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ROVE BEETLE (COLEOPTERA: STAPHYLINIDAE) ASSEMBLAGES IN HUMAN MODIFIED FOREST HABITATS

Egyetemi doktori (PhD) értekezés

NAGY D. DÁVID

Témavezető

Dr. Tóthmérész Béla
egyetemi tanár

DEBRECENI EGYETEM
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A doktori értekezés betétlapja

Ezen értekezést a Debreceni Egyetem Természettudományi Doktori Tanács a **Juhász Nagy Pál Doktori Iskola Kvantitatív és Terresztris Ökológia** programja keretében készítettem a Debreceni Egyetem természettudományi doktori (PhD) fokozatának elnyerése céljából.
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Tanúsítom, hogy **Nagy Dávid** doktorjelölt 2010-2013 között a fent megnevezett Doktori Iskola **Kvantitatív és Terresztris Ökológia** programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.
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Prof. Dr. Tóthmérész Béla
témavezető

A doktori értekezés betétlapja

ROVE BEETLE (COLEOPTERA: STAPHYLINIDAE) ASSEMBLAGES IN HUMAN MODIFIED FOREST HABITATS

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a Környezettudomány tudományágban

Írta: **Nagy Dávid** okleveles Biológus-ökológus
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(**Kvantitatív és Terresztris Ökológia** programja) keretében

Témavezető:
Prof. Dr. Tóthmérész Béla ....

A doktori szigorlati bizottság:
elnök: Dr. ....
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Dr. ....
A doktori szigorlat időpontja: 2014. április 16.

Az értekezés bírálói:
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1. Introduction

1.1. Urbanization and the GlobeNet project

The elimination or mitigation of adverse effects of urbanization is one of the major challenges for humanity. The human population and disturbance (urbanization, agriculture and forest management) increase every year in the world (United Nation 2012). Human influences create similar pattern and structure in landscape network, which change the natural habitats (Gilbert 1989). These alterations have significant effect on the whole biosphere. Thus, due to the conservation of wildlife it is necessary to investigate and better understand the human influences on the biodiversity. The urbanization goes with the increasing of quantitative and qualitative settlements. The destructive effects of urbanization were not observed with the presence of first settlements about 9000 years ago. However, these effects cause significant damage in the present, which is because of the fact that people try to serve the human demands against with other creatures during urbanization (Antrop 2000).

Proportions of the urban areas have been increasing explosively from the 20th century. The urban population can reach 6.2 billion by 2050 (United Nation 2012). The population growth and the attendant landscape management have strong effect on the whole living systems and their segments. During urbanization the natural habitats changed drastically; thus, creating many similar landscape patterns in worldwide. Urbanization gradient could differ in ecosystem types, but that shows similar structure all over the world. At the end of the gradient there is an undisturbed, natural rural habitat without buildings and artificial practises. It follows moderately disturbed suburban areas towards urban areas with increased human disturbances and decreased level of naturalness (McIntyre 2000). Therefore, the urbanization gradient could be useful on the investigation of effects of urbanization and human disturbances on wildlife (Magura et al. 2008a, McDonnell et al. 1997, Niemelä et al. 2000).

In 1998 Jari Niemelä and his colleagues organized a workshop about the monitoring of urbanization influences on biodiversity in Helsinki. The aim of the workshop was to develop a new international project (GlobeNet project), which could be used by different parts of the world with unified method and they could follow and reduce the effects of urbanization. Thus, they were looking for the answer whether human influences have similar effect on the biodiversity or rather have more important roles for the unique characteristics of local condition (elevation, climate, vegetation). The GlobeNet project (Global Network for monitoring landscape change) is a global network, which aims the investigation and evaluation of effects of changes inside the visually similar landscapes on biodiversity by the same sampling method (Niemelä et al. 2000).

Originally the protocol was built on ground beetles, because this group is diverse and reliably monitored. Carabid assemblages were investigated in cities of 9 countries (Belgium, Bulgaria, Canada, Denmark, England, Finland, Japan, Hungary and Romania) along an urbanization gradient (Gaublomme et al. 2008, Magura et al. 2010b, Magura et al. 2004). However, other taxa also respond sensitively on the disturbance by human activities. Thus, the project was also investigated on spiders (Finland and Hungary), isopods (Denmark and Hungary) and diplopods (Hungary) (Bogyó et al. 2015, Horváth et al. 2012, Magura et al. 2008a, Magura et al. 2010a).

Many hypotheses were stated on the effects of disturbance on the assemblages emphasizing the different aspects of relationship between the diversity and human disturbances; Tóthmérész and Magura (2009) provide a review of these hypotheses. These hypotheses overlap or supplement each other. Most of hypotheses based on overall species richness, which not always conclusive that those indicate the changes in the environmental habitats, because the response of specialist species with special habitat affinity and ecological demands could be varied (Lövei et al. 2006, Magura et al. 2010b). Thus, some species come to the front (generalist species, open-habitat species), while others keep back (forest specialist species) by effects of urbanization. These properties can neutralize to each other and the basic ecological patterns stay hidden (Magura et al. 2006b). If we want to get more details about the effect of human activities on the original habitat; it is necessary the investigation of taxa and species with different conditional and ecological demands (forest specialist species, thermophilous species, mycetophilous species).

The aim of this study was to investigate the effects of urbanization on rove beetles, a beetle taxon that has not yet been studied in the frame of the international Globenet project. In particular, we tested three classical and six novel hypotheses regarding the response of species to urbanization: (i) The increasing disturbance hypothesis claims that species richness monotonously decreases with the increasing levels of disturbance (Gray 1989). (ii) The intermediate disturbance hypothesis predicts that species richness is the highest in the moderately disturbed suburban area (Connell 1978). (iii) The habitat specialist hypothesis predicts that the species richness of forest specialist species decreases with the increasing disturbance (Magura et al. 2004). Our novel hypotheses are related to the habitat alteration caused by the urbanization. Urbanization radically alters the original habitat, the urban forest patches become more open, drier and warmer compared to the suburban and rural ones. Therefore, (iv) the richness of hygrophilous species should be the highest in the rural area (hygrophilous species hypothesis), while (v) the richness of thermophilous species should be the highest in the urban area (thermophilous species hypothesis). In the urban area and somewhat in the suburban area decaying organic material are usually removed during the management of forest patches. Therefore, (vi) the richness of saprophilous species (saprophilous species hypothesis), and (vii) the richness of species living in decaying plant debris (phytodetriticol species hypothesis) should be the highest in the less modified rural area. As ants and fungi prefer habitats with dense dead and decaying organic material, therefore (viii) the richness of myrmecophilous species (myrmecophilous species hypothesis), and (ix) the richness of species preferring the fungi (mycetophilous species hypothesis) also should be the highest in the rural area.

1.2. Effect of reforestation with native and non-native tree species

The increasing of human activities and associated multiple landscape management (urbanization, agricultural and forest management) can change drastically the original habitats. The intensive forest management is one of the most dangerous activities on the pattern and structure of natural landscape. The area of planted forests is increasing by 5 million hectares every year globally. In Europe there were more, than 59 million hectares forested area in 2010 (FAO 2010). 12% of forested areas were planted by introduced species (*Robinia pseudoacacia*, *Quercus rubra*, *Acer negundo*). In Hungary, the ratio of non-native species is nearly half of the planted areas (ÁESZ 2008). The reforestation with non-native species and the associated forest management practices (soil preparation, clear-cutting, grubbing, herb tilling) can change the abiotic (physical and chemical conditions) and biotic (interactions between plant or/and animal species) environmental conditions of the natural habitat (Mátyás 1996). These changes have drastic effects on the soil fauna (Finch 2005, Magura et al. 1997). Mainly the specialist, rare species are threatened, because these species respond sensitively to habitat alterations and the accompanying environmental changes (Magura et al. 2013). However, these can benefit to other species (invasive, ubiquist), which can adapt quickly to the unfavorable conditions (Pohl et al. 2007).

Moreover, the microhabitats and substrate materials, such as fungi, decaying wood materials, feces, nests and cavities are eliminated during the preparation of plantations (Bengtsson et al. 2000, Langor et al. 2008, Paillet et al. 2010). These components have vital role in the maintenance of biodiversity of lowland natural forests. Several specialist species depend on conditions provided by microhabitats and substrates. Due to the reforestation these components disappear from the managed forest area, which can decrease significantly the number of specialist, rare species (Paillet et al. 2010).

Previous studies showed that the reforestation with non-native species and the associated forest management have significant effects on ground-dwelling arthropods (Finch 2005, Magura et al. 1997, Niemelä et al. 1993). However, the majority of the published studies are based on ground beetles or spiders (Pohl et al. 2007). These taxa are probably less dependent on substrate materials than the saproxylic beetles, bryophytes, lichens and fungi, which show higher species richness in the unmanaged forests (Paillet et al. 2010). Therefore, it is also necessary to examine those taxa which are more sensitive to the substrates (Niemelä et al. 2007). Decaying material dependent species respond negatively to the reduction of habitat heterogenity and microhabitat availability (Hjältén et al. 2007, Johansson et al. 2007, Paillet et al. 2010). During timber-oriented forest management several macro- and microhabitats have been ruined, which are indispensable for the decaying material dependent and forest specialist species (Bengtsson et al. 2000, Langor et al. 2008, Paillet et al. 2010).

We compared rove beetle assemblages of four monospecific plantations with native oak (*Quercus robur* L.) and non-native tree species (black locust *Black locust* L., Scots pine *Pinus sylvestris* L., red oak *Quercus rubra* L.), in comparison to each other and to mature oak forest (*Convallario-Quercetum roboris)* as control. We tested the following hypotheses: the (i) overall number of rove beetle individuals and species should be the highest in the native oak forest. However, we assumed that (ii) native plantation is able to provide more suitable habitat for rove beetles than non-native plantations, resulting higher abundance and species richness. Heavy site preparation and post-treatments drastically modify the environmental conditions of original habitats. Therefore (iii) in accordance with hygrophilous species hypothesis the number of hygrophilous individuals and species should be higher in the mature oak forest than in the plantations (Magura et al. 2013). Furthermore, substrate materials and microhabitats for specialist rove beetle such as decaying materials, fungi and nests are eliminated by forest treatments. Thus, we assumed that (iv) the number of decaying material dependent (saprophilous, coprophilous and xylodetriticol) rove beetle individuals and species should be lower in the plantations compared to the mature oak forest (decaying material dependent species hypothesis). Moreover, we expected that (v) habitat characteristics, microclimate and soil pH value are important predictors for spatial distribution of rove beetles. After the reforestation the environmental conditions change and thus, (vi) there should be difference between the composition of rove beetle assemblages in plantations and the composition of assemblages in mature oak forest.

1.3. Role of forest edge in the maintenance of biodiversity

The forest edge is a transition zone between the adjoining forest and grassland habitat patches (Matlack 1993). Edges can cause changes in dynamic and ecological patterns of landscape, because those create fragmented habitats and possess specific vegetation structure and microclimate. Moreover, the edge can serve as shelter (source habitat or stepping-stone) during dispersal processes (den Boer 1981, Pulliam 1988) or may act as an ecological trap for some invertebrates by predators (Ries & Fagan 2003), when the adjoining habitats become unfavourable for organisms. Some species can associate with distinctive structure and/or microclimate of edges and generally they can be found in the edge (edge - associated species) (Horváth et al. 2002, Magura et al. 2001, Molnár et al. 2001). Thus, the forest edge can maintain specific species composition and increased diversity. The increasing human activities increases the number of edges and the landscape becomes more mosaic with smaller, homogenous patches, while the interior of patches become smaller or conversely bigger. Impacts of fragmentation by intensive forest management change the aboitic and biotic conditions of natural habitats and this have drastic effect on the flora and fauna (Ries et al. 2004). Therefore, understanding the ecology of habitat edges is important both for landscape ecology and for large-scale conservation and management decisions (Ries et al. 2004). Better understanding of ecological mechanisms of natural forest edges could be useful for creating suitable edge structure for conserving biodiversity in the intensive managed forests.

We tested the (i) edge effect hypothesis on rove beetles in forest-forest edge-grassland habitat complex, assuming that species richness is higher in the edge than in the adjoining habitats and/or that there are edge-associated characteristic species. We also studied (ii) the distribution of rove beetle assemblages in forest-forest edge-grassland habitats and (iii) identified the characteristic species of each habitat type using IndVal (indicator species analysis) methods.

1.4. Rove beetles as bioindicators

Rove beetles (Coleoptera: Staphylinidae) are one of the largest, cosmopolitan families of beetles with more than 46,200 species worldwide, approximately more than 1250 of which are found in Hungary (Ádám & Hegyessy 2001, Newton et al. 2001). They are usually easily distinguished form other beetles by their short elytra. The body length of adults varies between <1-60 mm in the Holarctic region. Their body shapes and coloring are variable, but most of them are ovoid or very elongate with dark or yellowish color.

