

1 **The influence of matrix and edges on species richness patterns of ground beetles**
2 **(Coleoptera, Carabidae) in habitat islands**

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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

50 **INTRODUCTION**

51

52 One of the most influential of ecological concepts is MacArthur and Wilson's Island
53 Biogeography Theory (MacArthur & Wilson, 1967). The original theory considered real
54 islands, but the concept was soon applied to habitat islands, and became an important study
55 topic with strong links to conservation biology (Harris, 1984). The major difference between
56 real and habitat islands is the nature of the surrounding matrix. In real islands, the surrounding
57 matrix is usually hostile to organisms occurring on islands (although whether this is a
58 significant barrier depends on the dispersal ability of the organisms concerned, see Báldi &
59 Kisbenedek, 1999). In the case of terrestrial habitat islands, the matrix is usually less hostile
60 (Gascon & Lovejoy, 1998; Ås, 1999; Hobbs, 2001) and can contain their set of species
61 ("matrix species"). Such matrix species can also occur in the habitat islands themselves.
62 Larger habitat islands or ones closer to a colonist source area do not always have more species
63 (Holt et al., 1995) but this could arise because of the indiscriminate inclusion of such "matrix
64 species" (Cook et al., 2002). Such results lead to a call for "further refinements of the
65 paradigm ...to adapt and broaden the theory. For island biogeography theory to be applied to
66 terrestrial habitat 'islands' which are heterogeneous and subject to edge effects,
67 methodological allowances need to be made for the likelihood that species can colonize the
68 'islands' from the sea..." (Cook et al., 2002).

69 Habitat fragments are not uniform, but have well-defined edges. Edges are transition
70 zones between adjacent habitats and form ecotones (Holland et al., 1991). Forest edges, for
71 example, have distinct microclimates, abrupt changes in light regimen, substrate, and water
72 conditions, and are generally rich in microhabitats (Murcia, 1995; Didham & Lawton, 1999).
73 This gives rise to "edge-preferring species", species that are characteristic of edge habitats
74 (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 pyraeaster*, *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

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

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), Húrka (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

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227

228 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., Dufrière, 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 Dufrière, 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 Scientiarum 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
<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> (Schrank, 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> (Schrank, 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> (Schrank, 1781)	Generalist species

BIOSKETCH

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