Island biogeography of temporary wetland carabid beetle communities

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Abstract

Aim The study tests if island biogeography is applicable to invertebrate communities of habitat islands in the agricultural landscape that are not fragments of formerly larger habitats.

Location Thirty temporary wetlands in the agricultural landscape of northeast Germany.

Methods The composition and species richness of carabid beetle communities was analysed. Habitat area, isolation, the density of temporary wetlands in the landscape, land-use intensity and the maximum duration of flooding were recorded as independent variables. Overall species richness and wetland species richness were studied in independent regression analyses. The community composition was analysed by means of a Canonical Correspondence Analysis (CCA). A partial CCA was used to analyse the effect of the distance to the edge of the field after removing impacts of other independent variables.

Results The area of the habitats and various measures of isolation (mean distances = 81–240 m) did not influence species richness or wetland species richness. The community composition was mainly determined by the land-use intensity, habitat area did not have significant effects, and the distance to the edge of the field was the only effective isolation parameter. Short-winged species were more often affected by the distance to the edge of the field than full-winged species.

Main conclusion There is evidence that the distances between the wetlands do not provide an effective barrier to the species dispersal and, therefore, metapopulation structures including subpopulations of multiple temporary wetlands might counteract local area effects on subpopulations. Short-winged species, however, might be more affected by isolation than full-winged species. As carabid beetle community structure in most early successional habitats is similar, these results may be representative of many agricultural landscape habitats. Nature conservancy concepts that aim to increase habitat area and habitat connectivity have successfully been applied to fragmented late-successional habitats. The present study indicates that such concepts do not necessarily result in higher diversity or larger populations in early successional habitats.

Keywords

Diversity, species richness, habitat connectivity, habitat fragments, isolation, species–area relationship, wetlands, agricultural landscape, ephemeral pools.

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INTRODUCTION

The theory of island biogeography predicts that species richness increases with island size and decreases with isolation (Preston, 1962; MacArthur & Wilson, 1963). Type 2 species–area relationships, which correlate total species richness and total area of island habitats (Rosenzweig, 1995), were originally used to explain variation in diversity on oceanic islands (MacArthur & Wilson, 1963, 1967; Simberloff, 1976), but they have subsequently been applied to habitat islands on the mainland (reviews in Connor and McCoy, 1979; Rosenzweig, 1995; Holt et al., 1999). This has led to a general acceptance of its relevance to applications in nature conservancy – generating a focus on increasing habitat area and decreasing isolation by habitat connectivity systems (Diamond, 1975; Simberloff & Abele, 1976, 1982; Spellerberg, 1991; Hovestadt et al., 1994; Jedicke, 1994; Pimm et al., 1995).

However, ecologists must face the question of whether this general simplification is acceptable, because its empirical base may be biased. Most studies have been carried out in vertebrate or plant communities, but little is known about the effect of island biogeographical parameters on invertebrates, which account for most overall diversity. Furthermore, most habitat islands studied can be characterized as fragments of formerly larger habitats (e.g. woodlands; Mader, 1981; Baz & Garcia-Boyero, 1995; Turner, 1996; Didham et al., 1998). This is in contrast to the situation of many habitat islands in the agricultural landscape like potholes (pools in glacier-shaped depressions) and temporary wetlands (ephemeral pools in ploughed field hollows), which are not fragments of formerly larger wetlands. There is very limited knowledge about the response of their communities to island biogeographical parameters.

Although most island biogeographical studies focus on diversity, empirical evidence suggests that different species respond differently to the same level of habitat isolation (e.g. Didham et al., 1998). There are, however, few studies on the responses of individual invertebrate species to isolation by agricultural fields. Accordingly, there is no consensus on which species are most susceptible to isolation. In vertebrate studies, it has been observed that large-bodied, poorly dispersing species, particularly in higher trophic levels, are mainly affected by isolation (review in Turner, 1996). As they are less capable of dispersing across large distances in a hostile landscape matrix, their local populations are more isolated and prone to extinction than populations of well-dispersing species. Although such generalities cannot yet be made for invertebrates, it has been shown that the survival of local carabid beetle populations in habitat patches depends on the species dispersal abilities (Den Boer, 1981, 1990).

This study investigates whether the concept of island biogeography applies to the carabid beetle communities of temporary wetlands. The following hypotheses were tested: (1) total species richness and wetland species richness increase with increasing habitat area and decreasing isolation, (2) the carabid community composition is influenced by habitat area and isolation, and (3) large-bodied and short-winged (poorly dispersing) species are more affected by isolation than the other species.

