

Effects of habitat fragmentation on carabids in forest patches

Tibor Magura^{1*}, Viktor Ködöböcz² and Béla Tóthmérész³ ¹Hortobágy National Park Directorate, Debrecen, Sumen u. 2, H-4024, Hungary ²Zoological Department of Debrecen University, Debrecen, PO Box 3, H-4010, Hungary ³Ecological Institute of Debrecen University, Debrecen, PO Box 71, H-4010, Hungary

Abstract

Aim The aim of this study was to test some of the classical rules of island biogeography for the carabid beetles (*Coleoptera: Carabidae*) in 15 forest patches during 1995–99.

Location The 15 forest patches studied are located on the Bereg Plain. The Bereg Plain is at the foot of the Carpathians, partly in Hungary and partly in the Ukraine. Even in recent times, the area was covered by continuous woodland of deciduous trees, and the species of the closed canopy deciduous forest of the hills and mountains were able to disperse from the Carpathians to these lowland forests. But now, because of agricultural activities and forest management, this woodland is fragmented into forest patches.

Methods The species–area and the number of species–distance to mainland relationships, and the influence of other factors like shape, isolation, and altitude above the sea level, on the number of species were studied. We have used three categories of species during the analyses: (i) total number of species; (ii) the number of species of the closed canopy deciduous forest of the hills and mountains (ForHim species); and (iii) the number of widely distributed generalist species (WidGe species).

Results There were positive, but statistically insignificant correlations between the distance to the Carpathians and the total number of species, and also between the distance to the Carpathians and the number of WidGe species. The correlation was negative for the number of ForHim species, and it was also not significant. There were significant negative correlation between both the total number of species and the number of WidGe species and the size of the forest patches, while there were significant positive correlation between the size of forest patch and the number of ForHim species. The number of ForHim species decreased significantly by the increase of isolation, while the number of WidGe species increased by the isolation. Shape of the forest patches, and their altitude above the sea level had no influence on the total species richness, the ForHim species richness, and the WidGe species richness. We have also proved that each of the total species richness, the ForHim species richness, and the WidGe species richness, is higher for many small forest patches than for one large patch of the same total area.

Main conclusions Our results suggest that historical reasons have a vital influence on the present species patterns. Moreover, in biogeographical studies we must distinguish between species which recognize the habitat as a patch or island and those that can survive in the neighbouring habitats as well. An ignorance of these two categories may disguise basic biogeographic rules.

Keywords

Carabid beetles, island biogeography, fragmentation, isolation, species–area relationship, edge-effect, habitat heterogeneity, subpopulations.

*Correspondence: Zoological Department of Debrecen University, Debrecen, PO Box 3, H-4010, Hungary. E-mail: magura@tigris.klte.hu

INTRODUCTION

There have been vital changes in forest and agricultural management of landscapes during the twentieth century. The new forms of agricultural activities and forest management have contributed largely to the fragmentation of natural habitats (Mader, 1980; Forman & Godron, 1986). There are two vital effects of fragmentation on living organisms. Firstly, the total area of the habitats sustaining the populations decreases. Secondly, these habitats tend to be more isolated (Saunders *et al.*, 1991; Halme & Niemelä, 1993).

The Bereg Plain is at the foot of the Carpathians, partly in Hungary and partly in the Ukraine, and it was covered by continuous woodlands of deciduous trees even during the 18–19th centuries. Because of the clear-felling of forests and agricultural activity, the former large forested areas are reduced to small isolated forest fragments separated by agricultural areas and by open seminatural assemblages. This particular situation provides excellent possibilities to test island biogeographical models and/or their predictions. When the Bereg Plain was covered by continuous forest, the species of the closed canopy deciduous forest of the hills and mountains were able to disperse from the Carpathians to these lowland forests. For these species the Carpathians were a potential colonization source (Varga, 1995; Magura *et al.*, 1997, 1999; Kődöböcz & Magura, 1999). Now, however, most of the species are widely distributed generalist species.

Studies on less mobile species, such as nonflying arthropods living on the soil surface, provide a useful measure of the impact of human-caused disturbances. Ground-dwelling carabid beetles (*Coleoptera: Carabidae*) are exceptionally useful study organisms for examining biogeographical topics

because they are diverse and abundant, their ecology and systematics are relatively well known, and they seem to be highly sensitive to the effects of landscape changes such as fragmentation (Niemelä *et al.*, 2000).

According to the predictions of island biogeography, the number of species supported by an island decreases with the distance from the continent (mainland) and it increases with the area of the island (MacArthur & Wilson, 1963, 1967). Therefore, it is negatively correlated with the distance and positively with the size of the island. Isolates, which are surrounded by different types of area/communities, can also be regarded as islands. We have tested these classical rules of island biogeography for the carabids of the Bereg Plain. Other authors have stressed the influence of other factors like shape (Laurence & Yensen, 1991), isolation (Vos & Stumpel, 1995), and altitude above the sea level (Báldi & Kisbenedek, 1999), on the number of species. We have also tested these factors.

