1 The influence of matrix and edges on species richness patterns of ground beetles 2 (Coleoptera, Carabidae) in habitat islands 3 Gábor L. Lövei^{1*}. Tibor Magura^{2,3}. Béla Tóthmérész⁴ and Viktor Ködöböcz² 4 5 ¹Department of Integrated Pest Management, Danish Institute of Agricultural Sciences, 6 Flakkebierg Research Centre, DK-4200 Slagelse, Denmark 7 ²Hortobágy National Park Directorate, Debrecen, P.O.Box 216, H-4002, Hungary; 8 ³Department of Zoology, Debrecen University, Debrecen, P.O.Box 3, H-4010 Hungary; 9 ⁴Ecological Institute, Debrecen University, Debrecen, P.O.Box 71, H-4010 Hungary; 10 11 Running head: Influence of matrix & edge on fragment species richness 12 13 Keywords: edge preferring species, forest patches, forest species, generalist species, island 14 biogeography 15 16 17 *Correspondence & proofs to: 18 Gábor L. Lövei 19 Department of Integrated Pest Management, Danish Institute of Agricultural Sciences, 20 Flakkebjerg Research Centre, DK-4200 Slagelse, Denmark 21 E-mail:gabor.lovei@agrsci.dk 22 Phone: +45-88993636 23 Fax. +45-88993501 24 25

ABSTRACT

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Aim The aim of this study was to analyse whether, and how, the inclusion of habitat 26 27 specialists and edge preferring species modifies the species-area relationship predictions of 28 the island biogeography theory for an insect group (ground beetles, Coloptera: Carabidae) 29 living in natural fragments. 30 Species - habitat island area relationships applied to terrestrial habitat islands can be distorted 31 by indiscriminate inclusion of all species occurring in the fragments. Matrices surrounding terrestrial habitat fragments can provide colonists that do not necessarily distinguish the 32 33 fragment from the matrix and can survive and reproduce there. Edge-preferring species can 34 further distort the expected relationship, as smaller fragments have larger edge/core ratios. 35 **Location** Nineteen forest fragments were studied in the Bereg Plain, Hungary and SW 36 Ukraine. This area contains natural forest patches, mainly of oak and hornbeam, and supports 37 a mountain entomofauna. 38 Methods Ground beetles (Carabidae) present in the 19 forest patches were categorised into 39 generalists, forest specialists, and edge-preferring species. We analysed the relationship 40 between species richness and fragment area using species richness in the different categories. 41 **Results** The assemblages contained a high share of generalist species (species that occur also 42 in the surrounding matrix). Forest patch size and the number of generalist species showed a 43 marginally significant negative relationship, indicating that generalist species were more 44 important in smaller patches. Forest specialist species richness was positively correlated with 45 patch area. Edge-preferring species were shown to influence the species-area relationship: the 46 number of edge-preferring species increased with the edge/area ratio. 47 Main conclusions Both generalist and edge preferring species can considerably distort the 48 species-area relationship. Island biogeography theory can be applied to habitat islands only if 49 the habitat islands are defined correctly from the viewpoint of the target species.

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INTRODUCTION

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One of the most influential of ecological concepts is MacArthur and Wilson's Island Biogeography Theory (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 their set of species ("matrix species"). Such matrix species can also occur in the habitat islands themselves. Larger habitat islands or ones 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", 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 hypothesise that the existence of edge-preferring species can also have important implications for the species richness-area relationship.

In the present contribution, 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 speciesarea relationship.

MATERIAL 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' ones as a consequence of human activities (Murcia, 1995). We used data collected over five years (1995-1999) from 19 forest patches (Table 1), with their size ranging from 41ha 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 by 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 studied forest fragments were dominated by oak (*Quercus robur*), with varying density of *Fraxinus angustifolia ssp. pannonica* and hornbeam (*Carpinus betulus*). In the shrub layer, *Pyrus pyraster*, *Crataegus monogyna*, *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 (depending on the area), scattered randomly within individual patches, and 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 we analyzed 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 1:25000 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

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

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 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