MATERIALS AND METHODS

Study sites

The study was carried out in the agricultural landscape of northeast Germany (between 53°22′N, 13°34′E and 52°22′N, 14°15′E) in the years 1998–2000. The study area is characterized by large-size fields, few hedges and woodlands, and a high density of potholes and temporary wetlands. Potholes are pools in depressions left behind by glaciers of the last ice age. Temporary wetlands (sometimes called vernal pools) are ephemeral pools or puddles that are typically located either in field-hollows or at the border of potholes. In contrast to potholes, temporary wetlands are cultivated and typically produce crops in dry years. During years of average or above-average precipitation, they usually occur every year at the same locations in the fields and retain surface water until spring or summer. In these years, the plant communities are dominated by annual therophytic species ranging between tall forbs (e.g. Matricaria maritima ssp. inodora, Bidens tripartita) or grasses (Elytrigia repens) and dwarf-rush species (Peplis portula, Juncus tenagaeia). The temporary wetlands are inhabited by highly diverse communities of Carabidae consisting of a mixture of typical field species (e.g. Carabus auratus, Pterostichus melanarius) with numerous wetland species (e.g. Agonum marginatum, Bembidion varium). In contrast to the wetland species, most field species have also been caught in the surrounding fields, although many of them had substantially lower abundances. Therefore, the temporary wetlands are isolated habitats for the wetland species and areas with higher density of the field species.

Historically, temporary wetlands were continually distributed across northern Germany (Klafs et al., 1973). As a consequence of their utility for agriculture, they were often drained and consequently disappeared from many predominantly western German landscapes. Different land-use systems in eastern Germany meant that the drainage of wetlands occurred on some highly productive agricultural areas, while in other regions, e.g. the study sites, the present abundance of temporary wetlands still accurately reflects the historical distribution.

Five study areas were chosen within northeast Germany and represent gradients of land-use intensity and density of temporary wetlands. The mapping of temporary wetlands was carried out by means of aerial photographs and field visits, and thirty study sites were randomly selected.

Sampling of carabid beetles

Five pitfalls were placed on each study site in a stratified random design in which the habitats were stratified with respect to the duration of flooding. One or two traps were placed in each stratum depending on the total number of

strata. They had a minimum distance of 5 m from each other to avoid mutual influence. The traps (white cups: diameter = 9.2 cm, 55% isopropanol with glycerine and detergent added) had transparent plastic lids as shelters to avoid damage by animals or precipitation. Samples were taken between mid-April and mid-July in each year. Each of the study sites was sampled for one trapping season. An extension of the trapping season in autumn was not included in the study because after the sites were harvested and ploughed, they lost their habitat island characteristics. The beetles caught in the pitfalls were collected every 14 days and identified to the species level.

Species classification

The nomenclature of carabid beetle species follows Scheffler *et al.* (1999). For species richness analyses, all carabid species caught were classified as either wetland species or non-wetland species, i.e. field species, according to their habitat preferences in the study region (Scheffler *et al.*, 1999). For community composition analyses, the thirty most abundant beetle species were used. The less abundant species were not classified, because their low abundances and low frequencies of occurrence on the study sites did not allow their inclusion in the subsequent statistical analyses. The thirty species studied were grouped with respect to their body size (large ≥ 6 mm; small < 6mm) and the development of their wings (full-winged or short-winged). First the species were classified as either macropterous, brachypterous or wing-dimorphic (Lindroth, 1949). Then, macropterous and brachypterous species were assigned to the groups of full-winged and short-winged species, respectively. For wing-dimorphic species, the wings of individuals in random subsamples were measured, and the species were subsequently grouped according to the dominant form of their wings. However, the wing development of these species may change considerably between genera-

tions. Accordingly, their classification as full-winged or short-winged species represents only the actual situation at the time the study was carried out.

Species richness

The samples were pooled to arrive at the observed species richness for each site, including wetland and non-wetland species. As the species accumulation curves indicated that this sampling strategy underestimated the true number of species, particularly in more diverse habitats, second order jackknife (Jack2) estimates were used to obtain more accurate results. This nonparametric estimator is based on the observed species richness (S_{obs}), the number of samples (m) and the numbers of species occurring in only one sample (Q_1) or in exactly two samples (Q_2) at the study site (Burnham & Overton, 1979). Extrapolated species richness (S_{ext}) is estimated as:

$$S_{ext} = S_{obs} \left(\frac{2m - 3}{m} \right) Q_1 - \left(\frac{(m - 2)^2}{m(m - 1)} \right) Q_2.$$

It has been shown that these estimates accurately match the results of pitfall trapping studies with higher sampling intensity (Brose, 2002). Although community evenness varied only moderately (range: 0.494–0.659), second order jacknife estimates that are most robust concerning differences in community evenness were chosen (Brose *et al.*, in press). The wetland species were similarly extrapolated, which led to measures of observed wetland species richness and extrapolated wetland species richness (Table 1).

