The associations between ground beetle (Coleoptera: Carabidae) communities and environmental condition in floodplain forests in the Pannonian Basin

JURAJ LITAVSKÝ1, OTO MAJZLAN1, SLAVOMÍR STÁŠIOV2, MAREK SVITOK2, 3 and PETER FEDOR1

1 Department of Environmental Ecology and Landscape Management, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, SK-842 15 Bratislava, Slovakia; e-mails: litavskyjuraj@gmail.com, oto.majzlan@uniba.sk, peter.fedor@uniba.sk
2 Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T.G. Masaryka 24, SK-960 53 Zvolen, Slovakia; e-mails: stasiov@tuzvo.sk, svitok@tuzvo.sk
3 Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

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Abstract. We studied assemblages of carabids in eight similar habitats, five in Slovakia and three in Serbia. The ground beetles were caught by pitfall traps from February 2015 until November 2016. We compared the incidence of Carabidae in floodplain forests and ecosystems alongside the River Danube in Slovakia and the Rivers Tisza and Begej in Serbia. We determined their association with anthropogenic effects, diversity of plants in the different vegetation layers, cover of vegetation layers (herbaceous plants, shrubs and trees), area of forest stands, circumference of forest stands, distance to forest edge, age of forest stands, depth of leaf litter and physico-chemical properties of soil and leaf litter (conductivity, pH, relative content of C, P and N). In total, 2,495 adult individuals of 110 species of carabids were collected. The total epigeic activity of the carabids was significantly and positively associated with the number of species of plants in E3 vegetation layer and the relative content of N, and negatively with the cover of the E1 layer. Species richness was significantly positively associated with the number of species of plants in the E2 layer and the pH of leaf litter, but an opposite trend in evenness.

INTRODUCTION

Currently, there are very few areas of floodplain forests left in Europe. The vast majority have been destroyed and many of the remaining fragments are in a poor condition. According to Abrahámová et al. (2014), they are among the most endangered natural ecosystems in Europe. Therefore, it is important to record the current conditions in these habitats over the widest possible area using important bioindicators such as Carabidae. This was the main reason for studying the alluvial soils of three rivers with analogous habitat characteristics, situated at the same latitude and approximately 400 km apart.

Carabidae are a taxonomically stable and well studied family, which because of their specific life strategies and ecological preferences in terms of humidity, temperature, shading, soil and vegetation (Migliorini et al., 2002; Rainio & Niemelä, 1998; Boháč, 2005; Schwerk, 2008; Vician et al., 2018) are frequently used for monitoring habitats. As the third largest Coleopteran family (Bouchard et al., 2017), with more than 40,000 species globally (Erwin, 1991; Loeve & Sunderland, 1996), carabids occur worldwide, from Arctic and alpine tundras to coastal areas, deserts and rainforests (Lövei & Sunderland, 1996). In various countries in different parts of the Pannonian Basin (Central Europe), ground beetles are abundant, with 619 species recorded in Serbia (Čurčić et al., 2007, 2018; Guéorguiev, 2008; Hlaváč & Magrini, 2016; Pavíc ević et al., 2018), 590 in Slovakia (Zahradník, 2017; Jászay & Jászayová, 2019) and 517 in Hungary (Horvatovich, 1993; Ádám, 1996).

Various insects, including beetles, are widely used to indicate specific habitat characteristics (Bishop et al., 2009), including environmental disturbance (Niemelä et al., 2000; Pearson & Cassola, 2005, 2007; Kaiser et al., 2009; Song et al., 2009; Negro et al., 2010; Vásquez-Vélez et al., 2010; Štefánič & Fedor, 2020), effects of management (Rushton et al., 1990; Jacobs et al., 2010; Kotze et al., 2011; Sklodowska, 2014; Ivanči Porhajašová et al., 2019), restoration (Rothenbücher & Schaefer, 2006; Babin-Fenske & Anand, 2010; Paolletti et al., 2010; Liu et al., 2013), forest fragmentation (Niemelä et al., 1988; Niemelä, 2001; Dubovský et al., 2010; Zvariková et al., 2016) or effects on agricultural ecosystems (Basedow, 1990; Kromp, 1999; Kagawa & Maeto, 2014; Ivanči Porhajašová et al., 2016). Some species of carabids are sensitive indicators of pollu-
tion (Garcia et al., 2010; Ito et al., 2010) and are used in studies on urban ecology (Eyre & Luff, 1990; Venn, 2003) and in ecological assessment.

