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PAPER



# The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands

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## ABSTRACT

**Aim** The aim of this study was to analyse whether, and how, the inclusion of habitat specialists and edge-preferring species modifies the species–area relationship predictions of the island biogeography theory for an insect group (ground beetles, Coleoptera: Carabidae) living in natural fragments. Species–habitat island area relationships applied to terrestrial habitat islands can be distorted by the indiscriminate inclusion of all species occurring in the fragments. Matrices surrounding terrestrial habitat fragments can provide colonists that do not necessarily distinguish the fragment from the matrix and can survive and reproduce there. Edge-preferring species can further distort the expected relationship, as smaller fragments have larger edge:core ratios.

**Location** Nineteen forest fragments were studied in the Bereg Plain, Hungary, and SW Ukraine. This area contains natural forest patches, mainly of oak and hornbeam, and supports a mountain entomofauna.

**Methods** Ground beetles (Carabidae) present in the 19 forest patches were categorized into generalists, forest specialists and edge-preferring species. We analysed the relationship between species richness and fragment area using species richness in the different categories.

**Results** The assemblages contained a high share of generalist species (species that occur also in the surrounding matrix). Forest patch size and the number of generalist species showed a marginally significant negative relationship, indicating that generalist species were more important in smaller patches. Forest specialist species richness was correlated positively with patch area. Edge-preferring species were shown to influence the species–area relationship: the number of edge-preferring species increased with the edge:area ratio.

**Main conclusions** Both generalist and edge-preferring species can considerably distort the species–area relationship. Island biogeography theory can be applied to habitat islands only if the habitat islands are defined correctly from the viewpoint of the target species.

## Keywords

Edge-preferring species, forest patches, forest species, generalist species, island biogeography.

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## INTRODUCTION

One of the most influential of ecological concepts is MacArthur & Wilson's theory of island biogeography (MacArthur & Wilson, 1967). The original theory considered real islands, but the

concept was soon applied to habitat islands and became an important study topic with strong links to conservation biology (Harris, 1984). The major difference between real and habitat islands is the nature of the surrounding matrix. In real islands, the surrounding matrix is usually hostile to organisms occurring

on islands (although whether this is a significant barrier depends on the dispersal ability of the organisms concerned; see Báldi & Kisbenedek, 1999). In the case of terrestrial habitat islands, the matrix is usually less hostile (Gascon & Lovejoy, 1998; Ås, 1999; Hobbs, 2001) and can contain its own set of species ('matrix species'). Such matrix species can also occur in the habitat islands themselves. Larger habitat islands or those closer to a colonist source area do not always have more species (Holt *et al.*, 1995), but this could arise because of the indiscriminate inclusion of such 'matrix species' (Cook *et al.*, 2002). Such results lead to a call for 'further refinements of the paradigm ... 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 colonize the 'islands' from the sea ...' (Cook *et al.*, 2002).

Habitat fragments are not uniform, but have well-defined edges. Edges are transition zones between adjacent habitats and form ecotones (Holland *et al.*, 1991). Forest edges, for example, have distinct microclimates, abrupt changes in light regimen, substrate and water conditions and are generally rich in microhabitats (Murcia, 1995; Didham & Lawton, 1999). This gives rise to 'edge-preferring species' that are characteristic of edge habitats (Odum, 1971; for insects: Magura *et al.*, 2001b). With the fragmentation of habitats, edges are becoming proportionately greater relative to interiors (Saunders *et al.*, 1991). We hypothesize that the existence of edge-preferring species can also have important implications for the species richness–area relationship.

In the present study, we evaluated the ground beetle (Coleoptera: Carabidae) fauna in natural forest patches (= habitat islands) in NE Hungary and SW Ukraine to examine the impact of matrix/generalist, forest specialist and edge-preferring species on the species–area relationship.