MATERIALS AND METHODS

Study area and sampling

Carabid assemblages of 15 forests of the Bereg Plain in Hungary and in the Ukraine were studied during the period of 1995–99 (Table 1 & Fig. 1). The Bereg Plain is the most humid (630–660 mm annual precipitation) and the coolest area of the Great Hungarian Plain. Originally *Salicetum triandrae*, *Salicetum albae-fragilis* and *Fraxino pannonicae-Ulmetum* forest associations were dominant along the rivers. Oak-hornbeam forest (*Quercus robori-Carpinetum*) is the most extensive forest type of the area. It is a relatively undisturbed, forested marginal area of the Great Hungarian Plain, which provides refuge for several endangered species

Table 1 Characteristics of the studied forest patches.

Forest	Area (ha)	Distance to the Carpathians (km)	Shape -index	Isolation -index	Height above the sea level (m)	Trapping year	Collected carabid species
Bockerek-forest	1249.66	36.91	3.66	0	101	1995	13
Déda-forest in Hungary	197.47	29.43	1.51	76.80	109	1995	18
Lónya-forest	1047.80	28.07	1.91	0	101	1995	17
Déda-forest in Ukraine	76.80	29.15	1.14	197.47	109	1996	17
Dobrony-forest	1191.67	9.94	1.85	0	103	1996	13
Peres-forest	249.97	12.08	1.26	0	101	1996	29
Rafajna-forest	1609.09	19.48	1.16	870.78	107	1996	18
Téglás-forest	41.19	15.20	1.14	0	102	1996	20
Dobrony-forest	1191.67	9.94	1.85	0	103	1997	13
Gút-forest	870.78	20.71	1.84	1609.09	108	1997	10
Alsóremete-forest	463.23	11.22	1.65	3995.46	136	1998	11
Beregújfalú-forest	3995.46	3.57	2.18	463.23	136	1998	12
Puskinó-forest	522.74	13.15	1.47	0	121	1998	14
Rafajna-forest	1609.09	19.48	1.16	870.78	107	1998	16
Puskinó-forest	522.74	13.15	1.47	0	121	1999	12
Beregújfalú-forest	3995.46	3.57	2.18	463.23	136	1999	12
Munkács-forest	179.68	9.99	1.29	1520.61	109	1999	14
Alsókerepec-forest	1520.61	7.58	1.55	616.40	109	1999	11
Gát-forest	436.72	15.04	1.74	1520.61	109	1999	12

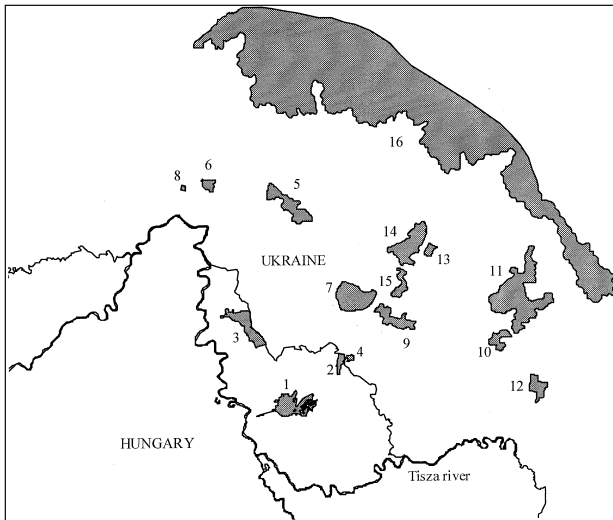


Figure 1 The studied forest patches in the Berek Plain. 1: Bockerek-forest, 2: Déda-forest on the Hungarian side, 3: Lónya-forest, 4: Déda forest on the Ukrainian side, 5: Dobrony-forest, 6: Peres-forest, 7: Rafajna-forest, 8: Téglás-forest, 9: Gút-forest, 10: Alsóremete-forest, 11: Beregújfalú-forest, 12: Puskinó-forest, 13: Munkács-forest, 14: Alsókerepec-forest, 15: Gát-forest and 16: Forest belt of the Carpathians.

of the fauna. There are also remarkable features of the carabid fauna of the studied region. Most of the species are generalist with wide distributions, characteristic both of forest and open areas of lowlands and hills. However, there are species which are characteristic of the closed canopy deciduous forest of the hills and mountains and usually do not occur in plain areas. The potential colonization source of these latter species is the Carpathians (Varga, 1995; Magura *et al.*, 1997, 1999; Ködöböcz & Magura, 1999). Based on these features of the fauna, we have used three categories of species during the analysis: (1) total number of species; (2) the number of species of the closed canopy deciduous forest of the hills and mountains (ForHim species in the followings); and (3) the number of widely distributed generalist species (WidGe species). This categorization is based on the paper of Szél (1996), using the bigeographical distribution of carabids in Hungary.

