Non-random colonization of habitat islands by carabid beetles

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The distribution of carabid beetles on habitat islands in Dutch polders was tested against the hypothesis that the habitat islands receive a 'continuous influx' of carabid beetles. The probability that a species colonizes islands is assumed to be proportional to its frequency in the species pool.

All the characters (number of species, community diversity, size distribution of beetles, and frequency of macropterous dimorphic and brachypterous beetles) analysed in the communities of carabid beetles on the habitat islands deviated from the pattern expected on the basis of random sampling of carabids from the species pool. The results suggest that some species are more successful than others in invading habitat islands. Smaller body size and long wings charactersize these successful carabids.

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1. Introduction

There is no compelling reason to invoke ecological factors to explain patterns of distribution of plants and animals on islands and insular habitats as long as a purely stochastic mechanism is sufficient to explain the patterns observed (Simberloff 1978a). For example, a basic difference between islands and the mainland is the fact that islands are smaller. Therefore, we expect that species numbers not only correlate with habitat diversity (Williams 1969) and immigration and extinction rates (MacArthur & Wilson 1967), but also simply with the number of individuals. This 'passive sampling' (Connor & McCoy 1979) of individuals of species from the recruiting area is based on the fact that large areas receive more immigrants than do smaller ones. "The idea that the species-area relationship is purely a sampling phenomenon should be considered as a null hypothesis, and all hypotheses invoking biological processes to explain the species-area realtionship should be considered as alternatives" (Connor & McCoy 1979:793; for more details of the criticism of the island biogeography, see also Simberloff 1978a,c, Connor & Simberloff 1978, Strong 1980, Gilbert 1980). As pointed out by Preston (1960, 1962) there is a relationship, although not a linear one, between the number of individuals sampled and the number of species encountered. Thus, while this hypothesis generates a positive correlation between island area (i.e., sample size, in numbers of individuals) and species number, it does not assume any complicated biological mechanisms behind the processes.

In this paper we test whether the 'sampling hypothesis' alone is sufficient to explain the number of carabid species on habitat islands in Dutch polder areas. The assumption of the null hypothesis is that the habitat islands receive a 'continuous influx' of carabid beetles in which different species are represented in the same proportion as they are found in the species pool. The sample size of each site is considered to be the number of individuals caught on the habitat islands. Thus our way of examining the colonization of the habitat islands is simply to construct by rarefaction communities of similar sizes (size judged by the number of individuals) as observed on the habitat islands. The observed and expected communities are then compared. Carabids are an excellent croup for this kind of study. The species represent a wide range of body sizes (2–35 mm) and have three different wing morph patterns, viz., macropterous (long-winged), brachypterous (only rudimentary wings) and dimorphic (specimens of both types) species. These characters reflect much of the feeding niches and dispersal abilities of the species

Table 1. Characterization of the habitat islands (study sites). The site code, short description of the site, sampling year, number of species (S) and number of individuals (I) encountered are given together with the description of the vegetation and some special characters for the 18 study sites. Data from Haeck (1971).

Site**	Year	S	I	Vegetation	Special characters
1 shell bank	1968	9	27	sparse grass	occasionally waterlogged
2 sandy island	1968	14	740	sparse grass	
3 soft clay terrain	1968	23	616	none to marsh vegetation	occasionally waterlogged
4 soft clay terrain	1968	30*	485*	none to marsh vegetation	
5 dike bank	1968	33	316	sparse grass	drifting sand
6 shell bank	1969	32	588	sparse grass	site 1 in 1968
7 sandy island	1969	35*	351	sparse grass	site 2 in 1968
8 sandy island	1968	14	58	none	drifting sand
9 grassy island	1968	34*	2021*	dense grass	4-year-old island
10 grassland	1968	36	3479	sparse grass	
11 grassland	1969	33	838*	grass and mosses	
12 grassland	1968	32	535	grass	
13 dike bank	1968	24	337*	deciduous shrubs	5-year-old thicket
14 reed land	1968	25	1677	dense reed and mosses	10-year-old thicket
15 wood	1964	40*	1329*	poplar, alder	6-year-old
16 wood	1968	39	572*	poplar, alder	site 15 in 1964
17 wood	1968	28*	732*	oak, ash, alder, spruce	14-year-old
18 wood	1968	27	412	poplar	