A number of endangered ground beetles, particularly species of *Abax* Bonelli, 1810, *Badister* Clairville, 1806, *Calosoma* Weber, 1801, *Carabus* Linnaeus, 1758, *Harpa
talus* Latreille, 1802, *Leistus* Frölich, 1799, *Platynus* Bonelli, 1810, *Pterostichus* Bonelli, 1810) and *Trechus* Clairville, 1806 are associated with natural forests (Boháč, 2005), which is an important factor when considering their conservation. There are a lot of studies on ground beetles in conservation. There are a lot of studies on ground beetles in

**MATERIAL AND METHODS**

**Sites studied**

This research was conducted at eight sites located on the alluvial soils of three rivers: the Danube in Slovakia and the Tisza and the Begej in Serbia) in different geographical regions, by analysing environmental parameters, such as anthropogenic effect, plant species diversity and cover of herbaceous plant layer (E), shrub layer (E2) and tree layer (E3), size of area, edge of area, circumference of area, age of trees, depth of leaf litter, pH of the soil and leaf litter, conductivity, content of P, N, C, H in the soil and leaf litter and their association with particular ground beetle communities.

**S1** – located near the overpass at Bajkalská Street (48°8’22.31”N, 17°8’57.03”E, 138 m a.s.l.) is a fragment of floodplain forest of the *Salici-Populetum* association, with a semi-open habitat and a slightly moist microclimate.

**S2** – located in the settlement Malé Pálenisko (48°8’11.54”N, 17°9’14.45”E, 132 m a.s.l.) is a semi-open habitat with a moist microclimate, situated near an old arm of the Danube River, with a fluctuating water level.

**S3** – a shrub–meadow ecotone located in the Dunajské Luhy Protected Landscape Area (48°06’21.13”N, 17°10’10.57”E, 131 m a.s.l.) is at the edge of a floodplain forest, with a medium-deep soil (30–60 cm).

**S4** – is near the waste incinerator in Bratislava (48°6’24.12”N, 17°10’9.68”E, 132 m a.s.l.) and is a semi-open xerothermic habitat on a gravel bar, with a shallow layer of soil (up to 30 cm).

**S5** – a hardwood floodplain forest, with a closed habitat and moist microclimate, located near the Biskupické Rameno oxbow lake (48°06’8.88”N, 17°10’29.77”E, 130 m a.s.l.).

**S6** – a closed habitat with moist microclimate, close to an oxbow lake on the Tisza River (45°22’50.76”N, 20°13’40.83”E, 74 m a.s.l.), which is frequently flooded in spring.

**S7** – a meadow-wetland ecotone located close to the dyke on the Tisza River (45°23’25.07”N, 20°13’16.15”E, 71 m a.s.l.).

The third site in Serbia (S8) is located in the protected area Carška Bara Special Nature Reserve, near the village of Belo Blato, close to the town of Zrenjanin, approximately 20 km from the sites studied along the Tisza River.

**S8** – a hardwood floodplain forest located near the Begej River (45°16’41.60”N, 20°24’58.56”E, 73 m a.s.l.) close to the Stari Begej oxbow lake.

**Fig. 1.** Aerial photograph and map showing the areas studied in the Danube River floodplain forests in Bratislava (Slovakia): S1–S5 – sites studied; AT – Austria; CZ – Czech Republic; HU – Hungary; PL – Poland; UA – Ukraine.

**Fig. 2.** Aerial photograph and map showing the areas studied in the floodplain forests near the Begej and Tisza Rivers (Serbia): S6–S8 – sites studied; AL – Albania; BA – Bosnia and Herzegovina; BG – Bulgaria; HR – Croatia; HU – Hungary; ME – Montenegro; MK – Republic of North Macedonia; RO – Romania.
More detailed information on the vegetation at these sites is presented in Litavský et al. (2018, 2021).