About half of species live in forest leaf litter or similar kinds of decaying plant matter. They are also commonly under the bark of trees, among rocks or sand by the edge of ponds and rivers. They form one of the most common and ecologically important insect components of the soil fauna (Boháč 1999). Most of them are predators of other arthropods, but some species are specialized in the utilize of other food resources, for example decaying material, pollen, fungi, algae as well as some species are ectoparasitoids (Pohl et al. 2008). The varied nutrition has important ecological roles in nutrient cycling and ecosystem productivity (Seevers & Herman 1978), which may affect the ecosystems services and the human well-being (Pejchar & Mooney 2009). Some rove beetle species are decaying material dependent. The properties of rove beetles are positive from investigational point of view; they can be found practically in all ecosystem types, they are diverse and abundant, taxonomically and ecologically (habitat requirements, ecological demands) well-known, being mobile and relatively short-lived, they adjust rapidly to changes in abiotic and biotic environmental variables and human disturbance (Boháč 1999, Magura et al. 2013). These properties mean that this taxon is especially useful for monitoring (Boháč 1999).

Majority of the published studies investigated human disturbances on ground beetles or spiders (Alaruikka et al. 2002, Finch 2005, Magura et al. 2000, Pohl et al. 2007). During the monitoring of habitats it is worth examining the rove beetles, because thanks for the various ecological demands they provide opportunities that examine other aspects of the treatment effects for the environment.

2. Material and methods

2.1. Sampling design along urbanization gradient in Debrecen, Hungary

The study area was in and around the city of Debrecen (47°32’N; 21°38’E), the second largest city of Hungary located in the eastern plains area near the country’s eastern border (Magura et al. 2004). Three forested areas, representing rural, suburban and urban habitats, were selected along a rural–urban gradient running from the adjacent Nagyerdő Forest Reserve to the city. These areas had formerly (a few hundred years ago) been part of a continuous aged (older than 100 years) native forest association. All sampled areas were larger than 6 ha (urban: 6-10 ha, suburban: 6-8 ha, rural: 6-12 ha). Intensity of urbanization was characterized by the ratio of the anthropogenically modified areas (buildings, roads and asphalt covered paths) to natural habitats, as calculated in a GIS (ArcGIS) based on an aerial photograph made in 2009. In the rural area none of the land was covered by built-up surfaces. In contrast, on average 30% of the suburban area was modified, and 60% of the surface area in the urban area was built up. In addition, the intensity of the habitat maintenance operations also differed among the three categories of land. In the rural area there were only occasional lowintensity forestry management operations. In habitat management of suburban forest, however, fallen trees and branches were removed, although understory vegetation was largely undisturbed. The urban forest patches were largely park-like; fallen trees and branches were regularly removed, the shrub layer was thinned and highly disturbed, and grass between urban forest patches was frequently mowed and removed. The distance between the sampling areas (rural, suburban and urban) was 1–3 km.

Two sites, at least 100 m apart, were selected within each of the three sampling areas. Rove beetles were collected using ten unbaited pitfall traps placed randomly at least 10 m apart from each other at each site. This resulted in a total of 60, 10 traps in two replicated forest stands at each stage of the gradient. All traps were at least 50 m from the nearest forest edge, in order to avoid any edge effects (Molnár et al. 2001). Pitfall traps were plastic cups (diameter 65 mm) containing about 100 ml of 4% formaldehyde as a killing-preserving solution. Traps were covered by a square (20 x 20 cm) of fiberboard to minimize the accumulation of litter and rain. Rove beetles species were collected fortnightly from the end of April to the end of October 2009.

2.2. Sampling design in native, non-native plantations and mature oak forest

Study area was located in the northern part of Debrecen (Eastern Hungary) in the Nagyerdő Forest Reserve Area. Here, the typical native association is lowland oak forest. Four plantations and mature oak forest were selected to investigate the impacts of reforestation on the rove beetle assemblages: (1) 135-year-old mature lowland oak forest as control. English oak was the most numerous tree species in the closed tree canopy layer; common hawthorn (*Crataegus monogyna*), elderberry (*Sambucus nigra*), field maple (*Acer campestre*) and black sherry (*Prunus serotina* Ehrh.) were most frequent in the shrub layer. The cover of herbs was moderate; the fallen, decaying wood materials were numerous. (2) 40-year-old native oak plantation established instead of mature native oak forest stands by planting acorns; the shrub layer consisted of scattered individuals of *P. serotina*, while in the herbaceous layer the *Alliaria petiolata, Urtica dioica, Impatiens parviflora, Dactylis polygama, Geum urbanum* were numerous. (3) 30-year-old black locust plantation was created after clear-cutting of native lowland oak forest stands. Boxelder and black sherry were most frequent in the shrub layer; the herb layer was dense (*Chelidonium majus, Bromus sterilis, Elymus caninum*) due to the openness of the plantations. (4) 39-year-old Scots pine plantation was established instead of native lowland oak forest stands. The shrub layer was consistent; in the undergrowth vegetation American pokeweed (*Phytolacca Americana*) dominated. (5) 31-year-old red oak plantation was created after clear-cutting of mature oak forest stands. The shrub and the herb layers were entirely missing because of the shading of the closed tree canopy.

For spatial replication two stands of all habitat types were investigated. The distance between the studied stands was greater than 300 metres. The soil type in the studied stands was identical, sandy soil with humus. During forest management the fallen, decaying woods were removed from the native and non-native plantations.

Rove beetles were collected at each stand using leaf litter sifter (Martin 1977). Litter sifter samples were taken randomly at least 15 m apart from each other. The litter samples were collected with a frame of sifter (25 x 25 x 5 cm). Litter and debris were sifted vigorously and stored in a bag which was sealed (Anderson & Ashe 2000).

Five litter sampling locations were selected at each stand. Overall there were 50 litter sifter samples (5 habitat types × 2 replicates × 5 samples). Litter sifter samples were collected every third week from April to October in 2011. For statistical analyses, we pooled samples for the whole year. All rove beetles taken in litter sifter samples were identified to species level using standard keys (Assing & Schülke 2011, Lohse 1974). Rove beetle species were classified according to their ecological demands based on Koch (1989) and Stan (2008). The saprophilous, coprophilous and xylodetriticol species were classified as decaying material dependent species.

We measured the cover of canopy, shrubs, herbs, leaf litter and decaying wood materials and the soil moisture, temperature and pH that can affect the spatial distribution of rove beetles (Irmler & Gürlich 2007, Magura et al. 2002). The soil temperature at 2 cm depth was measured in every sifting location on the sampling day of each month using a multifunctional electronic instrument (Voltcraft DT - 8820). We estimated the percentage cover of leaf litter, decaying wood materials, herbs, shrubs and tree canopy within a circle of 1m diameter around the sampling locations. Furthermore, we collected soil samples around every litter sampling location and we measured the moisture content and the pH value of soil in the laboratory using electrochemical method (Thomas 1996). We used the average of measurements over the season.

2.3. Sampling design in forest-forest edge-grassland habitat complex

The research area was located in the Hajdúság Landscape Protection Area (47°33'09"N, 21°56'18"E) in a lowland oak forest-forest edge-grassland habitat complex. Three habitat types were studied: (1) forest interior - a closed oak forest dominated by English oak with thick litter, an herb and shrub layer and 85 - 95% canopy cover; (2) forest edge - a shrubby forest edge with increased ground vegetation and a shrub layer (dominated by *Crataegus monogyna*, *Prunus spinosa* and *Rhamnus chatartica*); and (3) grassland - mesophilous grassland with dense herbaceous vegetation (dominated by *Festuca pratensis*, *Poa pratensis*, *Deschampsia caespitosa*).

We collected rove beetles using pitfall traps (diameter 65 mm) containing 100 ml of 70% ethylene glycol as a killing-preserving solution. The traps were covered with a square (20 x 20 cm) of fiberboard for protection from litter and rain (Spence & Niemelä 1994). We selected the study sites in the grassland and forest interior 25 m from the edge. The forest edge was 6-14 m wide. Ten traps were placed in parallel lines in each habitat type. Traps were placed at least 10 m apart from each other (Digweed et al. 1995). There were two spatial replicates of the sampling sites, and the distance between the spatial replicates was greater than 100 m. There were 60 traps altogether (2 spatial replicates × 3 habitat types × 10 traps). The traps were emptied every fourth week from the beginning of May to the end of October 2009. All rove beetle beetles in the samples were identified to the species level using standard keys (Assing & Schülke 2011, Lohse 1974).

3. Data analyses

3.1. Effect of urbanization on rove beetle assemblages

Catches were pooled for the year for analysis. We used nested (sites within sampling areas) GLMs to test differences in the overall rove beetle species richness and the species richness of the rove beetles with different ecological demands among the three areas and among the 6 sites. The response variable (species richness) was a Poisson distribution (with log link function), assuming that the mean and variance of the data were equal. However, because the variance is expected to be larger than the mean overdispersion was also incorporated into the model using quasi-Poisson distribution (Zuur et al. 2009). When the overall GLMs revealed a significant difference between the means, an LSD test was performed for multiple comparisons among means. Ecological demands of rove beetles (forest, hygrophilous, thermophilous, saprophilous, phytodetriticol, mycetophilous, and myrmecophilous species) were obtained from the literature (Irmler & Gürlich 2007, Koch 1989, Stan 2008) (were collected in Appendix Table A1).

Composition of rove beetle assemblages along the gradient was compared at trap level using nonmetric multidimensional scaling based on presence - absence data using the Rogers - Tanimoto index of similarity (Legendre & Legendre 1998). Analyses were performed using STATISTICA 8.0.

3.2. Effect of reforestation with native and non-native species

Generalized Linear Models (GLMs) were used to test differences in the number of rove beetle individuals and species between the five habitat types. In the model the factorial design was applied, where the habitat types and the spatial replicates were used as categorical variables. The response variables (number of individuals and species richness) were defined as following a Poisson distribution (with log link function; Zuur et al. 2009). When the overall GLMs revealed a significant difference between the means, a LSD test was performed for multiple comparisons among means.

Generalized Linear Models (GLMs) were also used to analyse the relationship between the eight environmental variables and the number of rove beetle individuals and species, using a multiple regression design (Wakefield 2013). We first fitted the full model containing all environmental variables. We evaluated models based on Akaike's Information Criterion (Akaike 1973), and accepted the model with the lowest AIC as the final model. In the final model the dependent variables (species richness and abundance) were regarded as following a Poisson distribution (with log link function).

Similarity of the species composition of litter sifter samples was calculated by the Bray-Curtis index of dissimilarity based on the abundances, and it was displayed by multidimensional scaling (NMDS) (Borcard et al. 2011). Analyses were performed using STATISTICA 8.0 and NuCoSA 1.05 (Tóthmérész 1993).

3.3. Effect of forest edge on rove beetle assemblages

For statistical analysis, we pooled the catches per trap for the entire year. Factorial GLMs were used to test the differences in the number of individuals and the species richness of rove beetles among the three habitat types (forest interior, forest edge and grassland). The response variables (number of individuals and species richness) were treated as a Poisson distribution with log link function (Zuur et al. 2009). When the overall GLMs revealed a significant difference between the means, an LSD test was performed for multiple comparisons among means. Analyses were performed using STATISTICA 8.0. The composition of rove beetle assemblages at the trap level was displayed using principal coordinates analysis (PCoA) based on a Bray-Curtis index of dissimilarity; PAST 3.01 software package was used.

IndVal (indicator species analysis) method was used to explore the characteristic species in the forest, forest edge, grassland habitats (Dufrêne & Legendre 1997). The

IndVal method uses a Monte Carlo permutation test to estimate the statistical significance of the species indicator value. We used the IndVal 2.0 package.

4. Results and discussion

4.1. Effect of urbanization on rove beetles

4.1.1. *Overall species richness*

Altogether 3105 individuals belonging to 84 species were trapped during the study (Appendix Table A1). This included 1,229 from 60 species in the rural area, 1204 individuals of 50 species in suburban forest and 672 individuals of 49 species in urban sites. The most numerous species was *Omalium caesum*; 761 individuals were trapped comprising 24.5% of the total catch and it was the most abundant species in all three sampling areas (Appendix Table A1). The overall species number decreased significantly from the rural sites to the urban ones ($\chi^2 = 75.7$; df = 2, 3; $p < 0.0001$, Fig. 1).

