



Carabid beetles among grassland - forest edge - beech forest habitats in Northern Hungary

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Abstract: Ground beetles were studied among grassland - forest edge - beech forest habitats in Hungary, using pitfall traps. We hypothesised that the activity density and species richness of carabids were the highest in the forest edge, the activity density and the number of forest species were decreasing, while the activity density and the number of generalist species increasing from the forest towards the grassland. Carabid assemblage of the grassland was the most diverse and the forest was the least diverse if measured by Rényi diversity. The average species richness per trap was significantly higher in the grassland and in the edge than in the forest. The number of forest species was significantly higher in the edge than elsewhere. The number of generalist species was highest in the grassland and decreased towards the forest. The activity density of carabids was significantly higher in the forest and in the forest edge than in the grassland. The activity density of forest species was higher in the forest and in the edge than in the grassland. The activity density of the generalist species was higher in the grassland than in the forest edge and in the forest. There were seven species characteristic to the grassland as identified by IndVal; two species were characteristic to the edge, and two species were characteristic both to the forest and the edge. We found that humidity was the highest in the forest; *Pterostichus oblongopunctatus* and *Molops piceus* were associated with the forest habitat, while *Abax ater* and *Pterostichus melanarius* were associated with the forest edge according to the RDA. The the shrub cover was the most relevant factor in the edge; *Abax ater* and *Pterostichus melanarius* were associated with this habitat.

Abbreviations: RDA—Redundancy Analysis.

Nomenclature: Hürka 1996.

Introduction

Edge habitats occur where two structurally dissimilar landscape components adjoin each other (Peltonen et al. 1997). The structure and diversity of invertebrate assemblages are characteristically altered in the edge habitat. Typically, species richness decreases with distance from the edge into the core habitat (Odum 1971, Ewers and Didham 2006). Forest edges are in the focus of both ecological studies and conservation efforts, because the progressive destruction and fragmentation of habitats led to an increase of forest edges in some areas, while in other areas they have disappeared (Magura et al. 2001a, Saunders et al. 1991).

Certain species are associated with edges (Lövei et al. 2006, Magura 2002); their distribution may be impacted by habitat fragmentation and edge effects (Jordán et al. 2006, Vasas et al. 2009). Understanding of how edge effects influence the ground-dwelling invertebrates will help in assessing the fragmentation impacts of different silvicultural options (Paillet et al. 2010) and also the ecological benefits of forest reserves such as wildlife habitat strips.

We tested how the carabid assemblage (Coleoptera: Carabidae) changes among the grassland - forest edge - forest habitats in the Zemplén Mountains, Northern Hungary. The research hypothesis was that the activity density and species richness of carabids and the activity density and species richness of forest species will be higher in the edge habitat, than in the grassland or in the forest. Previous studies (Lövei et al. 2006, Magura et al. 2001c) described that certain species could be characteristic for edges, thus we supposed that there are species specific to edges. We also intended to explore the structure of the carabid assemblages (species composition) in the edge habitat (i.e., edges can host species from the adjacent grassland and forest habitat).

Materials and methods

Study area and sampling design

We sampled carabids among a grassland, forest edge and forest interior by pitfall traps in Zemplén Mountains, Northern Hungary. The study area is located in the Gyertyánkúti meadows (coordinates: 48° 27' 37.62"N; 21° 21' 50.06"E) near Telkibánya village. The typical forest association was

beech forest (Aconito-Fagetum), with dense litter layer, and moderate understorey vegetation. The neighbouring area was a grassland with dense herbaceous vegetation (*Brachypodium pinnati* - *Calamagrosti arundinaceae*). The forest edge was characterized by moderate leaf litter layer. The shrub layer consisted mainly of hazelnut shrubs (*Corylus avellana*) and saplings of the canopy trees. The pitfall traps were arranged in a trapping station according to the habitat types containing ten pitfall traps. The distance between the traps in the trapping station was 10 m. The trapping stations were at least 50 m from each other. Three replicate transects of the trapping stations were installed across the studied habitat types (from the grassland toward the forest interior), 100 m apart from each other. The 90 pitfall traps were unbaited, consisting of plastic cups (diameter 100 mm, volume 500 ml) containing ethylene-glycol and water solution, and detergent (Spence and Niemelä 1994). The trapping period covered the whole snow-free season (from April to October in 2002) and the samples were collected monthly. For the numerical analysis, monthly samples were pooled. All carabid beetles taken in the pitfall traps were identified to species using standard keys (Hürka 1996). The following characteristics of the studied habitats were estimated within a 5 m radius around each trap: ground and air temperature, relative humidity, percentage cover of herbs and shrubs, percentage canopy cover, percentage leaf litter cover and woody debris and the number of potential prey items for carabids.