**Methods**

This research was carried out from February 2015 until November 2016. Ground beetles were captured using pitfall traps (Štašiov, 2015) consisting of plastic cups (diameter of opening 9 cm and volume 0.5 l) containing 1% formaldehyde as a fixative. At each site, five traps were set in a line at a distance of 5 m from each other. The traps were operational from February 2015 to November 2016 and emptied and refilled approximately at half-monthly intervals. The contents of the five traps at each site were pooled, which formed the sample for that date. The samples were sorted in the laboratory and the ground beetles subsequently identified to species according to Trautner & Geigenmüller (1987), Hürka (1996) and Müller-Motzfeld (2004). Specimens were fixed in 75% ethyl alcohol and deposited in the collection of the Faculty of Natural Sciences of the Comenius University in Bratislava. A list of species was drawn up following Lorenz (2019). In Table 1, for each species, we added its ecological characteristics. Farkaš et al. (2006) classify carabids into three groups: relict (R), adaptable (A) and eurytopic (E), based on their ecological valence and association with a particular habitat. Following Šustek (2000, 2004a, 2010, 2012), the humidity preferences of ground beetles were classified as either: 1 – strongly xerophilous, 2–3 – intermediate between strongly xerophilous and mesohygrophilous, 4–5 – mesohygrophilous, 6–7 – intermediate between mesohygrophilous and strongly hygrophilous, or 8 – strongly hygrophilous. In terms of dispersal ability, species were divided into three groups: (i) non-flying, (ii) flying and (iii) brachypterous, which occasionally fly (Hürka, 1992, 1996; Matalin, 2003; Šustek, 2012).

Samples of soil and leaf litter for chemical analyses were collected on June 8th 2016. More detailed information on the methods of analysis of the soil and leaf litter samples is given in Litavský et al. (2018, 2021).

We defined four levels of anthropogenic effect on the study area: level 1 – with minimum disturbance; level 2 – with grazing; level 3 – with infrequent movement of vehicles and minor solid waste pollution; level 4 – with solid waste pollution, frequent mowing and cutting and building activities.

Of the environmental factors that could affect the composition of carabid communities, we recorded species richness in individual layers, stand canopy of individual layers, anthropogenic effect, area of fragment, distance from another fragment (edge), length of the periphery of the fragment, age of trees at the sites and average depth of leaf litter, which are presented in Litavský et al. (2018, 2021).

During the vegetation period, we recorded plant species diversity in three vegetation layers (E1, E2, E3), as well as the covers of the tree, shrub and herbaceous plant layers, in both countries and within sites of constant size (400 m²). More information on the method of investigation of the vegetation is given in Litavský et al. (2021).

**Data analysis**

We calculated the diversity of the carabid communities in terms of species richness, Shannon diversity (Spellerberg & Fedor, 2003) and evenness (Jost, 2006; Tuominen, 2012; Fedor & Zvaříková, 2018). Species epigeic activity was the mean number of individuals caught per trap per day. Carabid community composition is summarized in the species-by-site matrix of epigeic activities.

Due to the relatively low number of sites sampled and the high number of environmental variables, we did not build models describing diversity and species composition, but adopted an exploratory approach and investigated all species-environment associations.

In order to investigate the diversity characteristics of communities (total epigeic activity, species richness, Shannon diversity and evenness), we produced a matrix of pairwise Spearman’s correlation coefficients between environmental variables and the diversity characteristics.

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance was used to visualize similarities in the composition of carabid communities. The vectors of environmental variables were projected onto ordinations in the directions of their maximum correlations with the configuration of sites. The statistical significance of fitted environmental vectors was evaluated using permutation tests (10,000 permutations).

This exploratory approach allowed us to investigate all species-environment associations without the risk of missing any important information caused, e.g., by the removal of highly correlated variables. Indeed, the results of such a heuristic analysis should be considered carefully and regarded as a process for generating hypotheses rather than a generalization to wider populations.

The analyses were performed in R (R Core Team, 2016) using the Hmisc (Harrell, 2016) and the Vegan libraries (Oksanen et al., 2016).