Our findings did not support the intermediate disturbance hypothesis, as the overall species richness of the rove beetles was not highest in the moderately disturbed suburban area. The Romanian research examining ground beetles (Tóthmérész et al. 2011) and the Hungarian research studying millipedes (Bogyó et al. 2015) were only ones of the published Globenet studies that supported the intermediate disturbance hypothesis. The other studies, similarly to our results, disprove this hypothesis (for ground beetles: Alaruikka et al. 2002, Gaublomme et al. 2008, Magura et al. 2004, Niemelä et al. 2002; for isopods: Magura et al. 2008a; for spiders: Alaruikka et al. 2002, Magura et al. 2010a). Thus, most of the published results contradicted the prediction of the intermediate disturbance hypothesis. Obvious reasons for the failure of the intermediate disturbance hypothesis may be due to the rather problematic quantification of the type, frequency and size of the disturbance events along the rural-suburban-urban gradients. Therefore, it is hard to arrange precisely the study areas along a disturbance continuum.

The richness of rove beetles increased significantly with decreasing urbanization. This is similar to results with ground beetles for which similar patterns have been reported from Belgium, Canada, Finland, Japan and the United Kingdom (Gaublomme et al. 2008, Niemelä et al. 2002). However, this pattern has not been consistently found. In studies of isopods (Hornung et al. 2007) and ground-dwelling spiders from Hungary (Horváth et al. 2012, Magura et al. 2010a), and ground beetles from Bulgaria and Denmark (Elek & Lövei 2007, Niemelä et al. 2002) there was no decreasing relationship between urbanization and species diversity. Urbanization generates several forms of disturbance, including loss, alteration, fragmentation and isolation of the original habitats, changes in temperature, humidity, edaphic conditions and air pollution (Niemelä 1999). Moreover, more frequent disturbance seems to homogenize urban forests patches, perhaps eliminating microhabitats favored by some species. Disturbances in urban and suburban areas are continuous, directed and long lasting, leading to decreased diversity (Niemelä et al. 2002).

Clearly, results from studies of overall species richness along the rural–urban gradient are inconsistent. For that reason it is likely that overall species richness itself is not easily interpreted as an indicator of the impacts of urbanization and accompanying disturbance. Some groups of species may decline with habitat loss (habitat specialists), while other species may increase in number (opportunistic species) because of the disturbance and habitat alteration caused by urbanization. Thus, impacts on species with different habitat affinity should be analyzed separately to better interpret the effects of urbanization.

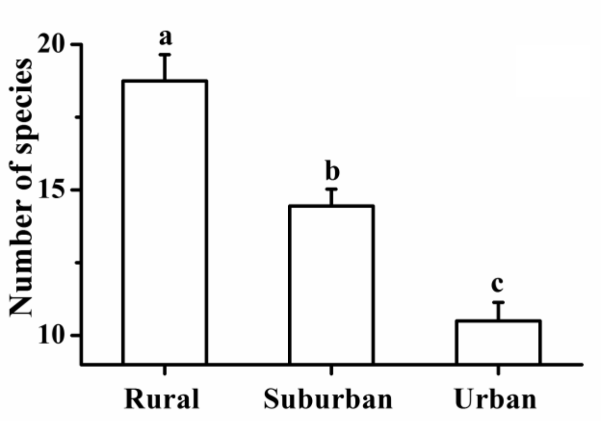

Fig. 1. Number of rove beetle species (±SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$).

4.1.2. *Species richness of forest specialist rove beetles*

The number of forest specialist rove beetle species was significantly lower in the heavily disturbed urban area compared to moderately and minimally disturbed suburban and rural area ($\chi^2 = 37.0$, df = 2, 3; $p < 0.0001$, Fig. 2). In Hungary the abundance of forest specialist terrestrial isopod species also decreased significantly from the rural area toward urban habitats (Magura et al. 2008a). No significant difference in the number of forest specialist spider species was reported across a rural–urban gradient in Finland, while in Hungary the number of forest specialist spiders was significantly highest in the rural area (Magura et al. 2010a). In general it appears that habitat modification associated with urbanization exerts a strong effect upon forest specialist species even in residual forest patches (Magura et al. 2010b, Niemelä & Kotze 2009).

Forest specialist species require a particular kind of environmental heterogeneity associated with provision of favorable microclimate, dead and decaying woods, and significant cover of leaf litter, shrubs and herbs, as in an undisturbed forest habitat (Desender et al. 1999). Urbanization appears to eliminate favorable microsites for forest specialist species and thus contributes to the decline of specialist species' richness in the assemblage. Others have demonstrated that rove beetles are especially sensitive to modification of forested habitat (Boháč 1999, Klimaszewski & Langor 2009, Pohl et al. 2008, Pohl et al. 2007), and the proportion of forest specialist rove beetle species decreased, as in the present study, with increasing urbanization in Berlin (Deichsel 2006).

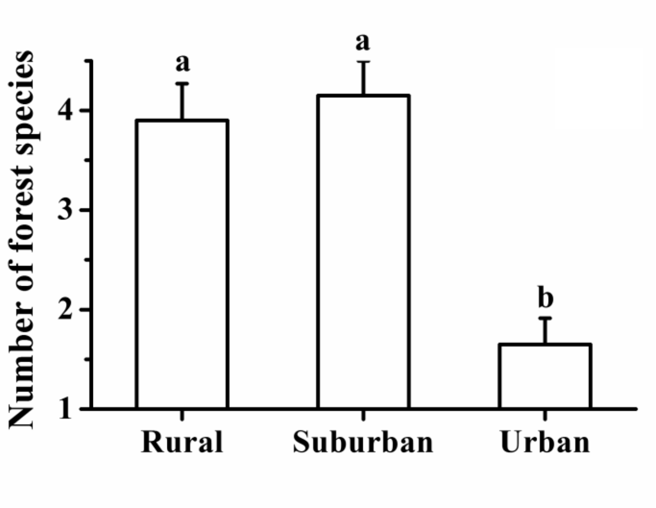

Fig. 2. Number of rove forest specialist rove beetle species (±SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$).

4.1.3. *Ecological demands of species indicating habitat alterations*

Our results showed that number of hygrophilous species decreased significantly from the rural area towards the urban forest ($\chi^2 = 60.0$; df =2, 3; $p < 0.0001$, Fig. 3A), while number of thermophilous species was significantly higher in the urban area compared to the suburban and rural forests ($\chi^2 = 7.7$; df=2, 3; $p = 0.0214$, Fig. 3B).

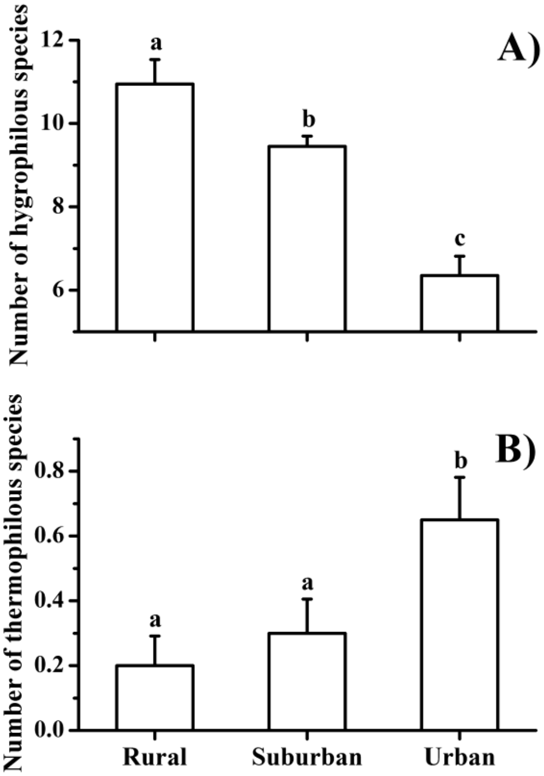

Fig. 3. Number of the hygrophilous rove beetle species (A) and the number of thermophilous rove beetle species (B) (±SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$).

Moreover, the number of species relating directly or indirectly to decaying organic materials also changed significantly along the gradient. Numbers of saprophilous, phytodetriticol species and myrmecophilous species were significantly highest in the rural area ($\chi^2 = 16.47$; df = 2, 3; $p = 0.0003$, $\chi^2 = 45.81$; df = 2, 3; $p < 0.0001$; $\chi^2 = 39.31$; df = 2, 3; $p < 0.0001$, respectively; Fig. 4A-C). The number of mycetophilous species did not differ between rural and suburban areas but was significantly higher than in the urban forest ($\chi^2 = 19.4$; df = 2, 3; $p < 0.0001$, Fig. 4D).

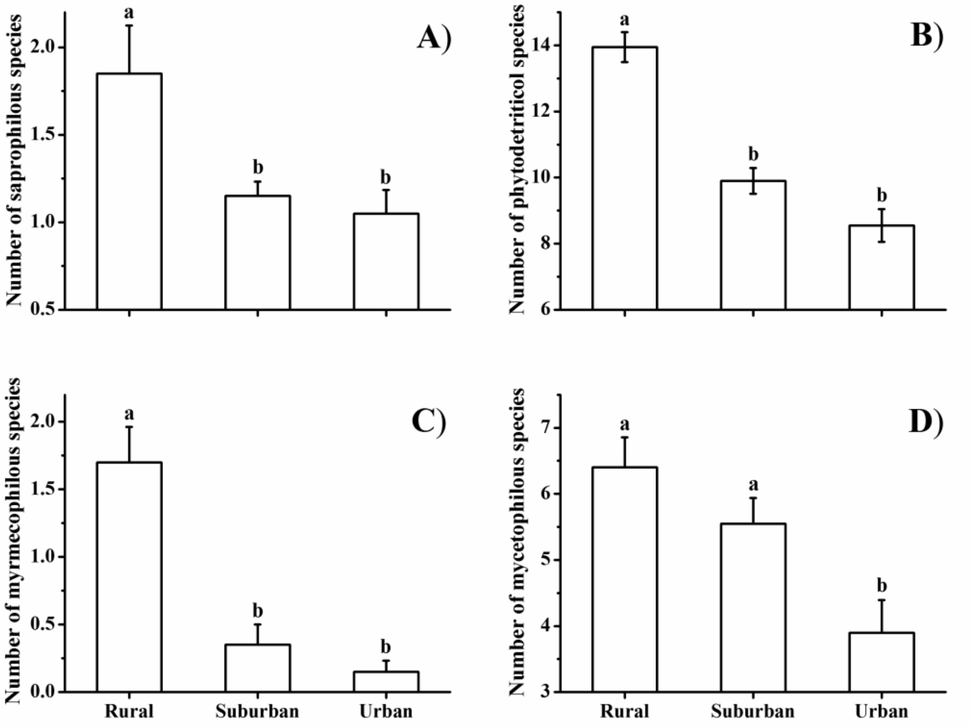

Fig. 4. Number of the saprophilous rove beetle species (A), the phytodetriticol rove beetle species (B), the myrmecophilous rove beetle species (C), and the mycetophilous rove beetle species (D) (±SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$).

Urbanization drastically modifies the original habitats (McKinney 2008), and in our study the nature of some of these changes was underscored by responses of sensitive species. For example, number of hygrophilous species was highest in the rural area, while the number of thermophilous species was highest in the urban area. The number of the species associated with decaying organic materials (saprophilous species, phytodetriticol species, myrmecophilous species and mycetophilous species) was also highest in the rural area and reached its lowest value in urban habitats. It seems that the fauna responded to increasing dryness and a general reduction in forest floor organic matter on the urban end of the gradient.

The urban forest studied here is considerably fragmented by paved footpaths, increasing edge habitat within the forest patches. This fragmentation together with cutting of the shrub layer, allows sunlight to penetrate more deeply, making urban forest patches drier and warmer (McDonnell et al. 1997). These features of urban patches support survival and/or immigration of open-habitat species that do best under lighter, warmer and drier conditions. Similar findings have been published for terrestrial isopods (Magura et al. 2008a), ants (Vepsäläinen et al. 2008), ground dwelling spiders (Magura et al. 2010a), ground beetles (Magura et al. 2008b, Magura et al. 2004, Tóthmérész et al. 2011), and weevils (Germann et al. 2008), suggesting that this situation applies quite generally to invertebrates in urban forest patches.

In both urban and suburban areas dead and decaying organic materials are commonly removed from forest patches as part of the management regime. Intensity of this sort of habitat management will be generally highest in urban areas, and in our study, it certainly decreased through suburban to rural areas. Decaying wood material provides favorable microclimate, shelter against predators, and sites suitable for feeding, aestivation, hibernation, overwintering, egg and larval development and thus, the number of the saprophilous rove beetle species decreased along the rural–urban gradient. Similarly to our finding, Vepsäläinen et al. (2008) reported that in urban environments ant species dependent on dead wood were very rare. Similar trend was reported for spiders as forest species requiring presence of dead and decaying wood materials were more species rich in the rural sites characterized by higher amounts of decaying woods (Magura et al. 2010a).

