1   **The influence of matrix and edges on species richness patterns of ground beetles**

2   **(Coleoptera, Carabidae) in habitat islands**

3

4   Gábor L. Lövei[1*], Tibor Magura[2,3], Béla Tóthmérész[4] and Viktor Ködöböcz[2]

5   [1]Department of Integrated Pest Management, Danish Institute of Agricultural Sciences,

6   Flakkebjerg Research Centre, DK-4200 Slagelse, Denmark

7   [2]Hortobágy National Park Directorate, Debrecen, P.O.Box 216, H-4002, Hungary;

8   [3]Department of Zoology, Debrecen University, Debrecen, P.O.Box 3, H-4010 Hungary;

9   [4]Ecological 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

25   **ABSTRACT**

26   **Aim** The aim of this study was to analyse whether, and how, the inclusion of habitat

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

32   terrestrial habitat fragments can provide colonists that do not necessarily distinguish the

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.

50

INTRODUCTION

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

75 becoming proportionately greater relative to interiors (Saunders et al., 1991). We hypothesise

76 that the existence of edge-preferring species can also have important implications for the

77 species richness-area relationship.

78   In the present contribution, we evaluated the ground beetle (Coleoptera: Carabidae)

79 fauna in natural forest patches (=habitat islands) in NE Hungary and SW Ukraine, to examine

80 the impact of matrix/generalist, forest specialist and edge preferring species on the species-

81 area relationship.

82

83

84 **MATERIAL AND METHODS**

85

86 **Study area and sampling**

87 We selected ground beetles (Carabidae) as test organisms. Ground beetles form a species-rich

88 beetle family, and are widespread in many types of habitats, including forest fragments (Lövei

89 & Sunderland, 1996). Forest fragments can be 'natural' habitat islands, formed naturally (e.g.

90 forest patches in lowlands), or 'artificial' ones as a consequence of human activities (Murcia,

91 1995). We used data collected over five years (1995-1999) from 19 forest patches (Table 1),

92 with their size ranging from 41ha to 3995 ha, located on the Bereg Plain in NE Hungary and

93 in SW Ukraine (Magura et al., 2001a). This is a relatively undisturbed, forested marginal area

94 of the Great Hungarian Plain. The "matrix" is composed by a mosaic of grasslands and non-

95 intensively cultivated fields. All the patches sampled were natural, although their degree of

96 isolation has probably changed during the gradual transformation of the landscape. The

97 studied forest fragments were dominated by oak (*Quercus robur*), with varying density of

98 *Fraxinus angustifolia ssp. pannonica* and hornbeam (*Carpinus betulus*). In the shrub layer,

99 *Pyrus pyraster*, *Crataegus monogyna*, *Euonymus europaeus*, *Corylus avellana* and *Cornus*

100   *sanguinea* were common, while the herb layer was moderate. The special feature of the

101   carabid fauna in these patches is the occurrence of species characteristic of closed-canopy

102   deciduous forests of hills and mountains. Such species do not usually occur in lowlands (Szél,

103   1996). We considered only these species to be "forest specialists". Beetles were collected

104   using unbaited pitfall traps, consisting of plastic cups with 70% ethylene glycol as a killing

105   and preserving solution. There were 9-18 traps/patch (depending on the area), scattered

106   randomly within individual patches, and were checked monthly from April to October.

107   Trapping effort per patch was somewhat uneven, due to logistical constraints, but this did not

108   influence the number of forest or edge species (results not shown). Further, as we sampled

109   monthly from April to October, and we analyzed species richness and not abundance, trap

110   density is unlikely to affect our results.

111

112   **Data analyses**

113   The area of the forest islands was measured using the ArcView GIS program package on a

114   digitized 1:25000 map. The area of the forest edge was calculated as the product of the

115   perimeter of the forest patches and the width of the forest edge, taken as 5 m. This width is

116   appropriate for ground beetles (Magura et al., 2000). The shape of forests was characterized

117   by the shape index (Patton 1975). It is defined as

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

119   where P is the perimeter of the forest patch (m), and A is patch area (ha). Its value is 1 for a

120   round-shaped forest fragment, while values greater than 1 represent deviation from circularity

121   (Laurence & Yensen 1991).