## MATERIALS AND METHODS

### Study area and sampling

We selected ground beetles (Carabidae) as test organisms. Ground beetles form a species-rich beetle family and are widespread in many types of habitats, including forest fragments (Lövei & Sunderland, 1996). Forest fragments can be 'natural' habitat islands, formed naturally (e.g. forest patches in lowlands), or 'artificial' islands as a consequence of human activities (Murcia, 1995). We used data collected over 5 years (1995–99) from 19 forest patches (Table 1), ranging in size from 41 ha to 3995 ha, located on the Bereg Plain in NE Hungary and in SW Ukraine (Magura *et al.*, 2001a). This is a relatively undisturbed, forested, marginal area of the Great Hungarian Plain. The 'matrix' is composed of a mosaic of grasslands and non-intensively cultivated fields. All the patches sampled were natural, although their degree of isolation has probably changed during the gradual transformation of the landscape. The forest fragments studied were dominated by oak (*Quercus robur*), with varying densities of *Fraxinus angustifolia* ssp. *pannonica* and hornbeam (*Carpinus betulus*). In the shrub layer, *Pyrus pyraeaster*, *Crataegus monogyna*,

**Table 1** Name, area-related characteristics, number of pitfall traps and number of ground beetle species by habitat affinity category captured in the forest fragments studied on the Bereg Plain, NE Hungary and Ukraine. Fragments are arranged by decreasing numbers of all carabid species caught

Site	Area (ha)	Perimeter (m)	Shape-index	Number of pitfall traps	Number of			
					All species caught	Forest specialist species	Edge preferring species	Generalist species
Peres	249	7,077	1.26	12	29	0	3	26
Téglás	41	2,588	1.14	12	20	0	3	17
Déda, Hungary	197	7,544	1.51	18	18	1	4	13
Rafajna, 1996	1609	16,467	1.16	12	18	6	2	10
Déda, Ukraine	76	3,555	1.14	12	17	1	5	11
Lónya	1047	21,871	1.91	18	17	2	5	10
Rafajna, 1998	1609	16,467	1.16	9	16	5	3	8
Puskinó, 1998	523	11,883	1.47	9	14	2	4	8
Munkács	180	6,145	1.29	9	14	5	3	6
Bockerek	1249	45,822	3.66	18	13	1	4	8
Dobrony, 1996	1191	22,672	1.85	12	13	2	3	8
Dobrony, 1997	1191	22,672	1.85	9	13	2	3	8
Beregújfalu, 1998	3995	48,954	2.18	9	12	4	3	5
Puskinó, 1999	523	11,883	1.47	9	12	2	3	7
Beregújfalu, 1999	3995	48,954	2.18	9	12	2	3	7
Gát	437	12,922	1.74	9	12	4	3	5
Alsóremete	463	12,594	1.65	9	11	3	5	3
Alsókerepec	1520	21,478	1.55	9	11	5	2	4
Gút	871	19,233	1.84	9	10	2	3	5

*Euonymus europaeus*, *Corylus avellana* and *Cornus sanguinea* were common, while the herb layer was moderate. The special feature of the carabid fauna in these patches is the occurrence of species characteristic of closed-canopy deciduous forests of hills and mountains. Such species do not usually occur in lowlands (Szél, 1996). We considered only these species to be 'forest specialists'. 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 patch<sup>-1</sup> (depending on the area) scattered randomly within individual patches, and these were checked monthly from April to October. Trapping effort per patch was somewhat uneven due to logistical constraints, but this did not influence the number of forest or edge species (results not shown). Further, as we sampled monthly from April to October and analysed species richness and not abundance, trap density is unlikely to affect our results.

### Data analyses

The area of the forest islands was measured using the ArcView GIS program package on a digitized 1 : 25,000 map. The area of the forest edge was calculated as the product of the perimeter of the forest patches and the width of the forest edge, taken as 5 m. This width is appropriate for ground beetles (Magura *et al.*, 2000). The shape of forests was characterized by the shape index (Patton, 1975). It is defined as:

$$AI = P / \left( 200 \cdot \sqrt{\pi \cdot A} \right)$$

where  $P$  is the perimeter of the forest patch (m) and  $A$  is patch area (ha). Its value is 1 for a round-shaped forest fragment, while values greater than 1 represent deviation from circularity (Laurence & Yensen, 1991).

