

## **The influence of matrix habitat on ground beetle (Carabidae) species richness patterns in habitat islands**

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### **Abstract**

The influence of matrix species on the species - area relationship was tested in a real habitat island situation. Ground beetles (Carabidae) were studied by pitfall trapping in lowland-growing mountain forest fragments in NE Hungary and the Ukraine. There were a total of 56 species, and 48 of these were classified as "matrix" species (not specialists of mountain forests). There was a significant negative correlation between forest fragment size and both the total number of species and the number of matrix species, while a significant positive correlation between the forest fragment size and the number of forest specialist species.

Because of their higher richness, matrix species inverted the slope of the species-area relationship.

**Key words:** Habitat fragmentation, forest fragments, matrix species, island biogeography theory, carabids

## Introduction

The theory of island biogeography (MacArthur & Wilson, 1967), although first suggested to describe species richness patterns on real islands, was soon extended to terrestrial habitat islands such as mountaintops (Diamond, 1981), nature reserves (Diamond & May, 1976), even agricultural fields (Risch, 1979). One major difference between real and habitat islands is the nature of the habitat separating them (Walter, 2004). Real islands are separated by water that cannot sustain dispersers that miss their island target. Also, immigration to the islands by organisms living in the habitat separating them (i.e. water) is not expected. Terrestrial habitat islands are separated by one or more different types of terrestrial habitat. This is termed the "matrix" in which the islands are embedded (Desender, 2005). This matrix is not necessarily hostile to dispersers, and they can survive there for variable periods of time. Species living in the matrix habitat can also colonise the habitat islands and even survive/reproduce there. The importance of the nature of the matrix connecting habitat islands is gradually realised (Desender, 2005). The relationship with habitat island features can be different by the island specialists and the species living in the matrix but also colonising the habitat island (thereafter called matrix species). These species perceive the habitat differently, and their reaction to habitat islands will also be different.

A detailed, experimental study of species dynamics on habitat islands, mainly concentrating on plants, is reported by Holt *et al.* (1995). In a recent publication, Cook *et al.* (2002) re-analysed this study and showed that the indiscriminate inclusion of matrix species present in habitat islands can distort the species - area relationship. When the matrix species were excluded, the significance of the species-area relationship increased. They conclude that: "further refinements of the paradigm are necessary to adapt and broaden the theory. For island biogeography theory to be applied to terrestrial habitat 'islands' which are heterogeneous and subject to edge effects, methodological allowances need to be made for the likelihood that species can colonise the 'islands' from the sea..." (Cook *et al.*, 2002).

In this contribution, we evaluated the effect of matrix species on the species-area relationship to test whether the relationships reported for plants in a manipulated, fine-scale "habitat island experiment" (Cook *et al.*, 2002) can also be detected for an arthropod group living in "real", large-scale habitat islands? We found that matrix species made a significant contribution to the ground beetle fauna in the large-scale fragmented forest habitat island setting and their indiscriminate inclusion can seriously distort the species-area relationship.

## Material and methods

### Study area and sampling

We selected ground beetles (Coleoptera, Carabidae) as test organisms. Carabids form a species-rich beetle family, and are widespread in many types of habitats, including forest fragments (Lövei & Sunderland, 1996). Forest fragments are 'real' habitat islands, formed either naturally, or as a consequence of human activities (Murcia, 1995). We used the carabid material collected over five years (1995-1999) from 19 forest fragments, ranging from 41ha to 3995 ha, located on the Bereg Plain (Magura *et al.*, 2001). The Bereg Plain is at the foot of the Carpathian Mountains, partly in NE Hungary and partly in the Ukraine. This is a relatively undisturbed, forested marginal area of the Great Hungarian Plain. Even in recent times, the area was covered by continuous woodland dominated by 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 lowlands. Due to agricultural activities and forest management in the 20<sup>th</sup> century, this once-continuous woodland became fragmented into patches. These patches of the original mountain forest are now embedded in a matrix of cultivated fields, meadows and other lowland forest patches. The remarkable feature of the carabid fauna is the occurrence of species characteristic of closed canopy deciduous forests of hills and mountains that usually do not occur in lowlands. The original mountain forest patches could be distinguished because they belong to the *Quercus robur*-*Carpinetum* association; the lowland-forest patches were here considered part of the matrix.

Beetles were collected using unbaited pitfall traps, consisting of plastic cups with 70% ethylene glycol as a killing and preserving solution. There were 9-18 traps/fragment, scattered randomly within individual fragments, and checked monthly from April to October. Further details on sampling and handling are in Magura *et al.* (2001).