Beetles were collected using unbaited pitfall traps consisting of plastic cups (diameter 100 mm, volume 500 mL) containing ethylene glycol as a killing preserving solution. There were nine to 18 traps in a forest, scattered randomly in a typical part of the forest. There was at least 10 m distance between the traps. Trapped individuals were collected monthly from April to October. All carabids taken in pitfall traps were identified to species using standard keys (Freude *et al.*, 1976).

Data analyses

Distances of the forest islands from the Carpathians, and their area, were measured by the ArcView GIS program

package on a digitized 1 : 25,000 map. Distance was calculated by taking the shortest possible distance between the Carpathians and the forest patch. The shape of forests was characterized by the shape index (Patton, 1975). It is defined as $P/(200 \times (\pi \cdot A)^{-1/2})$, where P is the perimeter of the forest patch in metre, and A is the area of it in hectares. Its value is 1 for a round shape forest, while values > 1 represent deviation from circularity (Laurence & Yensen, 1991). Isolation of a habitat island is most often measured as the distance to the nearest patch. Isolation of a habitat patch depends not only on the distance to the nearest patch, but on the area of the nearest patch, too. Namely, a larger habitat patch is more likely to have greater number of species that can colonize in the neighbouring patch. However, the distance between the adjacent patches is also relevant. In our study isolation of the forest patches was measured by the inverse isolation measure, as proposed by Vos & Stumpel (1995). It was defined as the total forest area within a radius of 600 m around the studied forest patch. This measure was used as an inverse of the isolation, because its value decreases as the isolation of the forest increases. The radius was chosen as 600 m, because even poor colonist forest specialists can cover this distance through inhospitable habitats. Cumulative number of species richness and the number of species in the categories in ranked sequences of patches from large-to-small and small-to-large were calculated to explore whether many small forest patches contain more species than one large patch of the same total area (Quinn & Harrison, 1988; Douglas & Lake, 1994; Honnay *et al.*, 1999).

Linear regression analysis was used to study the relationships between the studied variables (distance to the Carpathians, size of the forest island, shape index, inverse isolation index, altitude above the sea level) and the total number of carabid species of the island, the number of ForHim species, and the number of WidGe species. The dissimilarity of the species composition of forest patches was measured by the Hellinger distance, $d(\mathbf{p}, \mathbf{q})$, in the following way:

$$d(\mathbf{p}, \mathbf{q}) = 1 - \sum_{i=1}^S \sqrt{p_i \cdot q_i}$$

where p_i is the relative frequency of the species i in the first compared forest patch (\mathbf{p}), and q_i is the relative frequency of the species i in the second compared forest patch (\mathbf{q}), and S is the total number of species. Heterogeneity of the carabid fauna of the forest patches was characterized by the Whittaker's β -diversity (Whittaker, 1960), which is defined as the ratio of the total species pool and the average number of species of the patches and minus one. Its minimum is 0, and a large beta-diversity value means a large heterogeneity.

RESULTS

During the period of 1995–99, we have collected 10,983 individuals of 56 carabid species (see Appendix). There were four species identified at the Berek Plain, which are

usually characteristic to the closed forests of the hill and mountains. They are as follows: *Carabus intricatus* Linnaeus 1761; *Cychrus caraboides* (Linnaeus 1758); *Abax parallelus* (Duftschmid 1812); and *Cymindis cingulata* Dejean 1825. These are the first published occurrence of these species in a plain (lowland) situation. We have collected three more species which were recorded just once at the Hungarian Great Plain: *Carabus arcensis carpathus* Born 1902; *Pterostichus melas* (Creutzer 1799) and *Molops piceus* (Panzer 1793).

There were positive, but statistically insignificant correlations, between the distance to the Carpathians and the total number of species, and also between the distance to the Carpathians and the number of WidGe species. The relationship was negative for the number of ForHim species, and it also was not significant (Table 2).

Both the total number of species and the number of WidGe species are negatively correlated with the size of the forest patches. These relationships were significant. There was a significant positive correlation between the size of forest patch and the number of ForHim species (Table 2 & Fig. 2).

There was also a significant positive correlation between the number of ForHim species and the inverse isolation index. Therefore, the number of ForHim species decreased by isolation. Moreover, we have found a significant negative correlation between the number of WidGe species and the inverse isolation index. There was no significant correlation between the other factors (Table 2). We have further found a significant positive correlation between the distances of the patches and the dissimilarity of their species composition measured by the Hellinger distance ($r = 0.4654$, $F = 46.7232$, d.f. = 1,169, $P < 0.0001$; Fig. 3), which also stresses the effect of isolation.

A plot of the cumulative species richness of forest patches against the ranking of the size of the patches proved for each of the total species richness, the ForHim species richness, and the WidGe species richness, that many small forest patches contain more species than one large patch of the same total area (Fig. 4). Whittaker's beta-diversity of the carabid fauna was 2.8, suggesting high heterogeneity of the local fauna of the forest patches.