Linear regression analysis (on log-transformed data) was used to examine the relationships between the studied variables (area of the forest fragment, proportion of the edge area to the total fragment area, shape index) and the total number of carabid species in the fragment, the number of forest specialist species, the number of generalist (matrix) species and the number of edge-preferring species. The categorization of species is based on Szél (1996), Húrka (1996) and our previous studies at other sites in Hungary (Magura *et al.*, 2000, 2001b). Based on these, we classified species into categories as follows:

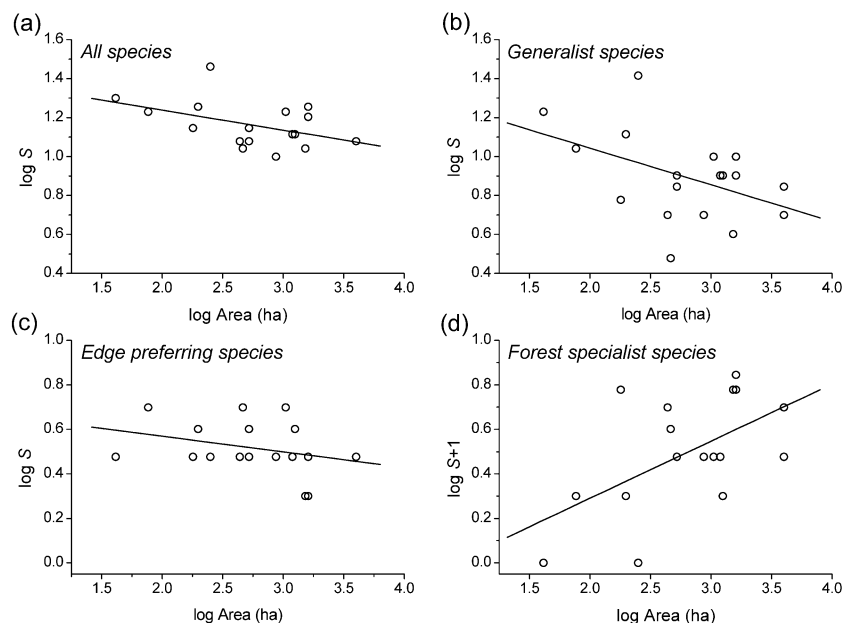
- forest specialists: species inhabiting hills and mountains that in our study area occur exclusively in the native deciduous forests;
- edge-preferring species: species reported as occurring at the edges of deciduous forest fragments; and
- generalist (matrix) species: species that occur reportedly in both forest and matrix (grasslands and cultivated land) equally.

### RESULTS

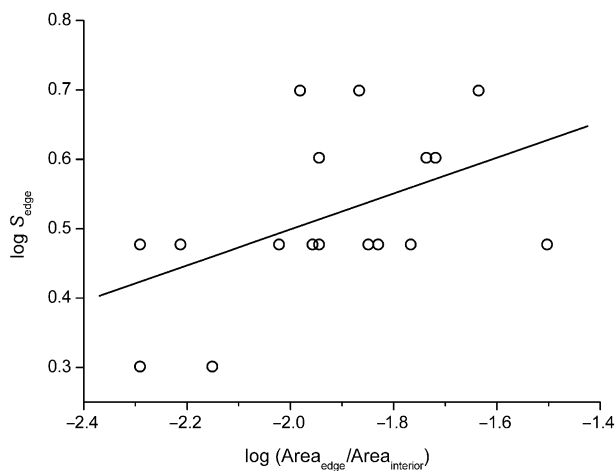
The species richness in all patches combined was 56 species, dominated by the 41 generalist (matrix) species (Appendix 1). Seven species were identified as edge-preferring species, comparable to the number of forest specialists (eight species).

