small and non-isolated or large patches of farmland (Figs. 2 and 3). However, the differences were not statistically significant. (One-way ANOVA: S_{obs}: $F = 2.06, p = 0.17$ and N: $F = 3.51, p = 0.06$). We also compared SIPs and SNIPs separately in both years. Neither the species number nor the number of individuals differed significantly in 1993 ($t = -1.33$, $p = 0.22$ for S_{obs} and: $t = 1.71$, $p = 0.125$ for N). In 1995, the trend was similar, and both S_{obs} ($t = -3.01, p = 0.013$) and N ($t = -4.58, p = 0.001$) differed (Fig. 2 and 3).

We also tested how species number in the patch correlated with farmland area in the matrix surrounding the patch with the data of 1995. Correlations were positive and highly significant at greater distances (1–2 km) (e.g. for the buffer of 1 000 m, $r = 0.846$. $p = 0.0005$, and 1 800 m, $r = 0.788$ $p = 0.0023$). In smaller buffers no significant correlation was found between species number and farmland area.

As the catch varied among fields, we calculated also the expected number of species with rarefaction (Simberloff 1978). The mean $E(S_{40})$ did not vary significantly among SIPs, SNIPs and LARGEs in 1993 (One-way ANOVA: $F = 0.78, p = 0.48$,) or between SIPs and SNIPs in 1995 ($t = -0.52, p = 0.62$) (Fig. 4).

In our data no difference was found between coarse (grain size > 0.2 mm) and fine soils (grain size < 0.2 mm) in species and individual numbers in either year (Mann-Whitney *U*-test: $p = 0.12$ for S_{obs} and $p = 0.12$ for N in 1993, in 1995: $p = 0.33$ for S_{obs} and $p = 0.33$ for N). In 1993, most of the sampling sites were in fine soils, and in 1995 in coarse soils (Table 1). Carex-type was not included in this analysis.

3.2. Occurrence of individual species: dispersal abilities and colonization success

Carabid beetles can be either brachypterous or macropterous, different species being either mono- or dimorphic. Only macropterous individuals are capable to fly and, consequently, expected to colonize isolated patches. We found only two open land

Table 3. The number of species caught in small patches according to their ranking into abundant, medium, and scarce abundance in the regional species pool (105 species) of farmland carabid fauna in Lammi.

Abundance rank	SIP	SNIP	LARGE
Abundant	23	26	29
Medium	16	22	23
Scarce	8	8	13

species which, according to Lindroth (1985, 1986) are constantly short-winged in Fennoscandia and Denmark. All other open land species caught were macropterous or classified as dimorphic. *Carabus cancellatus* (Ill.) (body size 22–27 mm, wings rudimentary) and *Dyschirius globosus* (Hbst.) (body size 2.2–3 mm, constantly short-winged in our area) (Lindroth 1985) were found in isolated patches as well as in less isolated and large patches. In all, 210 individuals of *D. globosus* were found in all but one SNIPs and two SIPs. The 104 individuals of *C. cancellatus* were caught in three of the SIPs and five of the SNIPs.

Pterostichus melanarius (Ill.), a dimorphic, but dominantly (98%) brachypterous species in Lammi (Laaka 1993), was found only in two SIPs. Four of the 47 individuals found in SIPs were macropterous. Two macropterous individuals of 145 were collected in two of the SNIPs as well.

3.3. Abundance of species in isolated patches

To study the effect of regional abundance on the probability of colonization of small patches of farmland, we collated a data base of 41 051 carabids (105 species) caught in pitfall trappings of our team in Lammi since 1987. These were ranked by abundance and divided into three classes with 35 species in each. We expected that the carabid community composition of the LARGEs would represent that of the source areas, because they were part of the five large field areas, situated around the SIPs or in the neighbourhood of SNIPs. The number of species in the three rank classes did not differ among SIPs, SNIPs or LARGEs significantly (Table 3, overall $\chi^2 = 0.90$, $P = 0.92$, $df = 4$). Hence, the isolation of the SIPs, SNIPs and LARGEs did not affect the colonization probability of abundant and scarce species.

We also compared the carabid assemblages in five of the SIP-patches which were studied both in 1993 and 1995. Our data suggest that the species which were rare in 1993 were less likely to be found in 1995 than the abundant ones (Table 4). We cannot conclude that they had gone extinct, but at least the population size had decreased to the extent that they could not be detected even though the sampling effort was higher in 1995. Instead, those species which occurred in larger numbers were found also in 1995.