Data analyses

Diversity of the pooled samples of the habitats was compared by the Rényi one-parametric diversity index family. In this case, not just one numerical value is used to characterize the diversity of an assemblage, but a family of diversity values (Tóthmérész 1995, 1998). This method can be used in a graphical form to visualize the diversity relations of assemblages (Lövei 2005, Ricotta 2005). It may be portrayed graphically by plotting diversities against a (scale) parameter. This curve is frequently mentioned as the diversity profile of the assemblage. Members of the one-parametric diversity index family have varying sensitivities to rare and abundant species as the scale parameter changes (Tóthmérész 1998). When the value of the scale parameter is zero, Rényi diversity represents the log-transformed species richness and is extremely sensitive to the contribution of the rare species to the diversity of the assemblage. When the value of the scale parameter approaches one, then the Rényi diversity is identical to the Shannon diversity, and is sensitive to the rare species, although less so than at zero. When the value of the scale parameter is two, the Rényi diversity is related to the quadratic (Simpson) diversity. In this case, the index starts to be more sensitive to the frequent species than to the rare ones. When the value of the scale parameter is further increased, the Rényi diversity is related to the Berger-Parker dominance index which is determined only by the relative abundance of the most common species.

The IndVal (Indicator Value) procedure (Dufrene and Legendre 1997) was used to determine which carabid species could be considered as a characteristic species of the studied habitats. IndVal is a quantitative characterisation of the idea of indicator species of classical phytosociology, based on a computerised randomisation procedure (Elek et al. 2001). The IndVal method proved to be useful in identifying characteristic species in field studies (Magura et al. 2000a, 2004, Schiegg 2000).

Analysis of variance (ANOVA) was used to test differences in the activity density and species richness per trap among the habitats (Sokal and Rohlf 1995). Carabid beetles were divided into three groups according to their habitat affinity based on the literature: forest species, generalists, and open-habitat species (Hürka 1996). Differences in the activity density and species richness in these groups were also tested by ANOVA. Normality of the data was tested by the Kolmogorov-Smirnov tests (Sokal and Rohlf 1995). When ANOVA revealed a significant difference, Tukey-type multiple comparisons were used to determine the significant differences between means (Sokal and Rohlf 1995).

To explore the relationship between the carabid assemblages and environmental variables (ground and air temperature, relative humidity, percentage cover of herbs and shrubs, percentage canopy cover, percentage leaf litter cover and woody debris and the number of potential prey items for carabids), we applied Redundancy Analysis (RDA, Palmer 1993); the species with fewer than 10 individuals collected were excluded from this analysis. The analyses were carried out in R 2.4.1 (R Development Core Team 2010) using the Vegan package (version 1.15-0, Oksanen et al. 2007).

Results

Altogether 31 species and 4696 individuals were captured. The three most dominant species were as follows: *Pterostichus burmeisteri*; *P. melanarius*, and *Molops piceus*. They represented 65% (3077 individuals) of the total catch (for further details, see Appendix 1). Based on the pooled samples of the habitats, the carabid assemblage of the grassland was the most diverse (Fig. 1). Total number of trapped

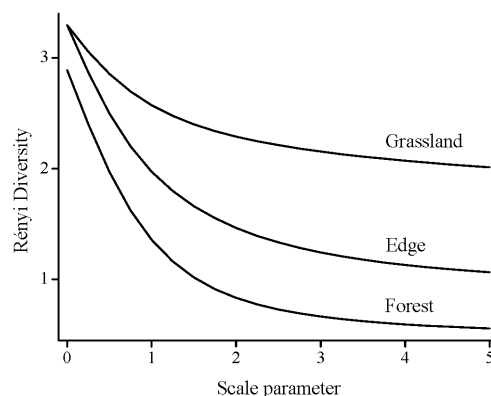


Figure 1. Diversity profiles of the carabid assemblages of the studied habitats by the Rényi one-parametric diversity index family.