There was a significant negative relationship between species richness and the area of forest concerning all captured carabid species ( $R = -0.49$ ,  $F_{(1,17)} = 5.22$ ,  $P = 0.04$ , Fig. 1a). Forest patch size and the number of generalist species showed a marginally significant negative relationship ( $R = -0.46$ ,  $F_{(1,17)} = 4.45$ ,  $P = 0.05$ , Fig. 1b). These species did not respond to these forest patches as if they were islands.

The number of edge-preferring species vs. the area of the forest patch showed a negative but not significant relationship ( $R = -0.33$ ,  $F_{(1,17)} = 2.09$ ,  $P = 0.17$ , Fig. 1c). The number of edge



**Figure 1** Relationship between habitat island area and species number in ground beetles (Carabidae) with different habitat affinities. The habitat islands are forest patches in NE Hungary and in SW Ukraine. (a) The relationship for all species was negative ( $R = -0.49$ ,  $F_{(1,17)} = 5.22$ ,  $P = 0.04$ ), caused mainly by the generalist species (b) ( $R = -0.46$ ,  $F_{(1,17)} = 4.45$ ,  $P = 0.05$ ). (c) Edge-preferring species did not show a significant relationship with area ( $R = -0.33$ ,  $F_{(1,17)} = 2.09$ ,  $P = 0.17$ ). (d) Forest specialist species showed a significant positive relationship with area ( $R = 0.56$ ,  $F_{(1,17)} = 7.80$ ,  $P = 0.01$ ).



**Figure 2** Relationship between number of edge-preferring species and area of edge in relation to the interior of the patch. The edge is defined as the outer 5 m of the fragment, and was calculated from the map of the actual patches (see Materials and Methods section for details). Smaller patches have relatively larger edge areas than large patches, and the importance of edge species increases correspondingly.

preferring species was unrelated to the shape index ( $R = 0.22$ ,  $F_{(1,17)} = 0.88$ ,  $P = 0.36$ ). However, the number of edge-preferring species is expected to be dependent not on the total area of the fragment, but rather on the ratio of the edge area to the total area. The smaller patches had a relatively larger edge area, and this was reflected by the significant positive relationship between the number of edge-preferring species and the edge:total area ratio ( $R = 0.51$ ,  $F_{(1,17)} = 5.84$ ,  $P = 0.03$ , Fig. 2). Furthermore, a significant negative relationship was found between the edge-preferring species:forest specialist species ratio and the patch size ( $R = -0.50$ ,  $F_{(1,17)} = 5.56$ ,  $P = 0.03$ ). All these results indicated the increasing importance of edge species with decreasing patch size.

There was a significant positive ( $R = 0.56$ ,  $F_{(1,17)} = 7.80$ ,  $P = 0.01$ ) relationship between the size of the forest patch and the number of forest specialist species (Fig. 1d).

## DISCUSSION

The original theory of island biogeography (MacArthur & Wilson, 1967) took into account size and isolation, but not the change in habitat quality that occurs near edges. This would have different consequences, depending on whether species avoid or are attracted to the specific edge type. We evaluated whether considering this aspect would modify or strengthen the expected relationship between area and species richness. Isolation in our setting was not relevant, as all fragments were relatively far from any potential 'source' area (the Carpathian Mountains).

The importance of edges has been recognized intuitively (Murcia, 1995), but studies of forest fragments are dominated by human-generated fragments (Desender, 2005) that are often without a natural edge, and a conceptual basis for edge studies

has been lacking until recently (Ries & Sisk, 2004). Our study demonstrated clearly the impact of both generalist and edge species on the shape and strength of the species–area relationship in forest fragments.

Comparing our results to those dealing with plants, there were remarkable differences in species composition by class. Among plants in Holt *et al.*'s (1995) experiments the share of generalist species was 23%, while in our material 73% of the species pool consisted of generalist species. In our study, the number of forest specialists and the number of edge-preferring species were almost equal, indicating that the latter formed a significant component of the fauna.