125 specialist species, the number of generalist (matrix) species, and the number of edge 126 preferring species. The categorisation of species is based on Szél (1996), Hůrka (1996) and 127 our previous studies at other sites in Hungary (Magura et al., 2000, 2001b). Based on these, 128 we classified species into categories as follows: 129 - forest specialists: species inhabiting hills and mountains that on our study area occur 130 exclusively in the native deciduous forests 131 - edge-preferring species: species reported as occurring in the edges of deciduous forest 132 fragments 133 - generalist (matrix) species: species that reportedly occur in both forest and matrix 134 (grasslands and cultivated land) equally. 135 136 **RESULTS** 137 The species richness in all patches combined was 56 species, dominated by the 41 generalist 138 (matrix) species (Table 1). Seven species were identified as edge-preferring species, 139 comparable to the number of forest specialists (8 species). 140 There was a significant negative relationship between the species richness and the area 141 of the forest concerning all captured carabid species (R = -0.49, $F_{(1,17)} = 5.22$, P = 0.04, Fig. 1a). 142 Forest patch size and the number of generalist species showed a marginally significant 143 negative relationship (R= -0.46, $F_{(1.17)}$ =4.45, P=0.05, Fig.1b). These species did not respond 144 to these forest patches as if they were islands. 145 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 146 number of edge specialist species was unrelated to the shape index (R=0.22, $F_{(1.17)}$ =0.88, 147 148 P=0.36). However, the number of edge preferring species is expected to be dependent not on 149 the total area of the fragment, but rather on the ratio of the edge area to the total area. The

smaller patches had 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=0.49, $F_{(1,17)}$ =5.44, P=0.03) relationship between the size of the forest patch and the number of forest specialist species (Fig. 1d).

DISCUSSION

The original Island Biogeography Theory (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 intuitively recognized (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 clearly demonstrated 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 is 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 nearly 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 reliably documented (Lövei & Sunderland, 1996) so the generalist species could be identified with confidence.

In spite of these differences, our results corroborated, for an insect group and real habitat islands, 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 not entirely new. Several authors studying ground beetles (Bauer, 1989; De Vries, 1994; Magura et al., 2001a) emphasized that during the study of habitat islands, 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 the total species richness and the 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, logically, is 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 structure 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 verified that not only the matrix /generalist species, but also the edgespecialist species can mask the relationship between species richness of carabids and the area of habitat islands.

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

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Site	Area	Perimeter (m)	Shape- index	Number of pitfall	Number of			
	(ha)				All species	Forest	Edge	Generalist
				traps	caught	specialist	preferring	species
						species	species	
Peres	249	7077	1.26	12	29	0	3	26
Téglás	41	2588	1.14	12	20	0	3	17
Déda, Hungary	197	7544	1.51	18	18	1	4	13
Rafajna, 1996	1609	16467	1.16	12	18	6	2	10
Déda, Ukraine	76	3555	1.14	12	17	1	5	11
Lónya	1047	21871	1.91	18	17	2	5	10
Rafajna, 1998	1609	16467	1.16	9	16	5	3	8
Puskinó, 1998	523	11883	1.47	9	14	2	4	8
Munkács	180	6145	1.29	9	14	5	3	6
Bockerek	1249	45822	3.66	18	13	1	4	8
Dobrony, 1996	1191	22672	1.85	12	13	2	3	8
Dobrony, 1997	1191	22672	1.85	9	13	2	3	8
Beregújfalu, 1998	3995	48954	2.18	9	12	4	3	5
Puskinó, 1999	523	11883	1.47	9	12	2	3	7
Beregújfalu, 1999	3995	48954	2.18	9	12	2	3	7
Gát	437	12922	1.74	9	12	4	3	5
Alsóremete	463	12594	1.65	9	11	3	5	3
Alsókerepec	1520	21478	1.55	9	11	5	2	4
Gút	871	19233	1.84	9	10	2	3	5

Figure legends

Figure 1 The 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 (panel 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 The relationship between the number of edge-preferring species and the 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 Material and Methods section for details). Smaller patches have relatively larger edge areas than large patches, and the importance of edge species correspondingly increases (R = 0.51, $F_{(1,17)} = 5.84$, P = 0.03).

