Effect Of Forest Fragmentation On Carabid Assemblages At Different Spatial Scale

Doktori (PhD) értekezés

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Természettudományi Kar
Debrecen, 2003.

Ezen értekezést a Debreceni Egyetem TTK Biológia doktori iskola Biodiverzitás doktori program Biocönózisok alprogramja keretében készítettem 1993-1997 között és ezúton benyújtom a KLTE doktori PhD fokozatának elnyerése céljából.

Debrecen, 2003. augusztus 25.

Molnár Tivadar

Tanúsítom, hogy Molnár Tivadar doktorjelölt 1999-2003 között a fent megnevezett doktori alprogram keretében irányításommal végezte munkáját. Az értekezésben foglaltak a jelölt önálló munkáján alapulnak, az eredményekhez önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.

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Debrecen, 2003. augusztus 25.

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INTRODUCTION

This thesis consists of four research papers (hereafter referred as *I-IV*) and a summary. The summary begins with a general background of the studies (forest fragmentation and their consequences). Further, the design and main results of the *studies I-IV* are presented, and these results are discussed in the context of habitat fragmentation.

Forest fragmentation

Habitat fragmentation is one of the most important causes of species declines and extinctions across the world (Saunders et al. 1991). Fragmentation reduces the total area of original habitat, creates isolated subpopulations, thus disrupting individual behaviour (e.g. Davies and Margules 1998), the exchange of genes between populations (e.g. Lacy and Lindenmayer 1995; Gaines et al. 1997), species interactions (e.g. Kruess and Tscharntke 1994; Arango-Velez and Kattan 1997; Lei and Hanski 1997) and ecological processes (e.g. Robinson et al. 1992). Thus, habitat fragmentation can influence an entire suite of processes, ranging from individual behaviour through population dynamics to ecosystem fluxes. The response of animal species to habitat fragmentation depends on their dispersal behaviour, their demography, their competitiveness, and on the size of the fragments (Kareiva 1987; Saunders et al. 1991). Furthermore, habitat fragmentation occurs on many different spatial scales (Simberloff 1988; Gibb and Hochuli 2002; Lord and Norton 1990; Kareiva and Wennergren 1995), and ranges from small breaks in an otherwise homogeneous habitat to widely scattered fragments in a surrounding area (Wiens 1989). For each species, the relevant spatial scale is different (Forman and Godron 1986; Wiens 1994). I studied the effects of habitat fragmentation on carabid beetles at meso and macro spatial scale.

Study of habitat fragmentation at meso spatial scale

One consequence of fragmentation and isolated habitat loss is decreasing fragment size, which leads to a decreasing proportion of interior habitat and increasing proportion of edge (Murcia 1995) (Saunders et al. 1991). Changes in abiotic and biotic conditions in the edge compared with the intact habitat are collectively called edge effects. Forest edges have distinctive microclimates, there are abrupt changes in light regimen, substrate, water conditions, and they are generally rich in microhabitats (Murcia 1995) there are changes in

radiation, predation, parasitism, and species interactions (Saunders et al. 1991; Murcia 1995). These factors are highly significant for small animals such as insects, especially of ground-dwelling beetles (Lövei and Sunderland 1996). Therefore the increased levels of human-induced disturbance at habitat edges also affect species composition (Kruger and Lawes 1997). To counteract the negative effects of edges it is important to understand how species respond to conditions in habitat edges (Haila et al. 1994). Therefore the goal of my studies *(I-III)* was to test the edge effect hypothesis for carabids (*Coleoptera: Carabidae*) along forest-grass transects. I also examined the environmental variables that may be important to control the distribution of ground-dwelling carabids, and thus can influence edge effect on carabid beetles. My hypothesis was that changes in carabids are most pronounced in forest edge characterised particular environmental conditions, and that according to the classical edge effect hypothesis the diversity of carabids will be higher in the forest edge than in the forest interior. Moreover, my objectives were to asses the extent of variation in distribution of carabid species along the transects, and to relate this to habitat characteristics and to spatial distribution of co-occurring carabid species.

Study of habitat fragmentation at macro spatial scale

Urbanisation and the loss of biotic diversity have a vital direct and indirect influence on the biosphere (Vida 1978). One of the leading causes of habitat fragmentation is urbanisation. Urban ecosystems are areas under profound and constant human activity. They are characterised by high-density human habitation, intense transport processes, and only remnants of natural habitats (McIntyre et al. 2001). Urban ecosystems contain spatially heterogeneous and temporally dynamic areas that differ from their surroundings and from the natural, intact habitats. Since urban development is both spreading and intensifying, knowledge about the functioning of urban ecosystems has vital importance in planning future urban development in order to minimise environmental impacts (McIntyre et al. 2001; Niemelä 2000). Despite their global ubiquity, relatively little is known about how arthropods respond to urbanisation (Eversham et al. 1996; Bolger et al. 2000;McIntyre et al. 2001; Gibb and Hochuli 2002), even though urbanisation is regarded as one of the leading causes of decline in arthropod diversity and abundance (Davis 1978; Pyle et al. 1981). Recently, a multi-national research framework to assess and compare the influence of urbanisation using a single group of invertebrates and standardised field methods has been initiated (GlobeNet, Niemelä et al. 2000). Carabids were selected as the key taxon since they were sufficiently varied both taxonomically and ecologically, abundant and sensitive to the changes of the

microenvironment and human disturbance (Scott and Anderson 2002). In the GlobeNet projects three kind of forested habitats (urban parks, suburban forested area, and rural forest), representing different levels of human disturbance and habitat fragmentation were selected (Niemelä et al. 2002). The patterns and responses of carabid assemblages along this urbanisation gradient may help guide management practices, especially in the case of urbanisation problems. The effects of urbanisation can be explored through investigations of biotic and abiotic changes along urban-to-rural gradients (McDonnell et al. 1997; Niemelä 1999, 2000; Niemelä et al. 2000). Several hypotheses try explain the effects of disturbance on biotic communities. In *study IV*, I tested the following predictions for carabids in urban environments: (1) diversity should be the highest in the suburban area according to the *intermediate disturbance hypothesis (IDH)* (Connell 1978) (2) diversity should decrease from a high in the rural area to a low in urban area *(increasing disturbance hypothesis)* (Gray 1987, 1989); (3) the abundance and species richness of the forestspecialist species should increase from the more disturbed urban area to the less disturbed rural one *(habitat specialist hypothesis)*; (4) opportunistic species should gain dominance in the urban area *(opportunistic species hypothesis)* (Gray 1989); (5) the mean body size of the species should decrease with increasing disturbance level, in our case from the rural to the urban area *(mean body size hypothesis)* (Gray 1989); (6) carabid assemblages should change along the urbanisation gradient and therefore there should be characteristic and/or key species of the stages of the studied gradient; and (7) certain environmental variables should predict the observed pattern of carabid abundance and species richness.

MATERIAL AND METHODS

Study area and sampling design

Studies I-III

Sampling area was located at the North Hungarian Mountain in the Aggtelek National Park, near the Mogyorós Peak (Haragistya). In this region oak-hornbeam forests (*Querco-Carpinetum*) and a grass association (*Polygalo majori-Brachypodietum pinnati*) are the most extensive. There are three habitat types on the research area:

(1) Grass (*Polygalo majori-Brachypodietum pinnati*), with dense herbaceous vegetation dominated *by Polygala major, Brachypodietum pinnatum, Filipendula vulgaris, Salvia pratensis, Inula hirta, Geranium sanguineum*. The litter layer, the shrubs and the canopy layer are missing in this habitat. Its area was approx. 40 ha.

(2) Forest edge, with dense herbaceous vegetation originating from the adjacent grass. The shrub layer is also dense in this habitat, consisting mainly of shrubs and saplings of the canopy trees *(Carpinus betulus, Corylus avellana* and *Prunus spinosa*). The litter layer is thick and the canopy layer is less closed than in the forest interior.

(3) Forest interior: oak-hornbeam forest, with thick litter layer, moderate herbaceous and shrub layer and with 85-95 % canopy cover. The size of the forest stand was greater than 100 ha.

Beetles were collected using unbaited pitfall traps, consisting of plastic cups (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution (Spence and Niemelä 1994).

In *study I* (in 1997) two parallel transects of pitfall traps were established with 8 traps in each of the 3 habitats.

In *study II* (in 1997-1998) the pitfall traps were arranged in a trapping station in each habitat, containing 5 traps. Three replicated transects of trapping stations were set across the studied habitats.

In *study III* (in 1999) three replicated parallel transects of pitfall traps were set across the three studied habitats. There were 42 traps placed along each transect (14 traps per habitat). Altogether there were 3×3×14=126 traps.

The transects were perpendicular to the forest edge. To provide adequate statistical independence for pitfall samples, transects and trapping stations were set at least 50 meter from each other (Digweed et al. 1995).

To study associations between the distribution of carabids and the environmental variables, I studied five environmental factors. I estimated the percentage cover of the leaf litter layer, the herbs, the shrubs and the canopy layer around each trap. I also studied the abundance of the potential food resources of the carabids (abundance of other invertebrate that fell in the traps). These invertebrates (e.g. *Lumbricidae, Mollusca, Isopoda, Chilopoda, Aranea,* and *Coleoptera* larvae) are surface dwellings, therefore they can be regarded as food source for the carabids. It was proved by serological method (Sergeeva 1994) that these invertebrates are prey for carabids. In *study II* the temperature of ground at 2cm depth, the air temperature on

the surface and the relative air moisture was measured near each trap monthly on a typical sunny day in the morning. The statistical analyses were based on averages.

Study IV

The study areas were in Debrecen (Eastern-Hungary), the second largest city of the country. Three forested sampling areas were selected along an urbanisation gradient within the boundaries of the city, and in the surrounding forest reserve. This represented urban, suburban and rural areas, according to the GlobeNet standard (Niemelä et al. 2000). In the urban park area, several paths with asphalt surface were created and the shrub layer was strongly thinned resulting in a park character, while in the suburban area the fallen trees were removed. All sampling sites were situated in continuous patches of forest dominated by English oak (*Quercus robur*) and covering at least an area of 6 ha. The typical, native forest association of the sampling sites was *Convallario-Quercetum* (Tóthmérész and Török 2003).

Four sites were selected within each sampling area. Carabid beetles were collected at each of the 4 sites of the 3 studied areas using pitfall traps. Ten traps were placed randomly at each site. This resulted in a total of 120 traps scattered along the urban-rural gradient. The pitfall traps were unbaited, consisting of plastic cups containing 75% ethylene glycol as a killing-preserving solution. The traps were covered with bark pieces to protect them from litter and rain (Spence and Niemelä 1994). Trapped beetles were collected fortnightly from the end of March to the end of November, 2001. For the numerical analyses I pooled samples from the whole year. Nine environmental factors were measured that can affect the distribution of carabid species (Thiele 1977; Lövei and Sunderland 1996). Ground temperature at 2cm depth, air temperature on the surface and relative humidity on the surface were measured adjacent to each trap monthly on a typical sunny day in the morning. The statistical analyses were based on averages. I also estimated the cover of leaf litter, decaying wood material, herbs, shrubs and canopy around the traps within a circle of 2m diameter. I also counted the number of potential prey for carabids (Sergeeva 1994).

Data analyses

In all study the IndVal (Indicator Value) approach was applied to find indicator species and species assemblages characterising the grass, the forest edge and the forest interior *(I, II and III)* respectively the urban, suburban and rural areas *(IV)*(Dufrêne and Legendre 1997). To

start of this approach consists of obtaining a classification of sample units using one of the classical methods of data analysis. I obtained a typology from the principal coordinates analysis using Bray-Curtis index of percentage similarity for carabid abundances.

Studies I-II

The species richness was characterised by the Shannon diversity. Analyses of variance (Kruskal-Wallis non-parametric ANOVA *(I)* respectively ANOVA, Friedman-test *(II)*) and Tukey-type multiple comparisons *(I, II)* were used to determine differences in the carabid diversity per trap and in the studied environmental variables between the three habitats of the transects. Spearman rank correlation *(I)* respectively multiple linear regression analyses *(II)* were used to study the relationships between the environmental measurements and the diversity of carabids (Zar 1984). Non-metric multidimensional scaling (MDS) based on the Rogers-Tanimoto similarity was used for species composition *(II)*. Principal coordinates analysis (PCoA) using the Bray-Curtis dissimilarity *(I)* respectively the Bray-Curtis and Matusita similarities *(II)* were used to assess similarities in abundances of carabids among the traps (Digby and Kempton 1987). I used the NuCoSA package (Tóthmérész 1993).

Study III

Principal coordinates analysis (PCoA) using the Bray-Curtis index of similarity was used for carabid abundances to asses similarities in carabid assemblages of the traps (Gauch 1986). I used the NuCoSA package (Tóthmérész 1993). To characterise the spatial distribution of carabids, I calculated the index of dispersion, Iδ, which is defined as the variance-to-mean ratio (Diggle 1983): $I_\delta = s^2 / \bar{x}$, where s^2 is the variance, and $\bar{x}$ is the average number of individuals. An Iδ value close to one indicates a random distribution. Iδ>1 indicates aggregated, while Iδ<1 indicates regular distribution. The departure from randomness can be tested by the test statistic $ID = (n-1)s^2 / \bar{x}$. It has approximately χ2 distribution with (n-1) degrees of freedom. This approximation is reasonable provided n>6 and $\bar{x}$>1.

Multiple regression was used to study whether any of the environmental measurements and of abundance of the other carabids could be used to predict distribution of a particular carabid species. Catches of the common carabid species were compared among the traps of each habitat with Kruskal-Wallis nonparametric ANOVA. A Tukey-type multiple comparison was

then used to compare catches from the habitat types (Sokal and Rohlf 1995). For the eighteen most frequent species the correlation between the number of trapped individuals and the degree of their aggregation was calculated by the Pearson's product-moment correlation. Before the calculations the number of individuals was transformed by a logarithmic transformation to provide normality. The correlation between the abundance of a species and number of traps from which it was recorded was calculated by the Spearman rank correlation. The analyses were done by the SPSS-PC program.