122   Linear regression analysis was used to examine the relationships between the studied

123   variables (area of the forest fragment, proportion of the edge area to the total fragment area,

124   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

146   negative, but not significant relationship (R= – 0.33, $F_{(1,17)}$=2.09, P=0.17, Fig. 1c). The

147   number of edge specialist species was unrelated to the shape index (R=0.22, $F_{(1,17)}$=0.88,

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

150   smaller patches had relatively larger edge area, and this was reflected by the significant

151   positive relationship between the number of edge-preferring species and the edge/total area

152   ratio (R=0.51, $F_{(1,17)}$=5.84, P=0.03, Fig. 2). Furthermore, a significant negative relationship

153   was found between the edge preferring species/ forest specialist species ratio and the patch

154   size (R= –0.50, $F_{(1,17)}$=5.56, P=0.03). All these results indicated the increasing importance of

155   edge species with decreasing patch size.

156   There was a significant positive (R=0.49, $F_{(1,17)}$=5.44, P=0.03) relationship between

157   the size of the forest patch and the number of forest specialist species (Fig. 1d).

158

159

160   **DISCUSSION**

161   The original Island Biogeography Theory (MacArthur & Wilson, 1967) took into account size

162   and isolation, but not the change in habitat quality that occurs near edges. This would have

163   different consequences, depending on whether species avoid or are attracted to the specific

164   edge type. We evaluated whether considering this aspect would modify or strengthen the

165   expected relationship between area and species richness. Isolation in our setting was not

166   relevant, as all fragments were relatively far from any potential „source" area (the Carpathian

167   Mountains).

168   The importance of edges has been intuitively recognized (Murcia, 1995) but studies of

169   forest fragments are dominated by human-generated fragments (Desender, 2005) that are

170   often without a natural edge, and a conceptual basis for edge studies has been lacking until

171   recently (Ries & Sisk, 2004). Our study clearly demonstrated the impact of both generalist

172   and edge species on the shape and strength of the species-area relationship in forest fragments.

173   Comparing our results to those dealing with plants, there were remarkable differences

174   in species composition by class. Among plants in Holt et. al.'s (1995) experiments, the share

175   of generalist species is 23%, while in our material, 73% of the species pool consisted of

176   generalist species. In our study, the number of forest specialists and the number of edge

177   preferring species were nearly equal, indicating that the latter formed a significant component

178   of the fauna.

179   We defined the habitat affinities of the three groups (forest and edge-preferring

180   species, generalist species) based on the literature and our earlier data. Even though we had no

181   parallel sampling in the matrix, the habitat affinities of ground beetles are well known and

182   reliably documented (Lövei & Sunderland, 1996) so the generalist species could be identified

183   with confidence.

184   In spite of these differences, our results corroborated, for an insect group and real

185   habitat islands, that the presence of generalist species can mask the species richness- area

186   relationship as stated by Cook et al. (2002). The distinction between matrix and "island"

187   species is warranted but not entirely new. Several authors studying ground beetles (Bauer,

188   1989; De Vries, 1994; Magura et al., 2001a) emphasized that during the study of habitat

189   islands, distinction should be made between species that truly perceive the habitat fragments

190   as islands (and are unable to survive in the surrounding matrix), and those that occur in both

191   the fragment and the matrix.

192   Cook et al. (2002) define "matrix" species as any species occurring outside their

193   experimental islands. This is a significant simplification as the mere occurrence in a habitat,

194   especially in mobile organisms, does not indicate ecological links to that habitat. There can be

195   a significant occurrence of "tourists" in arthropod assemblages (Novotny & Missa, 2000).

196   The removal of matrix species is expected to increase the strength of the relationship

197   between species richness and patch size (Cook et al., 2002). We demonstrated that after

198   removing not only the generalist/matrix species, but also the edge preferring species (retaining

199   only the forest species for which the habitat fragments are islands), the strength of the species

200   richness-area relationship increased. Moreover, the negative relationship between the total

201   species richness and the forest area became positive as predicted by the theory of island

202   biogeography.