Table 1. One-way ANOVA indicating differences in carabid activity density and average species richness of overall catches per trap, habitat affinity along the grassland (G) edge (E) and forest interior (F) transect. The last column of the table shows the significant differences based on Tukey (Honest Significant Difference) test ($p < 0.05$)

Characteristics	Variables	SS	d.f.	MS	F	p	Tukey test
<i>Species richness</i>							
Overall species richness	Habitats	232.86	2	116.43	19.57	<0.001	G=E>F
	Error	160.60	27	5.94			
Forest species	Habitats	48.46	2	24.23	7.31	0.002	E>G=F
	Error	89.40	27	3.31			
Generalists	Habitats	73.86	2	36.93	24.93	<0.001	G>E>F
	Error	40.00	27	1.48			
<i>Activity density</i>							
Overall activity density	Habitats	85487.3	2	42743.6	8.93	0.001	F=E>G
	Error	129222.2	27	4786.0			
Forest species	Habitats	80587.3	2	40293.6	13.48	<0.001	F=E>G
	Error	80650.6	27	2987.1			
Generalists	Habitats	11206.87	2	5603.43	9.85	<0.001	G=E>F
	Error	15356.50	27	568.76			

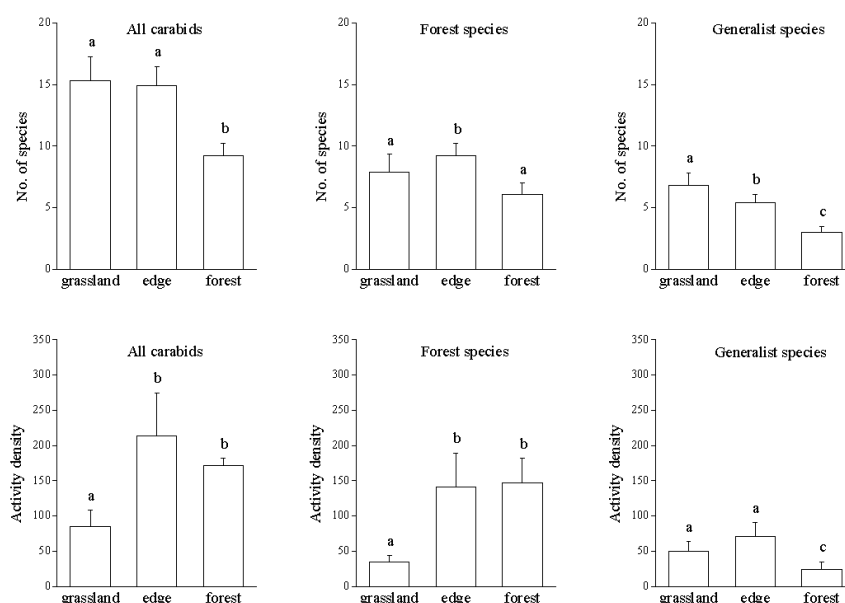


Figure 2. Average values (\pm SE) of the overall species richness, the species richness of forest carabids and generalist species and the overall carabid activity density, the activity density of forest and generalist species, along the grassland edge and forest interior transect. Different letters indicate significant differences based on Tukey (Honest Significant Difference) test ($p < 0.05$).

species was identical for the grassland and the forest edge. On the other hand, the carabid assemblage of the forest edge was less diverse than the grassland. The least diverse was the forest assemblage.

ANOVA showed that there were significant differences in the activity density and species richness of the traps among the habitats (Fig. 2, Table 1). The average number of species per trap was significantly higher in the grassland and the edge than in the forest. The mean number of forest specialist species per trap was higher at the edge than elsewhere. The mean number of habitat-generalist species per trap was highest in the grassland and decreased toward the forest (Fig. 2, Table 1).