We defined the habitat affinities of the three groups (forest and edge-preferring species, generalist species) based on the literature and our earlier data. Even though we had no parallel sampling in the matrix, the habitat affinities of ground beetles are well known and documented reliably (Lövei & Sunderland, 1996), so the generalist species could be identified with confidence.

In spite of these differences, for an insect group and real habitat islands our results corroborated that the presence of generalist species can mask the species richness–area relationship as stated by Cook *et al.* (2002). The distinction between matrix and 'island' species is warranted, but is not entirely new. Several authors studying ground beetles (Bauer, 1989; De Vries, 1994; Magura *et al.*, 2001a) have emphasized that during the study of habitat islands, a distinction should be made between 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.

Cook *et al.* (2002) define 'matrix' species as any species occurring outside their experimental islands. This is a significant simplification, as the mere occurrence in a habitat, especially in mobile organisms, does not indicate ecological links to that habitat. There can be a significant occurrence of 'tourists' in arthropod assemblages (Novotny & Missa, 2000).

The removal of matrix species is expected to increase the strength of the relationship between species richness and patch size (Cook *et al.*, 2002). We demonstrated that after removing not only the generalist/matrix species, but also the edge-preferring species (retaining only the forest species for which the habitat fragments are islands), the strength of the species richness–area relationship increased. Moreover, the negative relationship between total species richness and forest area became positive, as predicted by the theory of island biogeography.

Further, we demonstrated that the significance of the edge-preferring species within the fauna is related to the proportion of the edge area to the total fragment area. The relationship between the proportion of edge-preferring species and fragment size is, logically, a negative one: the smaller the fragment, the more significant are the edge species in the fauna. Their species richness or their density (Bender *et al.*, 1998) can increase. The area of the edge does not necessarily decrease with the decreasing fragment size, as it depends on the shape of the fragment, its area and the structure of the edge (Didham & Lawton, 1999).

It is probable that the relationship between patch area and edge species is not a simple one. Edge species require the presence of two

habitats with different structures and environmental conditions that together form the special 'edge' conditions (Ries & Sisk, 2004). If the fragment is too small the presence of one of these habitat types, the 'inner' one, can be absent. A forest patch needs to be of a minimum size to create conditions characteristic for forest interior, and this is not possible below a certain size. This minimum required size can vary depending on geographic location, habitat structure or the age of the fragment. Actual figures for ground beetles can be 0.5 ha (Mader, 1984) to tens of hectares (Niemelä, 2001). In our study the smallest fragment was 41 ha (Magura *et al.*, 2001a), sufficient for forest interior habitat to exist.

In summary, we have verified that not only matrix/generalist species but also edge-preferring species can mask the relationship between species richness of carabids and the area of habitat islands.

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Influence of matrix and edge on fragment species richness

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**Appendix 1** Habitat affinity categorization, based on literature and field sampling from other habitats evaluated by the IndVal method (Dufrêne & Legendre, 1997), of the collected carabid species in the Bereg Plain, NE Hungary and Ukraine, between 1995 and 1999.

Generalist species: species equally abundant in the forests and the matrix; forest specialist species: species appearing exclusively in the forests; edge-preferring species: species concentrating at the forest edge