### Data analyses

The area of the mountain forest islands was measured by the ArcView GIS program package on a digitised 1:25000 map. The 19 studied forest fragments were divided into three area categories (small: <500 ha, medium: 500-1500 ha, large: >1500 ha) and the mean species numbers in the different categories were compared using a one-way Analysis of Variance (ANOVA). Normal distribution of the data was achieved by  $\log(x+1)$  transformation. When ANOVA revealed a significant difference between the means, an LSD (least significant difference) test was performed for multiple comparison among means (Sokal & Rohlf, 1995).

Linear regression analysis was used to examine the relationships between the area of the forest fragment and the total number of carabid species in the fragment, the number of forest specialist species, and the number of matrix species. The categorisation of species is based on local habitat preference information, including Szél (1996), and our previous studies (Magura *et al.*, 2000, 2001).

## Results

The species richness in all fragments combined was 56 species, dominated by the 48 matrix species. Eight species were identified as mountain forest specialists: *Abax parallelus*, *Carabus arcensis*, *C. intricatus*, *Cychrus caraboides*, *Cymindis cingulata*, *Leistus piceus*, *Molops piceus*, and *Pterostichus melas*.

One-way ANOVA on the total species richness and the richness of matrix species did not indicate significant differences by fragment size class (Table 1). However, it detected significantly greater richness of the forest species in large patches than in the small and medium sized fragments (Table 1). There was also a significant difference by fragment size class in the ratio matrix species / total species: small and medium fragments had relatively more matrix species than large fragments.

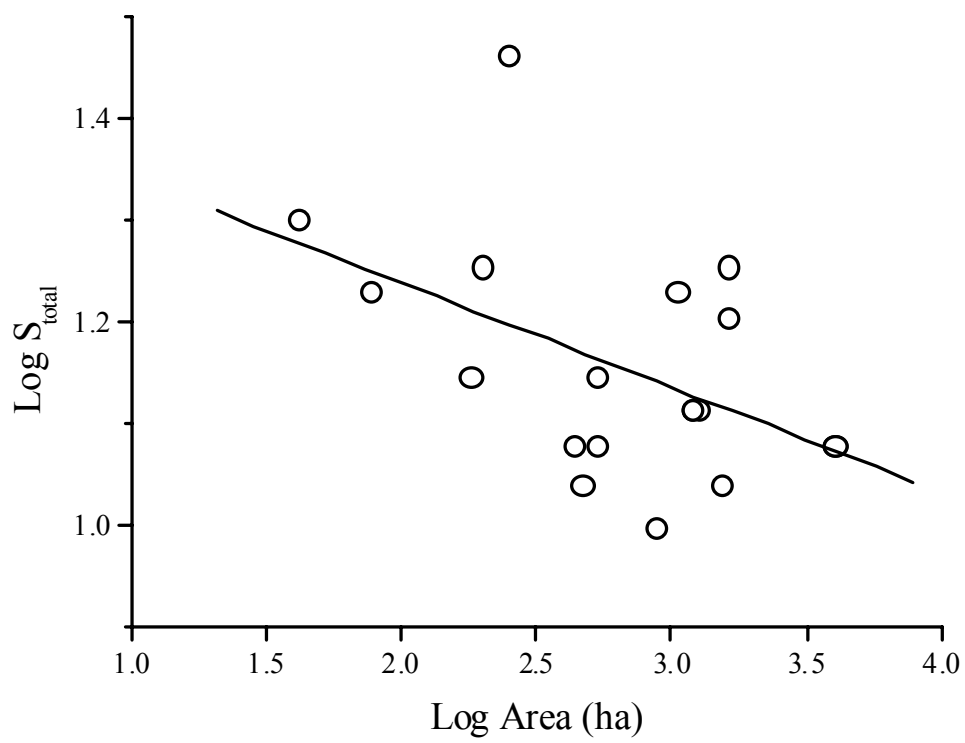
There was a significant negative ( $R=0.4846$ ,  $F(1,17)=5.2161$ ,  $p=0.0355$ ,  $n=19$ ) relationship between the size of the forest fragment and the total number of species (log-log scale, Fig. 1a).

Forest fragment size and the number of matrix species (Fig. 1b, log-log scale) showed a significant negative relationship ( $R=0.5372$ ,  $F(1,17)=6.8956$ ,  $p=0.0177$ ,  $n=19$ ). The forest fragment size and the ratio of matrix species to the total species showed a marginally significant negative relationship ( $R=0.4504$ ,  $F(1,17)=4.3275$ ,  $p=0.0529$ ,  $n=19$ ). The smaller the fragment, the larger part of the fauna belonged to the matrix species category.