Total activity density was significantly higher in the forest and at the forest edge than in the grassland. The activity density of forest species was highest in the forest and de-

creased toward the grassland. Significantly more individuals of generalist species were captured in the grassland and at the edge than in the forest.

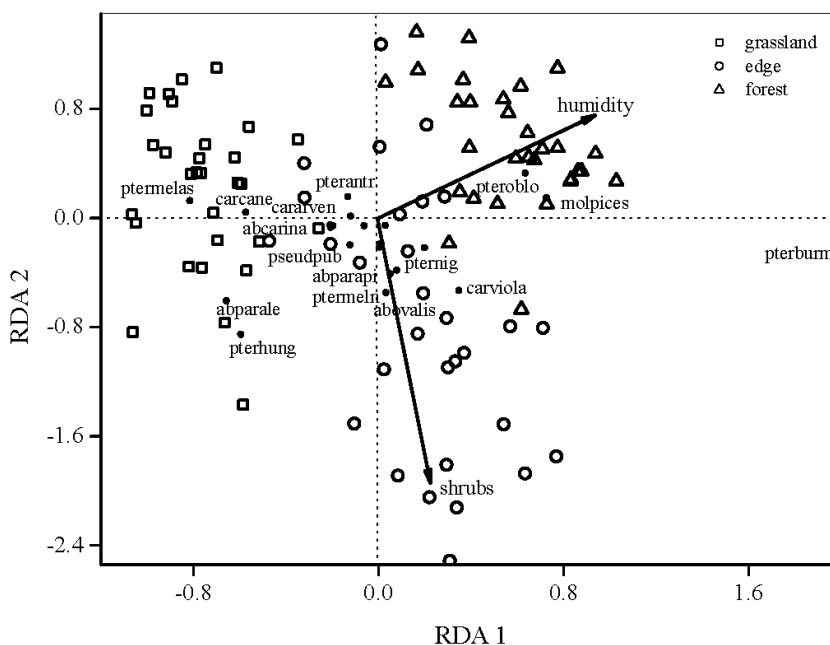
Significant characteristic species of the habitats were identified by the IndVal procedure. Seven characteristic species were identified by the IndVal method in the grassland, two for the edge, and two for the non-grassland (forest and the edge) habitats. No characteristic species were identified for the forest habitat (Table 2).

In the RDA ordination, the sum of all the unconstrained eigenvalues was 1.3 and the eigenvalues associated with the first two gradients were 0.5 and 0.3. These axes explained 39.9% cumulative variance of the species dataset and 50.1% cumulative variance of the species-environment relationships. Few species were strongly associated with particular

Table 2. Species character power for the studied sites. The IndVal column shows the species character value for the corresponding clustering level. In the last three columns, the first number indicates the number of trapped individuals and the second one corresponds to the number of traps where the species is present in this sample group. Only significant results ($p < 0.05$) are shown.

Species	IndVal	p	grassland	edge	forest
All habitats					
No species					
Grassland					
<i>Carabus cancellatus</i>	91.43	**	48/10	8/4	1/1
<i>Pterostichus melas</i>	86.23	**	103/9	7/4	2/2
<i>Abax schueppelli</i>	61.28	**	18/8	9/5	2/2
<i>Carabus arvensis</i>	60	**	15/7	5/4	0/0
<i>Carabus obsoletus</i>	53.62	**	18/7	10/5	1/1
<i>Trichotichnus laevicollis</i>	30	**	3/3	0/0	0/0
<i>Amara convexior</i>	28.42	**	9/3	1/1	0/0
Edge					
<i>Abax ovalis</i>	70	**	8/6	35/10	7/2
<i>Pterostichus niger</i>	41.67	**	3/2	15/5	0/0
Forest and Edge					
<i>Pterostichus oblongopunctatus</i>	81.14	**	2/2	17/7	67/10
<i>Cychrus caraboides</i>	67.31	**	2/2	23/9	12/6
Forest					
No species					