Study IV

I used nested analyses of variance (ANOVA) to test

- differences in the overall carabid abundance and species richness among the sampling areas and among the sites;

- differences in the number of individuals and species richness in three ecological groups (i.e. forest species, generalist species and openhabitat species) – into the carabid beetles were divided according to their habitat preference (Hůrka 1996);

- changes in carabid body size along the urban-rural gradient;

- the difference in the dominance structure among the sampling areas and among the sites;

- the ratio of the number of individuals of the opportunistic (generalist) carabid species to the total number of individuals for all the 120 traps.

The distribution of data used in the ANOVA model was normal (tested by the Kolmogorov-Smirnov test, Sokal and Rohlf 1995). When ANOVA revealed a significant difference between the means, an LSD (least significant difference) test was performed for multiple comparison among means. The composition of the carabid assemblages along the studied urbanrural gradient was compared at site level by cluster analysis based on presence-absence data using the Sørensen index of similarity and the group average fusion algorithm. Non-metric multidimensional scaling (MDS) was applied to assess similarities in the abundance of carabids among the sites using the Bray-Curtis index of dissimilarity (Legendre and Legendre 1998). The relationships between the environmental measurements and the abundance and species richness of carabids were examined by forward and backwards stepwise multiple linear regression analyses (Sen and Srivastava 1990). Forward stepwise multiple linear regression analysis provided a better fit; thus, I used this method as suggested by the statistical literature (Kutner et al. 1996).

RESULTS AND DISCUSSION

Forest fragmentation on meso-scale *(Studies I-III)*

Edge effects on carabids

The analyses of variance provided that there was variation in the carabid diversity among the habitats for the transects in 1997 *(I)* and in both years of *study II.* By the Tukey-type posteriori test it is evident that the Shannon diversity was significantly ($p<0.05$) higher in the forest edge and the grass than in the forest interior in both studies and years, but the differences in diversity between the forest edge and the grass were not significant *(Figure 1.)*. The same diversity pattern was shown by the pooled samples of the habitats. My results show that there is a significant edge effect on the carabid assemblages. The diversity increased along the transects from the forest interior towards the grass. The significant difference in species richness between the forest interior and the grassland is known from the literature. Similar results were published for forests and the surrounding open habitats (Halme and Niemelä 1993; Niemelä and Halme 1992; Levesque and Levesque 1994; Niemelä et al. 1992b; Segers and Bosmans 1982). I found no significant difference in the diversity of the grassland and the forest edge, which also corroborates the edge effect on carabids, because forested habitats usually are significantly less diverse than the open areas, as was reported by the above mentioned papers. Studying carabids of farmland-forest transects, similarly to my result, Bedford and Usher (1994) also reported that open habitat and forest edge have higher species richness than the forest interior. Báldi and Kisbenedek (1994), Butovsky (1994), Asteraki et al. (1995) also showed that diversity is higher in the forest edge than in the forest interior.

Ordination of the carabid assemblages and indicator species

According to the results of PCoA and MDS we can state that samples from the forest interior, forest edge and the grassland were different from each other. There was a linear gradient in the composition of the carabid assemblages along the transects, namely the carabid assemblages change gradually from the forest interior towards the grass along the transects *(Figure 2)*. The arch effect usually represents linear gradients (Gauch 1986). Instead of the almost continuous variation of the composition of the assemblage along the gradient, carabid

samples of the grass, the forest edge and the forest interior are separated from each other. The composition of the samples from the forest edge and the forest interior were more similar to each other than the samples from the edge and the grass.
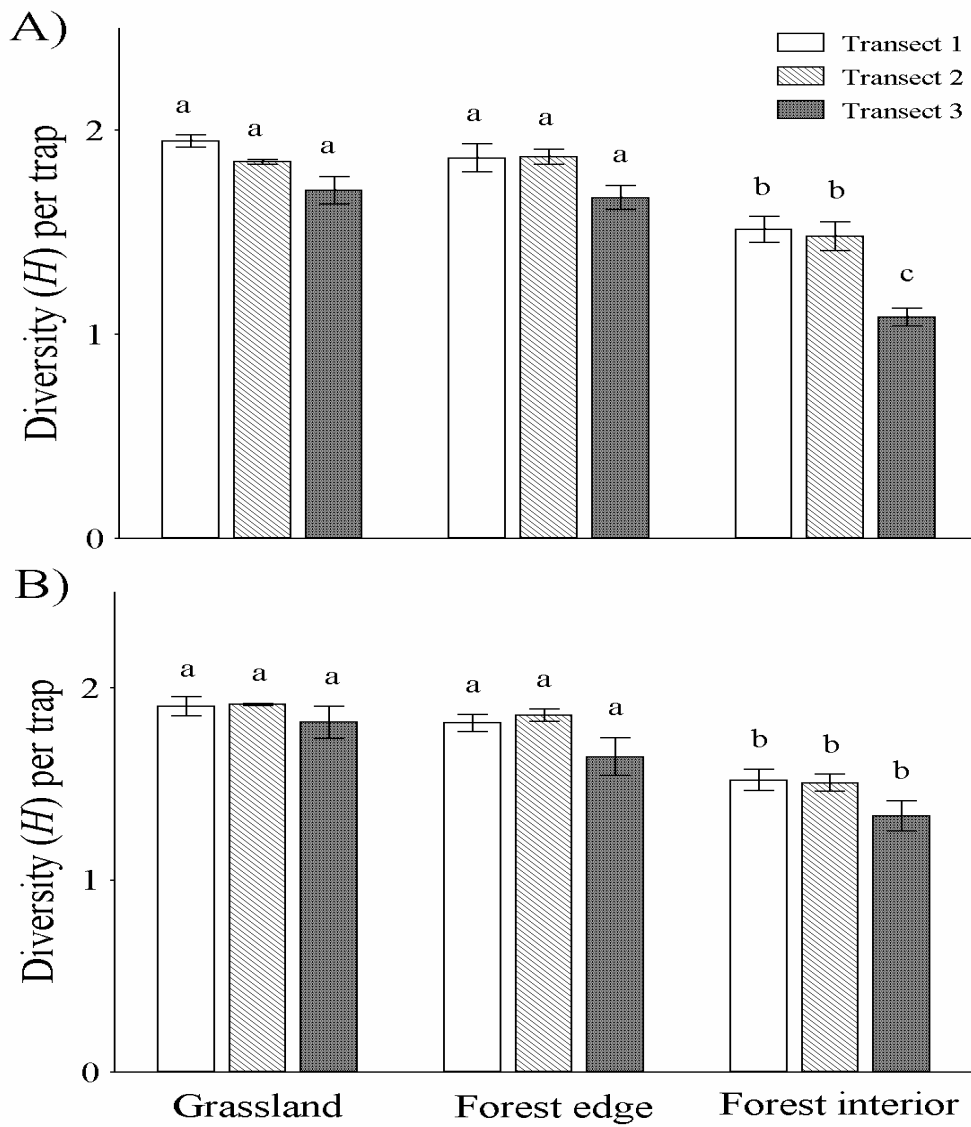
Figure 1. Average Shannon diversity of carabids per trap (with SE) in the studied habitats in 1997 (A) and in 1998 (B) in *study II*. Means with different letters indicate a significant (p<0.05) difference by Tukey-type multiple comparison.
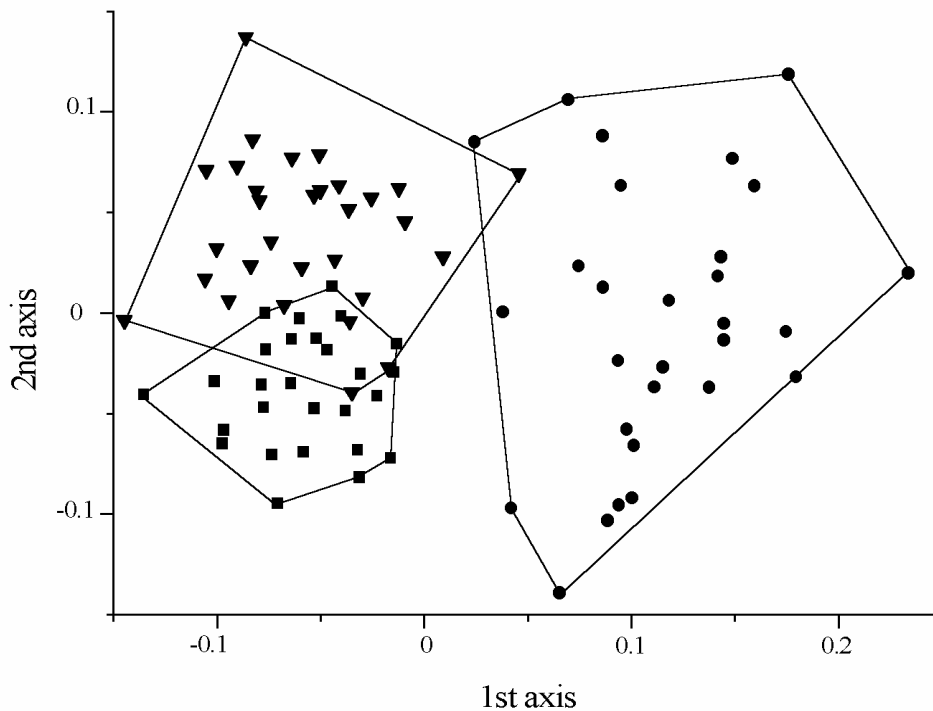
Figure 2. Ordination (MDS) of the pitfall catches based on species composition by the Rogers-Tanimoto similarity *(Study II)*. (●) Grassland; (▼) Forest edge; (■) Forest interior.

According their habitat preference the collected carabid species can be divided into five groups by indicator species analysis: (1) habitat generalists that occurred numerously in all habitat types; (2) grassland-associated species, that were recorded exclusively in the grassland or were the most abundant in the grassland; (3) forest generalists, that occurred exclusively in the forested habitats or were the most abundant in the forest habitats (forest interior and forest edge); (4) forest specialists that were captured numerously in the forest interior; and (5) edge-associated species that were recorded exclusively in the edge or were the most abundant in the forest edge *(I, II and III) (Table 1)*. However the analyses of indicator species show that all studied habitat types have characteristic assemblages of carabid species associated with them. On the studied scale the habitats are not isolated from each other and there appears to be dispersal between the adjacent habitats. The high diversity of the forest edge may be caused by small scale dispersal processes, as carabid beetles are able to cover large distance while looking for food (Baars 1979b; Magura 1995). Other efficient causes of the dispersal processes could be the exhibit density-dependent migration (Grüm 1971), aggregation in habitats with high amount of prey available (Bryan and Wratten 1984) and movement between reproduction habitat and hibernation habitat (Wallin 1986; Andersen 1997). The

changes of the monthly distribution pattern of carabids in the habitats suggesting that there must be seasonal movement between the adjacent habitats. In *study II* I analysed the indicator species separately for each month. *Pterostichus oblongopunctatus* was significant character species for the forest interior from March to April, and it was significant character species for the forested habitats (forest interior and forest edge) from May to June, while it was again a characteristic species for the forest interior from July to November. For the pooled samples it was significant characteristic species for the forested habitats. Similar behaviour was observed in the case of *Pterostichus burmeisteri*. Furthermore, with decreasing of canopy cover, the species typical mostly of open habitats (e.g. *Pterostichus melanarius*, *Synuchus vivalis*, *Harpalus rufipes and Carabus montivagus*) can immigrate into the forest edge increasing the diversity. Spence et al. (1996), studying carabids in a clear-cut area and in the adjacent residual pine forest, also reported that open-habitat species can colonize the forest edge due to less canopy closure and to changes in microclimate. Forest interior species (*Abax ovalis*, *Abax parallelus* and *Aptinus bombarda*) can also move into the forest edge. The discussed dispersal processes and the edge-associated species contribute to the increased diversity of carabids in the forest edge. Overall, edge effect on carabids is due in part to the presence of species characteristic of each of the adjacent habitats (forest interior and grassland) plus species inhabiting the edge. These edge species may find habitats at the edge that are not present in either habitat alone, or they may require two structurally different habitats in close proximity to one another.

In the three studies I found twenty-five common species and only six species showed different habitat preference by the analyses of indicator species. These differences could be explained with the low number of individuals in case of *Abax carinatus* and *Amara convexior.* These species are asymmetrical indicator, according to the IndVal terminology, which means that their presence cannot be predicted in all sites of one habitat, but contribute to the habitat specificity. Furthermore several studies state that 10 traps placed in a habitat is sufficient to obtain a quantitative picture about the ground beetle community of the habitat (Baars 1979a; Benest 1989; Refseth 1980). On the other hand my results show that this pitfall number seems insufficient if our goal is the examination of the small-scale distribution of the carabids. Since in *study III* was the number of the traps per habitat the highest (42 traps were arranged in each habitat), therefore the results of this study are the most reliable. Furthermore the small-scale dispersal processes between the habitats also could explain the differences between the habitat preference of a particular species. A different seasonal movement between years could lead to a different habitat preference along the years.

Spatial pattern of carabids along the transects

In *study III* I found a strong, positive correlation between the abundance of a species and number of traps from which it was recorded. The collected 40 species can be partitioned into four distinct groups according to their frequency of occurrence among the 126 traps. Two species (*Abax parallelepipedus* and *Molops piceus*) which were found in more than 100 traps and represented by a mean of more than 3 individuals per trap, were designated as habitat generalists and eudominant species. Five other species (*Pterostichus oblongopunctatus*, *Pterostichus burmeisteri*, *Carabus violaceus*, *Abax ovalis* and *Carabus hortensis*) that were captured in more than 55 traps with more than 1 individuals per trap can be mentioned as dominant species. Eleven other species, which were found in 20-40 traps and were represented by a mean catch of more than 0.15 individuals per trap, can be designated as subdominant species. The other 22 species that were captured in less than 20 traps with less than 0.15 individuals per trap, are rare species. The dominant and subdominant species of *study III* generally showed aggregated distribution. There were 19 cases where the statistical test was applicable and 18 distribution patterns out of 19 were significantly aggregated. Similarly to Niemelä and Spence (1994) I also found significant positive correlation between the number of individuals and the degree of aggregation for the eighteen studied species (*r*=0.6375, *p*=0.0033, *n*=19) *(III)*. This may be interpreted as more abundant species are more aggregated. Sometimes, variation in carabid catches among the fourteen traps in the same habitat was greater than the variation among habitats indicating the importance of strong microhabitat variations controlling carabid distribution. Differences among the habitats in the number caught individuals, on the other hand, were significant for all the dominant and subdominant species, except *Carabus convexus*, *Carabus nemoralis* and *Carabus intricatus (III)*. The analyses of indicator species and the variation in carabid catches among traps and habitats also show that the collected carabid species have a clear habitat and microsites preferences with specific environmental conditions. In the literature (Niemelä et al. 1985, 1996), four not mutually exclusive factors are mentioned that might explain the spatial distribution of carabid beetles: (1) autecological characteristics of the species, (2) small-scale dispersal, (3) interspecific interactions, and (4) differences in environmental conditions (habitat heterogeneity, food resources, microclimate, etc.).