Intensity of urbanization is a function of disturbance and the structural simplification of remaining habitat by management practices that remove not only the dead woody and herbaceous material, but the living trees, shrubs and herbs. These practices decrease the habitat quality of remaining habitats (McKinney 2008). In the present study, reductions in coarse woody material and litter doubtlessly were associated with decreasing of the richness of species using decaying plant debris as habitat (phytodetriticol species). Reductions in plant debris are also harmful for rove beetle larvae. As they are soil bound and less mobile than adults (Boháč 1999), disturbance of the litter and soil are important in determining their survival and thus adult population size. Together with similar findings for terrestrial isopods and millipedes (Riedel et al. 2009) and ants (Savitha et al. 2008) our results suggest that dense decaying plant debris and litter promote the establishment and maintenance of species rich assemblages.

Myrmecophilous rove beetles are specialized predators that eat ants or saprophages living on waste in or near ant nests (Boháč 1999). Lessard & Buddle (2005) and Vepsäläinen et al. (2008) reported decreased ant species richness in urban areas relative to surrounding rural areas, and that the decline varied directly with the degree of the urbanization. Vepsäläinen et al. (2008) also reported that ant species dependent on dead wood were rare or absent in urban areas that they studied. Therefore, significant impoverishment of the myrmecophilous rove beetle species in the urban forest patches was expected. The occurrence of aggressive, dominant and competitively dominant non-native species in urban areas could negatively affect not only the other ant species, but also the other ground-dwelling arthropods (Lessard & Buddle 2005).

Mycetophilous rove beetles live in or near fungi (Boháč 1999). Fungi are sensitive to environmental changes, specialized in substrate requirements, and depend on decomposing organic plant material as their living substrate (Rayner & Boddy 1988). Thus, urbanization is associated with decreases in abundance and species richness in urban areas (McDonnell et al. 1997). In consequence of the impoverishment of fungi at the urban forest patches, our hypothesis assumed significant decrease of the mycetophilous rove beetle species along the rural–urban gradient. Earlier results also showed that urbanization negatively affected both the fungivous microinvertebrates (nematods, microarthropods) and the fungi. Moreover, the larvae of the rove beetles are more sensitive to air pollution (Boháč 1999), so damage of the larvae could negatively affect the abundance and species richness of imagoes.

4.1.4. *Spatial pattern of rove beetle assemblages along the gradient*

Rove beetle assemblages of the rural, suburban and urban areas were clearly separated from each other by the ordination (Fig. 5). Assemblages from rural forests were separated from those of suburban and urban habitats along the first axis. Clearly, composition of the rove beetle assemblages of suburban and urban areas was more similar to each other than to the assemblages of the rural area.

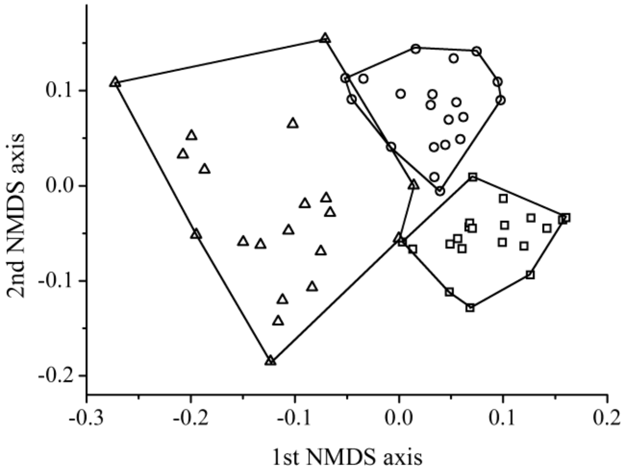

Fig. 5. Ordination (nonmetric multidimensional scaling using the Rogers-Tanimoto index of similarity) of the rove beetle assemblages along the studied rural-urban gradient (*open triangles:* rural traps, *open circles:* suburban traps, and *open squares:* urban traps).

4.2. Effect of reforestation with native and non-native species on rove beetles

4.2.1. *Rove beetles in the native and non-native plantations*

Altogether 1,542 individuals belonging to 92 species were collected by litter sifter. In the mature oak forest 60 species and 476 individuals were caught, while in the native oak plantation 44 species and 338 individuals were caught. 37 species and 265 individuals were captured in the black locust plantation; 33 species and 252 individuals were collected from the Scots pine plantation and 211 individuals belonging to 47 species were sampled in the red oak plantation. The most numerous species was *Gabrius osseticus,* which made up 8.2% of the total catch. This species was also the most numerous in the native oak plantation. *Sepedophilus pedicularius* was in the highest number in the black locust plantation, while in Scots pine plantation the *Pselaphus heisei* was the most frequent. In the red oak plantation *Omalium caesum* had a most frequent occurrence. In the mature oak forest *Geostiba circellaris* was the most numerous species (Appendix Table A2).

Despite the fact that the number of rove beetle individuals and species showed increase in the native oak plantation compared to non-native plantations, these were still significantly more in the mature oak forest, suggesting a partially recovery of rove beetle assemblages. (for the number of individuals: Wald statistic = 51.36; d.f. = 4,4; $p < 0.0001$; for the number of species: Wald statistic = 87.62; d.f. = 4,4; $p < 0.0001$, Fig. 6A and B). Similarly to our results, several previous studies also demonstrated that reforestation with non-native species does not provide suitable habitat for invertebrates and causes changes in ground-dwelling beetle assemblages compared to native forest stands (Magura et al. 2003, Paritsis & Aizen 2008, Roberge & Stenbacka 2014). The primary causes of rove beetle assemblage' collapse in the plantations may be the heavy mechanical site preparation before reforestation and cultivation by light tilling during the management of the plantations, originating drastic habitat alteration. Almost all studies have confirmed that clear-cutting of native forest and the subsequent treatments cause considerable changes in the structure and spatial pattern of ground-dwelling beetle assemblages, which are most markedly detectable in the early phase (1-3 years) of reforestation (Magura et al. 2003, Niemelä et al. 2007). However, after canopy closure (8-16 years after the planting) ground-dwelling beetle assemblages are not notably different, and they show partial recovery resulting similar species composition between forested stands of the ageing sequence (Magura et al. 2015, Taboada et al. 2008). By contrast, our results did not suggest that rove beetle assemblages altered drastically by clear-cutting recovered after 40 years of reforestation with native species.

However, it seems that reforestation with native oak can maintain higher rove beetle species richness compared to the non-native plantations (Fig. 6A and B). This can be explained by the fact that in native plantations after the canopy closure the plant and insect species may colonise easier from the nearby mature, native forests. These forest stands provide a local source of native dispersal agents, which result in rapid vegetation and climate regeneration within the native plantations (Brockerhoff et al. 2008). Thus, reforestation with native tree species facilitates the forest regeneration and accordingly to the recovery of ground-dwelling beetles after some ten years of clear-cutting (Buddle et al. 2006, Magura et al. 2015, Taboada et al. 2008). Moreover, the closed native plantation something is similar in environmental conditions (native humus, leaf litter and decaying woody materials, herbs) to the mature oak forest, contributing to the rapid recolonization and permanent populations of rove beetles. However, the microclimatic conditions, vegetation structural complexity and development of litter and humus layers can drastically alter in case of reforestation with non-native tree species (Brockerhoff et al. 2008). These alterations make the colonization of dispersal agents and regeneration of favourable climate very difficult from the nearby mature forests, preventing the development of appropriate conditions within the non-native plantations. As forest regeneration has not been implemented satisfactorily, the recovery of ground-dwelling beetles also does not proceed in non-native plantations (Magura et al. 1997, 2003).

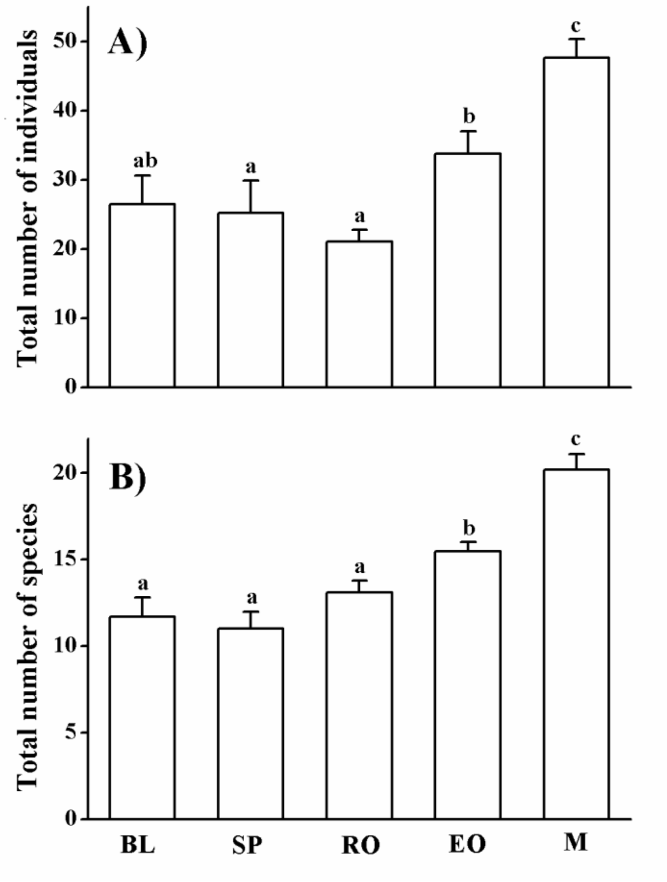

Fig. 6. Number of rove beetle individuals (A) and species (B) per sampling point (±SE) in the studied habitat types. Means with different letters indicate a significant ($p < 0.05$) difference by LSD test. Notations: BL – black locust plantation, SP – Scots pine plantation, RO – red oak plantation, EO – English oak plantation, M – mature oak forest.

4.2.2. *Richness of specialist species in native and non-native plantations*

Specialist species in forested habitats require microsites with a particular kind of environmental heterogeneity and presence of suitable substrate materials (Horváth et al. 2012). These variables provide favourable microclimate, shelter away from predators, and suitable stands for feeding and life cycle (aestivation, hibernation, overwintering, egg and larval development) of ground-dwelling beetles (Magura et al. 2013). Establishment of plantations and the accompanying intensive forest treatments cause unfavourable changes in the habitat structure altering the abiotic and biotic conditions of the habitats. These alterations promote the disappearance of the sensitive forest specialist species and accelerate the colonization of generalist, invasive species (Pohl et al. 2007, Toivanen et al. 2014). However, it has been reported that forest specialist beetles with high dispersal ability and less specific feeding habit can recover with canopy closing after a few years of reforestation (Magura et al. 2015). In our study the delayed recovery of the diversity and composition of rove beetles in the plantations were probably due to the less ecological flexibility of the specialist species.

In our study the number of hygrophilous rove beetle individuals and species were significantly the highest in the mature oak forest, moreover these were significantly higher in the native plantation compared to the non-native plantations (for the number of individuals: Wald statistic = 66.32; d.f. = 4,4; $p < 0.0001$, and for the number of species: Wald statistic = 59.66; d.f. = 4,4; $p < 0.0001$, respectively, Fig. 7A and B). There were no significant differences in these parameters among the non-native plantations.

The non-native tree species were planted in parallel rows in the plantations, furthermore spaces between the rows were regularly treated, which allow sunlight to penetrate more deeply, making the soil drier (Appendix Table A3). The humus content, the physical properties of the soil and the depth of tilth are important determinants of water supply of forests. Clear-cutting causes rapid degradation of humus that accumulated over several decades. Moreover, a striking part of residuary humus layer is eliminated during management of trunk tracts. These changes lead to soil acidification and decreasing of storage capacity for water in the plantations (Mátyás 1996). After the reforestation, the structure and composition of the non-native tree' litter and the regular cultivation by light tilling also influence the development of humus layer, further constraining the soil water storage capacity in plantations (Andersson et al. 2004, Keenan & Kimmins 1993). These are key factors in development of suitable microclimate for hygrophilous rove beetle species, because these species rather associated with lower under light and moister conditions. Thus, in the drier and warmer non-native plantations with poor water supply the colonization of the hygrophilous rove beetles are not supported even after the canopy closure.