203   Further, we demonstrated that the significance of the edge preferring species within the

204   fauna is related to the proportion of the edge area to the total fragment area. The relationship

205   between the proportion of edge-preferring species and fragment size, logically, is a negative

206   one: the smaller the fragment, the more significant are the edge species in the fauna. Their

207   species richness or their density (Bender et al., 1998) can increase. The area of the edge does

208   not necessarily decrease with the decreasing fragment size, as it depends on the shape of the

209   fragment, its area, and the structure of the edge (Didham & Lawton, 1999).

210   It is probable that the relationship between patch area and edge species is not a simple

211   one. Edge species require the presence of two habitats with different structure and

212   environmental conditions that together form the special "edge" conditions (Ries & Sisk,

213   2004). If the fragment is too small, the presence of one of these habitat types, the "inner" one

214   can be absent. A forest patch needs to be of a minimum size to create conditions characteristic

215   for forest interior, and this is not possible below a certain size. This minimum required size

216   can vary, depending on geographic location, habitat structure, or the age of the fragment.

217   Actual figures for ground beetles can be 0.5 ha (Mader, 1984) to tens of hectares (Niemelä,

218   2001). In our study, the smallest fragment was 41 ha (Magura et al., 2001a), sufficient for

219   forest interior habitat to exist.

220   In summary, we verified that not only the matrix /generalist species, but also the edge-

221   specialist species can mask the relationship between species richness of carabids and the area

222   of habitat islands.

223

224   **ACKNOWLEDGEMENTS**

227

REFERENCES

229   Ås, S. (1999) Invasion of matrix species in small habitat patches. *Conservation Ecology*

230   [online] **3**(1):1. http://www.consecol.org/vol3/iss1/art1 (accessed 5 July 2005)

231   Báldi, A., & Kisbenedek, T. (1999) Species-specific distribution of reed-nesting passerine

232   birds across reed-bed edges: effects of spatial scale and edge type. *Acta Zoologica Academiae*

233   *Scientiarum Hungaricae* **45**, 97–114.

234   Bauer, L.J. (1989). Moorland beetle communities on limestone 'habitat islands'. I. isolation,

235   invasion and local species diversity in carabids and staphylinids. *Journal of Animal Ecology*

236   **58**, 1077-1098.

237   Bender, D.J., Contreras, T.A., & Fahrig, L. (1998) Habitat loss and population decline: A

238   meta-analysis of the patch size effect. *Ecology* **79,** 517–533.

239   Cook, W.M., Lane, K.T., Foster, B. L., & Holt, R.D. (2002) Island theory, matrix effects and

240   species richness patterns in habitat fragments. *Ecology Letters* **5**, 619-623.

241   Desender, K. (2005) Theory versus reality: a review on the ecological and population genetic

242   effects of forest fragmentation on wild organisms, with an emphasis on ground beetles.,.

243   *European Carabidology 2003. Proceedings of the 11th European Carabidologists Meeting.*

244   (ed. by G.L. Lövei and S. Toft), pp. 49-72. Danish Institute of Agricultural Sciences Report

245   Series No. 114., Flakkebjerg, Slagelse.

246   De Vries, H.H. (1994) Size of habitat and presence of ground beetle species. In: *Carabid*

247   *beetles: ecology and evolution* (ed. by K. Desender, K., Dufrêne, M., Loreau, M., Luff, M.L.

248   and Maelfait, J-P.), pp. 253-259, Kluwer Academic Publishers, Dordrecht.

249 Didham, R. K. & Lawton, J. H. (1999) Edge structure determines the magnitude of changes in

250 microclimate and vegetation structure in tropical forest fragments. *Biotropica,* **31**, 17-30.

251 Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a

252 flexible asymmetrical approach. *Ecological Monographs,* **67**, 345–366.

253 Gascon, C., & Lovejoy, T.E. (1998) Ecological impacts of forest fragmentation in central

254 Amazonia. *Zoological Analysis of Complex Systems* **101,** 273–280.

255 Harris, L.D. (1984) *The fragmented forest: Island Biogeography and the preservation of*

256 *biotic diversity*. University of Chicago Press, Chicago, IL, U.S.A.