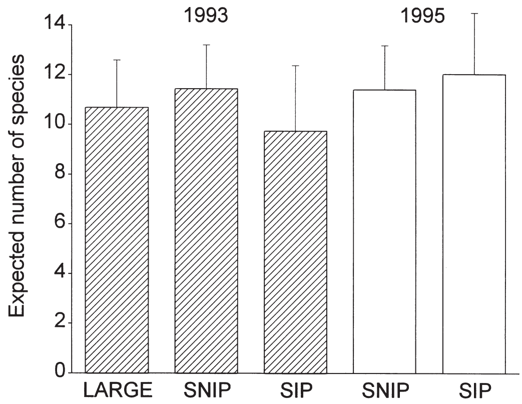

Fig. 4. Mean expected number of species and standard deviations in small isolated (SIP), small non-isolated patches (SNIPs) and fields in large patches of farmland (LARGE).

4. Discussion

In this study fields of equal size and a more or less similar habitat differed from each other in terms of species and individual number probably depending on landscape structure. More individuals and species were found in small patches, if there were other patches of farmland nearby. However, species number correlated positively with the number of individuals caught ($r = 0.691$, $p = 0.0001$, $df = 25$), indicating that species richness depends on sample size.

Intuitively, one would think that the larger the populations are the larger the catch would be. However, pitfall catches probably measure activity density rather than true densities and abundances of species (e.g. Luff 1987). As the habitat was standardized in our sampling design, the catch should not be biased among SIPs, SNIPs and LARGEs. Thus, the

Table 4. Mean abundance of the species found in 1993 and in 1995, and of the ones found in 1993 but not in 1995. Comparison is based on the Mann-Whitney *U*-test (*P*-value). S is the number of species.

Field	Species found in 1995			Species not found in 1995			*P*
	Mean	*S.D.*	S	Mean	*S.D.*	S	
SIP 1	6.57	11.66	7	1	0.00	3	0.008
SIP 2	10.90	23.72	10	1.82	2.04	6	0.048
SIP 3	3.70	2.91	10	1.5	1	4	0.07
SIP 4	22.83	36.95	6	2	2	4	0.06
SIP 5	5.63	5.17	11	1		1	0.17

species richnesses should be comparable with each other but insufficient in the sense of catching all but rather abundant species.

The correlation analysis revealed that when the buffer zone around the focal patch was large, species number and farmland area correlated positively. Because the patches chosen to be studied were isolated, the farmland area in the surroundings within distances up to 800 m was very scarce. Thus we cannot study the importance of nearby patches with these data. The between-patch scale concerns here mainly distances over 800 m.

The rarefactions did not reveal any differences between the expected species numbers. This may be a distortion due to the small sampling sizes which determined the expected number of species to be calculated for only 40 individuals. However, it may also indicate that community structures are more or less similar and are not affected by isolation.

One would have expected that brachypterous species would not have been found in isolated patches. The only two brachypterous open land species *Carabus cancellatus* Ill. and *Dyschirius globosus* (Hbst) were found in three of the isolated patches and in five of the isolated patches, respectively. In the case of dimorphic species, it is expected that after successful colonization their frequency is high (Niemelä & Spence 1991). In fact, the proportion of long-winged *Pterostichus melanarius* (Ill.) was 8.5% in SIPs which is much higher than what Laaka (1993) found in large patches of farmland elsewhere in Lammi (2%). The frequence in SNIPs (1.4%) is about the same as that in Laaka (1993). However, these figures are still much lower than the 60–70% proportion of macropters of *P. melanarius* found by Niemelä & Spence (1991) in remote populations in Canada.

How have *D. globosus* and *C. cancellatus* colonized the small isolated patches? We are able to recognize three possible explanations. Firstly, road verges may function as corridors. Secondly, the species may have arrived with humans, e.g., in vehicles, or with hay or earth transportations. Thirdly, it is possible that their populations are relicts from earlier times when there was a network of small patches (as revealed by maps from the 1930s) or when the landscape was more open in general as a result of former slash-and-burn cultivation.

Den Boer (1985, 1987) suggests that mean survival times for local populations of carabids only rarely exceed 100 years and most populations exist only for some decades. Having once colonized the patches, populations must have survived until these days unless they have been able to recolonize the patches after local extinction. Whether the survival possibilities are equally good in all the studied patches is doubtful. For instance, overwintering conditions for some species may be worse in small fields, if suitable field boundaries are not available (Desender *et al*. 1981, Sotherton 1984, 1985, Dennis *et al*. 1994).

To conclude, the isolation of small patches is an important factor in colonization dynamics. The community in distant fields was impoverished in terms of species richness. Colonization seems to be random in relation to abundance. However, the low number of individuals found in the isolated fields may be the result of some other characteristic but isolation. The quality of patches for carabids, for instance, may vary.

Even short wings did not prevent successful colonization by the two brachypterous open land species. However, when the wing length was studied in dimorphic species, *Pterostichus melanarius*, it appeared, that long wings may be a factor contributiong to colonization probability.

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