**RESULTS AND DISCUSSION**

During this research, a total of 2,495 adult carabids belonging to 22 tribes, 48 genera and 110 species were recorded. Seventy-nine species of ground beetles are recorded at the sites in Slovakia and 58 species at those in Serbia (Majzlan & Litavský, 2017), with 27 of the species occurring in both countries. The values of the total epigeic activity of ground beetles captured at individual sites during this research are shown in Table 1. The most abundant species was *Agonum fuliginosum* (Panzer, 1809) (487 adults recorded), which was recorded most abundantly near the oxbow lake on the Danube River (Biskupické Rameno) (55). The other dominant species were *Nebria brevicollis* (Fabricius, 1792) (247 adults), *Abax parallelepipedus* (Piller & Mitterpacher, 1873) (185 adults), *Carabus granulatus* Linneaus, 1758 (125 adults), *Pterostichus niger* (Schaller, 1783) (117 adults), *Patrobus atrorufus* (Strom, 1768) (114 adults), *Pterostichus melanarius* (Illiger, 1798) (108 adults), *Carabus coriaceus* Linneaus, 1758 (105 adults) and *Agonum micans* (Nicolai, 1822) (102 adults). No species was recorded at all the sites studied. The largest number of adult individuals was recorded at site S2 (967), which is a semi-open habitat with a moist microclimate and where the highest species richness of ground beetles was recorded (38 species). The lowest species richness of carabids was recorded at S4, which is a semi-open xerothermic habitat (23 species). In addition, we divided the ground beetles into different groups according to several criteria (Table 1). Based on their ecological valence and association with a particular habitat, we recorded 10 relict, 38 eurytopic and 62 adaptable species of carabids. In terms of their humidity preferences 24 were strongly xerophilous, 39 mesohygrophilous and 47 strongly hygrophilous species. With regard to their ability to fly, we recorded 20 brachypterous species that occasionally fly, 20 non-flying species and 70 species of ground beetles capable of flying.
Table 1. A list of the species of carabids collected, the total numbers of specimens and species, diversity measures of carabid communities recorded at the sites studied and their division according to ecological characteristics: Abbr. – abbreviations; * – published in Majzlan & Litavský (2017); EV – ecological valence of carabids and their association with habitats; R (relict), A (adaptable), E (eurytopic); HP – humidity preferences of carabids recorded: 1 – strongly xerophilous, 2–3 – intermediate between strongly xerophilous and mesohygrophilous, 4–5 – mesohygrophilous, 5–7 – intermediate between mesohygrophilous and strongly hygrophilous, 6 – strongly hygrophilous; FL – ability to fly: F (flying), N (non-flying), B (brachypterous, occasionally able to fly).
The associations between diversity characteristics and environmental variables were evaluated using correlation analysis. The total epigeic activity of carabids was significantly and positively associated with the number of species of plants in the E3 layer and pH of the leaf litter, while the trend in evenness was exactly the opposite. Analysis. The total epigeic activity of carabids was significantly and positively associated with the number of species of plants in the E3 layer and the pH of the leaf litter, while the trend in evenness was exactly the opposite. The results of our two-year research indicate that the floodplain forests and their ecotones alongside the Danube, the Tisza and the Begej Rivers provided appropriate conditions for ground beetle communities, based on their high species richness. Šustek (1994b) states that about 25–35 species of carabids are usually present at any one time at one locality under natural conditions, but in the best conserved floodplain forests the number of carabid species exceeds 40. We recorded the highest number of carabid species at S2 (38 species), S5 (36 species) and S6 (36 species) typical of stands with low treediversity. The most active carabid species, Trechus quadristriatus (Herbst, 1768) and Calathus melanocephalus (Linnaeus, 1758) and C. coriaceus were typical of stands with low leaf litter pHs. Agonum micans, A. fuliginosum, Platynus assimilis (Paykull, 1790), Acupalpus flavicollicus (Sturm, 1825), Dyschirus globosus (Herbst, 1784) P. atrorufus, Platynus rufus (Duftschmid, 1812) and N. brevicollis preferred fragments with high number of species of plants in the E3 vegetation layer.

Table 1 (continued).