257 Hobbs, R.J. (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic

258 invasions in southwestern Australia. *Conservation Biology* **15,** 1522–1528.

259 Holland, M.M., Risser, P.G. & Naiman, R.J. (1991) *Ecotones. The Role of Landscape*

260 *Boundaries in the Management and Restoration of Changing Environments*. London:

261 Chapman and Hall.

262 Holt, R.D., Robinson, G.R. & Gaines, M.S. (1995) Vegetation dynamics in an experimentally

263 fragmented landscape. *Ecology* **76**, 1610-1624.

264 Hůrka, K. (1996) *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlin, Czech

265 Republic.

266 Laurence, W.-F. & Yensen, E. (1991) Predicting the impacts of edge effects in fragmented

267 habitats. *Biological Conservation,* **55**, 45-67.

268 Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera:

269 Carabidae). *Annual Review of Entomology,* 41, 231-256.

270 MacArthur, R.H., & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton

271 University Press, Princeton, NJ, USA.

272 Mader, H-J. (1984) Animal habitat isolation by roads and agricultural fields. *Biological*

273 *Conservation,* **29**, 81-96.

274   Magura, T., Ködöböcz, V. & Tóthmérész, B. (2001a) Effects of habitat fragmentation on

275   carabids in forest patches. *Journal of Biogeography*, **28**, 129-138.

276   Magura, T., Tóthmérész, B. & Molnár, T. (2000) Spatial distribution of carabid species along

277   a grass-forest transects. *Acta Zoologica Academiae Scientiarium Hungariae*, **46**, 1-17.

278   Magura, T., Tóthmérész, B. & Molnár, T. (2001b) Forest edge and diversity: carabids along

279   forest-grassland transects. *Biodiversity and Conservation*, **10**, 287-300.

280   Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in*

281   *Ecology and Evolution,* **10**, 58–62.

282   Niemelä, J. (2001) Carabid beetles (Coleoptera, Carabidae) and habitat fragmentation: a

283   review. *European Journal of Entomology,* **98**, 127-132.

284   Novotny V, & Missa O. (2000) Local versus regional species richness in tropical insects: one

285   lowland site compared with the island of New Guinea. *Ecological Entomology,* **25**, 445-451.

286   Odum, E.P. (1971) *Fundamentals of Ecology*. London: Saunders.

287   Patton D.R. (1975) A diversity index for quantifying habitat edge. *Wildlife Society Bulletin,* 3,

288   171-173.

289   Ries, L., & Sisk, T.D. (2004) A predictive model of edge effects. *Ecology,* **85,** 2917–2926.

290   Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem

291   fragmentation: a review. *Conservation Biology,* **5**, 18–32.

292   Szél, Gy. (1996) Rhysodidae, Cicindelidae and Carabidae (Coleoptera) from the Bükk

293   National Park. In: *The fauna of the Bükk National Park* (ed. by S. Mahunka, L. Zombori, and

294   L. Ádám), pp. 159-222. Hungarian Natural History Museum, Budapest.

295   **Table 1** The name, area-related characteristics, the number of pitfall traps, and the number of ground beetle species by habitat affinity category

296   captured in the studied forest fragments on the Bereg Plain, NE Hungary and Ukraine. Fragments are arranged by decreasing number of all

297   carabid species caught.

298

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	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

299

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

BIOSKETCH

Gabor L. Lövei is Senior Scientist at the Danish Institute of Agricultural Sciences, where he leads research on agricultural biodiversity, biological control, biosafety of transgenic organisms and invasion biology.

Tibor Magura is field biologist at the Hortobágy National Park Directorate, and leader of the Carabidology Research Group at the University of Debrecen. His main research interests include the distribution, biogeography and ecology of ground beetles.

Béla Tóthmérész is professor of quantitative ecology at the Ecological Institute, University of Debrecen. His research interests include the theory of diversity, with special emphasis on scale-dependent characterisation, scalable proximity measures and the multivariate analysis of communities.

Viktor Ködöböcz is regional program manager of the Hungarian National Biomonitoring System at the Hortobágy National Park Directorate. He is currently working on his Ph. D. thesis about the biogeography of carabids. His main interests are taxonomy, faunistics and biogeography of ground beetles.