The observable small scale dispersal processes at the research area were discussed above.

At the studied spatial scale, the occurrence of other carabids was a significant predictor of the abundance of a particular dominant and subdominant species *(III)*. Most of the correlations

were positive, suggesting similar respond to habitat properties. Previous works (Niemelä et al. 1992b; Niemelä and Spence 1994) also reported few negative relationships. These relationships were usually between species of clearly different body sizes or seasonal activities, or both, and are probably better attributed to different microhabitat preferences than to effects of interspecific interactions. In *study III* there was a negative relationship between the spatial distribution of the small *Synuchus vivalis* and the much larger *Carabus arcensis* which also showed maximum activities at different times of the season. For similar reasons interspecific competition is not a likely explanation for the other pairs of species showing a significant negative relationship: *Carabus arcensis* and *Harpalus rufipes*; *Carabus montivagus* and *Harpalus rufipes (III)*.

Interspecific competition may be suspected to contribute to the negative relationship between *Molops piceus* and *Pterostichus burmeisteri* which are of similar size and showed similar habitat preference and similar patterns of seasonal activity. Other data sets (Magura and Molnár 1997; Magura and Tóthmérész 1997, 1998; Magura et al. 1997, 1998*a, b*) suggest that negative interactions are not a general feature of these two species. Niemelä (1988) and Niemelä and Spence (1994) also reported two carabid species with similar size and seasonal activity which showed negative interaction in a forest habitat, while these species in other forest associations showed a high overlap in spatial distribution and in seasonal activity (Niemelä et al. 1992*b*; Niemelä and Halme 1992) or there were no correlation between the occurrence of the two species (Niemelä et al. 1993). These facts suggest that the type of relationship between the occurrence of carabids may not be a general feature. The interactions can vary among habitat types with different environmental attributes. Further manipulative and non-manipulative studies are necessary to prove the presence of competition between *Molops piceus* and *Pterostichus burmeisteri* because distributional data (spatially non-overlapping distribution) are just the first step to evaluate the mechanism of interspecific competition *(III)*.

Environmental factors controlling carabids distribution and diversity

In *study I* I found, that the plant cover (leaf litter, herb or canopy cover) and prey abundance significantly influenced the diversity of ground beetles along the transects. On the other hand the results of *study II* showed that the relative air moisture, the ground temperature and the cover of the herbs were the most important factors determining the diversity of carabids along the studied transects. For this reason I examined whether any of the environmental

measurements could be used to predict distribution of a particular carabid species *(III)*. The results of the multiple regression analyses show that the relative cover of the leaf litter was a significant negative predictor for two carabid species *(Abax parallelepipedus* and *Aptinus bombarda)*. Cover of the herbs was a significant positive predictor for *Carabus coriaceus.* Relationship between the cover of shrubs and the carabids' catch was significant for two species (*Abax parallelepipedus* and *Molops piceus*). Canopy cover was a significant positive predictor for *Abax parallelepipedus*. Abundance of carabids' preys was a significant positive predictor for three carabids (*Carabus convexus*, *Harpalus rufipes* and *Synuchus vivalis (III)*.

The importance of the microclimate in structuring carabid assemblages is emphasized in previous studies (Néve 1994; Butterfield 1997). The positive relationship between the ground temperature and the carabid's diversity can be explained by the fact that higher ground temperature may provide favourable sites for aestivation, hibernation, egg and larval development (Thiele 1977). The significant positive correlation between the relative air moisture and the diversity of carabids is expected because higher air moisture may produce favourable microsites for carabids in the studied area.

The significant negative correlation between canopy cover and carabid diversity could be because ground beetles characteristic of grassland can colonize the forest edge if canopy closure is low and thus microclimate is more favorable for them. On the other hand the multiple regression analyses showed that canopy layer was a significant positive predictor for *Abax parallelepipedus*. This is a habitat generalist, but significantly more individuals were captured in the forest interior than in the other habitats, suggesting the importance of microsites preference within the movement area.

The negative correlation between leaf litter cover and ground beetle diversity was unexpected because it is argued that deep leaf litter layer enhances ground beetle diversity through producing favorable microsites (Niemelä and Spence 1994). However, Guillemain et al. (1997) showed that an increase in litter thickness was accompanied by a decrease in both total beetle abundance and species richness. The proportion of forest species has also increased, due to the disappearance of some ubiquitous species. At sites where litter got thicker, ubiquitous species tended to become less abundant and ultimately disappeared leaving only typical forest species in the assemblage. In the forest interior with thick litter, most habitat generalists, edge-associated species and grassland-associated species disappeared producing a decreased diversity of the assemblage. The significant negative association between leaf litter and *Abax parallelepipedus* and *Aptinus bombarda* is surprising. Loreau (1987) reported that *Abax parallelepipedus* is active mainly at the surface of the litter. Perhaps this species can

move easier in a habitat with limited litter layer. The same may be supposed for *Aptinus bombarda*.

The significant positive correlation between the diversity of carabids and the cover of herbs may be explained by the structure of habitats, as carabid beetles depend more on a habitat structure than on specific plant species (Spence et al. 1996). Previous works demonstrated that vegetation structure and its derived changes in microclimate (e.g. temperature and air moisture) are likely to be one of the most important factors controlling and structuring the distribution of carabids (Niemelä et al. 1992*a*; Šustek 1994; Verschoor and Krebs 1995; Magura et al. 1997, 2000). Greater heterogeneity of vegetation accompanied higher diversity value of the carabid assemblages (Bedford and Usher 1994; Blake et al. 1996). Liebherr and Mahon (1979), Refseth (1980), Parmenter and MacMahon (1984) and Niemelä et al. (1996) also pointed out that the diversity of carabids was related to the heterogeneity of the habitat. In the case of the forest edge it can be stated that the herbs from the adjacent grassland and the shrubs from the forest significantly contributed to the heterogeneity of the habitat and supported the development of microhabitats.

With the increasing of coverage of the vascular plants (cf. habitat heterogeneity) the microclimatic conditions become more favourable for the majority of carabids and their egg and larval development (Thiele 1977). As the majority of trapped carabids are non-specialised predators, scavengers or omnivores, percentage cover of the herbs may increase the amount of herbivorous invertebrate prey available for carabids and may provide a more uniform resource distribution in time (Niemelä and Spence 1994; Niemelä et al. 1994, 1996). The abundant prey through the smaller resource-overlap (MacMahon 1980; Parmenter and MacMahon 1984) and the decreased intra- and interspecific competition (Müller 1987; Loreau 1989, 1990) may explain the high diversity observed in the forest edge and grassland and the positive relationships between the abundance of carabids' preys and the four carabid species.

Forest fragmentation on macro-scale (*Study IV*)

Responses of carabids to urbanisation

Urbanisation causes several forms of disturbance, such as alteration, fragmentation and isolation of indigenous habitats, changes of temperature, moisture and edaphic conditions, and pollution (Gilbert 1989; Niemelä 1999). Gray (1989) hypothesised that in habitats influenced

by disturbance, overall diversity should decrease, opportunistic (generalist) species should gain dominance and the mean body size of species should decrease. My results did not confirm the increased disturbance hypotheses. The number of collected carabid species was significantly higher in the rural and the urban areas than in the suburban one *(Figure 3 A)*. The overall species richness of carabids was almost as high in the urban area as in the rural one *(Figure 3 D)*. Overall species richness changes along the disturbance gradient (urban-rural gradient) can be complex, because in a group of taxa, species richness may increase or decrease with disturbance depending on their habitat preference. Even basic biogeographical rules, such as the species richness – island size relationship can be masked if one does not take into account the ecological characteristics of the species studied (Magura et al. 2001). The initial hypothesis regarding forest specialists was confirmed: the number of forest species significantly increased from the urban to the rural area *(Figure 3 B)*. The number of open-habitat species was significantly higher in the urban area than in the suburban and rural areas *(Figure 3 F)*. These results indicate that human impacts caused a pronounced change in the carabid assemblages. Forest species require microsites with a particular kind of environmental heterogeneity (Desender et al. 1999). Changes caused by urbanisation eliminate favourable microsites, altering the original habitats. These disturbances damage the species most closely adapted to the original environment, here the forest species. The degree of disturbance is higher in the urban area, than in the suburban, and lowest in the rural area. This was also expressed by the difference in the species richness of forest carabids *(Figure 3 E)*. The remarkable alteration of the original habitats in the urban area was also reflected by the higher number of open-habitat species *(Figure 3 F)*. Urban parks contain several microhabitats that open-habitat species can colonise. Previously I also emphasised *(I, II, III)* that the number of openhabitat species increases as the closure of the forest stand decreases. Changes of carabid abundance along the urban-rural gradient showed a similar pattern *(Figure 3 C)*. The overall carabid abundance was significantly higher in the rural than in the urban and suburban areas *(Figure 3 A)*. The number of individuals of the forest species was also the highest in the rural area, while significantly more individuals of open-habitat species were collected from the urban than from the other areas *(Figure 3 B-C)*.
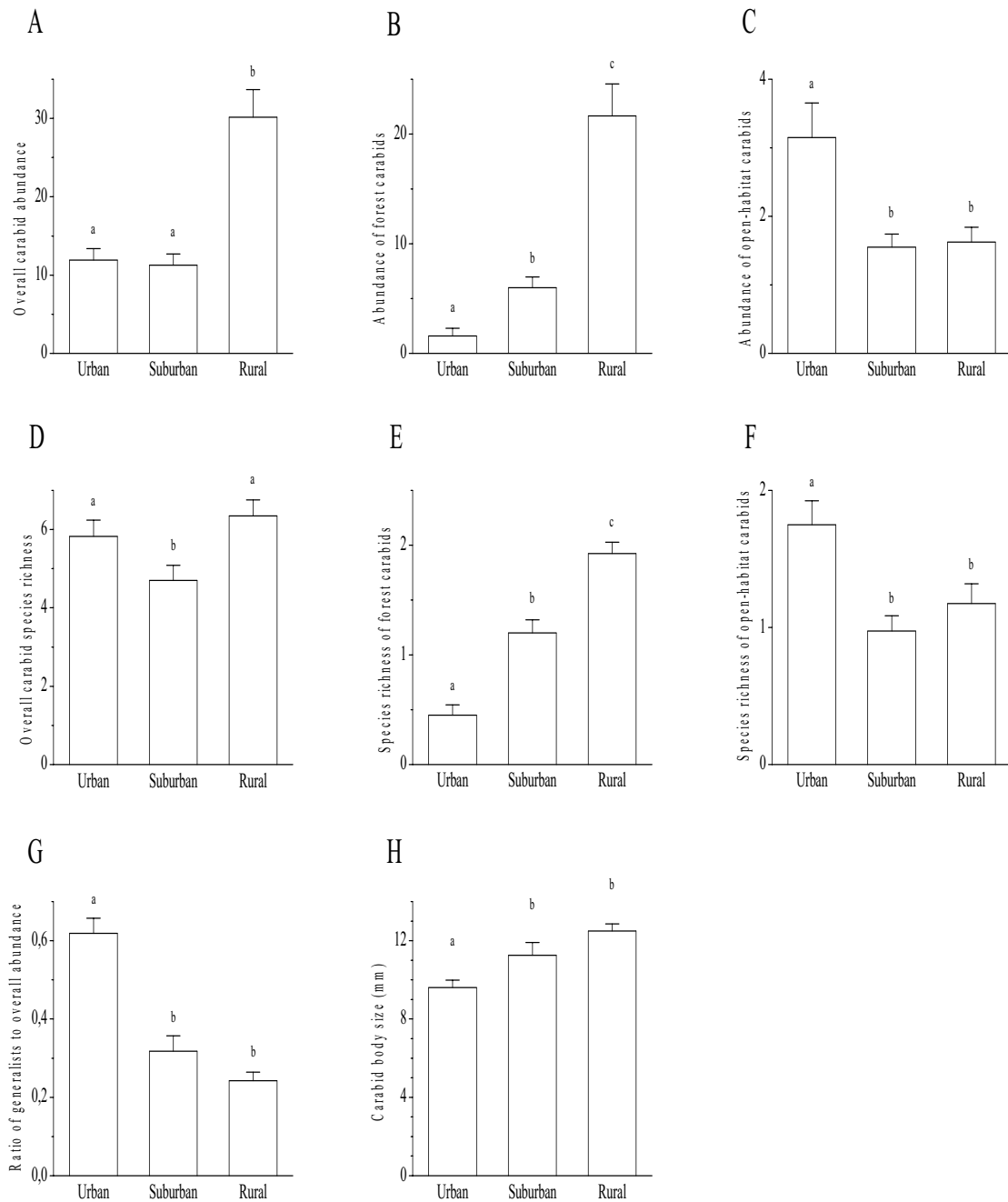
Figure 3. Average value (±SE) of the overall carabid abundance (A), the abundance of forest carabids (B), the abundance of open-habitat carabids (C), the overall carabid species richness (D), the species richness of forest carabids (E), and the species richness of open-habitat carabids (F) along the urban-suburban-rural gradient. Different letters indicate significant (p<0.05) differences based on the LSD (least significant difference) multiple comparison.