DISCUSSION

Species–distance relations

There were no significant correlations between the total number of species, the number of WidGe species and the distance to the Carpathians. There was negative correlation between the ForHim species and the distance to the Carpathians, although it was also not significant. This may be explained by the fact that the forest of the Carpathians are the source of the species characteristic of the closed canopy deciduous forest of hills and mountains, and they spread from there to the forests of Bereg Plain (Varga, 1995; Magura *et al.*, 1997, 1999; Kódoböcz & Magura, 1999). Therefore, the observed negative species number–distance to

Table 2 Relationships between the total species number, the number of species of the distribution categories (ForHim and WidGe species) and the studied variables (size of the forest patches, distance to the Carpathians, shape index, inverse isolation index, altitude above the sea level). The base of the logarithm is 10.

	Log (Area)	Log (Distance)	Shape	Log (Isolation)	Height above the sea level
Total species	$S = 25.68 - 3.87 \text{ Log (Area)}$ $r = 0.4636$ $F = 4.6539$ d.f. = 1,17 $P = 0.0456$	$S = 9.89 + 4.36 \text{ Log (Distance)}$ $r = 0.2742$ $F = 1.3822$ d.f. = 1,17 $P = 0.2559$	$S = 19.44 - 2.78 \text{ (Shape)}$ $r = 0.3602$ $F = 2.5350$ d.f. = 1,17 $P = 0.1298$	$S = 16.64 - 1.09 \text{ Log (Isolation)}$ $r = 0.3647$ $F = 2.6087$ d.f. = 1,17 $P = 0.1247$	$S = 33.40 - 0.17 \text{ (Height)}$ $r = 0.4508$ $F = 4.3367$ d.f. = 1,17 $P = 0.0527$
Forest species of the hills and mountains (ForHim species)	$S = -1.72 + 1.54 \text{ Log (Area)}$ $r = 0.4599$ $F = 4.5612$ d.f. = 1,17 $P = 0.0475$	$S = 4.47 - 1.67 \text{ Log (Distance)}$ $r = 0.2620$ $F = 1.2531$ d.f. = 1,17 $P = 0.2785$	$S = 3.44 - 0.52 \text{ (Shape)}$ $r = 0.1686$ $F = 0.4972$ d.f. = 1,17 $P = 0.4903$	$S = 1.28 + 0.79 \text{ Log (Isolation)}$ $r = 0.6621$ $F = 13.2667$ d.f. = 1,17 $P = 0.0020$	$S = -0.49 + 0.03 \text{ (Height)}$ $r = 0.1867$ $F = 0.6140$ d.f. = 1,17 $P = 0.4441$
Widely distributed generalist species (WidGe species)	$S = 26.85 - 5.23 \text{ Log (Area)}$ $r = 0.5192$ $F = 6.2742$ d.f. = 1,17 $P = 0.0227$	$S = 5.64 + 5.79 \text{ Log (Distance)}$ $r = 0.3021$ $F = 1.7067$ d.f. = 1,17 $P = 0.2088$	$S = 15.81 - 2.18 \text{ (Shape)}$ $r = 0.2338$ $F = 0.9832$ d.f. = 1,17 $P = 0.3353$	$S = 15.33 - 1.89 \text{ Log (Isolation)}$ $r = 0.5266$ $F = 6.5231$ d.f. = 1,17 $P = 0.0205$	$S = 33.71 - 0.19 \text{ (Height)}$ $r = 0.4333$ $F = 3.9300$ d.f. = 1,17 $P = 0.0638$

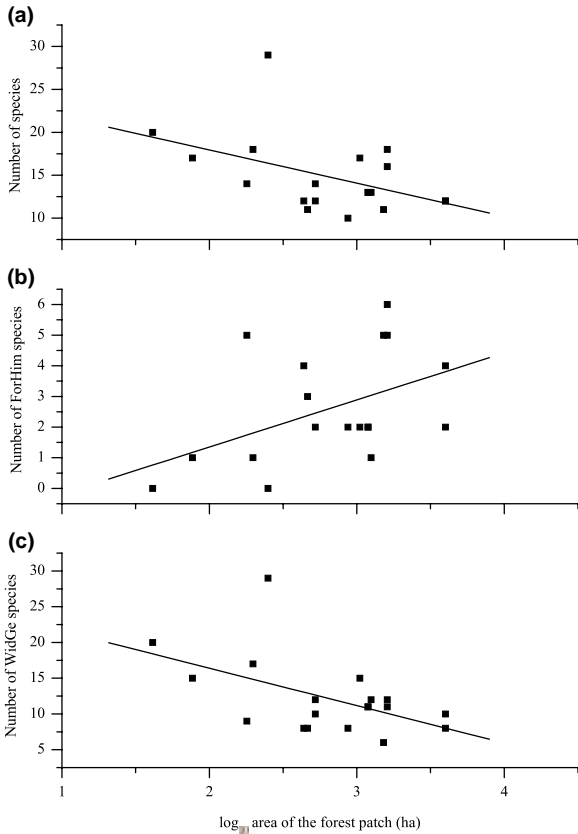


Figure 2 Species-area relationships for the three categories of species.