Measurement of environmental variables

The area of each site was measured in mid-March. The water edge at this time was used as the habitat boundary. The other island biogeographical parameters were determined

Table 1 Description, mean + SD and range of the variables. The values are based on thirty study sites and a total catch of 71,238 carabid beetles (136 species – including sixty-five wetland species)

Variable	Description	Mean ± SD	Range
Dependent variables			
S_{obs}	Observed species richness	43 ± 7	28–58
S_{ext}	Extrapolated species richness (Jack2 estimates)	56 ± 11	39–85
WS_{obs}	Observed wetland species richness	23 ± 7	10–38
WS_{ext}	Extrapolated wetland species richness (Jack2 estimates)	28 ± 10	10–48
Independent variables			
area (m²)	Habitat area	926 ± 568	50–2400
Distfield (m)	Distance to the edge of the field	83 ± 88	3–290
Distpot (m)	Distance to the next pothole	81 ± 135	5–600
Disttemp (m)	Distance to the next temporary wetland	240 ± 447	15–2000
Density 1	Density of temporary wetlands within 1 km²	4.5 ± 3	0–9
Density 1.5	Density of temporary wetlands within 1.5 km²	5.9 ± 4.2	0–18
Density 2	Density of temporary wetlands within 2 km²	6.9 ± 4.9	0–23
Density 5	Density of temporary wetlands within 5 km²	10.5 ± 6.9	0–25
Flooding	Maximum duration of flooding	2.9 ± 0.9	1–4
Intensity	Land-use intensity of the fields	43.6 ± 6.6	27.6–54.2

from digitalized 1 : 10,000 maps in ArcView GIS 3.0 (Table 1). Three distance measures were included: the distances to the edge of the field, to the next temporary wetland and to the next pothole (Table 1). As the density of habitats is important for metapopulation structures (Ouborg, 1993), four density measures of the temporary wetlands were included in the study (Table 1).

Two further variables were used to characterize habitat characteristics: the maximum duration of flooding and the land-use intensity. Both independent variables have a strong influence on temporary wetland plant communities (Brose, 2001). The minimum hydroperiod of the temporary wetlands was defined as mid-March. For each study site, the maximum duration of flooding was recorded as the number of months since the minimum hydroperiod, and it ranged between 1 (drying up by mid-April) and 4 months (drying up by mid-July). The land-use intensity for the fields was indicated by soil indices (ranging between zero for unproductive and 100 for productive soils), which provide information about the productivity of the soils and indicate the potential yield (Lieberoth, 1982). The soil indices are compound variables that combine measurements like, for example, the soil type and the texture. They are relative measures of land-use intensity that integrate various aspects of cultivation, such as crop type, potential yield, and consequent application of fertilizers and pesticides.

Data analyses

All variables were checked for normality and linearity by Kolmogorov–Smirnov tests. The variables disttemp, and distpot required natural logarithmic transformation to meet these assumptions (Table 1). The impacts of the independent variables on the dependent variables were tested in consecutive univariate regression analyses (Table 1). To test the dependence of species richness on habitat area, linear regression analyses were carried out in a double-log transformed data set and in a non-transformed data set. The influence of the distance and density variables on the dependent variables was tested in simple linear regression analyses.

The variation in the species composition between the study sites was analysed with Canonical Correspondence Analysis (CCA) and Detrended Correspondence Analysis (DCA) using the CANOCO program (version 4.0) (Ter Braak & Šmilauer, 1998). A reduced data set of the thirty most abundant species was used to exclude bias by rare species (Jongman et al., 1995). Prior to further analyses, the activity densities of the species were standardized to fifty sampling weeks, and all environmental variables were standardized to zero mean and unit variance. The CCA was carried out with a forward selection procedure that ranks the environmental variables according to their conditional eigenvalues. The significance at each step was tested with Monte Carlo permutation tests with 999 random permutations. Only variables with significant effects were included in a subsequent CCA with Hill's scaling.

A partial CCA was used to focus on an isolation variable of special interest, while the other variables were entered as co-variables. The species points in the ordination were subsequently projected onto the environmental arrow. The order of the projection points indicates an approximate ranking of the species centres of distributions along the gradient (Jongman et al., 1995). Extreme positions of species concerning this order were analysed with respect to differences from the remaining species in body size or wing development.

RESULTS

The carabid beetle fauna

In this study, a total of 71,238 carabid beetles comprising a total of 136 species – including sixty-five wetland species – were sampled. The carabid communities were dominated by typical field species (Appendix 1). The eight most abundant species were assessed with 51,294 individuals, 72% of the catch total. Fourteen of the thirty most abundant carabid species were characterized as wetland species (Appendix 1). Six of the thirty most abundant species were classified as wing-dimorphic. After a count of the relative proportions of large and short hind wings in random subgroups, they were classed as either full-winged or short-winged (Appendix 1). With respect to the thirty most abundant species, the community was dominated by full-winged (twenty-six species) and large species (twenty-one species) (Appendix 1).