Intermediate Disturbance Hypothesis (IDH)

Both my findings and those of Niemelä et al. (2002) contradict the IDH (Connell 1978). Species richness was not the highest in the moderately disturbed suburban areas as IDH predicts *(Figure 3 D)*. This may be explained partly by the fact that basal species in food webs probably conform to this hypothesis (Wootton 1998), but top consumers like carabids (Lövei and Sunderland 1996) do not. IDH is a general framework considering different kinds of disturbance without precise, verifiable details regarding the ecological mechanisms of the changes in species richness. The increase of richness may be ecologically important when only the species pool of the local, characteristic habitat type (conform to native fauna) is involved. However, invasion of the species from other habitat types or by generalist, opportunistic species would also increases species richness. The gain by the presence of these species could offset the disappearance of habitat specialists. According to the opportunistic species hypothesis (Gray 1989) the generalist (opportunistic) species should gain dominance with increasing disturbance within the assemblage. My results supported this prediction, as the ratio of the individuals of the opportunistic carabid species to the total number of individuals was significantly higher in the urban area than in the other ones *(Figure 3 G)*.

Mean body size hypothesis

My results were also coherent with the mean body size hypothesis (Blake et al. 1994; Gray 1989): the mean carabid body size was significantly higher in the less disturbed rural and suburban areas than in the more disturbed urban area *(Figure 3 H)*. Gray (1989) hypothesised that the mean size of the species should decrease in disturbed habitats. Disturbed habitats (Blake et al. 1994) as well as forests (Holliday 1991; Magura et al. 2002) support a carabid fauna with smaller average body size. Šustek (1987) also found that disturbance caused by urbanisation produced smaller average carabid body size. It may be expected that changes in body size distributions along the urban-rural gradient may reflect differences in resource availability and stability or habitat capacity (Niemelä et al. 2002). Blake et al. (1994) argued that larger carabids were predominantly autumn breeders with overwintering larvae and a longer larval period required an availability and stability of resources that was missing in disturbed habitats. Several field studies confirmed that the abundance of carabids that overwinter as larvae was higher in less disturbed habitats compared to more disturbed ones (Butterfield 1997; Lövei 1984; Magura et al. 2002). In woodlands, increasing organic matter is linked to increased carabid biomass, and this may contributes to the persistence of larger-

bodied carabids (Blake et al. 1994). In woodlands, the chief source of soil organic matter is from decaying plant material and it is possible that a high organic matter content is an indication of less disturbed forest habitats. At our sites, the rural area had significantly more herbs and decaying wood than the other areas and therefore probably more organic matter. This could contribute to the existence of larger carabids. The smaller mean body size in the urban area may also be explained with the flight ability, as species capable of flying are generally small-sized. The majority of open-habitat species collected in the urban area are able to fly which enables their rapid dispersal.

Changes in species structure

There is a marked separation among the sites along the urban-rural gradient. The four urban sites separated into a distinct cluster based on the species composition, while the suburban and rural sites formed the other cluster, indicating that urbanisation caused a pronounced change of carabid assemblages, as the urban sites separated from the suburban and rural sites *(Figure 4 A)*. The number of common species was high and equal for all the studied areas (21 species), while the number of differential species was very low for the suburban-rural areas (9 species) compared to the others (urban-suburban (27 species), and urban-rural (26 species)). The number of differential species was very uneven; the urban area had 22 differential species compared to the rural and suburban sites (5 versus 4 differential species, respectively). There was no such asymmetry between the rural-suburban areas. This is explained by the patterns of occurrence of carabid species along the urban-rural gradient. Forest species preferred the moderately disturbed or undisturbed areas (suburban and rural), while open-habitat species occurred mainly in the urban area. These changes along the urban-rural gradient and the different patterns of occurrence were confirmed by the results of the IndVal procedure. Five groups of species were distinguished: (1) habitat generalists that were numerous in all areas (e.g. *Harpalus tardus*, *Carabus violaceus*, *Platyderus rufus*); (2) species preferring the urban area, recorded exclusively or being most abundant in the urban area (e.g. *Amara convexior*, *Pterostichus melanarius*, *Anisodactylus nemorivagus*); (3) species characteristic of suburban-rural areas; (e.g. *Carabus convexus*, *Stomis pumicatus*, *Oxypselaphus obscurus*); (4) species preferring the suburban area; (e.g. *Harpalus luteicornis*, *Badister lacertosus*, *Amara consularis*); and (5) species characteristic of the rural area; (e.g. *Pterostichus oblongopunctatus*, *Ophonus nitidulus*, *Amara saphyrea*). The MDS ordination based on the abundance data revealed a linear gradient *(Figure 4B)*: the carabid assemblages changed
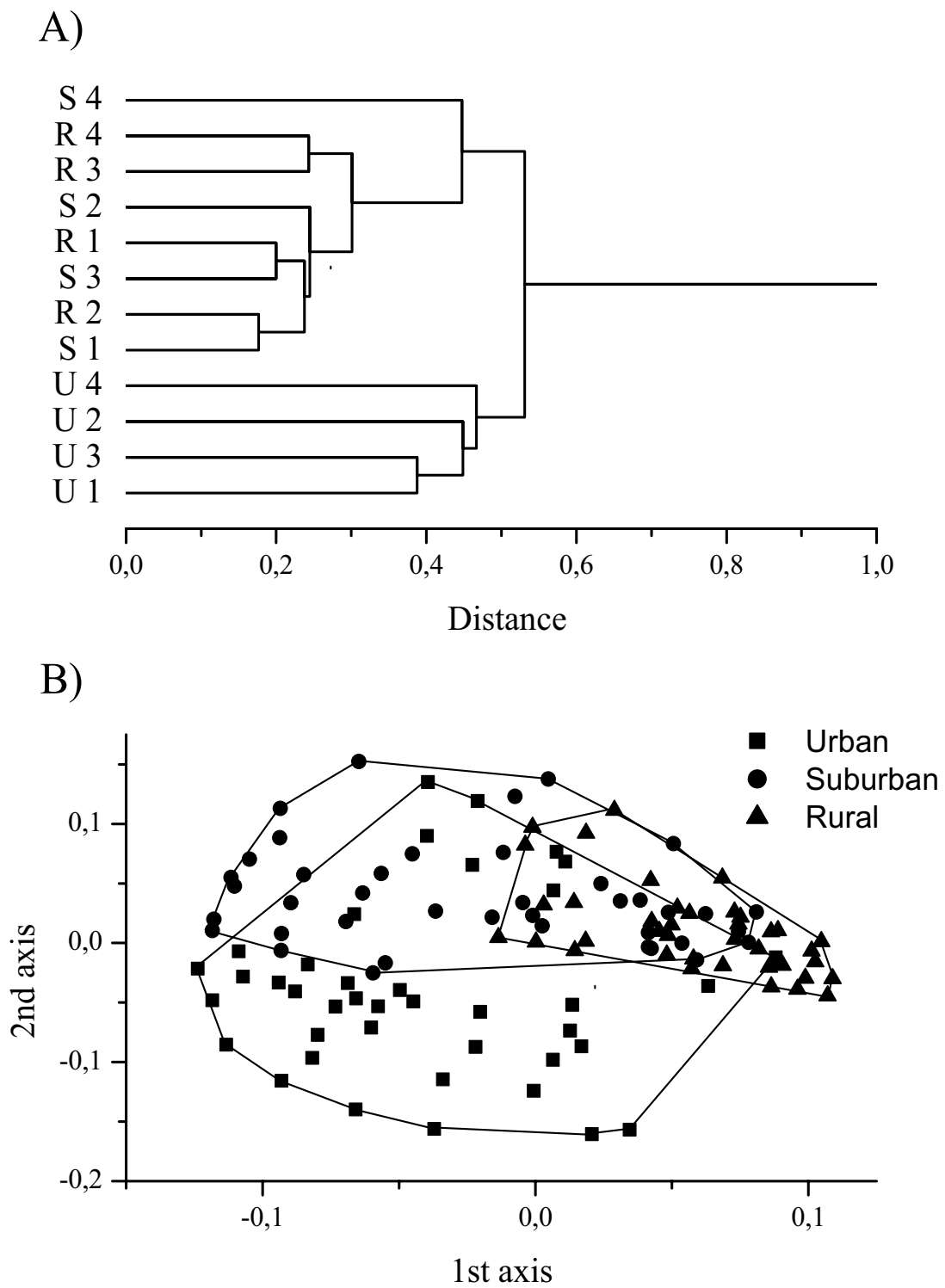
Figure 4. Cluster analysis of the carabid assemblages along the studied urbanrural gradient at site level using the Sørensen index of similarity and the group average fusion algorithm (A) and MDS ordination of the abundances using the Bray-Curtis index of dissimilarity (B).

gradually from the rural area towards the urban area. The heterogeneity of the carabid composition among the sites of the given area is highlighted by the size of the convex hull on the ordination graph. The larger size of the convex hull indicates a higher variability among the carabid composition of the traps. The size of the convex hull correlates with the ß-diversity and/or heterogeneity of the assemblages (Tóthmérész 1998). The size of the convex hull of the sites increased from the rural to the urban area, suggesting an increased heterogeneity and/or ß-diversity of the carabid composition along the urban-rural gradient *(Figure 4 B)*. High heterogeneity and ß-diversity among sites in the urban area was caused by the patchy environment. In the urban area, habitat patches with closed canopy co-occur with patches of moderate closure because of the walking paths and thinned shrubs. This patchiness facilitated the survival and persistence of forest species, generalist species as well as open-habitat species in the urban area. However, the species composition changed from site to site, causing high heterogeneity. The rural area had roughly identical habitat patches, therefore the dominant and subdominant generalist and forest species were relatively uniformly distributed leading to lower heterogeneity. The fact that many species of different origin (forest species, generalist species, open-habitat species) find suitable conditions in the urban area causes a relatively high α-diversity, while the considerable variety of habitat patches (e.g. natural and anthropogenically influenced and/or modified patches) and their associated species assemblages leads to high ß-diversity.

Environmental factors and carabids

Regression analyses showed that a significant proportion of the variation in abundance and species richness was associated with a particular kind of environmental heterogeneity, as reflected by the ground temperature, surface temperature, humidity, cover of leaf litter, decaying wood material, herbs, shrubs, canopy layer, and by the amount of potential prey.
The positive relationship between the ground temperature and the overall species richness can be attributed to the high number of generalist and open-habitat species in habitats with higher temperature. Open-habitat species prefer habitats with open or less closed canopy, where the sunlight can warm up the soil and they aggregate in these patches (Thiele 1977).
Relationships between humidity and the abundance of both overall carabids and the forest species were positive. Forest carabids generally favour habitats of higher humidity (Thiele 1977). The mainly nocturnal forest carabids also may prefer microsites with higher humidity during day-time. Certain generalist species also favour habitats with higher humidity. As

more than half of the collected individuals were forest carabids, it is plausible that the positive relationship between humidity and overall carabid abundance was caused by the positive relationship between humidity and the abundance of forest species. Leaf litter cover was not a significant predictor for either the abundance or the species richness of carabids, even though several studies emphasised the importance of leaf litter in the spatial pattern of occurrence in carabid beetles (Koivula et al. 1999; Magura et al. 2000; Antvogel and Bonn 2001). In the broad-leaved forests abiotic factors (temperature and humidity) altered by the leaf litter might play a more important role in carabid occurrence than leaf litter cover alone. In this study, humidity increased, while ground and surface temperature decreased with increasing leaf litter coverage. Both the abundance and species richness of open-habitat carabids decreased, while the number of forest carabid species increased as the amount of decaying wood material increased. Open-habitat carabids are not adapted to environment with dense decaying wood material. For forest carabids, decaying wood provides favourable microsites, shelter against predators, and sites for aestivation, hibernation, egg and larval development (Thiele 1977). Except for the number of open-habitat species, both the abundance and species richness of carabids increased as herb cover increased. These can be explained by the structure of habitats and by the increasing the amount of potential prey for carabids which can provide a more uniform resource distribution in time as it was discussed above. Canopy cover was a negative predictor for the overall carabid abundance, for the abundance of forest carabids and for the number of openhabitat species. Open-habitat species are adapted to an environment with limited or moderate canopy closure (Thiele 1977), so a negative correlation between their occurrence and the amount of canopy cover is not surprising. A more open canopy can produce a more heterogeneous habitat where both the generalist, the forest and the open-habitat carabids could find favourable microsites, resulting in a rich carabid assemblages. The negative correlation between the canopy cover and the abundance of forest carabids is unexpected because forest carabids generally prefer a closed canopy layer (Thiele 1977). There may also be a threshold level of canopy cover that forest species require, and above which the actual value of the canopy cover does not really matter. When the canopy cover is high enough to guarantee the typical microclimatic conditions inside the forest, other factors are becoming dominant in controlling the species richness of forest carabids. There was a significant positive relationship between the amount of potential prey items and both the overall carabid species richness and the number of forest carabid species. Several studies (Thiele 1977; den Boer 1985) emphasise the importance of abiotic environmental factors in carabid ecology but neglect the influence of biotic factors, such as the amount of carabid prey.

My result draws attention to the relevance of prey density in determining carabid species richness. Bryan and Wratten (1984) also reported that carabids may aggregate in microsites with plentiful prey. Verschoor and Krebs (1995), Guillemain et al. (1997) and Fournier and Loreau (1999) also emphasised that prey density plays a crucial role in carabid distribution. Through smaller resource-overlap (Parmenter and MacMahon 1984) and decreased intra- and interspecific competition (Müller 1987; Loreau 1989, 1990) the abundant prey can explain the high species richness observed in habitats with abundant prey.