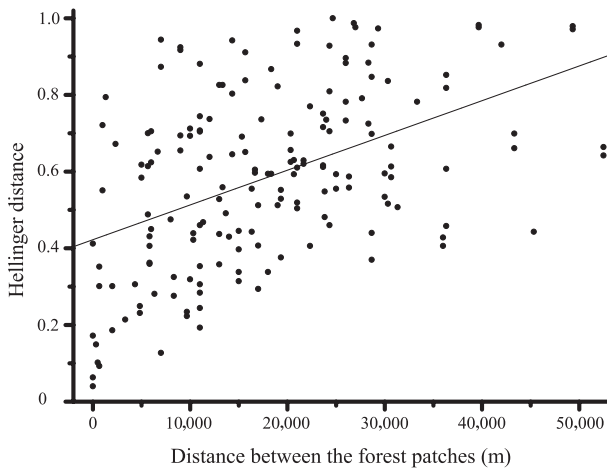


Figure 3 The correlation between the distance of forest patches and the dissimilarity of their species composition measured by the Hellinger distance.

the Carpathians relationship is consistent with the rules of dynamic biogeography: the number of species, characteristic to the source decreases as the distance to the source increases. This may be explained by historical reasons that

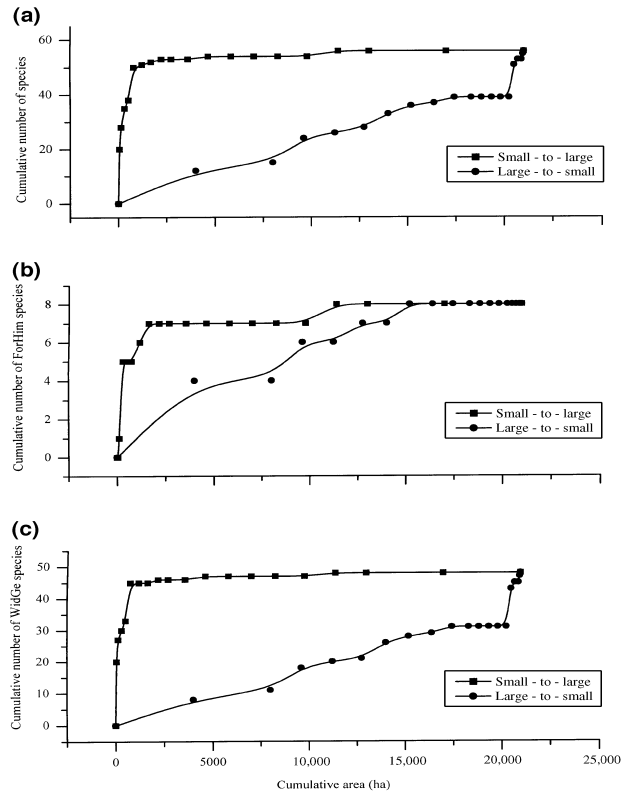


Figure 4 Small-to-large and large-to small cumulative area curves for the carabids of the forest patches.

the negative correlation is not significant. Nowadays, the distance between the woodlands of the Carpathians and the forest patches of the Bereg Plain are 2.5–33.5 km, and this region is covered by agricultural areas and open (herbaceous) assemblages. The forest specialist species are not able to spread over such a large areas, which are remarkably different in microclimate and vegetation structure from the forest. Nowadays, these forests are entirely isolated from the colonization source. Moreover, each of the forest patches is segregated by unpenetrable barriers (1–10 km wide agricultural area, or grasslands). Therefore, these patches do not serve as stepping stones (Den Boer, 1970) spreading from the Carpathians for the brachypterous species characteristic of the closed canopy forests of the hills and mountains. At the beginning of 1900s, when the forest stands were continuous, or partly continuous, these species were able to spread over the region. According to the prediction of island biogeography, the further the forest stand from the colonization source, then the less species are able to reach it. Summarizing, the distance to the Carpathians had significant influence to the composition of carabid fauna of the forest patches. Nowadays, it has no significant influence because of the isolation of the forest patches, but the negative relationship between the number of ForHim species and the distance to the Carpathians is still observable, although it is not significant statistically.