* Deviates from the column total given by Haeck (1971: table 1) but corresponds to the data in Haeck's table 1, and is the correct information (Jaap Haeck; personal communication).
** Sites 1–9 were classified as riparian, sites 10–12 as arable and sites 13–18 as woodland by Haeck (1971).

(Lindroth 1949, den Boer 1971, 1977, Haeck 1971). Thus, one can easily compare the fit of other characters, and not only the number of species in the rarefied sample, with the actual observations. Recently Drs Jaap Haeck and Rob Hengeveld have devoted themselves to uncover in greater detail the characters labelling the carabis colonizing the polder areas in The Netherlands (peronal communication).

2. Material and methods

2.1. Habitat islands

During the past 50 years the Dutch have been carrying on a large-scale programme to drain a former North Sea area (Zuidersee) for acricultural purposes. The potential of the reclaimed areas, called 'polders' (area 200–540 km²), for studies of habitat colonization by plants and animals was soon recognized (e.g., Feekes 1936, Feekes & Bakker 1954, Dammerman 1949, Mook 1971, Haeck 1971, Haeck et al. 1980, Nip-Van der Vort et al. 1979). When the water is drained, large island-like areas of clay become dry in areas which were previously covered by shallow water. Some of the deepest areas may remain wet for years. Thus, within a polder there is a gradient of habitat patches of different ages. The history of the polder systems provided the background for the studies by Haeck (1971), who started to follow the immigration of carabids into the habitat patches in the reclaimed Zuidelijk Flevoland polder (drained in 1968). On this polder he selected 9 study sites which varied in terms of their environmental characters and age. He further selected 9 study sites from the surroundings of the Zuidelijk polder (mainly from the Oostelijk Flevoland polder, constructed in 1957), which represented somewhat older habitat islands (Haeck 1971: table 1, fig. 5 and pp. 36–39). Haeck's 18 study sites form a gradient of habitat islands differing in age, and therefore in habitat characters (Table 1). Carabids were sampled from these stations during the whole season by a set of 5 pitfall traps on each. The traps were checked at intervals of 2 to 4 weeks, and all carabid specimens were identified and

counted. Haeck (1971: table 1) gives a comprehensive list of the carabid beetles from the 18 study sites. This material is used here for an analysis of the colonization of habitat islands by carabids. The number of species varied from 9 to 40 at each study site and totalled 93 species. The annual catch of specimens varied between 27 and 3 479. The study sites are briefly characterized in Table 1.

2.2. 'Species pool'

Den Boer (1970, 1971, 1977) sampled carabids intensively by pitfall-trapping in the area of Drenthe, The Netherlands, not far from the Zuidelijk Flevoland polder in 1959–67 (see den Boer 1971). The sampling methods were the same as those used by Haeck (1971). His study sites, ranging from sand dunes to old oak woods, form a gradient representative of habitat types present in the area (see the appendix in den Boer 1977). As the sites were selected in order to represent different habitats in the proportion to their occurrence in the area (den Boer 1977), these data serve ideally as a species pool from which the carabids may disperse and colonize the new polder. These data were also used by Haeck (1971) when he compared the patterns of carabid communities caught at the 18 habitat islands. A list of the 149 carabid species trapped and their trapping frequencies was provided by den Boer (1977: appendix) together with the wing morph of the species (i.e., macropterous, dimorphic, brachypterous).