The quantity, size and age of the decaying materials could be other important factors on the spatial pattern of specialist species (Hammond et al. 2004). The richness of specialist species (predators, fungivorous and scavengers) increases from habitat with fresh woody debris to habitat with highly decayed coarse woody debris (Hammond et al. 2004). The increasing microhabitat diversity within decayed woody debris created by fungi and arthropods provides suitable conditions for specialist rove beetle species (Siitonen 2001). Roberge & Stenbacka (2014) also showed that the abundance of wood- and cambium specialist beetles (including several rove beetle species) and the species richness of cambium-living beetles were significantly lower in introduced non-native lodgepole pine stands than in the native Scots pine ones.

Dead wood, humus, carrions, nests, feces and other special microhabitats or substrates are indispensable for specialist rove beetle species (Boháč 1999, Nadeau et al. 2015). These microhabitats and substrates were eliminated in the plantations during forest treatments, so the survival of specialist species was hampered. Moreover, establishment of monospecific plantations causes nutrient losses and leads to declines in soil fertility and biomass production, and it alters the microbial community that is known to be a major contributor of enzyme activities and decomposition process (Fang et al. 2013, Saswati & Vadakepuram 2010). Thus, habitat alterations can reduce and slow down nutrient cycling and decomposition processes in the plantations. Due to the removal of decaying materials and the changed decomposition processes by microbial community the number and quality of decayed materials are the highest in the mature oak forest compared to the plantations, contributing to the high diversity of the species associated with decaying organic materials. Although the cover of decaying wood materials were similar in the native and non-native plantation, the number of decaying material dependent species and their abundance were significantly higher in the native plantation compared to the non-native ones (for the number of individuals: Wald statistic = 50.04; d.f. = 4,4; $p < 0.0001$, and for the number of species: Wald statistic = 75.48; d.f. = 4,4; $p < 0.0001$, respectively, Fig. 7C and D). Native plant debris may be easier and more effectively processed by the native decomposers, creating decaying materials with higher quality (Rudgers & Orr 2009).

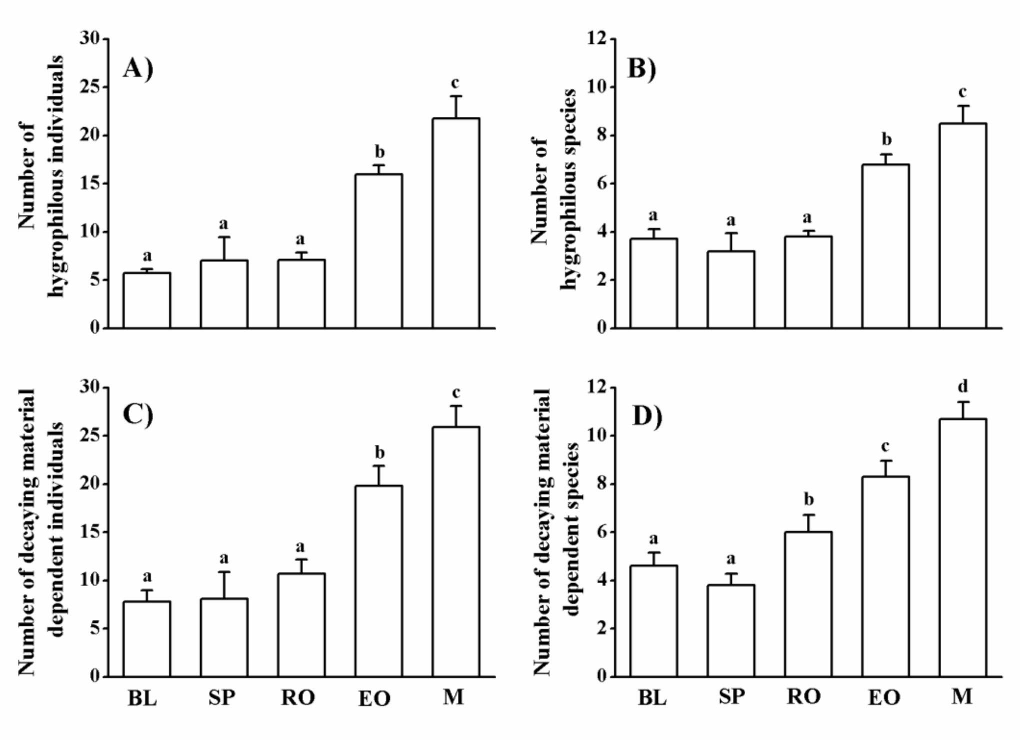

Fig. 7. Mean number of the hygrophilous rove beetle individuals (A) and species (B), and decaying material dependent rove beetle individuals (C) and species (D) (±SE) in the studied habitat types. Means with different letters indicate a significant ($p < 0.05$) difference by LSD test. Notations: BL – black locust plantation, SP – Scots pine plantation, RO – red oak plantation, EO – English oak plantation, M – mature oak forest.

4.2.3. *Species distribution and environmental variables in plantations*

Creating of plantations drastically altered the environmental condition characteristics of mature oak forest, resulting distinctive vegetation structure and microclimate in the studied plantations. These changes have important roles in the distribution of ground-dwelling beetles (Roberge & Stenbacka 2014). For example, tree canopy cover and cover of understory vegetation have effects on the amount of light penetrating, which could affect ground-dwelling beetles through differences in other related environmental variables (Elfving et al. 2001).

In our study we measured 8 environmental variables, which can affect the distribution of rove beetles (Appendix Table A3). The importance of environmental variables on the distribution of rove beetles was also emphasized by several previous studies (Boháč 1999, Irmler & Gürlich 2007). Rose (2001) underlined that leaf litter type and tree canopy cover are the most important factors determining the spatial distribution of rove beetles. Generalized linear models (GLMs) showed there was no significant correlation between the cover of litter, the canopy cover and the diversity of rove beetles. However, we demonstrated that the cover of shrubs was a positive predictor for the abundance and species richness of hygrophilous rove beetles, whereas the cover of herbs also showed a positive correlation with the overall number of individuals, the number of hygrophilous individuals and species and the number of decaying material dependent individuals (Appendix Table A4).The lime content and the pH of soils are other important predictors to the rove beetles' distribution (Buse & Good 1993, Irmler & Gürlich 2007). Accordingly, in our study the total number of species, the number of hygrophilous species and the number of decaying specialist individual and species increased as the soil pH increased (Appendix Table A4). Contrary to studies of both Szujecki (1966) and Irmler (1993), our results did not show significant correlation between the soil moisture and the diversity of rove beetles (Appendix Table A4). However, soil temperature showed a negative correlation with the abundance and species richness of rove beetles. Higher soil temperature may adversely influence the egg and larval development in the soil, and may cause a reduction in the number of sensitive rove beetle species (Boháč 1999, Ernsting & Isaaks 2000).

Rove beetle assemblages of the samples from the mature oak forest were strongly separated from the assemblages of the samples from the plantations along the first axis of the NMDS (stress value: 0.2516; Fig. 8). Rove beetle assemblages of the samples from the native oak plantation and red oak plantation were similar to each other. Results of the multidimensional scaling also highlighted that the rove beetles did not recover in the native and non-native plantations after 30-40 years of establishment. The structure of understory vegetation and environmental conditions differed between the studied habitats, which resulted in characteristic rove beetle assemblages. The delayed recovery of rove beetles may be attributed to the fact that the recovery of rove beetles with specific environmental and ecological demands may be longer.

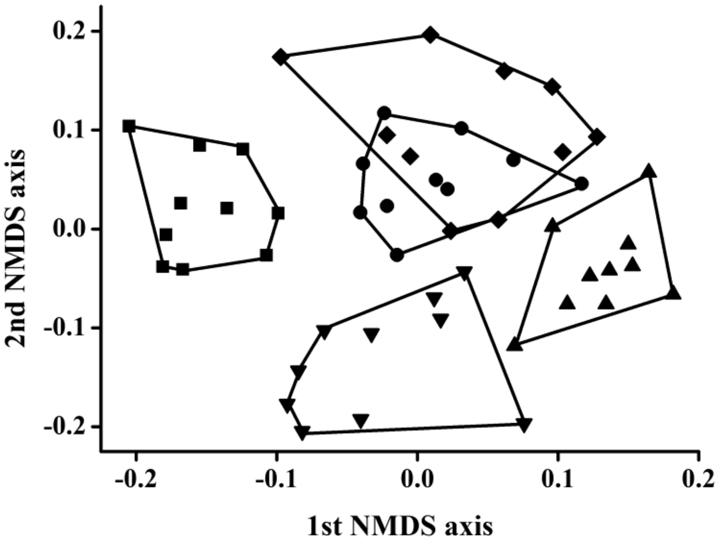

Fig. 8. Multidimensional scaling of the rove beetle assemblages based on the abundances using the Bray-Curtis index of dissimilarity. Notations: ▲ – black locust plantation, ▼ – Scots pine plantation, ♦ – red oak plantation, ● – native oak plantation, ■ – mature oak forest.

4.3. Effect of forest edge on the rove beetle assemblages

4.3.1. *Rove beetles in forest-forest edge-grassland habitat complex*

We collected 1458 rove beetle individuals and 87 species. *Staphylinus caesareus* was the most frequent species (11.2% of whole rove beetle catch). This species was also the most frequent species in the grassland habitat. At the edge, *Omalium caesum* was the most abundant, whereas *Oxypoda acuminata* was the most numerous in the forest interior (Appendix Table A5).

The GLMs showed that there were significant differences in the number of individuals and species richness among the habitats. The total number of rove beetle individuals was significantly lower in the grassland than in the edge and forest interior ($\chi^2 = 25.0$; df = 2; $p < 0.0001$, Fig. 9A). While the overall species richness was highest in the edge and the lowest species number was recorded in the grassland ($\chi^2 = 62.1$; df = 2; $p < 0.0001$, Fig. 9B).

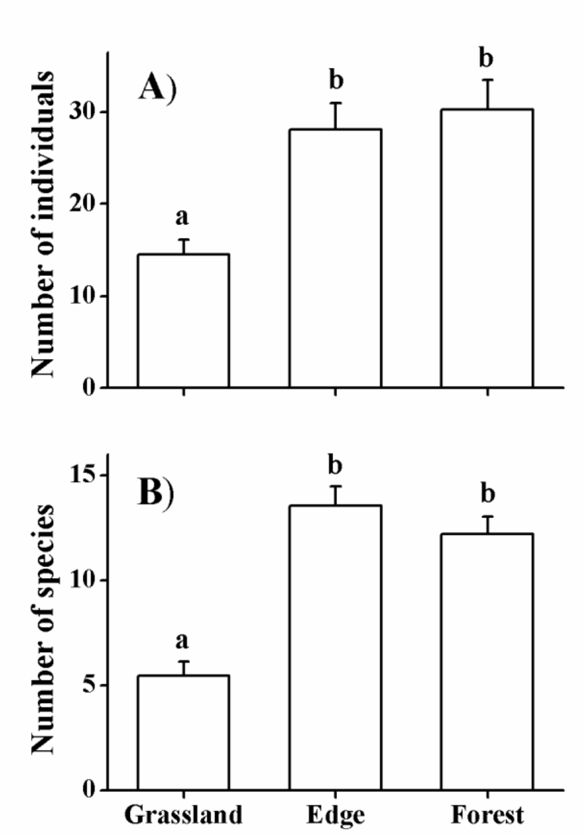

Fig. 9. Number of rove beetle individuals (A) and species (B) per trap (±SE) within the habitats. Means with different letters indicate a significant ($p < 0.05$) difference.

The composition of rove beetle assemblages changed slightly from the forest interior to the edge and drastically changed in the grassland (Fig. 10). The PCoA ordination revealed that the grassland assemblage separated from the forest interior and edge assemblages along the first axis. Thus, the compositions of the assemblages of the forest interior and edge were more similar to each other than to the grassland.

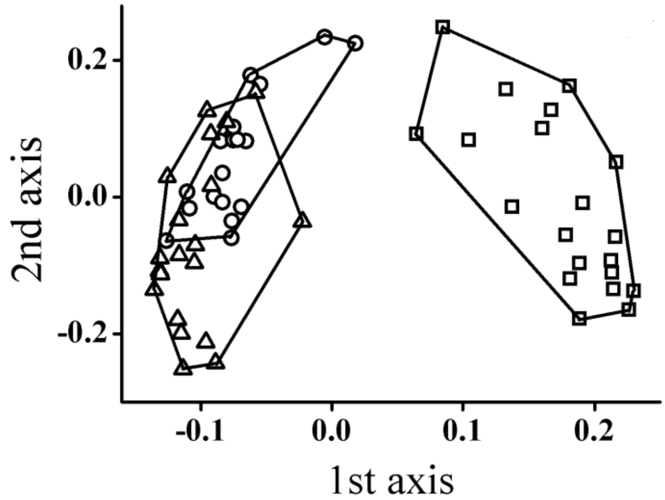

Fig. 10. Ordination (PCoA, Bray-Curtis dissimilarity) of the pitfall catches in case of rove beetles in forest-forest edge-grassland habitat complex. Notations: *unfilled squares* – grassland traps; *unfilled circles* – edge traps; and *unfilled triangles* – forest traps.