Figure 3. RDA tri-plot for the ground beetles. The arrows denote the increase of humidity and shrub cover. The eight-letter abbreviations indicate the following species: abcarina = *Abax carinatus*; abovalis = *Abax ovalis*; abparapi = *Abax parallelepipedus*; abparale = *Abax parallelepipedus*; cararven = *Carabus arvensis*; carcane = *Carabus cancellatus*; carviola = *Carabus violaceus*; pseudpub = *Pseudoophonus pubescens*; molpices = *Molops piceus*; pterhung = *Pterostichus hungaricus*; pternig = *Pterostichus niger*; pterantr = *Pterostichus anthracinus*; pterburm = *Pterostichus burmeisteri*; pteroblo = *Pterostichus oblongopunctatus*; ptermelas = *Pterostichus melas*; ptermeln = *Pterostichus melanarius*.



habitats and environmental factors. Humidity was higher in the forest than other habitats, and *Pterostichus oblongopunctatus* and *Molops piceus* were associated with this habitat (Fig. 3). Shrub cover was the most relevant environmental factor at the edge and *Abax parallelepipedus* and *Pterostichus melanarius* were associated with this habitat (Fig. 3). *Pterostichus melas* was captured more commonly in the grassland, but there were no environmental variables which strongly associated with this habitat.

Discussion

We found that the forest edges are not hosting as many carabids as expected based on previous studies from Hungary. The species richness and diversity pattern were similar

among the studied habitat types, suggesting that the grassland was similarly diverse like forest edges. We found a relatively few species with high activity density in the forest edges compared with grassland and forest habitats. Only two characteristic species were identified for forest edges. Previous studies (Máthé 2006, Magura 2002, Magura et al. 2002, Magura and Tóthmérész 1997, 1998) showed that activity density, species richness and diversity increases in the edge habitats. Based on these clues, we supposed that the activity density, species richness and diversity would be higher in forest edges.

We found by scale-dependent diversity characterization based on the Rényi diversity index family that the grassland was the most diverse, and the forest edge was less diverse

than the grassland based on the species pool of the habitats. In a beech forest in Transsylvania, Romania, the edge was the most diverse (Máthé 2006), and Magura and Tóthmérész (1998) also reported the same for an oak-hornbeam forest edge. These differences in diversity suggest that habitat associations may change, depending on the geographical factors and/or the particular forest and grassland types. This is also consistent with previous observations demonstrating that forest specialist species also maintain populations in the forest edge (Spence et al. 1996).

Comparing the average species richness of the traps, we found that overall species richness was significantly higher in the grassland and edge than in the forest. Magura (2002), Magura et al. (2002) and Magura and Tóthmérész (1998) also reported a similar pattern in the case of grassland–oak-hornbeam forest transects. Máthé (2006) found that the forest edge was significantly more species rich than the forest. Magura and Tóthmérész (1997, 1998) and Magura et al. (2001a) showed that the average species richness of the traps was higher in the forest edge than in the forest interior. These findings suggest that the edge effect also depends on the local carabid assemblage and on local vegetation.

The low species richness of the forest habitat suggested that fewer carabid species are adapted to relatively cool and dark forest habitats (Niemelä 1993). This most humid homogenous habitat is suitable for a carabid assemblage with low number of species, because of limited food sources as compared to the more open habitats, where more sources of food available (Koivula and Niemelä 2002).

We found that overall activity density was higher in the forest and in the forest edge than in the grassland. Magura (2002) and Magura et al. (2002) also reported similar pattern in the case of grassland - oak-hornbeam forest transects. We found that the activity density of forest species was higher at the forest edge and in the forest interior than in the grassland, similarly to Magura et al. (2002). The activity density of generalist species was significantly higher in the grassland and edge than in the forest. Magura (2002) reported that some generalist species were numerous in all habitats along grassland - oak-hornbeam forest transects.

The diversity pattern detected (i.e., grassland is the most diverse habitat) can be the consequence of the high evenness in the grassland because of the high activity density and moderate species richness. Similar pattern in species richness and activity density were reported for spiders by Liu et al. (2002). As a consequence, we found that our hypothesis is partly supported by the findings. Our results can also be explained by the local aspects in vegetation or geographical attributes. Ewers and Didham (2006) also showed that habitat edges are hyper-dynamic ecological systems, resulting in the destabilization of the animal population.