Species	Habitat affinity
<i>Abax carinatus</i> (Duftschmid, 1812)	Edge-preferring species
<i>Abax parallelepipedus</i> (Piller et Mitterpacher, 1783)	Generalist species
<i>Abax parallelus</i> (Duftschmid, 1812)	Forest specialist species
<i>Agonum micans</i> (Nicolai, 1822)	Generalist species
<i>Agonum moestum</i> (Duftschmid, 1812)	Generalist species
<i>Platynus obscurus</i> (Herbst, 1784)	Generalist species
<i>Amara saphyrea</i> Dejean, 1828	Generalist species
<i>Amara similata</i> (Gyllenhal, 1810)	Generalist species
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	Generalist species
<i>Badister bullatus</i> (Schränk, 1798)	Generalist species
<i>Bembidion biguttatum</i> (Fabricius, 1779)	Generalist species
<i>Blethisa multipunctata</i> (Linnaeus, 1758)	Generalist species
<i>Brachinus crepitans</i> (Linnaeus, 1758)	Generalist species
<i>Calosoma inquisitor</i> (Linnaeus, 1758)	Generalist species
<i>Carabus arcensis carpathus</i> Born, 1902	Forest specialist species
<i>Carabus cancellatus</i> Reitter, 1896	Generalist species
<i>Carabus clathratus</i> Linnaeus, 1761	Generalist species
<i>Carabus convexus</i> (Fabricius, 1775)	Edge-preferring species
<i>Carabus coriaceus</i> Linnaeus, 1758	Edge-preferring species
<i>Carabus granulatus</i> Linnaeus, 1758	Generalist species
<i>Carabus hampei ormayi</i> Reitter, 1896	Generalist species
<i>Carabus intricatus</i> Linnaeus, 1761	Forest specialist species
<i>Carabus ullrichi</i> Germar, 1824	Generalist species
<i>Carabus violaceus</i> Linnaeus, 1758	Generalist species
<i>Chlaenius nitidulus</i> (Schränk, 1781)	Generalist species
<i>Clivina fossor</i> (Linnaeus, 1758)	Generalist species
<i>Cychrus caraboides</i> (Linnaeus, 1758)	Forest specialist species
<i>Cymindis cingulata</i> Dejean, 1825	Forest specialist species
<i>Elaphrus cupreus</i> Duftschmid, 1812	Generalist species
<i>Harpalus latus</i> Linnaeus, 1758	Edge-preferring species
<i>Harpalus dimidiatus</i> (Rossi, 1791)	Generalist species
<i>Harpalus rufipes</i> (De Geer, 1774)	Edge-preferring species
<i>Licinus depressus</i> (Paykull, 1790)	Generalist species
<i>Leistus piceus</i> Frölich, 1799	Forest specialist species
<i>Molops piceus</i> (Panzer, 1793)	Forest specialist species
<i>Notiophilus palustris</i> (Duftschmid, 1812)	Generalist species
<i>Oodes helopioides</i> (Fabricius, 1792)	Generalist species
<i>Ophonus nitidulus</i> Stephens, 1828	Edge-preferring species
<i>Patrobus atrorufus</i> (Stroem, 1768)	Generalist species
<i>Platynus assimilis</i> (Paykull, 1790)	Generalist species
<i>Platynus krynickii</i> (Sperk, 1835)	Generalist species
<i>Platynus livens</i> (Gyllenhal, 1810)	Generalist species
<i>Poecilus cupreus</i> (Linnaeus, 1758)	Generalist species
<i>Pterostichus anthracinus</i> (Illiger, 1798)	Generalist species
<i>Pterostichus latoricaensis</i> Pulpan, 1965	Generalist species
<i>Pterostichus macer</i> (Marsham, 1802)	Generalist species
<i>Pterostichus melas</i> (Creutzer, 1799)	Generalist species
<i>Pterostichus melanarius</i> (Illiger, 1798)	Generalist species
<i>Pterostichus minor</i> (Gyllenhal, 1827)	Generalist species
<i>Pterostichus niger</i> (Schaller, 1783)	Edge-preferring species
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	Generalist species
<i>Pterostichus ovoideus</i> (Sturm, 1824)	Generalist species
<i>Pterostichus strenuus</i> (Panzer, 1797)	Generalist species
<i>Stomis pumicatus</i> (Panzer, 1796)	Generalist species
<i>Synuchus vivalis</i> (Illiger, 1798)	Generalist species
<i>Trechus quadristriatus</i> (Schränk, 1781)	Generalist species