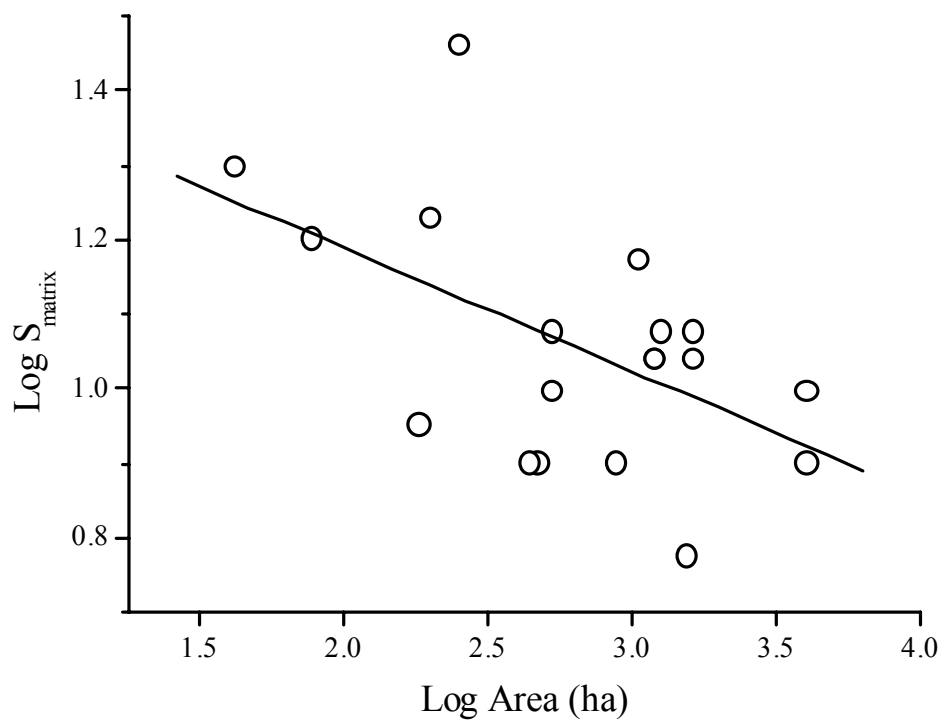
However, there was a significant positive ( $R=0.4925$ ,  $F(1,17)=5.4427$ ,  $p=0.0322$ ,  $n=19$ ) relationship between the size of the forest fragment and the number of forest specialist species (Fig. 1c, log-log scale).

**Table 1. Results of one-way ANOVAs on species numbers in relation to forest fragment size. The 19 studied forest fragments were divided into three groups: (Small: <500 ha, 7 fragments; Medium: 500-1500 ha, 7 fragments; Large: >1500 ha, 5 fragments) and the logarithm of the mean species numbers and the logarithm of matrix species/total species ratio were compared using a one-way ANOVA. If the one-way ANOVA indicated significant differences between samples, then an LSD (least significant difference) test was applied. Post hoc test results indicate which area group differs significantly ( $p<0.05$ ) from the others; for example, S=M<L indicates that species richness was significantly higher in large (L) forests than in the medium (M) and small (S) forests.**

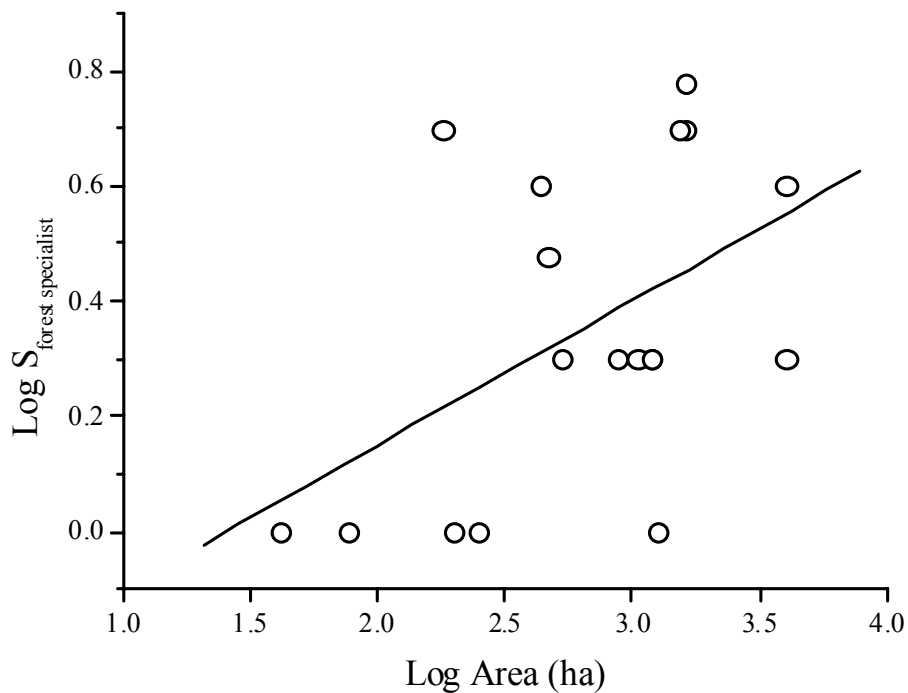
	Source	SS	d.f.	MS	F	p	Post hoc test
<i>All species</i>	Between Groups	0.036	2	0.018	1.767	0.203	
	Within Groups	0.165	16	0.010			
	Total	0.202	18				
<i>Matrix species</i>	Between Groups	0.080	2	0.040	1.920	0.179	
	Within Groups	0.332	16	0.021			
	Total	0.412	18				
<i>Forest species</i>	Between Groups	0.344	2	0.172	3.825	0.044	S=M<L
	Within Groups	0.719	16	0.045			
	Total	1.063	18				
<i>Matrix species / Total species ratio</i>	Between Groups	0.007	2	0.003	4.340	0.031	S=M>L
	Within Groups	0.012	16	0.001			
	Total	0.019	18				