| Species | Abbr. | EV | HP | FL | Sites | S1 | S2 | S3 | S4 | S5 | S6* | S7* | S8* |
|---------|-------|----|----|----|-------|----|----|----|----|----|-----|-----|-----|
| Harpalus latus (Linnaeus, 1758) | Hala | A | 4 | F | 1 | 1 | 6 | 4 | 8 | 0 | 0 | 0 | 20 |
| Harpalus rufipes (De Geer, 1774) | Haru | E | 4 | F | 1 | 0 | 2 | 3 | 37 | 3 | 5 | 0 | 51 |
| Laemostenus punctatus (Dejean, 1828) | Latepu | A | 4 | N | 0 | 0 | 0 | 0 | 12 | 0 | 3 | 0 | 15 |
| Leistus ferrugineus (Linnaeus, 1758) | Lefe | E | 4 | F | 0 | 0 | 0 | 0 | 4 | 0 | 3 | 0 | 8 |
| Leistus piceus Frölich, 1799 | Lepi | A | 6 | B | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 5 |
| Leistus rufomarginatus (Duftschmid, 1812) | Leru | R | 5 | F | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Loricera pilicornis (Fabricius, 1775) | Lopi | A | 4 | F | 1 | 2 | 0 | 0 | 0 | 5 | 8 | 0 | 2 |
| Myleostes maurus (Sturm, 1827) | Mima | E | 2 | B | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| Molops piceus (Panzer, 1793) | Mopi | A | 4 | N | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 2 |
| Nebria brevicollis (Fabricius, 1792) | Nebr | A | 6 | F | 3 | 218 | 0 | 0 | 15 | 5 | 0 | 6 | 247 |
| Neolithus bifigitus (Fabricius, 1775) | Nobi | A | 4 | B | 1 | 3 | 2 | 0 | 3 | 0 | 0 | 0 | 9 |
| Neolithus palustris (Duftschmid, 1812) | Nopa | E | 4 | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Oodes helioioides (Fabricius, 1792) | Oohe | A | 6 | F | 3 | 218 | 0 | 0 | 15 | 5 | 0 | 6 | 247 |
| Ophonus azureus (Fabricius, 1775) | Opaz | E | 2 | F | 0 | 0 | 0 | 0 | 1 | 37 | 0 | 0 | 38 |
| Ophonus puncticollis (Paykull, 1798) | Oppu | A | 7 | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Oxybelus obscurus (Herbst, 1784) | Oxob | A | 7 | B | 4 | 1 | 4 | 2 | 5 | 42 | 0 | 0 | 58 |
| Paradromius linears (Olivier, 1795) | Pali | E | 2 | B | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 3 |
| Patrobus atraurus (Strem, 1678) | Paat | A | 7 | B | 0 | 85 | 3 | 0 | 0 | 20 | 6 | 0 | 114 |
| Platyderus rufus (Duftschmid, 1812) | Plru | A | 3 | N | 1 | 37 | 0 | 3 | 2 | 8 | 0 | 0 | 51 |
| Platynus assimilis (Paykull, 1790) | Plas | A | 7 | F | 2 | 14 | 0 | 0 | 46 | 0 | 0 | 62 |
| Platynus livens (Gyllenhal, 1810) | Plii | R | 8 | F | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Poecilus cupreus (Linnaeus, 1758) | Pocu | E | 4 | F | 0 | 6 | 0 | 12 | 0 | 0 | 0 | 0 | 18 |
| Pterostichus arhacicus (Illiger, 1798) | Ptra | A | 8 | B | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Pterostichus macer (Marshaw, 1832) | Ptmr | A | 4 | F | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Pterostichus melanarius (Illiger, 1798) | Ptmn | E | 5 | B | 11 | 59 | 5 | 0 | 4 | 28 | 1 | 0 | 108 |
| Pterostichus niger (Schaller, 1783) | Ptni | A | 6 | F | 14 | 42 | 0 | 0 | 30 | 30 | 0 | 11 | 1758 |
| Pterostichus nigritus (Paykull, 1790) | Ptngr | E | 8 | B | 5 | 22 | 0 | 0 | 21 | 0 | 0 | 0 | 26 |
| Pterostichus oblongopunctatus (Fabricius, 1787) | Ptbp | A | 5 | N | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Pterostichus strenuus (Panzer, 1796) | Pstt | A | 7 | B | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| Pterostichus vermicus (Panzer, 1796) | Ptvm | A | 8 | B | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| Stenolophus hisutus (Herbst, 1794) | Sthi | A | 8 | F | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Stenolophus skirshmainius Stephens, 1828 | Stski | A | 4 | F | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Symotus obscuroguttatus (Duftschmid, 1812) | Syob | A | 5 | F | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| Symotus pallipes Dejean, 1825 | Sypa | A | 5 | B | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| Tachys bicinctus (Duftschmid, 1812) | Tabi | A | 8 | N | 5 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Tachys ausstriacus Dejean, 1831 | Trau | E | 5 | B | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Trechus pulchellus Putzeys, 1845 | Trpu | A | 5 | N | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Trechus quadriradiatus (Schrank, 1781) | Trqu | E | 4 | F | 0 | 4 | 0 | 0 | 0 | 3 | 5 | 7 | 19 |
| Shannon diversity index | 2.316 2.165 2.829 2.829 2.711 2.516 2.477 2.876 |
| Evenness | 0.739 0.595 0.868 0.902 0.756 0.714 0.779 0.905 |
that we recorded a higher total species richness of carabid communities and environmental variables recorded at the sites studied in Slovakia and Serbia: s – soil; l – leaf litter; E1, E2, E3 [%] – canopy of individual vegetation layers; Σ species (E1, E2, E3) – species richness of individual vegetation layers; pHH2O – acidity of the supernatant of a suspension of soil and H2O (ratio 1:2.5); k [mS.cm–1] – conductivity of H2O extract (P – phosphorus; N – nitrogen; C – carbon; H – hydrogen. Statistically significant correlations (α = 5%) are highlighted in bold.