2.3. Methods

Our method follows the assumption that each species has a probability of immigration and also of colononization of a habitat island proportional to its frequency in the species pool. Thus, in order to examine whether or not the communities of carabid beetles on habitat islands are random samples of the species pool, we have to identify the frequencies of the species in the assumed species pool. As indicated above, den Boer's (1977) data on the distribution and frequency of 149 carabid species in the Dutch mainland fulfil this criterion. Using the standard rarefaction procedures (Simberloff 1978b) one can estimate how many species (S_r) a rarefied sample of I_r individuals would contain from a larger sample of I individuals and S species However, as Simberloff (1978b)

points out, this type of rarefaction gives only the number of species (with a variance) as a function of the number of individuals. But since we are also interested in certain other properties of the rarefied sample, we wrote a computer program to calculate the community diversity (exp H', where H' is the Shannon function), the size distribution of carabid beetles, and the frequency of wing morphs (individuals from macropterous, brachypterous and dimorphic species) in the rarefied samples. In fact, the method is similar to that used by Simberloff (1970), which, in turn, was a computerized extension of the method of Williams (1964).

The rarefaction runs were computed so that individuals were selected randomly from the species pool in which all species were represented in proportion to their known frequencies. We rarefied three types of artificial communities, each having a different species pool: A) all species had an equal probability, independently of their wing morph, of invading the habitat islands; B) only species which are potentially able of flying (Lindroth 1949, den Boer 1971, 1977, 1979, Haeck 1971, but see den Boer et al. 1980), viz., macropterous and dimorphic ones, were included; C) only macropterous species were included. The last procedure underestimates the numbers of potential colonists, but it was considered necessary because it is impossible afterwards to distinguish which proportion of the individuals in dimorphic species are able to fly. In each run the rarefaction was computed 100 times, the means and standard deviations being given for each of the habitat islands (used in statistical comparisons).

3. Results

As the first step of our analysis we ordinated the 18 sampling sites on the basis of the structure (species composition and species abundance) of the carabid communities. We used principal component analysis, the three first components explaining 75 % of the variation. Haeck (1971) classified sites 1–9 as riparian (i.e., unstable), 10–12 as arable (somewhat older, with permanent vegetation) and 13–18 as "more or less woodland" (sites within wooded areas). In our ordination, sites 13–18 scored low values on the 1st and 3rd components, but high values on the 2nd component (except site 18). High values for sites 7,9 and 11 were found on the 3rd component, while the rest of the sites were scattered on the 1st component. Thus, only the woodland sites clustered into one clearly sparated group (Fig. 1).

Whether or not we included brachypterous carabids to the species pool, the hypothesis of proportional colonization probabilities of different species on the habitat islands failed to explain the observed numbers of species. In all cases the observed numbers of species were significantly lower than expected on the basis of random sampling from the species pool (Fig. 2). Rarefaction C (species pool = macropterous species only) resulted in a better fit between observed and expected numbers of species: observed values were lower than expected in 16 cases (Fig. 2), but only 8 of the differences (sites 2, 3, 9, 10, 13, 14, 17, 18) were statistically significant (at least at the 5 % level; t-tests). Although sites 5
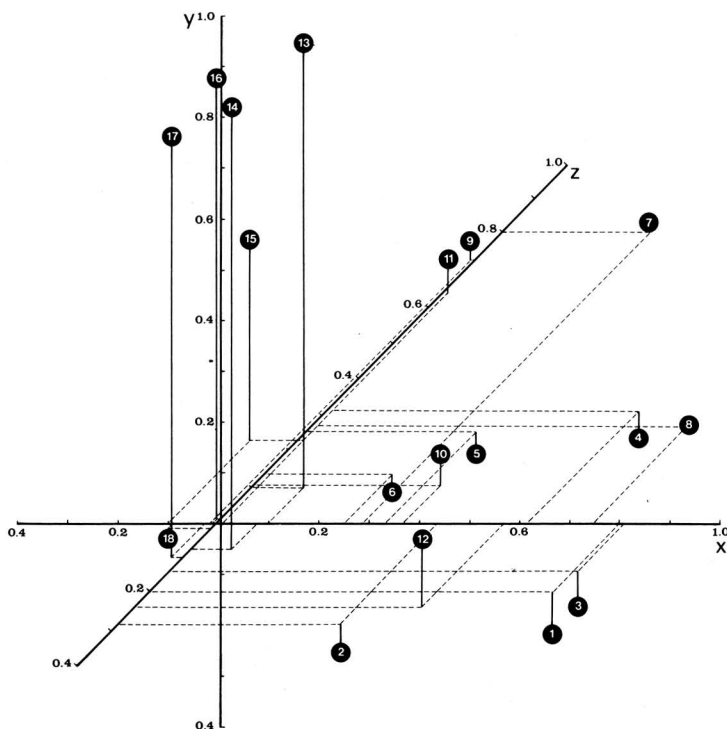