**Figure 1a.**



**Figure 1b.**



**Figure 1c.**

**Figure 1. Relationship between the area of forest fragment and the number of (a) total ground beetle species; (b) matrix species, (c) forest specialist species on the Bereg Plain in NE Hungary and Ukraine, 1995-1999. All regressions are significant (details see in the text).**

## Discussion

Several of the relationships found in forest fragments between habitat island area and species numbers in the NE Hungarian Plain ran contrary to the expected positive relationship. Larger fragments had fewer ground beetle species. This pattern was caused by the matrix species that were more common in smaller fragments. The number of forest specialists and habitat area showed a positive relationship, conforming to the conventional prediction of the island biogeography theory. The distinction between matrix and "island" species is warranted but not entirely new. Several authors studying ground beetles (Bauer, 1989; De Vries, 1994; Magura *et al.*, 2001) emphasised that during the study of habitat islands, distinction should be made among species of different habitat affinity. There are species that truly perceive the habitat fragments as islands, and are unable to survive in the surrounding matrix, and those that occur in both the fragment and the matrix. Matrix species did not perceive the fragment as an island.

There can be remarkable differences in the relative importance of the matrix species in comparison to plants. In Holt *et al.*'s (1995) experiments, the share of matrix species was 23%, while in our material 86% of the species pool consisted of matrix species. This deviation in the share of matrix species could be a general difference between groups of low mobility (plants) vs. high mobility (insects). It may also be due to a large pool of open-area generalist species compared to forest species among carabid beetles. If a similar analysis was made on xylophagous beetles (such as Cerambycidae), we would not expect matrix species to invert the relationship, simply because there would be few matrix species.

The definition of "matrix" species can be based on different considerations. For example, Cook *et al.* (2002) define 'matrix' species as any species occurring outside their experimental islands. This was based on empirical data, yet it is a significant simplification. The mere occurrence in a habitat, especially for mobile organisms, does not indicate ecological links to that habitat. There can be a significant share of "tourists" in arthropod assemblages (Novotny & Missa, 2000). We defined the habitat affinities (forest specialists, matrix species) based on the literature and our earlier data. We had no parallel sampling in the matrix of this landscape to prove that the matrix species really occurred outside the fragments. However, the habitat affinities of ground beetles are well known and reliably documented (Lövei & Sunderland, 1996) so the allocations could be made with confidence. We believe that a quantitative statistical method such as TWINSpan (Hill *et al.*, 1975) or the IndVal procedure (Dufrêne & Legendre, 1997) would be able to identify true matrix species more precisely.

We should also emphasise the special nature of the studied forest fragments. These forest fragments represent remnants of the Carpathian high mountain forests growing on the lowland (Magura *et al.*, 2001). There were other types of forest fragments in the area, but carabids occurring in these forested fragments were considered matrix species. "Forest specialists" in our context meant species that are restricted to these special types of forests.

In Cook *et al.*'s (2002) experiments, the removal of matrix species increased the strength of the relationship between the species richness and patch size. We note, however, that the relationship remained non-significant. In our study, the relationships were significant, and the impact was even more dramatic: when the matrix species were excluded from the analysis the whole relationship was turned around.

The smallest fragment in our study was still much larger (41 ha) than the assumed minimum necessary for self-sustaining ground beetle populations (about 1 ha, Mader 1984). Including smaller fragments could possibly strengthen the relationship documented.

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