CONCLUSION

Management and conservation of forest edges

My research pointed out that forest edges may have a crucial role in the maintenance and preservation of diversity of carabids, therefore their conservation is essential. Many carabid species characteristic of grassland and forest interior can disperse into the forest edge. Thus, forest edges have viable populations of carabids of the adjacent habitats. Therefore, they may also serve as "source" habitat (sensu Pulliam 1988) or "stepping-stones" (sensu den Boer 1970) for dispersal processes, contributing to the recolonization of carabid species in the adjacent habitats after local extinction (den Boer 1981) or destruction of suitable habitats (e.g. burning, ploughing, grazing, timbering etc.). These data indicate a considerable potential of the forest edges for succession and regeneration of adjacent disturbed sites. This feature of the forest edge may also be applied for conservation purposes. Landscape management schemes attempt to create more diverse vegetation in the poorly developed edges by sowing or planting shrubs and by cutting adjacent forest trees to reduce shading. Anderson and Carter (1987) also reported that diversity of plants and butterflies can be maintained and encouraged by management practice that widening or shaping the edges. The edges could have also negative effects, when in consequence of forest fragmentation they are becoming proportionately greater relative to interiors (Saunders et al. 1991). Edge habitats were found unsuitable for species requiring interior habitat (Demaynadier and Hunter 1998; von Sacker 1998), and consequently such species may be lost if fragments become to small (Haila 1999). Forest managers should minimize adverse edge effects by, for example, leaving fragments large enough to maintain specialists of the forest interior (Spence et al. 1996; von Sacker 1998). With help of well-designed studies that are able to determine which patterns are universal to

the edges in general, and the factors that potentially modulate edge effects in each particular case, we will able to design general management plans for conservation purposes.

Preservation biodiversity in the urban landscape

My results showed that urbanisation had an effect on carabid assemblages. Species richness as well as the composition were changed along the urban-suburban-rural gradient. Forested urban areas were still relatively species-rich, but the majority of the observed species invaded from the surrounding habitats (generalists and open-habitat species). In contrast the number of native forest carabid species significantly decreased along the disturbance gradient. Urban green areas, including the studied forested areas, contribute to the quality of urban life and thus should be conserved. Apart from the recreational importance of the urban green areas, they provide suitable habitats for many carabid species living in undisturbed or moderately disturbed areas (e.g. meadows, grasslands, pastures, agricultural areas) surrounding the city. Moreover, urban green areas could support rare species. In the present study I collected *Pterostichus melas* from the urban area. In Hungary, this species occurs mainly in the hills and mountains and only few lowland occurrences were known. However, as my results also demonstrated, urbanisation could be one of the leading causes of decline in indigenous arthropod diversity and abundance (Davis 1978; Pyle et al. 1981). How can the biodiversity preservation function of urban parks be enhanced? I suggest that extensive alteration of habitat structure (e.g. by strong thinning and removing decaying wood material) and creating too many asphalt-covered paths should be avoided. Change in habitat structure causes changes in the microclimatic, abiotic and biotic conditions of the area. All these changes affect forest carabids directly. Creating too many paths with asphalt surface also influences carabid beetles indirectly by fragmentation. The division of the original forests into smaller, isolated patches results in a loss of forest species through a reduction in the habitat area, an increase in remnant isolation and a decrease in habitat connectivity (Didham et al. 1996). Forest patches divided by asphalt-covered paths are isolated from each other, as carabids usually do not cross such roads (Mader 1984; Mader et al. 1990). The population size of forest carabid species in isolated patches could decrease because the patches are too small to maintain viable populations and because there is too little dispersal between patches. Small populations of forest carabids in isolated patches are at greater risk of local extinction through stochastic population fluctuations than are the larger populations (den Boer 1985; Niemelä et

al. 1994). Judicious habitat management can both serve the demand of city-dwellers for recreation and the maintenance of biodiversity.

Overall, my results suggest that carabids are useful as an indicator group to asses the environmental variation, as they show different habitat choices. My studies imply that distribution of carabids is determined not only by abiotic environmental factors, like soil types and soil properties (Luff et al. 1989, 1992; Niemelä et al. 1992*b*; Eyre and Luff 1994; Šustek 1994), microclimatic conditions (Niemelä et al. 1986; Müller-Motzfeld 1989; Spence et al. 1996), heterogeneity of vegetation (Niemelä 1990; Blake et al. 1996), cover of decaying woods and leaf litter (Niemelä et al. 1992*a*; Eyre and Luff 1994) but also by biotic factors, like distribution of other ground-dwelling animals (e.g. ants; Niemelä et al. 1992*a*), abundance of carabids' preys (Niemelä et al. 1986; Halme and Niemelä 1993; Guillemain et al. 1997), intraspecific competition (Müller 1986; Loreau 1990) and interspecific competition (Lenski 1982, 1984; Loreau 1989). Thiele (1977) and den Boer (1981, 1985) emphasize the priority of abiotic factors in the determination of carabid distribution and in the organisation. My result stresses that a synthesis is needed, which integrates competition with other abiotic and biotic ecological factors. This synthesis would help a lot in understanding community organisation of carabids, but in this respect, we are still at the beginning (Niemelä 1993).

SUMMARY

Study of habitat fragmentation at meso spatial scale

One consequence of fragmentation and isolated habitat loss is decreasing fragment size, which leads to a decreasing proportion of interior habitat and increasing proportion of edge. Therefore forest edges are a focus of conservation research, important to wildlife management and there is an increasing need for their appropriate management. Classical edge effect hypothesis states that diversity is higher in ecotones than in adjacent habitats. The goal of the studies was to test this hypothesis for carabids and to analyse of ground-beetle distribution along forest-grass transects. My objectives were to assess the extent of variation in distribution for carabids, and to relate this to habitat characteristics and to spatial distribution of co-occurring carabid species. I also examined the environmental variables that may be important to control the distribution of ground-dwelling carabids, and thus can influence edge effect on carabid beetles. Sampling area was located at the North Hungarian Mountain in the Aggtelek National Park, near the Mogyorós Peak (Haragistya). There are three habitat types on the research area: (1) Grass, (2) Forest edge, (3) Forest interior. Parallel transects of pitfall traps were set across the three studied habitats. The transects were perpendicular to the forest edge.

My results show that there is a significant edge effect on the carabid assemblages at the research area. The Shannon diversity was significantly higher in the forest edge and the grass than in the forest interior. Edge effect on carabids is due in part to the presence of species characteristic of each of the adjacent habitats plus species inhabiting the edge. These edge species find habitats at the edge that are not present in either habitat alone, or they require two structurally different habitats in close proximity to one another. The high diversity of the forest edge may be caused by small scale dispersal processes. On the studied scale the habitats are not isolated from each other and there appears to be dispersal between the adjacent habitats. The changes of the monthly distribution pattern of carabids in the habitats suggesting that there must be seasonal movement between the adjacent habitats as it was proved in case of *Pterostichus oblongopunctatus* and *Pterostichus burmeisteri*.

The carabid assemblages change gradually from the forest interior towards the grass along the transects. In spite of the almost continuous variation of the composition of the assemblages, carabid samples of the grass, the forest edge and the forest interior are separated from each

other. All studied habitat types have characteristic assemblages of carabid species associated with them.

According their habitat preference the collected carabid species can be divided into five groups: (1) habitat generalists; (2) grassland-associated species; (3) forest generalists; (4) forest specialists; and (5) edge-associated species. The collected carabid species have a clear habitat and microsites preferences with specific environmental conditions. Sometimes, variation in carabid catches among the traps in the same habitat was greater than the variation among habitats indicating the importance of strong microhabitat variations controlling carabid distribution. At the studied spatial scale, the occurrence of other carabids was a significant predictor for the abundance of a particular dominant and subdominant species. Most of the correlations were positive, suggesting similar respond to habitat properties. However interspecific competition may be suspected to contribute to the negative relationship between *Molops piceus* and *Pterostichus burmeisteri* which are of similar size and showed similar habitat preference and similar patterns of seasonal activity. The plant (leaf litter, herb or canopy) cover and prey abundance, the relative air moisture, the ground temperature were the most important factors determining the diversity of carabids along the studied transects. I examined whether any of the environmental measurements could be used to predict distribution of a particular carabid species The relative cover of the leaf litter was a significant negative predictor for *Abax parallelepipedus* and *Aptinus bombarda*. Cover of the herbs was a significant positive predictor for *Carabus coriaceus*. Relationship between the cover of shrubs and the carabids' catch was significant for *Abax parallelepipedus* and *Molops piceus*. Canopy cover was a significant positive predictor for *Abax parallelepipedus*. Abundance of carabids' preys was a significant positive predictor for *Carabus convexus*, *Harpalus rufipes* and *Synuchus vivalis*.

Study of habitat fragmentation at macro spatial scale

One of the leading causes of habitat fragmentation is urbanisation. Urban ecosystems contain spatially heterogeneous and temporally dynamic areas that differ from their surroundings and from the natural, intact habitats. Despite their global ubiquity, relatively little is known about how arthropods respond to urbanisation, even though urbanisation is regarded as one of the leading causes of decline in arthropod diversity and abundance. Three kinds of forested habitats (urban parks, suburban forested area, and rural forest), representing different levels of human disturbance and habitat fragmentation were selected to study the patterns and responses of carabid assemblages along this urbanisation and habitat fragmentation gradient. The study areas were in Debrecen (Eastern-Hungary), the second largest city of the country. The following predictions were tested for carabids in urban environments: (1) diversity should decrease from a high in the rural area to a low in urban area *(increasing disturbance hypothesis)*; (2) diversity should be the highest in the suburban area according to the *intermediate disturbance hypothesis (IDH)*; (3) the abundance and species richness of the forestspecialist species should increase from the more disturbed urban area to the less disturbed rural one *(habitat specialist hypothesis)*; (4) opportunistic species should gain dominance in the urban area *(opportunistic species hypothesis)*; (5) the mean body size of the species should decrease with increasing disturbance level, in our case from the rural to the urban area *(mean body size hypothesis)*; (6) carabid assemblages should change along the urbanisation gradient and therefore there should be characteristic and/or key species of the stages of the studied gradient; and (7) certain environmental variables should predict the observed pattern of carabid abundance and species richness.

My results did not confirm the increased disturbance hypotheses. The number of collected carabid species was significantly higher in the rural and the urban areas than in the suburban one. The increased disturbance hypothesis regarding forest specialists was confirmed: the number of forest species significantly increased from the urban to the rural area. My results contradict the Intermediate Disturbance Hypothesis (IDH). Species richness was not the highest in the moderately disturbed suburban areas as IDH predicts. The opportunistic species hypothesis was supported, as the ratio of the individuals of the opportunistic carabid species to the total number of individuals was significantly higher in the urban area than in the other ones. That means the generalist (opportunistic) species gained dominance with increasing disturbance within the assemblage. My results were also coherent with the mean body size

hypothesis: the mean carabid body size was significantly higher in the less disturbed rural and suburban areas than in the more disturbed urban area.

Changes caused by urbanisation altered the original habitats. Human impacts caused a pronounced change in the carabid assemblages. These disturbances damage the species most closely adapted to the original environment, here the forest species. The degree of disturbance is higher in the urban area, than in the suburban, and lowest in the rural area. The carabid assemblages changed gradually from the rural area towards the urban area. The heterogeneity of the carabid composition of the sites along the urban-rural gradient increased from the rural to the urban area. The high ß-diversity in the urban area was caused by the patchy environment. This patchiness facilitated the survival and persistence of forest species, generalist species as well as open-habitat species in the urban area. However, the species composition changed from site to site, causing high heterogeneity. The rural area had roughly identical habitat patches, therefore the dominant and subdominant generalist and forest species were relatively uniformly distributed leading to lower heterogeneity. The number of differential species was very uneven; the urban area had 22 differential species, while the number of differential species was very low (5 resp. 4) for the suburban-rural areas. This is explained by the patterns of occurrence of carabid species along the urban-rural gradient. Forest species preferred the moderately disturbed or undisturbed areas (suburban and rural), while open-habitat species occurred mainly in the urban area. Five groups of species could be distinguished according their habitat preference: (1) habitat generalists; (2) species preferring the rural area; (3) species characteristic of suburban-rural areas; (4) species preferring the suburban area; and (5) species characteristic of the urban area.

A significant proportion of the variation in abundance and species richness was associated with a particular kind of environmental heterogeneity. There was positive relationship between the ground temperature and the overall species richness. The humidity was significant negative predictor for the abundance of both overall carabids and the forest species. Both the abundance and species richness of open-habitat carabids decreased, while the number of forest carabid species increased as the amount of decaying wood material increased. Except for the number of open-habitat species, both the abundance and species richness of carabids increased as herb cover increased. Canopy cover was a negative predictor for the overall carabid abundance, for the abundance of forest carabids and for the number of openhabitat species. There was a significant positive relationship between the amount of potential prey items and both the overall carabid species richness and the number of forest carabid species.

ÖSSZEFOGLALÁS

Az élőhelyek feldarabolódásának a futóbogarakra gyakorolt hatását tanulmányoztam négy vizsgálatban *(I-IV)* mezo és makro térbeli léptékben.

Az élőhelyek fragmentálódásának mezo skálán történő vizsgálata *(I-III)* során a klasszikus szegélyhatás hipotézist teszteltem futóbogárközösségeken és elemeztem a futóbogarak térbeli eloszlását erdő-gyep transzektek mentén, továbbá vizsgáltam, a térbeli eloszlásban mutatkozó eltéréseket és megpróbáltam mindezt megmagyarázni az élőhely jellemzőiben mutatkozó különbségekkel, illetve a fajok közötti interakciókkal. Vizsgáltam azon környezeti tényezőket, melyek fontosak lehetnek a talajfelszínén mozgó futóbogarak szempontjából és így befolyásolhatják a szegélyhatást.

Az élőhelyek fragmentálódásának makro skálán történő vizsgálata *(IV)* során a fragmentációnak egyik fő előidéző okának, az urbanizációnak a futóbogarakra gyakorolt hatásait vizsgáltam. Három erdei élőhelyet választottam ki (egy városi parkot, egy külvárosi erdős területet, és egy városon kívüli erdőt), melyek az ember által okozott zavarás és a fragmentáció különböző fokát képviselik. A következő predikciókat teszteltem futóbogarakon a városi élőhelyeken: (1) a *növekvő zavarás hipotézis*ének megfelelően a diverzitásnak csökkennie kell városon kívüli élőhely magas értéktől a városi park alacsony értéke felé; (2) a diverzitásnak a külvárosi területen kell a legnagyobbnak lennie a *közepes zavarás hipotézis*ének megfelelően; (3) az erdei specialista fajok egyed- és fajszámának növekednie kell a leginkább zavart városi élőhelytől a legkevésbé zavart városon kívüli felé *(habitat specialista hipotézis)*; (4) az opportunista, generalista fajok lesznek dominánsak a város park élőhelyein (*generalista fajok arányának hipotézise*); (5) az átlagos testméretnek csökkennie kell a növekvő zavarás következtében, esetünkben a városon kívüli felől a városi park felé *(átlagos testméret hipotézis)*; (6) a futóbogár együttesek összetétele változni fog az urbanizációs gradiens mentén ennek következtében a vizsgált gradiens különböző fokain karakterisztikus és/vagy kulcs fajoknak kell lenniük; és (7) kapcsolat lesz bizonyos környezeti tényezők és a futóbogarak egyed- és fajszáma között.