Species richness and response to area and isolation

There was a gradient of observed species richness ranging from sites with twenty-eight species, resembling those of conventional parts of the fields, to highly diverse sites with fifty-eight species (Table 1). However, the species accumulation curves were not saturated. The extrapolated species richness had a minimum of thirty-one and a maximum of eighty-five species, and in this case, the accumulation curves indicated beginning saturation. The results for wetland species were similar (Table 1).

The island biogeographical parameters are listed in Table 1. The area of most study sites was below 1000 m². Habitat area did not have a significant influence on the dependent variables – neither in the double-log transformed nor in the non-transformed data set (linear regression analyses, $P > 0.05$, $n = 30$). Most of the isolation distances were <100 m (Table 1). In regression analyses, there were no significant impacts of the isolation distances and the density measures on the dependent variables (linear regression analyses, $P > 0.05$, $n = 30$). Accordingly, there was no increase in species richness or wetland species richness with increasing habitat area or decreasing isolation.

Relationship of species composition to environmental gradients

In the subsequent analyses, two of the thirty temporary wetlands studied were excluded. One study site led to extreme influences of the variable distances to the next

Table 2 CCA: forward selection summary, weighted correlation matrix of the independent variables with the first two axes and inflation factors of the variables. Correlations and inflation factors are only shown for significant variables. λ_a, increase in eigenvalue (additional fit); P, significance level of the conditional effects (Monte Carlo permutation tests with 999 random permutations). Variable abbreviations according to Table 1

No.	Variable	λ_a	P value	Axes 1	Axes 2	Inflation factor
1	Intensity	0.11	0.010	−0.4205	0.1154	1.026
2	Distfield	0.11	0.010	0.5302	−0.0542	1.091
3	Density 5	0.09	0.035	−0.2504	0.4922	1.307
4	Distpot	0.09	0.020	−0.3459	−0.2310	1.316
5	Flooding	0.09	0.025	−0.3044	−0.1736	1.059
6	Density 1	0.06	0.070			
7	Distwet	0.05	0.130			
8	Density 2	0.05	0.165			
9	Density 1.5	0.05	0.165			
10	Area	0.04	0.170			

pothole (forty-six times) and temporary wetland (seventy-eight times) indicating an extraordinary isolation in comparison with the other study sites. The other study site showed extremely low species abundance values, although the number of species was not markedly lower. In a CCA analysis with forward selection, the independent variables intensity (land-use intensity), distfield (distance to the edge of the field), density 5 (density of temporary wetlands within 5 km²), distpot (distance to the next pothole) and flooding (maximum duration of flooding) explained significant variation in beetle species composition (Table 2). The other

independent variables did not have significant conditional effects and were not included in further analyses.

In a subsequent CCA, the sum of all canonical eigenvalues was low (0.486), but the eigenvalues of the first four axes (0.233, 0.117, 0.083, 0.031) were similar to the eigenvalues for the respective DCA axes (0.296, 0.146, 0.049, 0.03). This indicates that the environmental variables chosen explain a substantial part of the overall variation in species composition. In DCA, the lengths of the first two ordination axes were above 2 SD (2.481, 2.159) and, accordingly, most of the response curves are considered to be unimodal (Jongman *et al.*, 1995). The inflation factors of the five environmental variables were below 2 indicating that the remaining internal correlations in the data set were low (Table 2). The first two axes accounted for 27% of the variance in the species data as measured by weighted averages with respect to the five environmental variables. As indicated by their low eigenvalues, the third and the fourth axes were of minor importance, only adding 8% to the explained variance in the species data.