Our findings the overall species richness of rove beetles was highest in the forest edge. Several previous studies demonstrated the edge effect hypothesis on carabids (Elek & Tóthmérész 2010, Magura & Tóthmérész 1998). However, there are only few studies that have investigated this in rove beetles (Golden & Crist 2000, Pohl et al. 2007). Pohl et al. (2007) showed that the species richness was slightly higher in the open habitat than in the forest area, but there were no other clear trends. The forest area within at least 10 m of the edge may be colonized by open habitat species and is not suitable habitat for all the forest species (Pohl et al. 2008). Thus, the rove beetle assemblage of the forest edge was more closely related to the open habitat assemblages than to the deep forest assemblages (Pohl et al. 2007). By contrast, we found that the rove beetle assemblage of the edge was more similar to the forest assemblage than to the grassland assemblage. Similar to our results several studies (in case of carabid) also showed that the assemblage of edge was more similar to the assemblage of forest interior (Magura et al. 2001, Molnár et al. 2001).

4.3.2. *Characteristic species of forest-forest edge-grassland habitat complex*

Five groups of the characteristic species were identified by the IndVal method: (1) habitat generalists that were present in high numbers in all habitat types (five rove beetle species); (2) forest specialists that were captured numerously in the forest interior (three significant rove beetle character species); (3) forest generalists that occurred exclusively or numerously in the forest interior and forest edge and were not present or rare in the grassland habitats (twelve significant rove beetle character species); (4) edge-associated species that were recorded exclusively in the edge or were abundant in the edge and were sparse or missing in the adjacent habitats (eight significant rove beetle character species: *Tasgius winkleri, Falagrioma thoracica, Tasgius melanarius, Olophrum assimile, Platydracus fulvipes, Pella limbatus, Quedius limbatus, Oxypoda longipes*); and (5) grassland-associated species that were found exclusively in the grassland or were abundant in the grassland (eight significant rove beetle character species, see Appendix Table A5).

The ordination and the IndVal method demonstrated that there were characteristic assemblages of the habitats (Fig. 10. and Appendix Table A5). Similar to our results, Koch (1989) and Stan (2008) reported that the rove beetle species *Oxypoda acuminata* and *Othius punctulatus* were forest specialist species. Several edge-associated species (*Tasgius winkleri, Falagrioma thoracica* and *Tasgius melanarius*) were present in both the open and/or forest areas. Previous studies also showed that these species can be found in all three habitat types (Koch 1989). However, these species were specifically associated with the edge and may disperse to the adjacent habitats during activity season. In the case of ground beetles Magura et al. (2001) also found seasonal dispersal between the adjacent habitats due to the annual changes of habitat structure and environmental conditions. Moreover, our results supported the findings of Koch (1989) that *Staphylinus caesareus, Tasgius pedator, Philonthus concinnus* and *Philonthus corruscus* mainly prefer the open habitats.

In the case of ground beetles Niemelä (1988) reported that small scale dispersal between habitat patches influenced their composition and structure. Thus, the dispersal processes may increase the diversity in the edge as the ground-dwelling beetles cover a long distances for food and/or habitats (reproduction and hibernation) and exhibit density-dependent migration and aggregation in habitats with large amounts of available prey (Magura et al. 2001). *Oxypoda acuminata, Othius punctulatus* and *Sepedophilus marshami* were significant character species for the forest interior (Appendix Table A5). However, these species also immigrate into the forest edge. Furthermore, there were several open-habitat species in the edge from the surrounding grassland habitat (*Tasgius pedator, Drusilla canaliculata*). Several previous studies showed that open-habitat species can colonize the forest edge due to changes in the habitat structure and microclimate (Murcia 1995, Pohl et al. 2007, Spence et al. 1996). Spence et al. (1996) also showed that forest specialist species have important roles in the maintenance of populations in the forest edge. Pohl et al. (2007) showed that the edges may not suitable habitat for the forest specialist rove beetle species. We found that three characteristic rove beetle species of the forest interior (*Oxypoda acuminata, Othius punctulatus* and *Sepedophilus marshami*) were also present in the forest edge.

The edge-associated species and the species from the surrounding habitats contribute to the increased diversity of ground-dwelling beetles in the forest edge. The species richness of rove beetles showed no significant difference between the forest interior and the edge. However, based on the results of the IndVal analysis, several species were significantly associated with the forest edge, which indicates an edge effect. Forest edges have a distinctive structure and microclimate and can thus provide suitable sites for the feeding and life cycle processes of edge-associated species.

5. Management implications and conclusion

Our results show that urbanization had a strong effect on rove beetles, with their overall species richness decreasing significantly with urbanization. Thus, this group, although not frequently used as such, are reliable indicators of urbanization.

Species composition of rove beetle assemblages changed remarkably along the studied rural-suburban-urban gradient, something that is likely to reflect disproportionate effects on species associated with organic matter and the degree of openness in forest habitats. We conclude that overall species richness is not a sufficient indicator of urbanization and its accompanying disturbance. Therefore, species with different habitat affinity should be analyzed separately to evaluate the real effects of urbanization. In this way we showed, that in accordance with the habitat specialist hypothesis, the number of forest specialist rove beetle species was significantly lower in the heavily disturbed and altered urban area compared to the suburban and rural area. Besides the habitat affinity of the species, the ecological demands of the species are also important. Namely, species with different ecological demands may also response variously to the urbanization and the accompanying processes. Thus, ecological demands of the species should be considered to detect accurately those environmental variables that drastically changed during urbanization.

Our results also demonstrated that clear-cutting of mature oak forest stands, creating of native or non-native plantations and the post-treatments of the plantations (removal of herbs, shrubs and fallen woods) had detrimental effects on the rove beetle assemblages. These habitat alterations change the original vegetation structure and the environmental variables, furthermore they reduce and slow down nutrient cycling and decomposition processes (Barlow et al. 2007, Jha et al. 1992, Roberge & Stenbacka 2014). These changes significantly influenced the hygrophilous and decaying material dependent rove beetles. However, it seems that these species recover easier in the native plantation than in the non-native ones. Based on our results, it is not advisable the further establishment of non-native plantations, because local rove beetle diversity and environmental services could be better enhanced in native broadleaved plantation than in non-native ones. It should be noted that although native oak plantation may be able to replace some important ecosystem functions, however the total recovery of rove beetles is likely to take much longer time. The main reason for this is the heavy mechanical soil preparations before reforestation and the removal of decaying materials during forest managements. Therefore, it is necessary to introduce new and more efficient forestry practices maintaining or even enhancing biodiversity (Magura et al. 2006a).

Natural and human disturbances (burning, grazing, mowing) have effects on natural habitats. These processes can change the abiotic and biotic environmental variables, which may have an influence on arthropods. In the case of habitat alteration in the adjacent habitats, forest edges can ensure food resources and protection to th rove beetle species that are characteristic of grassland and forest interior habitats (Magura et al. 2001). Thus, the forest edges have viable populations from the adjacent habitats and these can serve as a source habitat or stepping-stone for dispersal processes (den Boer 1981, Pulliam 1988). Furthermore, after the restoration of degraded habitat, the forest edges can contribute to the recolonization of rove beetle species in the adjacent habitats. Our results suggest that forest edge may play a vital role in the maintenance and preservation of the diversity of rove beetles. Thus, in forests with poorly developed edges (plantations and managed forests) it is necessary to create a more diverse edge by sowing or planting herbs and shrubs (Magura et al. 2001). Several previous studies noted that the diversity of plants and ground-dwelling beetles can be maintained and encouraged by suitable management practice and controlled habitat treatments (Anderson & Carter 1987, Golden & Crist 2000, Ingham & Samways 1996, Magura et al. 2001).

Summary

The aim of this study was to investigate the effects of human modified habitats on rove beetle assemblages by pitfall trapping and leaf litter sifting methods in forested areas. Species composition and distribution of rove beetles proved to be an important indicator in the disturbance researches. In the dissertation the scientific results are the following:

First, in the urbanization study we compared the rove beetle assemblages along an rural-suburban-urban gradient. The overall species richness of rove beetles was the highest in the undisturbed rural area, while it decreased towards suburban area to the urban one with higher human disturbances. The number of forest specialist species was higher in the rural and suburban areas, than in the urban one. Thus, the increasing disturbance hypothesis and the habitat specialist hypothesis were proved. Moreover there were 6 hypotheses (hygrophilous species hypothesis, thermophilous species hypothesis, saprophilous species hypothesis, phytodetriticol species hypothesis, myrmecophilous species hypothesis, mycetophilous species hypotheses) examined based on ecological demands of rove beetle species. The number of hygrophilous species was the highest in the rural area, while the richness of thermophilous species was higher in the urban one. The richness of species directly or indirectly feeding on decaying organic materials was also the highest in the rural area compared to the urban one. Our results showed that the overall species richness of rove beetles could be an important indicator, but it is not the most appropriate indicator of the effects of urbanization and accompanying disturbance. Therefore, it is necessary to examine habitat affinity and ecological demands of the species, which can give more information what habitat properties and environmental variables change drastically during urbanization.

Second, rove beetle assemblages of four monospecific plantations with native (English oak) and non-native tree species (black locust, Scots pine, red oak) were compared to each other and to mature oak forest as control. Results showed that the total number of individuals and species were higher in the mature forest than in the plantations. During reforestation of native forest with non-native tree species the substrate materials and microhabitats (decaying materials, fungi, nests) for the rove beetles are eliminated and these alterations mitigate the heterogeneity of habitats. This impoverishment in heterogeneity has effects on the ground-dwelling meso- and macroinvertebrates. GLM analyses showed that both number of hygrophilous and decaying material dependent individuals and species were the highest in the mature forest compared to the plantations. Moreover, our results also confirmed that reforestation with native species provide more suitable habitat for rove beetles than non-native plantations. However, it seems that rove beetle assemblages could not

recover after 40 years of reforestation with native species due to their specific ecological demands. The most influencing environmental factors of distributions of rove beetles were the ground temperature, soil moisture and pH. Rove beetle assemblages of the native forest and plantations were clearly separated from each other, suggesting that 30 - 40 years of reforestation is not enough to the total recolonization of plantations by rove beetles.

Third, the forest edges have important role in the maintenance of biodiversity. Thus, it is necessary to know more details about the ecological mechanisms in forest edge. The edge effect hypothesis was tested on rove beetles using pitfall traps in forest-forest edge-grassland habitat complex. The number of rove beetle individuals was the highest in the forest habitat and it was the lowest in the grassland, while the number of rove beetle species was higher in the forest edge, but there was no significant difference between the forest interior and forest edge. However, based on IndVal method, there were eight significant rove beetle character species (*Tasgius winkleri, Falagrioma thoracica, Tasgius melanarius, Olophrum assimile, Platydracus fulvipes, Pella limbatus, Quedius limbatus, Oxypoda longipes*), which indicate an edge effect. Moreover, eight grassland characteristic rove beetle species and three forest character rove beetle species were identified. Principal coordinates analysis (PCoA) based on a Bray-Curtis index of dissimilarity showed that the composition of the assemblages of the forest interior and edge were more similar to each other than to the grassland.

Összefoglalás

Az urbanizáció kedvezőtlen hatásainak megszüntetése vagy enyhítése az egyik legnagyobb kihívás az emberiség számára. Vizsgálatunkban az urbanizáció holyvákra gyakorolt hatását vizsgáltuk Debrecenben és környékén. Három eltérő mértékű emberi zavarásnak kitett terület holyvaegyütteseit hasonlítottuk össze egy urbanizációs grádiens mentén: A (1) természetközeli állapotú erdő nem volt épületek és mesterségesen kialakított úthálózatok által feldarabolva, valamint az emberi zavarás mértéke alacsony volt. A (2) városszéli erdőt föld utak és épületek tagolták, az emberi zavarás mértéke pedig mérsékelt volt. A (3) városi erdős park emberi zavarásnak erősen kitett volt, jelentős részét épületek és aszfaltozott sétányok tagolták. A holyvák fajszáma a természetközeli állapotú erdőben volt a legnagyobb, míg a városi erdős parkban a legalacsonyabb. Az erdei élőhelyekhez kötődő specialista fajok száma szignifikánsan nagyobb volt a természetközeli és kertvárosi erdőkben, mint a városi erdős parkban. Eredményeink megerősítik a növekvő zavarási hipotézist és az élőhely specialista hipotézist, amik szerint a teljes fajszám és az erdei specialisták fajszáma az emberi zavarástól mentes természeközeli állapotú erdőben a legnagyobb. A nedvességkedvelő fajok száma szignifikánsan csökkent, míg a melegkedvelő fajoké növekedett a természetközeli erdőtől a városi parkerdő irányába. A bomló szubsztrátot kedvelő (szaprofág) holyvák fajszáma, a növényi törmeléklakók fajszáma, a gombakedvelők fajszáma és a hangyakedvelő holyvák fajszáma csökkent a zavarás növekedésével. A városi és kertvárosi területek holyvegyütteseinek fajösszetétele jobban hasonlított egymáshoz, mint a természetközeli állapotú erdő holyváinak fajösszetételéhez. Eredményeink azt mutatják, hogy az urbanizáció hatására a természetközeli erdőre jellemző mikroélőhelyek eltűnnek, csökken a mozaikosság és mindez a specialista holyvafajokat érinti a leghátrányosabban.