Fig. 1. Ordination of the habitat islands by principal component analysis. The results are given in a three-dimensional form (x = PC I, y = PC II, z = PC III). The woodland sites (13–18) cluster around PC II, the rest are more or less scattered.
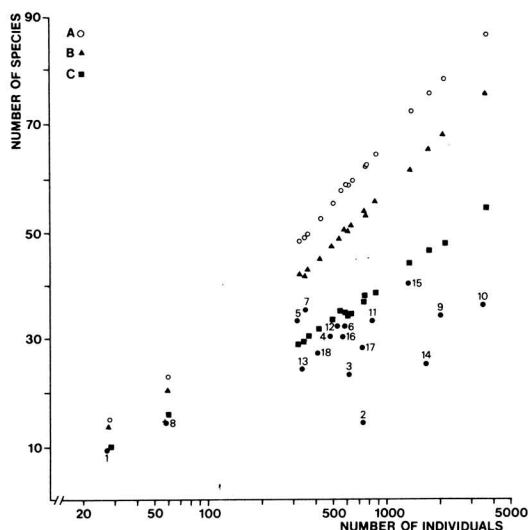
Fig. 2. Number of carabid species plotted against the long-number of individuals in the 18 habitat islands. Results of different rarefaction runs are given (A = species pool includes macropterous, dimorphic and brachypterous species, B = species pool includes macropterous and dimorphic carabids, C = species pool includes macropterous carabids only). The observed numbers are given with dots (1–18).

The rarefaction models (A and B) show a stable increase in the log number of individuals of dimorphic species as a function of the log number of individuals of macropterous species (Fig. 4; only the results of run B are given here). However, again the pattern observed deviates from that expected, for the woodland habitats have more and the other habitats less individuals of dimorphic species than expected (Fig. 4.)

The expected size distributions of carabid beetles are given for runs A and B only; again the observed patterns deviate from the expected ones (Fig. 5). Except at sites 9, 10 and 18, all distributions are skewed towards smaller size.

4. Discussion

All the characters analysed in the island communities of carabid beetles deviated clearly from the patterns expected on the basis of random sampling of carabids from the "species pool". The first two parameters analysed (number of species, community diversity) suggest that there are several species that are unable to invade the newly emerged habitat islands. The relatively low community diversities, in comparison to the expected ones, further suggest that the species abundance relations in the habitat islands do not
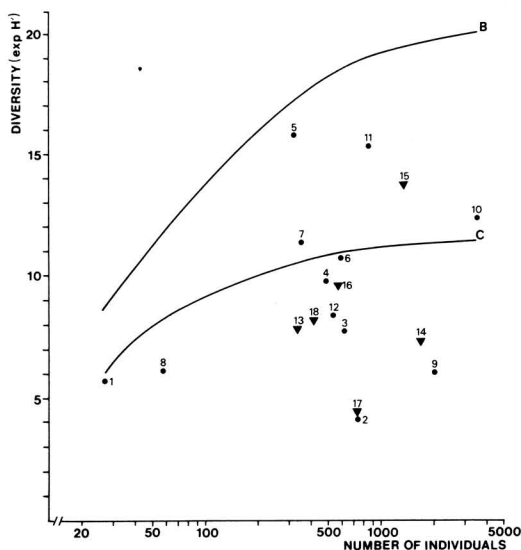
and 7 had higher observed species numbers than those expected, the differences were insignificant. Note, however, that rarefaction C is based on an unrealistically small species pool, as all sites also have dimorphic carabids, and some of the sites (15, 16 and 18) have even a very small number of brachypterous species (Haeck 1971: table 1). Thus, the assumption that only monomorphic macropterous species are able to colonize the habitat islands must be considered unrealistic. Furthermore, the rarefaction models suggest a monotonic increase in species number as a function of the logarithm of the number of individuals (Fig. 2). However, only half of the variation in the number of species observed on the habitat islands was explained by the variation in the logarithm of the number of individuals ($r^2 = 0.47$; d.f. 16; $p < 0.01$).