Responses of individual species to the gradients

In the biplot of species points and environmental arrows (Fig. 1), the species points are placed as weighted averages with respect to the each of the environmental variables. The arrows show the orientation of the environmental variables in the biplot. Concerning their response to the environmental variables, the species may be classified into three groups. The first group consists of hygrophilous riparian species (*Anisodactylus binotatus*, *Acupalpus parvulus*, *Elaphrus riparius*, *Bembidion varium*, *B. articulatum*) that are placed in the
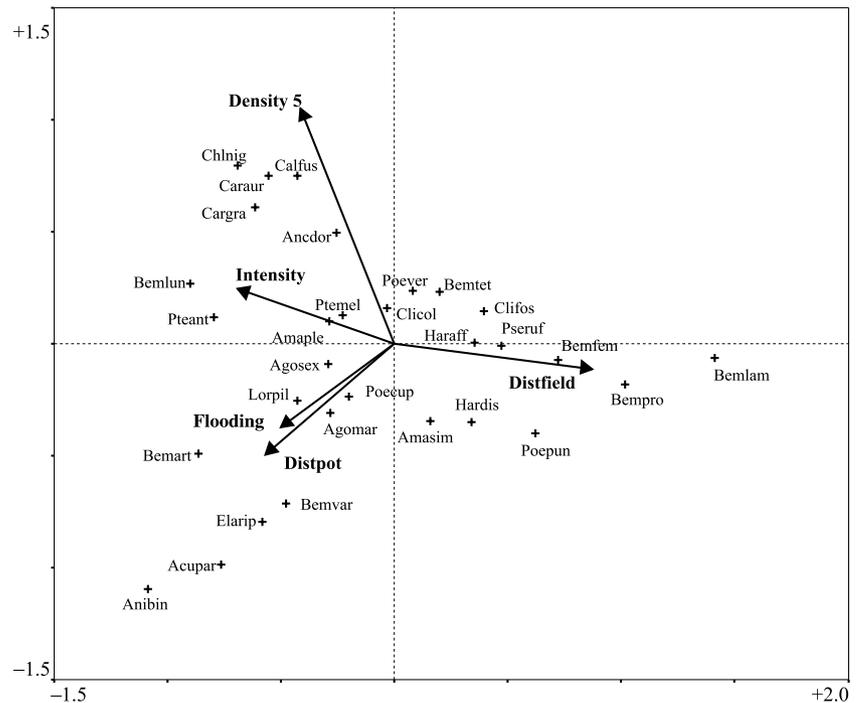

Figure 1 CCA ordination diagram with the thirty most abundant carabid species (see Appendix 1 for species names) and the environmental variables (variable abbreviations according to Table 1).
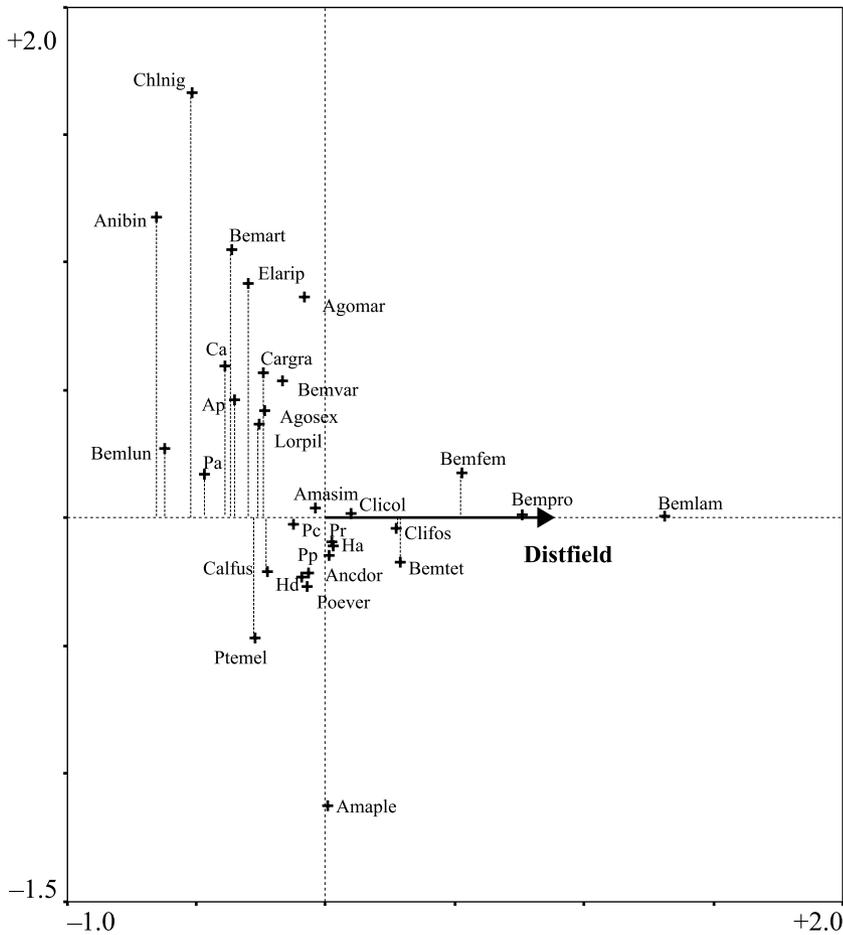
Figure 2 Partial CCA ordination diagram with the thirty most abundant carabid species (see Appendix 1 for species names), the environmental variable distance to the edge of the field (distfield), and the co-variables density of temporary wetlands within 5 km², distance to the next pothole, maximum duration of flooding, and land-use intensity. The projections of the species points on the first axes indicate their approximate ranking along the gradient of distance to the edge of the field. The projections are shown for the species with extreme positions on the gradient.