Őshonos kocsányos tölgyes állományok és telepített, azonos korú őshonos (kocsányos tölgy) és tájidegen (akác, erdeifenyő és vöröstölgy) ültetvények holyvaegyütteseit vizsgáltuk avarrostás mintavétellel. Eredményeink azt mutatják, hogy a holyvák faj- és egyedszáma szignifikánsan kisebb volt az ültetvényekben, mint az őshonos tölgyes állományokban. A holyvák teljes fajszáma nagyobb volt az őshonos ültetvényekben, mint a tájidegen ültetvényekben. A nedvességkedvelő és a bomló anyagokat kedvelő holyvák faj- és egyedszáma szintén szignifikánsan kisebb volt az ültetvényekben, mint az őshonos kocsányos tölgyesben. Továbbá mind a nedvességkedvelő mind pedig a bomló anyagokat kedvelő holyvák faj- és egyedszáma szignifikánsan nagyobb volt az őshonos ültetvényekben, mint a tájidegen ültetvényekben. Az NMDS ordináció (Bray-Curtis hasonlóság függvény alapján) azt mutatta, hogy az őshonos kocsányos tölgy holyvaegyüttese jelentősen elkülönült az ültetvények holyvaegyütteseitől. Eredményeink az mutatták, hogy az

őshonos állományok helyére telepített tájidegen fafajok hatással vannak a talajlakó holyvaegyüttesekre és 40 évvel a tarvágást követően sem képesek regenerálódni. Ugyanakkor fontos megemlíteni, hogy az őshonos fafajokkal történő telepítések megfelelőbb körülményeket biztosítanak a holyvák számára, mint a tájidegen ültetvények. Az erdőkezelések során eltávolított speciális élőhelyek (kidőlt fák, gombák, fészkek) csökkentik a természetes élőhelyek heterogenitását, ami leginkább a ritka, specialista fajok fennmaradását veszélyeztetik.

Az erdőszegélyeknek fontos szerepe van a biodiverzitás fenntartásában. A szegélyhatás hipotézis szerint a biologiai sokféleség az erdőszegélyben nagyobb, mint a szomszédos élőhelyeken. Vizsgálatunk során holyvaegyütteseken teszteltük a szegélyhatás hipotézist talajcsapdás mintavétellel. Három eltérő élőhelytípusban vizsgáltuk a holyvaegyütteseket: (1) Erdő – zárt alföldi tölgyes, vastag avar, lágyszárú és cserjeborítással, valamint 85-95%-os borítottságú lombkorona szinttel. (2) Erdőszegély – cserjés erdőszegély megnövekedett lágyszárú és cserjeborítással. (3) Gyep – közepesen nedves gyep sűrű lágyszárú vegetációval. Eredményeink mutatták, hogy a holyvák egyedszáma az erdőben volt a legnagyobb és a gyepben volt a legkisebb. A holyvák fajszáma az erdőszegélyben volt a legnagyobb, de nem volt szignifikáns különbség az erdő és az erdőszegély holyváinak fajszáma között. A főkoordináta analízis (PCoA, Bray-Curtis hasonlóság függvény alapján) azt mutatta, hogy az erdőszegély és az erdő holyvaegyütteseinek összetétele jobban hasonlított egymásra, mint a gyep holyvaegyüttesére. Az IndVal módszer alapján kimutattunk nyolc nyílt élőhelyhez kötődő és három erdőhöz kötődő karakterfajt. Továbbá nyolc erdőszegélyhez kötődő karakterfajt (*Tasgius winkleri, Falagrioma thoracica, Tasgius melanarius, Olophrum assimile, Platydracus fulvipes, Pella limbatus, Quedius limbatus, Oxypoda longipes*) is kimutattunk, amelyek jelzik a szegélyek holyvaegyütteseket befolyásoló hatását. Eredményeim alapján látható, hogy az erdőszegélyek fontos szerepet játszanak a holyvák sokféleségének megőrzésében, ezért érdemes figyelmet fordítani az intenzív erdőgazdálkodás során létrejövő strukturálatlan, jellegtelen erdőszegélyek heterogenitásának növelésére.

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Appendix

Table A1. Habitat affinity, ecological demands and the trapped number of individuals of the rove beetle species along the urbanization gradient. Notations: R = Rural, S = Suburban, U = Urban, For = Forest species, Hyg = Hygrophilous species, The = Thermophilous species, Sap = Saprophilous species, Phy = Phytodetriticol species, Myc = Mycetophilous species, and Myr = Myrmecophilous species.

Species	Habitat affinity and ecological demands	R	S	U
Abemus chloropterus	For, Hyg	62	115	28
Aleochara erythroptera	Hyg, Myc, Phy	6	1	0
Anotylus rugosus	Hyg, Myc, Phy, Sap	5	1	1
Anthobium atrocephalum	Phy	14	16	11
Astenus immaculatus	Hyg, Phy	1	0	3
Atheta gagatina	Myc, Phy	1	1	9
Atheta sodalist	For, Myc, Phy	0	4	1
Atheta triangulum	Myc, Phy, Sap	4	2	4
Bolitochara bella	Myc	1	0	0
Byraxis curtisii orientalis	Phy	1	2	0
Dropephylla ioptera	For, Hyg, Myc,	0	1	0
Drusilla canaliculata	Phy	1	0	0
Enalodroma hepatica	For	1	0	1
Gabrius osseticus	Hyg, Phy	89	11	5
Geostiba circellaris	Hyg, Myc	3	2	3
Gyrohypnus angustatus	Hyg, Phy	24	58	81
Habrocerus capillaricornis	Myc, Phy	2	3	1
Heterothops dissimilis	Phy	7	1	2
Ilyobates bennetti	Hyg, Phy	13	15	0
Ilyobates nigricollis	For, Hyg, Phy	0	4	1
Lathrobium brunnipes	Hyg, Phy	4	0	0
Lathrobium geminum	Hyg, Phy	14	0	1
Liogluta granigera	Myc, Phy	4	0	0
Liogluta longiuscula	Hyg, Myc, Phy	90	49	20
Mocyta fungi	Hyg, Myc, Phy	6	1	0
Mocyta orbata	Hyg, Myc, Phy	3	1	0
Mycetoporus eppelsheimianus	For, Myc	1	0	2
Mycetoporus erichsonanus	Myc	0	1	0
Mycetoporus forticornis	For, Hyg	0	1	0
Mycetoporus Lepidus	Phy	0	4	0
Mycetota laticollis	Phy	0	0	1
Ocalea badia	Hyg, Phy	2	0	0

Ocypus brunnipes	For, Hyg, Myc, Phy	0	2	6
Ocypus mus	For, Myc	7	40	0
Ocypus nitens	For, Hyg	21	43	1
Oligota pusillima	Myc, Phy	0	1	0
Omalium caesum	Hyg, Myc, Phy	257	277	227
Omalium rivulare	Hyg, Myc, Phy, Sap	142	156	90
Ontholestes haroldi	Phy	73	231	50
Othius punctulatus	For, Phy	16	4	0
Oxypoda abdominalis	Myc, Phy	2	8	0
Oxypoda acuminate	Hyg, Myc, Phy	87	13	22
Oxypoda longipes	Phy	0	1	0
Oxypoda opaca	Myc, Phy	5	0	0
Oxypoda vittata	Myr	30	5	1
Paederus balcanicus	Hyg	0	0	1
Pella laticollis	Myr	10	0	0
Pella lugens	Myr	39	4	1
Pella ruficollis	For, Myr	7	0	0
Philonthus carbonarius	Phy	1	0	0
Philonthus intermedius	Phy, Sap	1	0	0
Philonthus laminates	Myc, Phy, Sap	4	0	0
Philonthus succicola	Myc, Phy	1	0	0
Philonthus tenuicornis	Myc, Phy	0	1	0
Phyllodrepa floralis	Phy	1	0	0
Platydracus fulvipes	For, Hyg	5	14	4
Platystethus cornutus	Hyg	0	1	0
Pselaphus heisei	Phy	0	1	0
Quedius curtipennis	Hyg, Phy	18	4	1
Quedius fuliginosus	Hyg, Phy	2	0	1
Quedius limbatus	For, Hyg, Myc	2	5	0
Quedius longicornis	Hyg	0	0	2
Quedius molochinus	Hyg, Phy	3	0	0
Quedius ochripennis	Phy	0	0	1
Quedius scintillans	Phy	0	1	2
Rugilus rufipes	Hyg, Phy	26	78	24
Sepedophilus marshami	Myc, Phy	2	2	4
Sepedophilus obtusus	Phy, The	0	1	2
Staphylinus erythropterus	For, Hyg	9	0	1
Stenus humilis	Hyg, Phy	2	0	9
Stenus ludyi	For, Hyg, Phy	3	0	2
Stenus ochropus	Hyg, The	0	0	1

Sunius fallax	Phy	0	0	4
Tachinus rufipes	Myc, Sap	10	0	0
Tachyporus formosus	For, Hyg	3	0	0
Tachyporus hypnorum	Hyg, Myc, Phy	0	2	1
Tachyporus nitidulus	Myc, Phy	0	1	0
Tasgius melanarius	Phy	21	5	2
Tasgius morsitans	Phy, The	5	6	16
Tasgius winkleri	Phy	0	0	2
Xantholinus dvoraki	Phy	0	0	1
Xantholinus linearis	Phy	1	0	2
Xantholinus tricolor	For, Phy	53	3	15
Zyras haworthi	Myr, The	1	0	1

Table A2. Ecological demands and the number of individuals of sampled rove beetle species. Notations: BL – black locust plantation, SP – Scots pine plantation, RO – red oak plantation, NO – native oak plantation, M – mature oak forest, h – hygrophilous species; d – decaying material dependent species (* not available information).

Species	Ecological demands	BL	SP	RO	NO	M
Alaobia scapularis		2	0	0	0	0
Aleochara bipustulata	d	0	0	0	1	0
Aleochara lanuginosa	d	1	0	0	0	0
*Amauronyx maerkelii**		0	0	0	0	1
Anthobium atrocephalum	d	0	3	0	4	6
Atheta benickiella		0	0	0	0	1
Atheta gagatina	d	0	2	6	2	2
Atheta ganglbaueri		0	0	1	0	0
Atheta harwoodi	d	0	0	0	0	1
Atheta sodalist		0	0	1	0	0
Atheta voeslauensis		0	0	5	1	0
*Batrisodes adnexus**		0	0	0	0	1
Bolitobius castaneus		1	0	0	1	1
Bolitochara bella	d	0	0	2	1	1
Brachida exigua		0	0	2	0	3
*Bryaxis sp 1.**		0	17	0	0	17
*Bryaxis sp 2.**		2	2	2	0	15
*Bryaxis carinula**		2	8	3	15	18
*Bryaxis curtisii orientalis**		0	9	1	7	13
Dropephylla ioptera	d	0	0	0	0	12
Falagrioma thoracica		0	0	0	0	1
Gabrius osseticus	h, d	19	13	19	44	32
Geostiba circellaris	h, d	0	20	0	4	50
Gyrohypnus angustatus	h	1	1	0	0	2
Gyrophaena fasciata		0	0	0	1	0
Gyrophaena joyi		0	0	1	0	0
Gyrophaena joyioides		0	0	0	0	3
Habrocerus capillaricornis	d	0	0	4	1	12
Heterothops dissimilis	d	11	2	5	19	2
Ischnosoma splendidum	h, d	0	4	0	1	0
Lathrobium geminum	h, d	0	0	0	4	0