The rarefactions (only cases B and C considered here) suggest the diversity of the communities (given as exp H', where H' is the Shannon function) to be a simple function of the logarithmic number of individuals. However, the observed figures clearly deviate from this pattern (Fig. 3), as no significant correlation was found between the log number of individuals and species diversity ($r^2 = 0.07$; d.f. 16). It is worth mentioning that the woodland habitats do not show higher diversities than the less stable habitats (Fig. 3).

Fig. 3. Diversity (exp H', where H' is the Shannon function) as a function of the log number of individuals in the 18 habitat islands (the woodland sites are indicated with triangles). The continuous lines show the results of the rarefaction runs (B = species pool includes macropterous and dimorphic carabids, C = species pool includes macropterous carabids only).
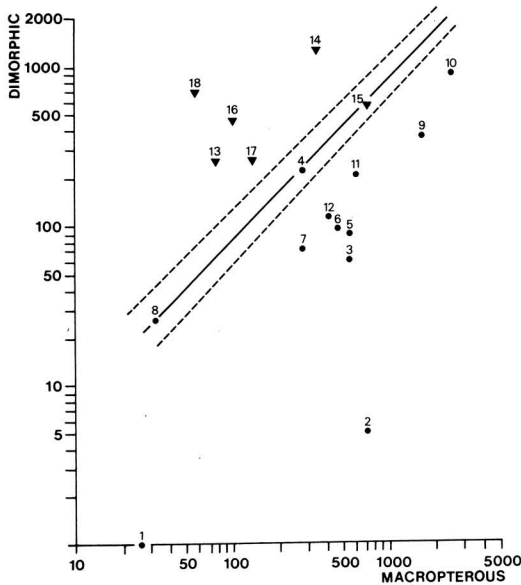
Fig. 4. The relationship between the number of macropterous and dimorphic individuals in the 18 habitat islands. The woodland sites are indicated with triangles. The line shows the expexted values (± standard deviation) based on the rarefaction B (species pool = macropterous and dimorphic carabids).

pool than others, though this is probably a result of some biological properties of the species. In all of the habitat islands examined here, the number of species observed was far from the expected value, as were the other characters of the carabid communties analysed. This allows the rejection of stochastic sampling processes as a sufficiently suitable mechanism for structuring the composition of the fauna of the habitat islands.