One of the main aspects in the ecology of edges is that interactions between the species are less stable; thus the species composition is more variable in the edges than in the adjacent homogenous habitats (Didham et al. 1998). It is impor-

tant to know that the species use these habitats temporarily or they could be characteristic for these habitats.

Analyses by IndVal and the RDA showed that two out of the three studied habitat types had a characteristic carabid species associated with them. Molnár et al. (2001) and Magura et al. (2001a) also reported that the ordinations separated the traps of the habitats. Using the IndVal method, we identified two significant edge-associated species (*Abax ovalis*, *Pterostichus niger*). Magura et al. (2000b, 2001b), Máthé (2006) and Molnár et al. (2001) also captured *Pterostichus niger* exclusively in the forest edges. However, their results showed that *Abax ovalis* was a forest species (Magura et al. 2001a, Molnár et al. 2001). As a consequence, we found that our hypothesis was supported by our results.

We found slight evidence for contributing the natural edges to the conservation of ground beetles among a beech forest, forest edge and the adjacent grassland habitats in the Zemplén Mountains, Hungary. We found that the forest edge is moderately species-rich but, abundant (i.e. high activity density) habitat from the point of view of the carabids, but this pattern shows particular variation based on habitat affinity of the collected species. Only two characteristic species were identified, but most of the collected species could appear in this habitat. Our results suggest that the studied forest edges is penetrable for most of the carabid species. This can be explained by the reciprocal positive edges response, where complementary resource use among the adjacent habitat types resulted the higher activity density in habitat edges (Rand et al. 2006).

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References

- Didham, R. K., P. M. Hammond, J. H. Lawton, P. Eggleton and N.E. Stork. 1998. Beetle responses to tropical forest fragmentation. *Ecol. Monogr.* 68: 295-323.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for the flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.
- Elek, Z., T. Magura and B. Tóthmérész. 2001. Impacts of non-native Norway spruce plantation on abundance and species richness of ground beetles (Coleoptera: Carabidae). *Web Ecology* 2: 32-37.
- Ewers, R.M. and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. rev.* 81: 117-142.
- Hürka, K. 1996. *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlin, Czech Republic.
- Jordán, F., T. Magura, B. Tóthmérész, V. Vasas and V. Ködöböcz 2007. Carabids (Coleoptera: Carabidae) in a forest patchwork: a connectivity analysis of the Bereg Plain landscape graph. *Landscape Ecol.* 22: 1527-1539.
- Koivula, M. and J. Niemelä. 2002. Boreal carabid beetles (Coleoptera, Carabidae) in managed spruce forests - a summary of Finnish case studies. *Silva Fenn.* 36: 423-436.