Species–area relations

Many published papers in zoology report positive correlations between the total number of species of the habitat island and the size of the island (Brown, 1971; Faeth & Kane, 1978; Mader, 1980; Nilsson *et al.*, 1988). A few papers do not corroborate this relationship between the number of species and area (Hopkins & Webb, 1984; Mader, 1984; Bauer, 1989; De Vries, 1994). We found a significant negative relationship between the size of habitat island and the total number of species. This is the opposite of the prediction of the classical theory of island biogeography. Bauer (1989) also finds a significant negative relationship between the patch size and the total number of species of carabids of isolated limestone outcrops and adjacent peat. Halme & Niemelä (1993), studying the fauna of conifer fragments report that the number of carabid species decreases as the patch size of the conifer forest increases. Bauer (1989) and De Vries (1994) stress that there should be a difference between species which recognize the habitat as a patch or island, and those which can survive in the neighbouring habitats as well. The ignorance of these two categories may disguise the real patterns. For the ForHim species, the forest patches studied are islands, while the WidGe species can survive in the neighbouring habitats. There is a significant positive correlation between the number of species and the size of the forest patch for ForHim species. The correlation is significantly negative for WidGe species. Bauer (1989) observes a similar pattern. There is a significant negative correlation between the size of limestone outcrops and those widely distributed carabid and staphylinid species that can survive in the neighbouring peat. There is a significant positive relationship between the size of limestone outcrops and the limestone specialist carabids and staphylinids that are restricted to limestone outcrops. Usher *et al.* (1993) also found that only the species richness of farm woodland carabids correlated positively with the area of woodland, while the total number of arthropod species did not correlate. Similar patterns exist for the carabid data set of conifer forest patches published by Halme & Niemelä (1993). There is a negative correlation between the number of widely distributed species and the size of the conifer forest patches and a positive correlation between the number of species of the forest species and the patch size.

The above patterns also occur in other types of habitats, like conifer forest patches, limestone outcrops and the neighbouring peat, and farm woodland patches. This pattern is related to the following factors, which are discussed in details below: (1) edge effect (2) habitat heterogeneity; and (3) asynchrony of subpopulations and (4) isolation.

Habitat islands consist of edge zones and core zones. Several studies demonstrate that edges of the forest stands have greater species richness than the forest interior (Helle & Muona, 1985; Bedford & Usher, 1994; Magura & Tóthmérész, 1997, 1998; Magura *et al.*, 2001). This feature can be explained by the fact that the forest edge has species characteristic of the adjoining habitat and edge-associated species. These edge-associated species may require the

particular abiotic and biotic environmental conditions resulting from the proximity of two structurally different habitats (Murcia, 1995). However, forest edges have an inverse effect on the forest biota. Previous studies analysing carabid beetles prove that with decreasing area of forest patches the number of generalists species increases, while the species richness of the forest specialists decreases (Mader, 1980; Halme & Niemelä, 1993; Usher *et al.*, 1993; Spence *et al.*, 1996). Our results also demonstrate that the number of WidGe species significantly increases, while the number of the ForHim species significantly decreases as the area of the forest patches decreases (Table 2 & Fig. 2). These facts can be explained by the increase of the edge-area ratio and the decrease of the area of the forest patches. Increased edge-area ratio and decreased forest area produce microclimatic conditions of the forest stands that make possible the colonization by generalist species (Halme & Niemelä, 1993; Spence *et al.*, 1996). The decrease of the core zone (forest interior) and the decrease of the habitat heterogeneity also have harmful impacts on the forest specialist species (Murcia, 1995; Spence *et al.*, 1996; Davies & Margules, 1998). According to Laurence & Yensen (1991) the shape index to some extent expresses the edge-area ratio of a forest patch. We have not found significant relationships between the shape index and the number of the total species, the WidGe or the ForHim species. Blouin & Connor (1985) examine the relationship between species richness and island shape expressed by the shape index and conclude that the island shape does not explain a significant amount of the variation in species richness. Perhaps the application of a suitable measure of the edge-area ratio, such as the total length of edges wider than 2 m, as proposed by Honnay *et al.* (1999), can reveal the relationship between the edge to area ratio of forest patch and the species richness of carabids in the studied region.

It is a general rule that with the increase of the area the habitat heterogeneity also increases (Forman & Godron, 1986). In this paper, significant positive relationship between the area of the forest patch and the number of ForHim species can also be explained by the habitat heterogeneity. De Vries & Den Boer (1990) prove that *Agonum ericeti* (Panzer 1809) needs a minimum area of habitat because this species requires special environmental conditions (microclimate, dead and decaying trees, cover of leaf litter and herbs, etc.). Niemelä *et al.* (1987) published similar results for *Agonum mannerheimii* (Dejean 1828). In the present study *Carabus intricatus* Linnaeus 1761 (a ForHim species) requires dead and decaying trees for its existence because this species overwinters in these trees. A larger forest patch is more likely to have greater habitat heterogeneity permitting the forest specialists to find their special microhabitat (Magura *et al.*, 2000). This fact can explain the significant increase in the number of ForHim species with the increase of the forest patch area.