Liogluta granigera		0	0	0	0	14
Liogluta longiuscula	h	0	0	0	0	3
Medon fusculus		0	0	0	3	21
Metopsia similis	d	24	28	12	23	15
Mocyta fungi	h, d	1	2	3	20	6
Mocyta negligens		0	0	0	0	1
Mocyta orbata	h, d	3	0	0	3	8
Mycetoporus erichsonanus		0	0	1	0	1
Mycetoporus eppelsheimianus		0	1	2	5	1
Mycetoporus forticornis		0	0	1	0	0
Mycetota laticollis	d	0	0	0	1	0
Ocalea badia	h	0	0	1	1	6
Ocypus mus		0	0	1	0	0
Ocypus nitens	h	3	0	0	0	1
Omalium caesum	h, d	1	1	24	22	35
Omalium oxyacanthae	d	0	0	1	0	0
Omalium rivulare	h, d	0	0	2	0	8
Ontholestes haroldi	d	4	1	3	2	0
Othius punctulatus		0	1	6	2	1
Oxypoda abdominalis		6	0	7	7	1
Oxypoda acuminata	h, d	1	0	4	3	5
Oxypoda flavicornis	h	0	1	1	0	3
Oxypoda opaca	d	0	0	1	1	0
Oxypoda praecox	h	0	9	0	0	0
Pella laticollis		0	0	0	0	33
Pella ruficollis		0	0	0	0	8
Philonthus cognatus	d	1	0	0	0	0
Phyllodrepa melanocephala	d	0	0	0	0	4
Pselaphus heisei		9	54	8	6	26
Quedius curtipennis	h, d	0	0	0	0	1
Quedius fuliginosus	h	0	0	0	0	1
Quedius limbatus	h, d	1	3	6	17	33
Quedius scintillans	d	0	0	1	0	2
Rugilus rufipes	h, d	1	0	3	9	9
Rugilus subtilis	d	2	0	1	1	0
Sepedophilus marshami		5	10	19	28	5
Sepedophilus immaculatus	d	0	0	2	0	0
*Sepedophilus obtusus**		10	3	15	17	0
Sepedophilus pedicularius		44	1	2	0	0

Sepedophilus testaceus		0	0	4	1	1
Scaphium immaculatum		3	2	2	1	0
Scaphidium quadrimaculatum		0	0	1	0	1
Stenus ater	h	1	0	0	0	0
Stenus clavicornis		1	0	0	0	0
Stenus humilis	h	17	8	3	11	0
Stenus ludyi	h	3	7	0	7	1
Stenus ochropus		31	19	3	4	1
Sunius fallax		41	9	11	21	6
Tachinus fimetarius	d	0	0	1	0	1
Tachyporus atriceps		0	8	0	0	2
Tachyporus chrysomelinus	d	0	0	0	1	0
Tachyporus hypnorum	h, d	4	1	5	13	13
Tachyporus nitidulus	d	1	1	2	1	1
Tasgius morsitans		0	0	0	0	1
Thinonoma atra	h	0	0	0	0	1
Xantholinus dvoraki		4	0	0	0	0
Xantholinus linearis	d	2	0	0	0	0
Xantholinus longiventris	h, d	1	0	0	0	0
Xantholinus tricolor		1	1	0	0	0
Zyras collaris	h	0	0	0	1	0
Zyras haworthi		0	0	0	0	1
Total number of species		37	33	47	44	60
Total number of individual		265	252	211	338	476

Table A3. Average values (±SE) of the studied environmental variables.

Environmental variables	Black locust plantation	Scots pine plantation	Red oak plantation	Native oak plantation	Mature oak forest
Canopy cover (%)	55.3 ± 2.9	49.2 ± 3.1	83.8 ± 1.2	70.0 ± 4.7	62.9 ± 7.3
Cover of shrubs (%)	34.3 ± 7.7	36.5 ± 5.6	14.1 ± 4.3	32.2 ± 8.0	50.7 ± 6.0
Cover of herbs (%)	23.3 ± 4.5	15.9 ± 2.1	7.3 ± 2.8	12.6 ± 2.1	12.2 ± 3.3
Cover of leaf litter (%)	87.8 ± 3.2	86.0 ± 5.0	93.1 ± 4.4	92.6 ± 2.7	78.0 ± 5.9
Cover of decaying wood materials (%)	7.2 ± 1.7	10.7 ± 1.2	9.0 ± 1.2	7.7 ± 0.9	14.1 ± 1.6
Soil moisture (%)	6.6 ± 0.6	10.2 ± 1.2	4.0 ± 0.2	7.6 ± 0.5	13.4 ± 0.8
Soil temperature (°C)	17.5 ± 0.1	16.4 ± 0.1	16.1 ± 0.2	16.3 ± 0.1	15.8 ± 0.1
Soil pH	5.1 ± 0.1	4.4 ± 0.0	5.0 ± 0.1	5.0 ± 0.1	5.6 ± 0.2

Table A4. Relationship between the number of rove beetle individuals, species and the studied variables by generalized linear models (GLMs) using the multiple regression design and the forward stepwise model building. Significant negative (–) and significant positive (+) relationships are marked.

		Total no. of individuals	Total no. of species	No. of hygrophilous individuals	No. of hygrophilous species	No. of decaying material dependent individuals	No. of decaying material dependent species
Test of the model	*r*	0.6379	0.6847	0.6541	0.6500	0.6392	0.6619
	F	4.9166	13.534	6.5815	8.2312	6.0808	11.957
	p	<0.001	<0.0001	<0.001	<0.0001	<0.001	<0.0001
	df	6, 43	3, 46	5, 44	4, 45	5, 44	3, 46
Canopy cover (%)		not entered	not entered	not entered	not entered	not entered	not entered
Cover of shrubs (%)		ns	not entered	+*	+*	ns	ns
Cover of herbs (%)		+*	ns	+*	+*	+*	not entered
Cover of leaf litter (%)		not entered	not entered	not entered	not entered	not entered	not entered
Cover of decaying wood materials (%)		ns	not entered	ns	not entered	ns	not entered
Soil moisture (%)		ns	not entered	not entered	not entered	not entered	not entered
Soil temperature (°C)		–**	–***	–***	–***	–***	–***
Soil pH		ns	+***	ns	+*	+*	+***

*: p<0.05, **: p<0.01, ***: p<0.001; ns: not significant; not entered: the variable was not entered into the model.

Table A5. Indicator power of the rove beetle species for the habitats. The IndVal column shows the species indicator value for the corresponding clustering level. In the cells of the table, the first number indicates the number of specimens present, and the second number corresponds to the number of traps where the species was present in this sample group.

Staphylinidae	IndVal	$p < 0.05$	Grassland	Edge	Forest
All habitat					
Ocypus nitens	13.33	NS	2/2	4/4	2/2
Ischnosoma splendidum	10.00	NS	1/1	4/3	2/2
Rabigus pullus	6.67	NS	2/2	0/0	2/2
Paederus littoralis	3.33	NS	1/1	1/1	0/0
Zyras collaris	3.33	NS	1/1	0/0	1/1
Forest					
Oxypoda acuminate	77.48	**	3/3	13/7	99/18
Othius punctulatus	47.50	**	0/0	3/2	19/11
Sepedophilus marshami	30.59	**	0/0	4/4	13/8
Lathrobium brunnipes	15.00	NS	0/0	0/0	6/3
Quedius fuliginosus	15.00	NS	0/0	0/0	4/3
Enalodroma hepatica	11.25	NS	0/0	1/1	3/3
Geostiba circellaris	10.00	NS	0/0	0/0	2/2
Philonthus succicola	10.00	NS	0/0	0/0	3/2
Staphylinus erythropterus	8.33	NS	0/0	1/1	5/2
Atheta gagatina	5.00	NS	0/0	0/0	1/1
Habrocerus capillaricornis	5.00	NS	0/0	0/0	1/1
Lordithon lunulatus	5.00	NS	0/0	0/0	1/1
Mocyta fungi	5.00	NS	0/0	0/0	1/1
Proteinus brachypterus	5.00	NS	0/0	0/0	5/1
Quedius ochripennis	5.00	NS	0/0	0/0	1/1
Sunius fallax	5.00	NS	0/0	0/0	1/1
Tachyusa scitula	5.00	NS	0/0	0/0	1/1
Forest and edge					
Xantholinus tricolor	88.36	**	5/4	47/18	86/20
Omalium caesum	75.92	**	4/3	89/16	60/16
Gabrius osseticus	65.00	**	2/2	31/14	21/14
Anthobium atrocephalum	63.09	**	1/1	29/12	37/14
Omalium rivulare	60.00	**	0/0	25/10	51/14
Ilyobates nigricollis	59.95	**	1/1	25/12	22/13
Rugilus rufipes	58.14	**	3/1	25/11	55/14

Quedius curtipennis	45.00	**	0/0	9/8	11/10
Liogluta longiuscula	40.20	**	1/1	17/8	18/9
Lathrobium geminum	39.46	**	1/1	8/6	18/11
Oxypoda abdominalis	30.00	**	0/0	7/5	14/7
Tasgius morsitans	22.50	**	0/0	10/5	4/4
Anotylus rugifrons	12.50	NS	0/0	3/3	2/2
Oxypoda preacox	12.50	NS	0/0	3/3	2/2
Mycetoporus eppelsheimianus	10.00	NS	0/0	2/2	2/2
Stenus humilis	10.00	NS	0/0	2/2	2/2
Mycetoporus punctus	7.50	NS	0/0	1/1	3/2
Brachygluta fossalata	5.00	NS	0/0	1/1	1/1
Bryoporus cernuus	5.00	NS	0/0	1/1	1/1
Metopsia similis	5.00	NS	0/0	1/1	1/1
Oxypoda vittata	5.00	NS	0/0	1/1	1/1
Edge					
Tasgius winkleri	43.75	**	1/1	14/10	1/1
Falagrioma thoracica	42.65	**	0/0	29/10	5/4
Tasgius melanarius	38.70	**	3/3	19/11	5/3
Olophrum assimile	37.65	**	1/1	16/8	0/0
Platydracus fulvipes	33.75	**	0/0	12/9	4/4
Pella limbatus	30.00	**	0/0	17/6	0/0
Quedius limbatus	20.00	**	0/0	5/4	0/0
Oxypoda longipes	19.44	**	0/0	7/5	2/2
Gyrohypnus angustratus	15.00	NS	0/0	3/3	0/0
Ilyobates bennetti	15.00	NS	0/0	5/3	0/0
Ontholestes haroldi	15.00	NS	0/0	16/3	0/0
Stenus ludyi	15.00	NS	0/0	3/3	0/0
Aleochara erythroptera	5.00	NS	0/0	1/1	0/0
Atheta triangulum	5.00	NS	0/0	1/1	0/0
Bolitochara bella	5.00	NS	0/0	1/1	0/0
Ocalea badia	5.00	NS	0/0	1/1	0/0
Ocypus brunnipes	5.00	NS	0/0	1/1	0/0
Ocypus fuscatus	5.00	NS	0/0	1/1	0/0
Oxypoda opaca	5.00	NS	0/0	1/1	0/0
Oxypoda vicina	5.00	NS	0/0	1/1	0/0
Pella laticollis	5.00	NS	0/0	4/1	0/0
Pella lugens	5.00	NS	0/0	3/1	0/0
Quedius cinctus	5.00	NS	0/0	1/1	0/0
Quedius scintillans	5.00	NS	0/0	1/1	0/0

Xantholinus linearis	5.00	NS	0/0	1/1	0/0
Grassland					
Staphylinus caesareus	94.71	**	163/19	0/0	1/1
Tasgius pedator	47.37	**	18/10	2/2	0/0
Drusilla canaliculata	41.62	**	28/11	15/8	3/2
Dinaraea angustula	25.00	**	7/5	0/0	0/0
Quedius molochinus	24.50	**	7/7	6/5	0/0
Philonthus concinnus	20.00	**	4/4	0/0	0/0
Falagria sulcatula	16.67	**	5/4	2/2	0/0
Philonthus corruscus	15.00	**	3/3	0/0	0/0
Xantholinus longiventris	14.00	NS	7/3	1/1	0/0
Philonthus carbonarius	10.00	NS	2/2	0/0	0/0
Platydracus stercorarius	10.00	NS	2/2	0/0	0/0
Rugilus similis	10.00	NS	2/2	0/0	0/0
Aleochara curtula	7.27	NS	4/2	3/2	0/0
Bisnius spermophilii	5.00	NS	1/1	0/0	0/0
Micropeplus porcatus	5.00	NS	1/1	0/0	0/0
Ontholestes murinus	5.00	NS	1/1	0/0	0/0
Philonthus debilis	5.00	NS	1/1	0/0	0/0
Stenus clavicornis	5.00	NS	1/1	0/0	0/0
Stenus providus	5.00	NS	1/1	0/0	0/0