APPENDIX. Habitat affinity categorisation, based on literature and field sampling from other habitats evaluated by the IndVal method (Dufrene & Legendre, 1997), of the collected carabid species in the Bereg Plain, NE Hungary and Ukraine, between 1997 -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
Abax carinatus (Duftschmid, 1812)	Edge preferring species
Abax parallelepipedus (Piller et Mitterpacher, 1783)	Generalist species
Abax parallelus (Duftschmid, 1812)	Forest specialist species
Agonum micans (Nicolai, 1822)	Generalist species
Agonum moestum (Duftschmid, 1812)	Generalist species
Platynus obscurus (Herbst, 1784)	Generalist species
Amara saphyrea Dejean, 1828	Generalist species
Amara similata (Gyllenhal, 1810)	Generalist species
Anisodactylus binotatus (Fabricius, 1787)	Generalist species
Badister bullatus (Schrank, 1798)	Generalist species
Bembidion biguttatum (Fabricius, 1779)	Generalist species
Blethisa multipunctata (Linnaeus, 1758)	Generalist species
Brachinus crepitans (Linnaeus, 1758)	Generalist species
Calosoma inquisitor (Linnaeus, 1758)	Generalist species
Carabus arcensis carpathus Born, 1902	Forest specialist species
Carabus cancellatus Reitter, 1896	Generalist species
Carabus clathratus Linnaeus, 1761	Generalist species
Carabus convexus (Fabricius, 1775)	Edge preferring species
Carabus coriaceus Linnaeus, 1758	Edge preferring species
Carabus granulatus Linnaeus, 1758	Generalist species
Carabus hampei ormayi Reitter, 1896	Generalist species
Carabus intricatus Linnaeus, 1761	Forest specialist species
Carabus ullrichi Germar, 1824	Generalist species
Carabus violaceus Linnaeus, 1758	Generalist species
Chlaenius nitidulus (Schrank, 1781)	Generalist species
Clivina fossor (Linnaeus, 1758)	Generalist species
Cychrus caraboides (Linnaeus, 1758)	Forest specialist species
Cymindis cingulata Dejean, 1825	Forest specialist species
Elaphrus cupreus Duftschmid, 1812	Generalist species
Harpalus latus Linnaeus, 1758	Edge preferring species
Harpalus dimidiatus (Rossi, 1791)	Generalist species
Harpalus rufipes (De Geer, 1774)	Edge preferring species
Licinus depressus (Paykull, 1790)	Generalist species
Leistus piceus Frölich, 1799	Forest specialist species
Molops piceus (Panzer, 1793)	Forest specialist species
Notiophilus palustris (Duftschmid, 1812)	Generalist species
Oodes helopioides (Fabricius, 1792)	Generalist species
Ophonus nitidulus Stephens, 1828	Edge preferring species
Patrobus atrorufus (Stroem, 1768)	Generalist species
Platynus assimilis (Paykull, 1790)	Generalist species
Platynus krynickii (Sperk, 1835)	Generalist species
Platynus livens (Gyllenhal, 1810)	Generalist species

Poecilus cupreus (Linnaeus, 1758)	Generalist species
Pterostichus anthracinus (Illiger, 1798)	Generalist species
Pterostichus latoricaensis Pulpan, 1965	Generalist species
Pterostichus macer (Marsham, 1802)	Generalist species
Pterostichus melas (Creutzer, 1799)	Generalist species
Pterostichus melanarius (Illiger, 1798)	Generalist species
Pterostichus minor (Gyllenhal, 1827)	Generalist species
Pterostichus niger (Schaller, 1783)	Edge preferring species
Pterostichus oblongopunctatus (Fabricius, 1787)	Generalist species
Pterostichus ovoideus (Sturm, 1824)	Generalist species
Pterostichus strenuus (Panzer, 1797)	Generalist species
Stomis pumicatus (Panzer, 1796)	Generalist species
Synuchus vivalis (Illiger, 1798)	Generalist species
Trechus quadristriatus (Schrank,, 1781)	Generalist species

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