ANYAG ÉS MÓDSZER

Vizsgálati terület és gyűjtési módszer

A vizsgálataim során a futóbogarak gyűjtésére csalogatóanyag nélküli talajcsapdákat alkalmaztam, melyek 75%-os etilén-glikolt tartalmaztak ölő- és tartósítófolyadék gyanánt. A csapdákat fakéreggel fedtem le, hogy megóvjam őket az eső okozta felhígulástól és a belehulló lombavartól és egyéb növényi részektől. A csapdákat a hómentes időszak alatt (márciustól novemberig) működtettem.

I-III. vizsgálat

A kutatási terület az Aggteleki-karszton helyezkedett el, az Aggteleki Nemzeti Parkban a Mogyorós-bércen. Ezen a területen a legkiterjedtebb társulás a gyertyános-tölgyes (*Querco-Carpinetum*) és a mérsékelten száraz gyep (*Polygalo majori-Brachypodietum pinnati*). Ennek megfelelően a kijelölt kutatási területen három élőhelyet vizsgáltam:

(1)   Gyeptársulás (*Polygalo majori-Brachypodietum pinnati*), mely az alábbi gyakori növényekkel jellemezhető: *Polygala major, Brachypodietum pinnatum, Filipendula vulgaris, Salvia pratensis, Inula hirta, Geranium sanguineum.* A lombavar réteg, a csejék és a fák hiányoztak e területről.

(2)   Erdőszegély, ahol a szomszédos gyepből származó lágyszárúak magas borítását figyelhettük meg, ugyanakkor a cserjék borítása is magas volt (a cserjeszint domináns tagjai: *Carpinus betulus*, *Corylus avellana* és *Prunus spinosa*). A lombavarréteg viszonylag vastag, összefüggő volt, míg a fák záródása kisebb volt, mint az erdőfolt belsejében.

(3)   Erdő belseje. A tanulmányozott erdőrész egy gyertyános-tölgyes volt, dús avarréteggel, mérséklet lágyszárú és cserje borítással. A lombkoronaszint záródása 85-95 % volt.

A *I. vizsgálat*ban (1997-ben) 2 párhuzamos transzektet jelöltem ki, ezek mentén helyeztem el a talajcsapdákat, mindegyik élőhelyen 8-8 csapda volt az egyes transzektekben, (azaz összesen 2×3×8=48 talajcsapda).

A *II. vizsgálat* során (1997-1998) három transzekt mentén 5-5 csapda volt az egyes élőhelyeken, (összesen 45 csapda)

A *III. vizsgálatban* (1999) a csapdákat három transzekt mentén helyeztem el. Mindegyik tanulmányozott élőhelyen tizennégy darabot. Így összesen 3×3×14=126 csapda üzemelt.

Ahhoz, hogy a futóbogarak térbeli eloszlása és a környezeti változók közötti kapcsolatot tanulmányozhassam, becsültem a lombavarréteg, a lágyszárúak és a cserjék százalékos

borítását, továbbá a lombkoronaszint záródását is mindegyik csapda környezetében. Továbbá megszámláltam a talajcsapdába esett valamennyi élőlényt, mely a futóbogarak szempontjából potenciális táplálékként szolgálhat. Ilyen élőlénynek számítanak az alábbi taxonok egyedei: *Lumbricidae*, *Mollusca*, *Isopoda*, *Chilopoda*, *Aranea* és *Coleoptera* lárvák. Azért ezeket a csoportokat tekintettem zsákmányállatoknak, ugyanis ezek is a talajfelszínen mozognak, ugyanakkor szerológiai módszerekkel igazolták, hogy a futóbogarak valójában fogyasztják ezeket a gerinctelen állatokat. A *II. vizsgálat*ban ezeken kívül még mindegyik csapda mentén mértem a talajhőmérsékletet illetve a talajfelszínen a levegő hőmérsékletét és páratartalmát.

IV. vizsgálat

A kutatási terület Debrecenben volt. Három erdei élőhelyet választottam ki egy urbanizációs gradiens mentén (egy városi parkot, egy külvárosi erdős területet, és egy városon kívüli erdőt), melyek az ember által okozott zavarás és a fragmentáció különböző fokát képviselik. A városi parkban számos aszfaltozott sétány volt és a cserjéket is erősen meggyérítették, hogy park jelleget adjanak a területnek, a külvárosi területről pedig a kidőlt fákat távolították el. Mindegyik mintavételi terület az eredeti kocsányos tölgyes erdővel kapcsolódó erdőrészben helyezkedett el és legalább 6 hektáros volt. Ezek mindegyikében négy mintavételi helyet választottam ki, amelyeken belül 10-10 csapdát helyeztem el véletlenszerűen. Kilenc környezeti változót vizsgáltam melyek hatással lehetnek a futóbogarak térbeli eloszlására. Azaz mértem a talaj hőmérsékletét, a levegő hőmérsékletét és páratartalmát a talajfelszínen, becsültem a lehullott, illetve korhadó fák mennyiségét, a lombavarréteg, a lágyszárúak és a cserjék százalékos borítását, továbbá a lombkoronaszint záródását is mindegyik csapda környezetében, tanulmányoztam a futóbogarak lehetséges táplálékforrásának csapdánkénti mennyiségét is.

Adatelemzések

Mindegyik vizsgálatban a karakterfaj-elemzést *(IndVal)* használtam, hogy az adott élőhelyekre jellemző karakterfajokat és faj-együtteseket azonosítsam. A karakterfaj-elemzések során főkoordináta analízist (Bray-Curtis távolságfüggvény) használtam a gyűjtési egységek klasszifikációjára, azaz azoknak mintavételi pontoknak, illetve helyeknek a csoportosítására, melyekre karakterfaj(oka)t kerestem.

I-II vizsgálat

Ahhoz, hogy a szegélyhatást futóbogár közösségek esetén vizsgálhassam, a transzektek mentén a három élőhely Shannon-diverzitását hasonlítottam össze egymással. Tukey-próbát *(I, II)* használtam annak meghatározásához, hogy vannak-e különbségek a transzektek mentén az egyes habitatokban a talajcsapdánkénti futóbogár diverzitásban és a vizsgált környezeti változókban. Spearman rangkorrelációt *(I)* illetve többszörös lineáris regresszió-analízist használtam annak kimutatására, hogy van-e valamilyen összefüggés a környezeti változók és a futóbogarak diverzitása között. Nem metrikus sokdimenziós skálázást (MDS) (Rogers Tanimoto hasonlóságfüggvénnyel) alkalmaztam a fajösszetétel vizsgálatára *(II)*. Főkoordináta-analízist (PCoA) végeztem a Bray-Curtis *(I, II)* illetve Matusita *(II)* távolságfüggvény felhasználásával a csapdánkénti futóbogár egyedszámok felhasználásával, hogy kimutassam az egyes csapdák hasonlóságát.

III. vizsgálat

A csapdák futóbogár anyagának összehasonlítását főkoordináta analízis (PCoA) segítségével, a Bray-Curtis távolságfüggvény alkalmazásával végeztem. A futóbogarak térbeli eloszlásának jellemzésére a diszperziós indexet használtam, amely a variancia és az átlag hányadosaként definiált: $I_\delta = s^2 / \overline{x}$, ahol s^2 a variancia, míg $\overline{x}$ az egyedszámok átlaga, amely a variancia és az átlag hányadosaként definiált: $I_\delta = s^2 / \overline{x}$, ahol s^2 a variancia, míg $\overline{x}$ az egyedszámok átlaga. I_δ egyhez közeli értéke random eloszlásra utal. $I_\delta > 1$ aggregált, míg $I_\delta < 1$ szabályos eloszlást jelez. A teljes randomitástól való eltérés a következő statisztika felhasználásával tesztelhető: $ID = (n-1)s^2 / \overline{x}$. Ez a statisztika megközelítően χ^2 eloszlást mutat (n-1) szabadsági fokkal. Az említett statisztika csak akkor ad valós eredményeket, ha $n > 6$ és $\overline{x} > 1$.

Annak tesztelésére, hogy az egyes futóbogárfajok térbeli eloszlását meghatározhatják-e a vizsgált környezeti tényezők illetve más futóbogárfajok előfordulásai többszörös regresszió-analízis használtam. A tömeges futóbogár fajok habitatonkénti egyedszámait a Kruskal-Wallis nem-paraméteres ANOVA és a Tukey-teszt segítségével hasonlítottam össze. A gyakori futóbogár fajok csapdázott egyedszáma és aggregáltságának foka közötti kapcsolatot a Pearson-féle korrelációval vizsgáltam. A futóbogár fajok egyedszáma és a csapdák száma (melyből az adott faj előkerült) közötti korrelációt a Spearman-féle rang korrelációval vizsgáltam.

IV. vizsgálat

Beágyazott (nested) ismétléses (repeated) ANOVA-t használtam annak tesztelésére:

- hogy vannak-e különbségek a futóbogarak egyed- és fajszámában a mintavételi területek között;
- hogy mutatkoznak-e különbségek az egyed- és a fajszámokban a három ökológiai csoportban (azaz erdei fajok, generalista fajok és nyílt területek fajai), amelyekbe a futóbogarakat az élőhelypreferenciájuk alapján soroltam;
- hogyan változik a futóbogarak testmérete az urbanizációs gradiens mentén;
- hogy vannak-e eltérések a dominancia struktúrában a mintavételi területek és helyek között;
- milyen az opportunista (generalista) fajok egyedszáma az összegyedszámhoz viszonyítva.

Az ANOVA modellben használt adatok eloszlása normális volt (Kolmogorov-Smirnov próbát alkalmaztam a teszteléshez). Amikor az ANOVA eredményei azt mutatták, hogy szignifikáns különbségek vannak az átlagok között, akkor LSD tesztet (least significant difference) használtam az egyes mintavételi területek közötti különbség kimutatására. A futóbogár együttesek összetételét a mintavételi helyek között a vizsgált urbanizációs gradiens mentén clusteranalízissel hasonlítottam össze a prezencia-abszencia adatok alapján Sørensen távolságfüggvény és csoport átlag fúziós módszer (group average fusion algorithm) segítségével. MDS-t alkalmaztam Bray-Curtis távolságfüggvény felhasználásával a futóbogarak egyedszámainak a mintavételi helyek közötti összehasonlítására. A környezeti változók és a fajok egyed- és fajszáma közötti kapcsolatok feltárására többszörös lineáris regresszió-analízist alkalmaztam.

EREDMÉNYEK
Az erdő fragmentálódás hatásai mezo skálán (I-III vizsgálat)
Eredményeim igazolják, hogy a kutatási területen szignifikáns szegélyhatás figyelhető meg a futóbogár együttesek esetén. A Shannon diverzitás szignifikánsan nagyobb volt az erdőszegélyben és a gyepben, mint az erdő belsejében. Az erdőszegély és a gyep diverzitása közötti különbségek nem voltak szignifikánsak, amely szintén alátámasztja a futóbogaraknál talált szegélyhatást, mivel az erdei élőhelyek rendszerint jóval kevésbé diverzek, mint a nyílt területek *(I, II)*. A megfigyelt szegélyhatás egyrészt a szomszédos élőhelyek (gyep, és erdő belseje) fajainak jelenlétéből adódik, de ehhez nagymértékben hozzájárulnak a szegélyhez kötődő fajok is. Ezek a szegélyfajok olyan élőhelyet találnak a szegélyben, amely a szomszédos élőhely egyikében sincs meg, illetve ezek a fajok igénylik a két, strukturálisan különböző habitat egymáshoz való közelségét. Az erdőszegélyben tapasztalt magas diverzitási értékek a kis térbeli léptékű diszperziós mozgásoknak is köszönhetők. A tanulmányozott

térbeli skálán a különböző élőhelyek (gyep, erdőszegély, erdő belseje) természetesen nem függetlenek egymástól, azaz a szomszédos habitatok között megfigyelhető a futóbogarak mozgása, diszperziója. A futóbogarak térbeli eloszlási mintázataiban mutatkozó havonkénti változások azt mutatják, hogy szezonális mozgások vannak a szomszédos élőhelyek között, amint azt a *II. vizsgálat* során a *Pterostichus oblongopunctatus* és *Pterostichus burmeisteri* esetében kimutattam.

A csapdák futóbogár együttese fokozatosan változik az erdő belsejétől a gyep felé a transzektek mentén. Az együttesek összetételében megfigyelhető szinte fokozatos változás ellenére a gyep, a gyep, az erdőszegély és az erdő belseje csapdáinak futóbogár mintái szeparálódnak egymástól. Azonban az erdőszegély futóbogár mintái hasonlóbbak az erdő mintáihoz, mint a gyep mintáihoz. Az ordinációs, valamint a karakterfaj-elemzések azt mutatják, hogy a tanulmányozott élőhelytípusok jellegzetes futóbogár közösségekkel jellemezhetők, amelyek az adott élőhelyhez kötődnek. A gyűjtött futóbogár fajokat a habitat preferenciájuk alapján öt csoportba sorolhatjuk: (1) habitat generalisták; (2) gyepre jellemző fajok; (3) erdei generalisták; (4) erdei specialisták; és (5) szegélyhez kötődő fajok. A karakterfaj elemzés eredményei és a talajcsapdák és habitatok közötti egyedszámbeli eltérések is azt mutatják, hogy a gyűjtött futóbogár fajok jellegzetes habitat-, illetve mikrohabitat preferenciával rendelkeznek, tehát olyan habitatokban, mikrohabitatokban csoportosulnak, ahol a környezeti változók bizonyos kombinációja fordul elő és a változók bizonyos megkívánt értékkel jellemezhetők. Néha az ugyanazon az élőhelyen lévő tizennégy-tizennégy csapdát összehasonlítva, a futóbogarak egyedszámában nagyobb volt az eltérés, mint a különböző élőhelyeken lévő 14-14 csapda között, jelezve a mikrohabitatok fontosságát a futóbogarak térbeli eloszlásában *(III)*. A *III. vizsgálatban* a domináns és szubdomináns futóbogár fajok esetén aggregált volt a tipikus térbeli eloszlás (19 esetből 18 térbeli mintázat szignifikánsan aggregált volt). Továbbá szignifikáns pozitív összefüggés volt egy adott faj egyedeinek száma és a faj aggregációjának foka között *(III)*. Ezt úgy lehet értelmezni, hogy minél tömegesebb egy faj annál aggregáltabb az eloszlása.