In the discussion of island biogeography theory much criticism has been raised about drawing conclusions without testing any null hypotheses. We agree that the proper way to test a hypothesized factor is to create an *a priori* null hypothesis and to try to falsify it. However, the proposed null hypothesis should not only be correspond to those in the hypothetical rarefied communities.
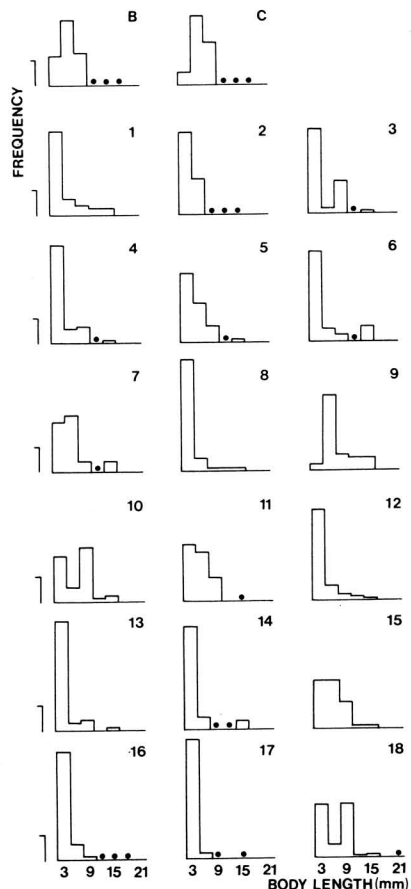
As shown by the frequency distributions of carabid sizes in the habitat islands, the beetles most successful in establishing populations are small (body length 3-6 mm). This pattern is in accordance with the predictions of the r-K theory derived from the MacArthur--Wilson model (Pianka 1970). Although the community diversity of the woodland sites did not fit the pattern "stable habitats — higher diversity", the proportion of dimorphic species is higher in the woodland sites than in the riparian and arable habitat islands. Furthermore, the habitat islands with brachypterous carabids (15, 16, 18) are all woodland sites. This observation agrees with Järvinen & Vepsäläinen (1976), Southwood (1977), Solbreck (1978) and Vepsäläinen (1978), who, among others, have suggested that stable habitats favour allocation to efficiency in resource utilization rather than migration.

The hypothesis that island species composition is merely a result of a stochastic sampling process implies no deterministic component, the only limitation being that an abundant species in the species pool has a greater chance to be included in the island fauna. We ignore the question of why some species are more numerous in the species

Fig. 5. Observed size frequencies of carabids at the 18 habitat islands (solid circles = frequency of the size class less than 3 %). The expected frequency distributions are shown at the top of the figure (B = species pool includes macropterous and dimorphic carabids, C = species pool includes macropterous carabids only). The frequency scale is 20 %.

simple, but should also be plausible and testable (Grant & Abbott 1980). We agree with Simberloff (1978a) that if stochastic processes suffice to simulate the species patterns observed on islands and insular habitats, then no biologically-based explanations should be invoked. However, care should be taken when formulating the stochastic hypotheses so that they do not have any determinsistic components (cf., Simberloff's 1978a: model II). Furthermore, when arguing in favour of stochastic null hypotheses (Connor & Simberloff 1978), the interpretation of results should be made with proper statistical analyses (Hendrickson 1981, Alatalo 1982).

As our analyses have shown, some characters (e.g., body size) of the carabid beetles are good indicators of their ability to colonize newly emerged habitat islands. Haeck (1971), Haeck et al. (1980), den Boer (1977, 1979), Hengeveld & Hogeweg (1979), and Jaap Heck and Rob Hengeveld (pers. comm.) in particular, have analysed the characteristics of carabids in polder areas in detail, and therefore we do not repeat the analysis here. Instead we briefly summarize their results. Haeck (1971, see especially Haeck et al. 1980) and den Boer (1971, 1977) analysed the distribution of carabid beetles on a local scale, whereas the approach by Hengeveld & Hogeved (1979) was more global. However, the conclusions of both approaches are the same [Jaap Haeck and Rob Hengeveld (pers. comm.)]: the colonization of the habitat islands is an outcome of the ease of

migration. The colonization into a new polder area is mainly affected by habitat factors, viz., species colonizing the habitat islands originate from unstable habitats, and thus a high potential for dispersion is a necessity of life in habitats of these types. In fact, these conclusions can also be drawn from the data on distribution of carabid beetles on true islands in the Baltic (see Lindroth 1949:198 ff.).

Although we can conclude that the sampling hypothesis by Connor & McCoy (1979) did not explain the colonization of the habitat islands by carabid beetles we were unable to identify the fit of Williams's (1964) habitat diversity hypothesis, or that of the equilibrium hypothesis (MacArthur & Wilson 1967). For testing these hypotheses, more details of the habitat islands and carabid beetles are needed. However, it is evident that biological characters of the species have to be included in any models attempting to explain the species composition of carabid communities on the habtitat islands in the Dutch polders.

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