lower left of the biplot, which is positively correlated with the duration of flooding and the distance to the next pothole. The second group of typical field species (*B. lampros, B. properans, B. femoratum, Poecilus punctulatus*) was ordinated to the right of the origin, and correlated with high distances of the temporary wetlands to the edge of the field and low land-use intensities. The third group consists of a mixture of wetland species (*B. lunulatum, Pterostichus anthracinus, Carabus granulatus, Chlaenius nigricornis*) and field species (*Carabus auratus, Calathus fuscipes*). These species were placed in the left and the upper left of the biplot that is correlated with high land-use intensities, low distances of the temporary wetlands to the edge of the field, and high densities of temporary wetlands within 5 km². No species were ordinated to the upper right of the origin, which indicates low distances to the next pothole. Although the riparian species were ordinated to areas of high distances to the next pothole (see above), the distance to the next pothole was not entered in further analyses, because there was no indication of a negative isolation effect mediated by high distances to the next pothole.

The interpretation of the biplot (Fig. 1) was complicated by the fact that the responses to the distance to the edge of the field (distfield) coincided inversely with a gradient of responses to land-use intensity (intensity). To get information about the species responses to isolation, a partial CCA was carried out with the distance to the edge of the field as the only environmental variable, and the other four independent variables as co-variables (Fig. 2). The species distributions were ordered along the first axis in response to the distance to the edge of the field. Five species were placed at the very right edge of the biplot, which was correlated with high distances of the wetlands to the edge of the fields (mainly consistent with the above mentioned second group of typical field species). Thirteen species were characterized as isolation-influenced species (at the very left of the biplot indicating negative responses to the distance to the edge of the field; Fig. 2). Only three of these thirteen species were small. Although this might indicate an increased proportion of large species in this group of isolation-influenced species, there was no significant difference when compared with the group of the remaining, non-isolation-influenced species (eleven large and six small species) ($\chi^2 = 5.24$, d.f. = 1, $P = 0.69$, Fisher's exact test). Furthermore, four of the thirteen isolation-influenced species were short-winged, whereas all the remaining seventeen non-isolation-influenced species were full-winged. This difference between the two species groups was significant ($\chi^2 = 6.04$, d.f. = 1, $P = 0.026$, Fisher's exact test).

DISCUSSION

Species richness and habitat area

In contrast to the initial hypothesis, there was no increase in species richness or wetland species richness with increasing habitat area. One might expect that a higher sampling intensity could have resulted in significant species–area relationships. In fact, as indicated by the species–accumulation curves, the observed species richness seriously underestimated the true species richness in the more diverse communities. The Jack2 estimates, however, predict accurately and precisely the results of studies with higher sampling intensity (Brose, 2002; Brose *et al.*, in press). As there were no significant correlations between habitat area and the extrapolated-dependent variables, it is unlikely that a higher sampling intensity would have resulted in significant species–area relationships. The lack of species–area relationships was surprising, because plant species richness of the temporary wetlands was significantly correlated with habitat area (Brose, 2001). Accordingly, the present results do not support the hypothesis that the strength of species–area relationships increases with trophic rank (Holt *et al.*, 1999). Furthermore, the present results are in contrast to studies carried out in woodland and heathland fragments (e.g. Mader, 1981; Den Boer, 1990; De Vries *et al.*, 1996). Potential explanations include the following: (1) fragmented habitats are not only influenced by insularization but also by habitat loss, (2) these dynamics lead to supersaturated biotas in habitat fragments – reflecting former conditions in larger habitat areas – with extinction dynamics that are strongly correlated with area (Wilcox & Murphy, 1985). In contrast to fragmented habitats, temporary wetlands – like most habitats in agricultural landscapes – have never been connected to each other. Taking into account that they have never been part of a former large-size wetland, their size is considered to be relatively stable in comparison with fragmented habitats like woodlands. Taking into account this comparatively stable size of the habitats and the dominance of full-winged species in the communities, these communities may be well adapted to survive in patchy landscapes. Accordingly, their situation is not comparable with a dynamic loss of species in supersaturated biotas of habitat fragments, and habitat area might be of minor importance for the extinction dynamics (Simberloff & Abele, 1982). Based on studies of fragmented habitats, increasing the area of natural or semi-natural habitats to keep population sizes of the inhabiting species above minimum levels has been stressed as a principal goal of nature conservation (Diamond, 1975; Simberloff & Abele, 1976; Spellerberg, 1991; Hovestadt *et al.*, 1994; Jedicke, 1994; Pimm *et al.*, 1995). The present study provides evidence that the application of this concept to habitat islands in agricultural landscapes that are not influenced by fragmentation, is of questionable relevance. In particular, metapopulation structures might counteract local area effects on subpopulations via rescue effects (Holt, 1993). Studies showing that interaction groups of carabid beetles containing a high number of gradually merging subpopulations spread the risk of extinction over a large part of the metapopulation support this conclusion (den Boer, 1981, 1990). Hence, it is most likely that species richness is determined by (1) parameters at larger spatial scales that influence the entire metapopulation (Brose, in press), and (2) qualitative habitat characteristics like vegetation structures (Brose, 2003).