- Liu W-X., Fang Hao W., Guo J-Y., Lövei G.L. 2002. Spiders and their seasonal dynamics in transgenic Bt. vs. conventionally managed cotton fields in north-central China. *European Arachnology* 2002. pp. 337-342.
- Lövei, G. 2005. Generalised entropy indices have a long history in ecology – a comment. *Community Ecol.* 6: 245-247.
- Lövei, G.L., T. Magura, B. Tóthmérész and V. Kódöböcz. 2006. The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecol. Biogeogr.* 15: 283-289.
- Magura, T. 2002. Carabids and forest edge: spatial pattern and edge effect. *Forest Ecol. Manag.* 157: 23-37.
- Magura, T. and B. Tóthmérész. 1997. Testing edge effect on carabid assemblages in an oak-hornbeam forest. *Acta Zool. Acad. Sci. Hung.* 43: 303-312.
- Magura, T. and B. Tóthmérész. 1998. Edge effect on carabids in an oak-hornbeam forest at the Aggtelek National Park (Hungary). *Acta Phytopathol. Entomol. Hung.* 33: 379-387.
- Magura, T., V. Kódöböcz and Zs. Bokor. 2001c. Effects of forestry practices on carabids (Coleoptera: Carabidae) - Implication for nature management. *Acta Phytopathol. Entomol. Hung.* 36: 179-188
- Magura, T., B. Tóthmérész. and Zs. Bordán. 2000a. Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biodivers. Conserv.* 93: 95-102.
- Magura, T., B. Tóthmérész and Zs. Bordán. 2002. Carabids in an oak-hornbeam forest: testing the edge effect hypothesis. *Acta Biologica Debrecina* 24: 55-72.
- Magura, T., B. Tóthmérész and Z. Elek. 2004. Effects of leaf-litter addition on carabid beetles in a non-native Norway spruce plantation. *Acta Zool. Acad. Sci. Hung.* 50: 9-23.
- Magura, T., B. Tóthmérész and T. Molnár. 2000b. Spatial distribution of carabid species along grass-forest transects. *Acta Zool. Acad. Sci. Hung.* 46: 1-17.
- Magura, T., B. Tóthmérész and T. Molnár. 2001a. Edge effect on carabids along forest-grass transects. *Web Ecology* 2: 7-13.
- Magura, T., B. Tóthmérész and T. Molnár. 2001b. Forest edge and diversity: carabids along forest-grassland transects. *Biodivers. Conserv.* 10: 287-300.
- Máthé, I. 2006. Edge effect on carabids along forest-grass transects. *Community Ecol.* 7: 91-97.
- Molnár, T., T. Magura, B. Tóthmérész and Z. Elek. 2001. Ground beetles (Carabidae) and edge effect in oak-hornbeam forest - grassland transects. *Eur. J. Soil Biol.* 37: 297-300.
- Niemelä, J. 1993. Mystery of the missing species: species - abundance distribution of boreal ground beetles. *Ann. Zool. Fenn.* 30: 169-172.
- Odum, E.P. 1971. *Fundamentals of Ecology*. Saunders, London.
- Oksanen, J., R. Kindt, P. Legendre and R.B. O'Hara R.B. 2007. *Vegan: Community Ecology Package version 1.8-6*. <http://cran.r-project.org/>
- Paillet, Y., L. Berges, J. Hjältén, P. Ódor, C. Avon, M. Bernhardt-Römermann, R-J. Bijlsma, L. De Bruyn, M. Fuhr, U. Grandin, R. Kanka, L. Lundin, S. Luque, T. Magura, S. Matesanz, I. Mészáros, M-T. Sebastia, W. Schmidt, T. Standovár, B. Tóthmérész, A. Uotila, F. Valladares, K. Vellak, R. Virtanen 2009. Does biodiversity differ between managed and unmanaged forests? A meta-analysis on species richness in Europe. *Conserv. Biol.* 24, 101-112.
- Palmer, M. W. 1993. Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.
- Peltonen, M., K. Heliövaara and R. Väisänen. 1997. Forest insects and environmental variation in stand edges. *Silva Fenn.* 31: 129-141.
- R Development Core Team (2010). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>.
- Rand T. A., Tylianakis J. M. and Tschamtker T. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9:03-614.
- Ricotta, C. 2005. On parametric diversity indices in ecology: A historical note. *Community Ecol.* 6: 241-244.
- Saunders, D.A., R.J. Hobbs and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5: 18-32.
- Schiegg, K. 2000. Are there saproxylic beetle species characteristic of high dead wood connectivity? *Ecography* 23: 579-587.
- Sokal, R. R. and F.J. Rohlf. 1995. *Biometry*. Freeman, New York.
- Spence, J.R. and J. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Entomol.* 126: 881-894.
- Spence, J.R., D.W. Langor, J. Niemelä, H.A. Cárcamo and C.R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33:173-184.
- Tóthmérész, B. 1995. Comparison of different methods for diversity ordering. *J. Veg. Sci.* 6: 283-290.
- Tóthmérész, B. 1998. On the characterization of scale-dependent diversity. *Abstracta Botanica* 22: 149-156.
- Vasas, V., T. Magura, F. Jordán, and B. Tóthmérész. 2009. Graph theory in action: evaluating planned highway tracks based on connectivity measures. *Landscape Ecol.* 24: 581-586.

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Appendix

The species and their activity density caught in during the study in Zemplén Mountains, Hungary, 2002. The file may be downloaded from the web site of the publisher at www.akademiai.com.