A vizsgált térbeli léptékben bizonyos futóbogár fajok jelenléte szintén befolyással bírt a domináns és szubdomináns futóbogár fajok egyedszámára és térbeli eloszlására *(III)*. A legtöbbje ezeknek a korrelációknak pozitív volt, utalva arra, hogy ezek a fajpárok hasonlóan reagáltak a habitat tulajdonságaira, a környezeti változók heterogenitására. Viszont interspecifikus kompetíciót feltételezhetünk a *Molops piceus* és a *Pterostichus burmeisteri* térbeli eloszlása esetén kimutatott negatív kapcsolat hátterében. Ugyanis az említett két faj hasonló testméretű, hasonló a habitat preferenciájuk és szezonális aktivitásuk *(III)*. Más

adathalmaz azonban azt mutatja, hogy a negatív kapcsolat nem egy általános törvényszerűség a két fajra nézve.

Az *I. vizsgálat*ban a lombavarrétegnek és a lágyszárúaknak a borítása, a lombkorona záródása és a potenciális zsákmányállatok mennyisége, míg a *II. vizsgálat*ban a levegő relatív páratartalma, a talaj hőmérséklete és a lágyszárúak borítása voltak a vizsgált transzektek mentén a futóbogarak diverzitását meghatározó legfontosabb faktorok. A *III. vizsgálat*ban tanulmányoztam, hogy a környezeti tényezők hatással vannak-e az egyes futóbogár fajok térbeli eloszlására. A többszörös lineáris regresszió-analízis szignifikáns negatív viszonyt mutatott ki a lombavar százalékos borítása és az *Abax parallelepipedus* és az *Aptinus bombarda* esetén. A lágyszárúak borítása pozitívan (szignifikánsan) befolyásolta a *Carabus coriaceus* egyedszámát. A cserjék és a futóbogarak egyedszáma között szignifikáns pozitív kapcsolat volt két faj esetén (*Abax parallelepipedus* és *Molops piceus*). A lombkorona záródása szignifikáns pozitív tényező volt az *Abax parallelepipedus* esetén. Szignifikáns pozitív kapcsolat volt a zsákmányállatok száma és három futóbogár faj egyedszáma között (*Carabus convexus*, *Harpalus rufipes* és *Synuchus vivalis*) *(III)*.

Az erdő fragmentálódás hatásai makro skálán (IV. vizsgálat)

Eredményeim nem támasztják alá a növekvő zavarás hipotézist. A gyűjtött futóbogarak száma szignifikánsan nagyobb volt a városi és városon kívüli, mint a külvárosi mintavételi területen. A városi mintavételi terület futóbogarainak összfajszáma majdnem olyan magas volt, mint a városon kívülieké. A futóbogarak összegyedszáma szintén szignifikánsan nagyobb volt a városon kívüli mintavételi területen, mint a városi és külvárosiakon. Azonban a növekvő zavarás hipotézise igazolódik az erdei specialista fajok tekintetében: az erdei specialista fajok száma szignifikánsan emelkedik a városi mintavételi területtől a városon kívüliek felé. A nyílt területekre jellemző fajok száma szignifikánsan magasabb volt a városi, mint a külvárosi és városon kívüli mintavételi területen. Az erdei fajok egyedszáma szintén a városon kívüli területen volt a legnagyobb, míg a nyílt területekre jellemző fajokat tekintve szignifikánsan több egyedet gyűjtöttem ezekből a városi mintavételi helyekről, mint a többi területről. Eredményeim nem igazolják a közepes zavarás hipotézisét. A fajgazdagság nem a közepesen zavart külvárosi mintavételi helyeken volt a legnagyobb, ahogyan ezt a hipotézis alapján várnánk. Azonban a kapott eredmények megerősítik a generalista fajok arányának hipotézisét, azaz a generalista fajok egyedszáma az összegyedszámhoz viszonyítva szignifikánsan nagyobb volt a városi, mint a többi mintavételi helyeken. Ami azt jelzi, hogy a generalista (opportunista fajok) az együtteseken belül dominánsakká váltak a növekvő zavarás következtében. Az átlagos testméret hipotézise is

igazolást nyert: a futóbogarak átlagos testmérete szignifikánsan nagyobb volt a kevésbé zavart városon kívüli és külvárosi mintavételi területen, mint a zavartabb városiban. Feltételezhető, hogy a testméret-eloszlásban az urbanizációs gradiens mentén bekövetkező

változások a források rendelkezésre állásában, stabilitásában vagy az élőhelyek eltartó képességében meglévő különbségeket tükrözik. A városi területen megfigyelhető kisebb átlagos testméret a röpképességgel is magyarázható, mivel a röpképes fajok általában kisméretűek. A városi mintavételi területen fogott, nyílt területekre jellemző fajok nagy többsége röpképes, ezáltal gyors diszperzióra képesek.

Kimutattam, hogy az urbanizáció az eredeti élőhelyeket megváltoztatta. Az emberi tevékenység hatásai kifejezett változásokat idéztek elő a futóbogár együttesekben. Ezek a zavarások negatívan érintik az eredeti élőhelyhez legjobban alkalmazkodott fajokat, esetünkben az erdei fajokat. A zavarás mértéke legnagyobb a városi élőhelyeken, kisebb a külvárosiakban, és a városon kívüliek esetében a legkisebb. Az eredeti élőhely jelentős mértékű megváltozását mutatja a városi mintavételi területen a nyílt területek fajainak nagy egyedszáma is. Jelentős elkülönülés figyelhető meg a mintavételi helyek között az urbanizációs gradiens mentén. A négy városi mintavételi hely egy elkülönült csoportot (clustert) képez a fajösszetétel alapján, míg a külvárosi és városon kívüli mintavételi helyek alkotják a másik csoportot (clustert), azt jelezve, hogy az urbanizáció kifejezett változást idézett elő a futóbogár együttesek összetételében. A közös fajok száma nagy és azonos volt az összes vizsgált területen. A differenciális fajok száma egyenlőtlen volt: a városi területen sok (22) olyan fajt találtunk, melyek nem fordultak elő sem a városon kívüli, sem a külvárosi mintavételi helyeken, ezzel szemben alacsony (5 ill. 4) volt a számuk a külvárosi-városon kívüli területeken. Ez az urbanizációs gradiens mentén a futóbogarak megjelenésének mintázatával magyarázható. Az erdei fajoknak a kevésbé zavart vagy nem zavart élőhelyek (külvárosi, városon kívüli) felelnek meg, míg a nyílt területekre jellemző fajok főleg a városi területen fordultak elő. A gyűjtött fajokat élőhely preferenciájuk alapján öt csoportba osztottam: (1) habitat generalisták; (2) városon kívüli területeket kedvelő fajok; (3) a külvárosi – városon kívüli területek karakterisztikus fajai; (4) a külvárosi élőhelyeket kedvelő fajok; (5) a városi területre jellemző fajok. A nem metrikus skálázás eredménye egy lineáris gradiens jelenlétéről tanúskodik: a futóbogár együttesek fokozatosan változtak a városon kívüli terület felől a városi felé. Azt is kimutattam, hogy az egyes mintavételi helyeken a futóbogár együttesek összetételének heterogenitása növekedett az urbanizációs gradiens mentén a városon kívüli terület felől a városi felé. A városi terület magas ß-diverzitását az élőhely foltossága magyarázza. Ez a foltosság teszi lehetővé úgy az erdei fajok, mint ahogy a generalista és nyílt

területekre jellemző fajok jelenlétét és túlélését, ugyanakkor a fajösszetétel mintavételi helyről-helyre változik, ami a magas heterogenitást idézi elő. A városon kívüli terület nagyjából azonos élőhelyfoltokkal jellemezhető, ezért a domináns és szubdomináns generalista és erdei fajok viszonylag azonos eloszlása alacsonyabb heterogenitáshoz vezet.

Bebizonyosodott, hogy szignifikáns pozitív összefüggés volt a talaj hőmérséklete és a futóbogarak fajszáma között. A levegő páratartalma pozitívan (szignifikánsan) befolyásolta mind a futóbogarak összegyedszámát, mind pedig az erdei fajok egyedszámát. A nyílt területekre jellemző fajoknak az egyed- és fajszáma is csökkenést mutatott, viszont az erdei fajok száma növekedett a lehullott illetve korhadó faanyag növekvő mennyiségével. A nyílt területekre jellemző fajok számának kivételével, a futóbogaraknak mind az egyed-, mind pedig a fajszáma növekedett a növekvő lágyszárú borítással. A lombkoronazáródás negatívan befolyásolta a futóbogarak összegyedszámát, az erdei fajok abundanciáját és a nyílt területekre jellemző fajok számát. Eredményeim azt mutatják, hogy a biotikus tényezőknek, úgymint a potenciális zsákmányállatok számának, is fontos szerep jut a futóbogarak fajgazdagságának meghatározásában. Szignifikáns pozitív összefüggés volt a potenciális zsákmányállatok száma és a futóbogarak összegyedszáma és az erdei fajok fajszáma között.

REFERENCES

Andersen, A. 1997. Densities of overwintering carabids and staphylinids (Col., Carabidae and Staphylinidae) in cereal and grass fields and their boundaries. J. Appl. Ent. 121: 77–80.

Anderson, M.A. and Carter, C.I. 1987. Shaping ride sides to benefit wild plants and butterflies. In Wildlife Management in Forests (D.C. Jardine, ed) pp. 66–80. Lancaster: Institute of Chartered Forests.

Antvogel, H. and Bonn, A. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24: 470–482.

Arango-Velez N, Kattan G.H. 1997 Effects of forest fragmentation on experimental nest predation in Andean cloud forest. Biol. Conserv. 81: 137–143

Asteraki, E.J., Hanks, C.B. and Clements, R.O. 1995. The influence of different types of grassland field margin on carabid beetle (Coleoptera, Carabidae) comminities. Agric. Ecosystems Environ. 54: 195–202.

Baars, M.A. 1979a: Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia, 41: 25-46.

Baars, M.A. 1979b Patterns of movement of radioactive carabid beetles. Oecologia 44: 125–140.

Báldi, A. and Kisbenedek, T. 1994. Comparative analysis of edge effect on bird and beetle communities. Acta Zool. Acad. Sci. Hung. 40: 1–14.

Bedford, S.E. and Usher, M.B. 1994. Distribution of arthropod species across the margins of farm woodlands. Agric. Ecosystems Environ. 48: 295–305.

Benest, G. 1989. The sampling of a carabid community: II. Traps and trapping. Revue d'Écologie et de Biologie du Sol, 26: 505-514.

Blake, S., Foster, G.N., Eyre, M.D. and Luff, M.L. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiologia 38: 502–512.

Blake, S., Foster, G. N., Fisher, G. E. J. and Ligertwood, G. L. 1996. Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland. Ann. Zool. Fennici 33: 139-147.

Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A. and Case, T.J. 2000. Arthropods in urban habitat fragments in southern California: Area, age, and edge effects. Ecological Applications 10: 1230–1248.

Bryan, K.M. and Wratten, S.D. 1984. The responses of polyphagous predators to spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. Ecol. Entomol. 9: 251–259.

Butovsky, R.O. 1994. Carabids in roadside ecosystems: perspectives of bioindication. In Carabid Beetles: Ecology and Evolution (K. Desender et al., eds) pp. 241–246. Dordrecht: Kluwer Academic Publishers.

Butterfield, J. 1997. Carabid community succession during forestry cycle in conifer plantations. Ecography 20: 614–625.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Davies, K.F. and Margules, C.R. (1998) Effects of habitat fragmentationon carabid beetles: experimental evidence. Journal of Animal Ecology 67: 460–471

Davis, B.N.K. 1978. Urbanisation and the diversity of insects. In: Mound L.A. and Waloff N. (eds), Diversity of Insect Faunas. Blackwell, London, UK, pp. 126–138.

Demaynadier, P.G. and Hunter, M.L. Jr. 1998. Effects of silvicultural edges on the distribution of and abundance of amphibians in Maine. Conservation Biology 12: 340-352.

den Boer, P.J. 1970. On the significance of dispersal power for populations of carabid–beetles (Coleoptera, Carabidae). Oecologia 4: 1–28.

den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50: 39–53

den Boer, P.J. 1985. Fluctuations of density and survival of carabid populations. Oecologia 67: 322-330.

Desender, K., Ervynck, A. and Tack, G. 1999. Beetle diversity and historical ecology of woodlands in Flanders. Belgian Journal of Zoology 129: 139–156.

Didham R.K., Ghazoul J., Stork N.E., Davis A.J. 1996. Insects in fragmented forests: a functional approach. Trends in Ecology and Evolution 11: 255–260.

Digby, P.G.N. and Kempton, R.A. 1987. Multivariate Analysis of Ecological Communities. London: Chapman and Hall.

Diggle, P.J. 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, London, 148 pp.

Digweed, S.C., Currie, C.R., Cárcamo, H.A. and Spence, J.R. 1995. Digging out the digging–in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). Pedobiol. 39: 561–576.

Dufrêne, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Eversham B.C., Roy D.B. and Telfer M.G. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Annales Zoologici Fennici 33: 149–156.

Eyre, M.D. and Luff, M.L. 1994. Carabid species assemblages of North-East England woodlands. In Desender, K. et al. (eds): Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, pp. 277-281.

Forman, R.T.T. and Godron, M. 1986. Landscape ecology. Wiley, New York

Fournier, E. and Loreau, M. 1999. Effects of newly planted hedges on ground-beetle diversity (Coleoptera, Carabidae) in an agricultural landscape. Ecography 22: 87–97.