Species richness and isolation

Economic pressures are responsible for the ongoing trend of increasing field sizes. It is an open question in agricultural landscape research whether it has an impact on the communities of agricultural habitats. Surprisingly, despite the large size of the fields in the study area, there were no significant relationships between carabid species richness and the isolation parameters. In a previous study, it was shown that the isolation parameters did not have an influence on plant species richness (Brose, 2001). This supports the general pattern that in contrast to oceanic islands, the species richness of habitat islands on the mainland is seldom influenced by isolation (Ouborg, 1993; Rosenzweig, 1995). A potential explanation arises from the fact that the mean isolation distances in the present study were between 81 and 240 m, which is much less than the distances included in most studies on actual islands. However, Nilsson *et al.* (1988) found that on islands no more than 4 km off the mainland, there was no depressing effect of isolation on species richness. This supports the interpretation that the lack of a depressing isolation effect on habitat islands on the mainland is caused by the smaller distances.

In some studies on forest fragmentation, isolation has been cited as an important variable that influences local levels of diversity (Burel, 1989; Turner, 1996). Potential explanations for why the current results differ include: (1) woodlands are surrounded by habitats hostile to most of their species, whereas temporary wetlands are part of a landscape matrix that is habitable for the field species that constitute a substantial part of its communities (Appendix 1), (2) in contrast to carabid communities of woodlands (Burel, 1989), the high percentage of full-winged species in the present study indicates a high dispersal efficiency (see den Boer *et al.*, 1980; den Boer, 1990 for a discussion of wing development and dispersal). Such dominance of full-winged carabid species is characteristic for most habitats in early successional stages, whereas most species occupying old, stable habitats are either brachypterous or wing-dimorphic (den Boer, 1990). As most habitats in agricultural landscapes are in early successional stages, the present results might be more representative of other carabid communities than those from studies on woodland fragments. As a result of the depressing effect of isolation on the species richness in woodland fragments, habitat connectivity systems have been claimed to be beneficial to sustaining species diversity in agricultural landscapes (e.g. Jedicke, 1994). The present study, however, does not support this nature conservancy concept.

Species composition and environmental variables

In contrast to the initial hypothesis, habitat area and most of the island biogeographical parameters did not have significant impacts on carabid community composition. The results suggest that community composition is mainly determined by the land-use intensity, consistent with many studies on the consequences of agricultural landuse (review in Kromp, 1999). The distance to the edge of the field was the only isolation parameter with considerable effects on the community composition (see below). While it has been shown that the maximum duration of flooding is the most important parameter affecting the plant communities of the temporary wetlands (Brose, 2001), its effect on the carabid beetle communities was of minor importance. As the total explained variation was low, it is most likely that the community composition may be determined by qualitative habitat characteristics – like the specific land-use (Kromp, 1999) or vegetation structures (Brose, 2003) – or at larger spatial scales where landscape parameters might influence the composition of the metapopulation (Brose, in press).

Individual species responses to isolation

The results indicate that the carabid beetle species studied were not negatively influenced by the distance to the next pothole. This result suggests that this variable does not have an isolation effect on the carabid communities studied. Accordingly, the distance to the edge of the field was the only effective isolation parameter. Surprisingly, there was a positive correlation between the abundances of some typical field species and the distance from the temporary wetland to the edge of the field. This isolation variable, however, was negatively correlated with the land-use intensity. Therefore, it is most likely that the effects on the carabid species abundances are mainly mediated by a negative response to land-use intensity, which is consistent with previous studies (Kromp, 1999). In contrast to this, increasing distances to the edge of the field influenced some species negatively (isolation-influenced species). It has been pointed out in several studies that most of the typical carabid field species hibernate in the field margins (e.g. Sotherton, 1985; Pfiffner & Luka, 2000). As these species subsequently migrate back into the fields, increasing distance to the edge of the field has been cited by several authors to explain the slower migration of non-flying arthropods into fields in spring (Coombes & Sotherton, 1986; Thomas et al., 1991). In accordance with this, the present study has shown that in the group of isolation-influenced species the relative proportion of short-winged species was significantly higher. The results support the hypothesis that flying species are less affected by isolation than poorly dispersing species, which has been observed in studies on vertebrates (see Turner, 1996). As a note of caution, however, it has to be emphasized that the classification of wing development in the present study represents the actual situation in the populations studied. The wing development of wing-dimorphic species may change considerably between generations. Therefore, wing-dimorphic species classified as full-winged may well be mainly short-winged in similar studies or under different habitat conditions. In the present study, however, the results indicate that the fraction of full-winged individuals did not change for any of the wing-dimorphic species studied in the three study years. Accordingly, it is most likely that similar results can be obtained in any study under similar experimental conditions. Furthermore, it has to be emphasized that the aim of the present study was the documentation of ecological patterns in the actual populations, which does not provide any evidence on evolutionary trends. A further generalization arisen from vertebrate studies is that large-bodied animals are more affected by isolation. The present results do not support this conclusion. This might be explained by the body sizes of carabid beetles that are generally small in comparison with vertebrates.