A theory proposed by Den Boer (1981, 1985) may also explain the significant positive relationship between the area of the forest patch and the number of ForHim species. According to this theory, the number of interaction groups

(subpopulations) of a large habitat patch may fluctuate in an asynchronous way. Thus, when the size of a subpopulation decreases, that of another subpopulation increases. If a population consists of several interaction groups (so-called multipartite population) and the numbers of subpopulations fluctuate differently, then the survival time of the composite population may significantly increase. Den Boer (1985) by simulation of the fluctuation of the observed population size, shows that survival time of a population consisting of only one interactive group is merely a few decades or less. According to Den Boer (1981, 1985), out of the factors that can determine the number of subpopulations in a composite population, the one of most importance is the area of the habitat. Therefore, it is expected that the survival time and the extinction rate of a population are greatly influenced by the area of the habitat (MacArthur & Wilson, 1967; Den Boer, 1981; De Vries & Den Boer, 1990). In the present situation, the ForHim species in larger forest patches probably consist of more subpopulations, therefore their survival time is longer.

The significant positive relationship between the inverse isolation index and the number of ForHim species emphasizes that increased isolation of a forest patch significantly decreases the number of ForHim species present there. Thus, the isolation also has a remarkable effect on the carabid fauna of a forest patch. If a ForHim species becomes extinct in a given small forest patch because of one of the above mentioned factors (edge-effect, decrease of the habitat heterogeneity and synchronicity of the subpopulations) or combination of these factors, then this extinct ForHim species cannot recolonize in the forest patch because the forest patch is isolated. ForHim species are large and wingless, so they are poor colonists. Therefore, the continuous and expanded agricultural area and grasslands between the Carpathians, and the forest patches, are impenetrable barriers for these species. The same is true for the area between the forest patches, namely these areas are also barriers for the ForHim species. Therefore, the recolonization of the ForHim species in a given forest patch through the 'from patch to patch' mechanism [cf. stepping stones Den Boer (1970)] is also prevented. By contrast, the good colonist WidGe species may more easily colonize in the 'empty' forest patches (Spence *et al.*, 1996).

Implications for nature conservation

Our study shows that carabid species characteristic of closed canopy deciduous forest of hills and mountains still persists in the isolated forest patches of the Bereg Plain. These species are not typical in other lowland areas of Hungary. Moreover, according to the prediction of Higgs & Usher (1980), many small forest patches contain more species than one large patch of the same total area. This is explained by the heterogeneity of the region studied. It is also confirmed by the high value of β -diversity of the fauna of the forest patches. Usually, just a quarter of the total species pool was present in a forest patch in the region studied. The relatively low ratio of the species present in a patch compared with the species pool is not related to the small size of a patch,

because the number of species of the patches is negatively related to the size of the forests (Fig. 2). Therefore, the large heterogeneity of the fauna is explained by isolation and other historical reasons.

For the conservation of the carabid species characteristic of the deciduous forests of hills and mountains in this region the following measures are recommended from the point of view of an active nature conservation management programme:

- (1) All of the forest patches should be preserved to serve as a source habitat;
- (2) Our results show a significant positive relationship between the number of carabid species characteristic of the deciduous forest of hills and mountains and the area of forest patches. Therefore, the additional fragmentation of the forest patches has to stop for the conservation of these species to be successful;
- (3) In the forest patches, mainly in the patches with a small area, a large area-to-edge ratio is recommended contributing to the recolonization of the species characteristic of the deciduous forest of hills and mountains;
- (4) Corridors of forest should be established to connect forest patches with one another and with the Carpathians. Creation of windbreaks between the forest patches might seem a reasonable solution because several studies have proved that forest specialist carabids can migrate great distance in windbreaks (Burel, 1989; Gruttke, 1994; Šustek, 1994). However, the distance between the source of the colonization (the Carpathians) and the forest patches, and between each of the forest patches is considerable (1–30 km). The creation of windbreaks is thus not sensible. The planting of forest stands composed of native deciduous trees between the source of colonization and the forest patches, or between each of the forest patches, may be a useful, alternative solution. The distance between these plantings, as stepping stones (Den Boer, 1970), is recommended to be 500–600 m, because the poor colonist forest specialists can cover this distance through the inhospitable habitats (Thiele, 1977). The realization of the above mentioned recommendation may contribute to the connection of the carabid populations living in the isolated forest patches. This connection can support the survival of the carabid species characteristic of the deciduous forest of hills and mountains and the maintenance and conservation of biodiversity.

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BIOSKETCHES

Tibor Magura (PhD) is currently the regional programme manager of the Hungarian National Biomonitoring System at the Hortobágy National Park Directorate. He is the head of the Carabidological Research Group at the University of Debrecen. His main research interests are the faunistics, the biogeography and the ecology of carabid beetles.

Viktor Ködöböcz is a PhD student at the Department of Zoology at the University of Debrecen. He is writing his thesis on the biogeography of carabids. His main fields of interest are faunistics, the biogeography and the ecology of carabid beetles.

Béla Tóthmérész is professor of quantitative ecology at the Ecological Institute of the Debrecen University. He has published papers on diversity measurement, with special emphasis on scale-dependent characterization, as well as scalable proximity measures and multivariate analyses of ecological communities.