Gaines, M.S., Diffendorfer, J.E., Tamarin, R.H. and Whittam, T.S. 1997. The effects of habitat fragmentation on the genetic structure of small mammal populations. J. Hered. 88: 294–304

Gauch, H.G. 1986. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, 298 pp.

Gibb H. and Hochuli D.F. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106: 91–100.

Gilbert, O.L. 1989. The Ecology of Urban Habitats. Chapman and Hall, London, UK.

Gray J.S. 1987. Species-abundance patterns. In: Gee J.H.R. and Giller P.S. (eds), Organization of Communities, Past and Present. Blackwell Scientific Publications, Oxford, UK, pp. 53–67.

Gray J.S. 1989. Effects of environmental stress on species rich assemblages. Biological Journal of the Linnean Society 37: 19–32.

Grüm, L. 1971. Spatial differentiation of the Carabus L (Carabidae, Coleoptera) mobility. Ekol. Polska 19: 1–34.

Guillemain, M., Loreau, M. and Daufresne, T. 1997. Relationships between the regional distribution of carabid beetles (Coleoptera: Carabidae) and the abundance of their potential prey. Acta Oecologica 18: 465-483.

Haila, Y. 1999. Islands and fragments. Pages 234-264 in M.L. Hunter Jr. ed. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, United Kingdom.

Haila, Y., Hanski, I.K., Niemelä, J., Punttila, P., Raivio, S. and Tukia, H. 1994. Forestry and boreal fauna: matching management with natural forest dynamics. Annales Zoologici Fennici 31: 187-202.

Halme, E. and Niemelä, J. 1993. Carabid beetles in fragments of coniferous forest. Ann. Zool. Fennici 30: 17-30.

Holliday, N.J. 1991. Species responses of carabid beetles (Coleoptera, Carabidae) during postfire regeneration of boreal forest. The Canadian Entomologist 123: 1369–1389.

Hůrka, K. 1996. Carabidae of the Czech and Slovak Republics. Kabourek, Zlin, Czech Republic.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326: 388–390

Kareiva, P. and Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302

Koivula, M., Punttila, P. and Niemelä, J. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22: 424–435.

Kruess, A. and Tscharntke, T. 1994. Habitat fragmentation, species loss, and biological control. Science 264:1581–1584

Kruger, S.C. and Lawes, M.J. 1997. Edge effect at an induced forest-grassland boundary: forest birds in the Ongoye Forest Reserve, KwaZulu-Natal. South African Journal of Zoology 32:82-91.

Kutner, M., Nachtschiem, C., Wasserman, W. and Neter, J. 1996. Applied Linear Statistical Models. McGraw-Hill, Boston, USA.

Lacy, R.C. and Lindenmayer, D.B. 1995. A simulation study of the impacts of population subdivision on the mountain brushtail possum, Trichosurus caninus Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. II. Loss of genetic variation within and between subpopulations. Biol Conserv 73:131–142

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier Science, Amsterdam, The Netherlands.

Lei, G.C. and Hanski, I. 1997. Metapopulation structure of Cotesia melitaearum, a specialist parasitoid of the butterfly Melitaea cinxia. Oikos 78:91–100

Lenski, R.E. 1982. Effects of forest cutting on two Carabus species; evidence for competition for food. Ecology 63: 1211-1217.

Lenski, R.E. 1984. Food limitation and competition: a field experiment with two Carabus species. J. Anim. Ecol. 53: 203-216.

Levesque, C. and Levesque, G.Y. 1994. Abundance and seasonal activity of ground beetles (Coleoptera: Carabidae) in a raspberry plantation and adjacent sites in southern Québec (Canada). J. Kansas Entomol. Soc. 67: 73–101.

Liebherr, J. and Mahon, J. 1979. The carabid fauna of the upland oak forest in Michigan: survey and analysis. The Coleopterists Bulletin 33: 183–197

Lord, J.M. and Norton, D.A. 1990. Scale and the spatial concept of fragmentation. Conserv Biol 4:197–202

Loreau, M. 1987. Vertical distribution of activity of carabid beetles in a beach forest floor. Pedobiol. 30: 173-178.

Loreau, M. 1989. On testing temporal niche differentiation in carabid beetles. Oecologia 81: 89–96.

Loreau, M. 1990. Competition in a carabid beetle community: a field experiment. Oikos 58: 25-38.

Lövei, G.L. 1984. Ground beetles (Coleoptera: Carabidae) in two types of maize fields in Hungary. Pedobiologia 26: 571–64.

Lövei, G.L. and Sunderland, K.D. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41: 231–256.

Luff, M.L., Eyre, M.D. and Rushton, S.P. 1989. Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in north-east England. J. Biogeogr. 16: 121-130.

Luff, M.L., Eyre, M.D. and Rushton, S.P. 1992. Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). J. Environ. Management 35: 301-315.

MacMahon, J.A. 1980. Ecosystem over time: Succession and other types of change. In:Waring RH (ed) Forests: Fresh Perspectives from Ecosystem Analysis, pp 129–136. Oregon State University Press, Corvallis

Mader, H.J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81–96.

Mader, H.J., Schell, C. and Kornacker, P. 1990. Linear barriers to arthropod movements in the landscape. Biological Conservation 54: 209–222.

Magura, T. 1995. Wanderungsverhalten und Ortstreue der Arten Abax ater und Abax ovalis (Coleoptera: Carabidae). Folia Ent. Hung. 56: 89–99.

Magura, T. and Molnár, T. 1997. Comparison of the carabid fauna of the Ménes-valley and a higher karst plateau (Coleoptera: Carabidae). In Tóth, E. & Horváth, R. eds: Research in Aggtelek National Park and Biosphere Reserve. Aggtelek National Park Directorate, Jósvafő, pp. 117-122.

Magura, T. and Tóthmérész, B. 1997. Testing edge effect on carabid assemblages in an oak-hornbeam forest. Acta zool. hung. 43: 303-312.

Magura, T. and Tóthmérész, B. 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., Elek, Z. and Tóthmérész, B. 2002. Impacts of non-native spruce reforestation on ground beetles. European Journal of Soil Biology 38: 291–295.

Magura, T., Ködöböcz, V. and Tóthmérész, B. 2001. Effects of habitat fragmentation on carabids in forest patches. Journal of Biogeography 28: 129–138.

Magura, T., Tóthmérész, B. and Bordán, Zs. 1997. Comparison of the carabid communities of a zonal oak–hornbeam forest and pine plantations. Acta Zool. Acad. Sci. Hung. 43: 173–182.

Magura, T., Tóthmérész, B. and Bordán, Zs. 1998*a*. Edge effect on carabid assemblages in a deciduous forest. In Brunnhofer, V. & Soldán, T. eds: Book of Abstracts, VIth European Congress of Entomology. České Budějovice, 1998. August 23-29. 715 p.

Magura, T., Tóthmérész, B. and Bordán, Zs. 1998*b*. Effects of non-native spruce plantation and nature management practice on Carabidae (Coleoptera). In Brunnhofer, V. & Soldán, T. (eds): Book of Abstracts, VIth European Congress of Entomology. České Budějovice, 1998. August 23-29. 716 p.

Magura, T., Tóthmérész, B. and Bordán, Zs. 2000. Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. Biological Conservation 93: 95–102.

McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M. and Medley K. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1: 21–36.

McIntyre, N.E., Rango, J., Fagan, W.F. and Faeth, S.H. 2001: Ground arthropod community structure in a heterogeneous urban environment. Landscape and Urban Planning 52: 257–274.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10: 58–62.

Müller, J.K. 1986. Anpassungen zur intraspezifischen Konkurrenzverminderung bei Carabiden (Coleoptera). Zool. Jb. Syst. 113: 343-352.

Müller, J.K. 1987. Period of adult emergence in carabid beetles: an adaptation for reducing competition? Acta Phytopathologica et Entomologica Hungarica 22: 409–415

Müller-Motzfeld, G. 1989. Laufkäfer (Coleoptera:Carabidae) als pedobiologische Indikatoren. Pedobiol. 33: 145-153.

Néve, G. 1994. Influence of temperature and humidity on the activity of three Carabus species. In Carabid Beetles: Ecology and Evolution (K. Desender et al., eds) pp. 189–192. Dordrecht: Kluwer Academic Publishers.

Niemelä, J. 1988. Carabid beetles in shore habitats on the Åland Islands, SW Finland: the effect of habitat availability and species characteristics. Acta Oecol./Oecol. Gener. 9: 379-395.

Niemelä, J. 1990. Effect of changes in the habitat on carabid assemblages in a wooded meadow on the Åland Islands. Notulae Entomol. 69: 169-174.

Niemelä, J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? Oikos 66: 325-335.

Niemelä, J. 1999. Ecology and urban planning. Biodiversity and Conservation 8: 119–131.

Niemelä, J. 2000. Is there a need for a theory of urban ecology? Urban Ecosystems 3: 57–65.

Niemelä, J. and Halme, E. 1992. Habitat associations of carabid beetles in fields and forests on the Åland islands, SW Finland. Ecography 15: 3–11.

Niemelä, J. and Spence, J.R. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. Ecography 17: 166–175.

Niemalä, J., Haila, Y., Halme, E., Pajunen, T. and Punttila, P. 1992a. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. Journal of Biogeography 19: 173–181.

Niemelä, J., Haila, Y. and Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19: 352–368.

Niemelä, J., Haila, Y. and Ranta, E. 1986. Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Åland Islands, SW Finland. Ann. Zool. Fennici 23: 289-296.

Niemelä, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., New, T., Penev, L., Samways, M. and Spence, J. 2000. The search for common anthropogenic impacts on biodiversity: a global network. Journal of Insect Conservation 4: 3–9.

Niemelä, J., Kotze, J.D., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D. and Montes de Oca, E. 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology 17: 387–401.

Niemelä, J., Langor, D. and Spence, J.R. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conserv. Biol. 7: 551-561.

Niemelä, J., Ranta, E. and Haila, Y. 1985. Carabid beetles in lush forest patches on the Åland Islands, south-west Finland: an island-mainland comparison. J. Biogeography 12: 109-120.

Niemelä, J., Spence, J.R., Langor, D., Haila, Y. and Tukia, H. 1994. Logging and boreal ground–beetle assemblages on two continents: implications for conservation. In Perspectives in Insect Conservation (K. Gaston et al., eds) pp. 29–50. Andover: Intercept.

Niemelä, J., Spence, J. R. and Spence, D.H. 1992b. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. Can. Ent. 124: 521-540.

Parmenter, R.R. and MacMahon, J.A. 1984. Factors influencing the distribution and abundance of ground-dwelling beetles (Coleoptera) in a shrub-steppe ecosystem: The role of shrub architecture. Pedobiologia 26: 21–34.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652–661.

Pyle, R., Bentzien, M. and Opler, P. 1981. Insect conservation. Annual Review of Entomology 26: 233–258.

Refseth, D. 1980. Ecological analyses of carabid communities - Potential use in biological classification for nature conservation. Biological Conservation, 17:131-141.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. and Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257:524–526

Saunders, D.A., Hobbs, R.J. and Margules, C.R. 1991 Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32

Scott, W.A. and Anderson, R. 2002: Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. Biological Conservation 110: 197–210.

Segers, R. and Bosmans, R. 1982. Diversity and similarity between 7 sampling sites at the "Moer", Bornem (Belgium) based on pitfall trapping of Staphylinidae, Carabidae (Coleoptera) and Araneae. Biol. Jahresbericht 50: 202–216.

Sen, A. and Srivastava, M. 1990. Regression Analysis: Theory, Methods and Applications. Springer, New York, USA.

Sergeeva, T.K. 1994. Seasonal dynamics of interspecific trophic relations in a carabid beetle assemblage. In Desender, K. et al. (eds): Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, pp. 367-370.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annu Rev Ecol Syst 19:473–511

Sokal, R.R. and Rohlf, F.J. 1995. Biometry. W.H. Freeman, New York, USA. pp310

Spence, J.R., Langor, D.W., Niemelä, J., Cárcamo, H.A. and Currie, C.R. 1996. Northern forestry and carabids: the case for concern about old-growth species. Annales Zoologici Fennici 33: 173–184.

Spence, J.R. and Niemelä, J. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. Can. Ent. 126: 881–894.

Šustek, Z. 1987. Changes in body size structure of carabid communities (Coleoptera, Carabidae) along an urbanisation gradient. Biológia (Bratislava) 42: 145–156.

Šustek, Z. 1994. Windbreaks as migration corridors for carabids in an agricultural landscape. In Desender, K. et al. (eds): Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, pp. 377-382.

Thiele, H.U. 1977. Carabid Beetles in Their Environments. Springer, New York, USA.

Tóthmérész, B. 1993. NuCoSA 1.0: Number Cruncher for Community Studies and other Ecological Applications. Abstracta Botanica 17: 283-287.

Tóthmérész, B. 1998. On the characterization of scale-dependent diversity. Abstracta Botanica 22: 149–156.

Tóthmérész, B. and Török, P. 2003: Comparative analysis of the vegetation of the Nagyerdő forest along an urban-rural gradient. Community Ecology (submitted).

Verschoor, B.C. and Krebs, B.P.M. 1995. Diversity changes in a plant and carabid community during early succession in an embanked saltmarsh area. Pedobiologia 39: 405–416.

Vida, G. 1978: Genetic diversity and environmental future. Environmental Conservation 5: 127–132.

von Sacker, A. 1998. Interior habitat in J. Voller and S. Harrison, eds. Conservation biology principles for forested landscapes. University of British Columbia Press, Vancouver Canada, pp.130-145.

Wallin, H. 1986. Habitat choice of some field–inhabiting beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entomol. 11: 457–466.

Wiens, J.A. 1989. Spatial scaling in ecology. Funct Ecol 3:385–397

Wiens, J.A. 1994. Habitat fragmentation: island versus landscape perspectives on bird conservation. Ibis (Suppl) 137:97–104

Wootton, J.T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. The American Naturalist 152: 803–825.

Zar, J.H. 1984. Biostatistical Analysis. London: Prentice Hall International.

Acknowledgements

APPENDIX