CONCLUSIONS

The results of the present study do not support conventional nature conservation concepts for agricultural landscapes that focus on habitat area and habitat-connectivity systems. There was no significant influence of the island biogeographical variables on species richness, and the impact on community composition was low. It was observed that short-winged (poorly dispersing) species are mainly affected by isolation. A comparison with other island biogeography studies has shown that the need for habitat connectivity is habitat-specific as forest species respond differently to isolation than species of habitats in early successional stages. The high proportion of full-winged species (good dispersers) at the temporary wetlands might be responsible for this difference. The documented community responses to island biogeographical parameters might be representative for early successional habitats in the agricultural landscape. The high mobility of the carabid species studied and the lack of habitat area or isolation effects on the communities suggest the existence of interaction groups of carabid beetles containing a high number of gradually merging subpopulations (den Boer, 1981, 1990). Accordingly, the extinction risk of the species might be spread over a large part of the metapopulation. Then, it is most likely that variables at larger spatial scales that influence the entire metapopulation and qualitative habitat characteristics like specific land-use systems are more important for the communities studied than island biogeographical variables. It is evident that future research should directed towards (1) macroecological conditions affecting the metapopulations (e.g. Brose, in press), and (2) habitat qualities that are important for the coexistence of the species (e.g. Brose, 2003). Such studies might have more profound implications for nature conservancy and biodiversity management in the agricultural landscape than concepts following the present paradigm of increasing habitat area and connectivity.

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BIOSKETCH

Ulrich Brose is a community ecologist with interest in theoretical and empirical ecology. Current research topics are species–area relationships, island biogeography, estimating species richness by extrapolations, non-linear dynamics in complex networks and diversity and stability of large food webs.

Appendix 1 The thirty most abundant carabid beetle species. ind., total number of individuals caught; frequency, number of study sites with occurrences; wetland, wetland species; p, proportion of full-winged species in the subsample; n, number of individuals in subsample; b, brachypterous; m, macropterous; l, large; s, small

Species	Abbreviations	ind.	frequency	Wetland	Wings (p/n)	size
Pterostichus melanarius	Ptemel	16904	30		b (0%/668)	l
Poecilus cupreus	Poecup/Pc	7828	30		m	l
Pseudoophonus rufipes	Pseruf/Pr	7011	30		m	l
Bembidion lampros	Bemlam	4949	27		m (70%/1125)	s
Bembidion tetracolum	Bemtet	4699	30		m (100%/355)	l
Bembidion properans	Bempro	4165	27		m (59%/265)	s
Clivina fossor	Clifos	3116	30		m (97%/121)	s
Carabus auratus	Caraur/Ca	2622	30		b	l
Elaphrus riparius	Elarip	2331	30	x	m	l
Bembidion varium	Bemvar	2175	30	x	m	s
Agonum marginatum	Agomar	2137	30	x	m	l
Anchomenus dorsalis	Ancdor	2043	30		m	l
Harpalus affinis	Haraff/Ha	1754	29		m	l
Loricera pilicornis	Lorpil	945	30	x	m	l
Bembidion femoratum	Bemfem	650	22	x	m	s
Amara plebeja	Amaple	635	21		m	l
Clivina collaris	Clicol	493	28	x	m	s
Anisodactylus binotatus	Anibin	482	24	x	m	l
Carabus granulatus	Cargra	471	26	x	m	l
Poecilus versicolor	Poever	410	19		m	l
Pterostichus anthracinus	Pteant/Pa	410	24	x	b (28%/18)	l
Calathus fuscipes	Calfus	404	27		b	l
Agonum sexpunctatum	Agosex	356	21	x	m	l
Amara similata	Amasim	298	23		m	l
Bembidion lunulatum	Bemlun	281	24	x	m	s
Poecilus punctulatus	Poepun/Pp	281	12		m	l
Harpalus distinguendus	Hardis/Hd	275	19		m	l
Chlaenius nigricornis	Chlnig	256	20	x	m	l
Acupalpus parvulus	Acupar/Ap	191	20	x	m	s
Bembidion articulatum	Bemart	169	15	x	m	s