| Environmental variable | Epigeic activity | Species richness | Shannon diversity index | Evenness |
|------------------------|------------------|-----------------|-------------------------|---------|
| Anthropological effect  | 0.01             | −0.19           | −0.59                   | −0.26   |
| E1 [%]                 | −0.75            | −0.55           | 0.12                    | 0.51    |
| E2 [%]                 | 0.61             | 0.69            | −0.25                   | −0.51   |
| E3 [%]                 | 0.25             | 0.07            | −0.05                   | −0.22   |
| Σ species (E1)         | −0.49            | −0.12           | 0.23                    | 0.42    |
| Σ species (E2)         | −0.54            | −0.32           | 0.02                    | 0.02    |
| Σ species (E3)         | 0.84             | 0.82            | −0.33                   | −0.71   |
| Area [m²]              | 0.14             | 0.06            | 0.19                    | 0.05    |
| Edge of area [m]       | −0.17            | −0.22           | 0.38                    | 0.19    |
| Circuit of area [m]    | 0.12             | −0.17           | 0.12                    | 0.17    |
| Age [year]             | 0.66             | 0.40            | −0.56                   | −0.66   |
| Leaf litter depth [cm] | 0.60             | 0.42            | −0.16                   | −0.49   |
| pHH2O/l               | −0.27            | 0.16            | −0.10                   | −0.05   |
| pHH2O/s               | 0.56             | 0.75            | 0.44                    | 0.73    |
| k [mS.cm–1]/s         | 0.48             | 0.28            | −0.26                   | −0.21   |
| k [mS.cm–1]/l         | 0.05             | −0.27           | −0.17                   | 0.26    |
| P [mg.kg–1]/s         | 0.07             | −0.14           | −0.10                   | 0.14    |
| P [mg.kg–1]/l         | −0.06            | −0.48           | 0.00                    | 0.38    |
| N [%]/s               | 0.54             | 0.19            | −0.06                   | −0.30   |
| N [%]/l               | 0.71             | 0.60            | −0.38                   | −0.52   |
| C [%]/s               | 0.60             | 0.53            | −0.45                   | −0.69   |
| C [%]/l               | −0.21            | −0.58           | −0.10                   | 0.14    |
| H [%]/s               | 0.62             | 0.16            | −0.19                   | −0.24   |
| H [%]/l               | 0.00             | −0.31           | 0.14                    | 0.14    |

There was a statistically significant negative association between total epigeic activity of ground beetles and the cover of the herbaceous plant layer (E1). This can be explained by the fact that density of vegetation, especially that of the herbaceous plant layer, can affect predator activity (the majority of carabids), by making it difficult for them to move on the surface of the soil. The decrease in epigeic activity of soil-dwelling beetles with increase in the density of vegetation is also reported by Heydemann (1957), Honek (1988), Humphrey et al. (1999) and Thomas et al. (2006). For example, Honek (1988) reports that some staphylinids and most species of carabids prefer sparse rather than dense stands. Zou et al. (2013), however, report that the density of herbaceous plants had little effect on the beetle activity in the Changbai Mountains.