Appendix Number of individuals and the distribution category of the collected carabid species in the Bereg Plain during the period of 1995–99. Legends: ForHim species – species of the closed canopy deciduous forest of the hills and mountains; WidGe species – widely distributed generalist species.

Species	Number of individuals	Distribution category in the studied area
<i>Abax carinatus</i> (Duftschmid 1812)	1260	WidGe species
<i>Abax parallelepipedus</i> (Piller et Mitterpacher 1783)	34	WidGe species
<i>Abax parallelus</i> (Duftschmid 1812)	643	ForHim species
<i>Agonum micans</i> (Nicolai 1822)	30	WidGe species
<i>Agonum moestum</i> (Duftschmid 1812)	683	WidGe species
<i>Platynus obscurus</i> (Herbst 1784)	7	WidGe species
<i>Amara saphyrea</i> Dejean (1828)	21	WidGe species
<i>Amara similata</i> (Gyllenhal 1810)	2	WidGe species
<i>Anisodactylus binotatus</i> (Fabricius 1787)	1	WidGe species
<i>Badister bullatus</i> (Schrank 1798)	1	WidGe species
<i>Bembidion biguttatum</i> (Fabricius 1779)	14	WidGe species
<i>Blethisa multipunctata</i> (Linnaeus 1758)	1	WidGe species
<i>Brachinus crepitans</i> (Linnaeus 1758)	10	WidGe species
<i>Calosoma inquisitor</i> (Linnaeus 1758)	32	WidGe species
<i>Carabus arcensis carpathus</i> (Born 1902)	1369	ForHim species
<i>Carabus cancellatus</i> (Reitter 1896)	722	WidGe species
<i>Carabus clathratus</i> (Linnaeus 1761)	10	WidGe species
<i>Carabus convexus</i> (Fabricius 1775)	79	WidGe species
<i>Carabus coriaceus</i> (Linnaeus 1758)	226	WidGe species
<i>Carabus granulatus</i> (Linnaeus 1758)	141	WidGe species
<i>Carabus hampei ormayi</i> (Reitter 1896)	21	WidGe species
<i>Carabus intricatus</i> (Linnaeus 1761)	32	ForHim species
<i>Carabus ullrichi</i> (Germar 1824)	199	WidGe species
<i>Carabus violaceus</i> (Linnaeus 1758)	791	WidGe species
<i>Chlaenius nitidulus</i> (Schrank 1781)	51	WidGe species
<i>Clivina fossor</i> (Linnaeus 1758)	4	WidGe species
<i>Cychrus caraboides</i> (Linnaeus 1758)	66	ForHim species
<i>Cymindis cingulata</i> (Dejean 1825)	1	ForHim species
<i>Elaphrus cupreus</i> (Duftschmid 1812)	1	WidGe species
<i>Harpalus latus</i> (Linnaeus 1758)	16	WidGe species
<i>Harpalus dimidiatus</i> (Rossi 1791)	1	WidGe species
<i>Harpalus rufipes</i> (De Geer 1774)	267	WidGe species
<i>Licinus depressus</i> (Paykull 1790)	5	WidGe species
<i>Leistus piceus</i> (Frölich 1799)	12	ForHim species
<i>Molops piceus</i> (Panzer 1793)	74	ForHim species
<i>Notiophilus palustris</i> (Duftschmid 1812)	2	WidGe species
<i>Oodes helopioides</i> (Fabricius 1792)	5	WidGe species
<i>Ophonus nitidulus</i> Stephens 1828	5	WidGe species
<i>Patrobus atrorufus</i> (Stroem 1768)	8	WidGe species
<i>Platynus assimilis</i> (Paykull 1790)	18	WidGe species
<i>Platynus krynickii</i> (Sperk 1835)	43	WidGe species
<i>Platynus livens</i> (Gyllenhal 1810)	20	WidGe species
<i>Poecilus cupreus</i> (Linnaeus 1758)	148	WidGe species
<i>Pterostichus anthracinus</i> (Illiger 1798)	193	WidGe species
<i>Pterostichus latoricaensis</i> (Pulpan 1965)	8	WidGe species
<i>Pterostichus macer</i> (Marsham 1802)	4	WidGe species
<i>Pterostichus melas</i> (Creutzer 1799)	2148	ForHim species
<i>Pterostichus melanarius</i> (Illiger 1798)	59	WidGe species
<i>Pterostichus minor</i> (Gyllenhal 1827)	2	WidGe species
<i>Pterostichus niger</i> (Schaller 1783)	196	WidGe species
<i>Pterostichus oblongopunctatus</i> (Fabricius 1787)	903	WidGe species
<i>Pterostichus ovoideus</i> (Sturm 1824)	151	WidGe species
<i>Pterostichus strenuus</i> (Panzer 1797)	27	WidGe species
<i>Stomis pumicatus</i> (Panzer 1796)	18	WidGe species
<i>Synuchus vivalis</i> (Illiger 1798)	53	WidGe species
<i>Trechus quadristriatus</i> (Schrank, 1781)	145	WidGe species