The significant positive association between both total epigeic activity and species richness of ground beetles, and plant species richness in the E1 vegetation layer is probably due to the longer period of shading (earlier budding of different species of trees and late leaf fall), which ensure more stable and humid microclimatic conditions for a longer period, as well as a greater food supply as a high tree diversity results in a richer leaf litter. Pearce et al. (2003) also point out that some ground beetles may also benefit from increased tree species richness. Vehviläinen et al. (2008) confirm that carabids differ significantly in their preferences for stands composed of particular, yet different, species of trees. During a study of the effects of river and floodplain restoration on riparian ground beetles, Januschke & Verdonschot (2016) revealed that the

Table 2. Matrix of Spearman correlation coefficients between sum of the diversity characteristics of carabid communities and environmental variables recorded at the sites studied in Slovakia and Serbia: s – soil; l – leaf litter; E1, E2, E3 [%] – canopy of individual vegetation layers; Σ species (E1, E2, E3) – species richness of individual vegetation layers; pHH2O – acidity of the supernatant of a suspension of soil and H2O (ratio 1:2.5); k [mS.cm–1] – conductivity of H2O extract (P – phosphorus; N – nitrogen; C – carbon; H – hydrogen. Statistically significant correlations (α = 5%) are highlighted in bold.

Fig. 3. Two-dimensional component of a non-metric multidimensional scaling (NMDS) of carabid communities recorded at the sites studied in Slovakia and Serbia, based on Bray-Curtis distances of epigeic activities. The vectors of significant environmental variables are fitted onto the ordination in the direction of their maximum correlation with site scores. The scores of the most active species were added as the weighted averages of site scores. Final stress value is displayed. S1–S8 – sites studied; Σ species (Ei) – number of species of plants in Ei vegetation layer; pHH2O/l – acidity of the supernatant of a suspension of leaf litter and H2O (ratio 1:2.5). For abbreviations of species names see Table 1.
encroachment of woody vegetation results in a decrease in species richness of carabid beetles. According to Šustek (2005), carabid communities in forest ecosystems consist of heliophobic species that prefer areas shaded by trees or at least by dense shrub vegetation. It is cooler in the shade, which slows down the drying out of the surface of the soils and leaf litter, reduces evaporation and improves the water balance in the stand. For this reason, the association of individual species with the presence of tree cover are to some extent positively associated directly with the species’ moisture requirements.

In addition to the effect of plants, ground beetle communities are also affected by properties of the soil and leaf litter. Nitrogen is an essential element for organisms. This is supported by the statistically significant positive associations between the total epigeic activity of carabids and the nitrogen content of leaf litter. The nitrogen content of the leaf litter may indirectly affect (through saprophagous prey of ground beetles) the food supply of carabid beetles. Leaf litter rich in N is an attractive food for saprophages that use the nitrogen in their own physiological processes (Vician et al., 2018). Therefore, this material decomposes more rapidly due to the activity of saprophages (Wittich, 1942, 1943). Dunger (1958) stresses the importance of nitrogen as the main element determining animal production and sources of food for invertebrates, including ground beetles. Vician et al. (2018) also report statistically significant associations between the content of N in the leaf litter and species richness, Shannon diversity and species composition of carabid beetle communities at nine stands in the Borová Hora Arboretum (Central Slovakia).

The composition of carabid beetle communities was also associated with the pH of the leaf litter, with a significant positive association between species richness of ground beetles and leaf litter pH, but the opposite trend in species evenness (Table 2). Vician et al. (2018) note that a floodplain forest in which leaf litter had a high pH also had a high species richness of ground beetles. Magura et al. (2003) also point out that leaf litter has a positive effect on carabid species richness.

Most studies on marshes and floodplain forests record mainly hygrophilous and mesohygrophilous species of ground beetles (Šustek, 1994a, e, 2004b; Šejnohová, 2006; Lik, 2010; Igondová & Majzlan, 2015). In the current study, there was also a predominance of hygrophilous and mesohygrophilous over xerophilous species of ground beetles, with hygrophilous species making up 42.7%, mesohygrophilous 35.5% and xerophilous 21.8%, i.e., a ratio of 2 : 1.6 : 1, respectively.

In terms of the carabids’ ecological valence and their association with a particular habitat, most (62) (56.4%) were adaptable, 38 (34.5%) were eurytopic and 10 (9.1%) were relict species. Relict species of carabid were mostly recorded near the oxbow lakes on the Danube (S5), the Tisza (S6) and the Begej Rivers (S8). This indicates these forest stands are ecologically stable. In comparison, Igondová & Majzlan (2015) did not record any relict species of ground beetles in the carabid communities during a one-year study of the Šuja peat bog (northern Slovakia). In relation to their ability to fly, of the species of carabid recorded (70) (63.6%) were able to fly, 20 (18.2%) were brachypterous and occasionally fly, and 20 (18.2%) were non-flying. Arndt & Hielscher (2007) conclude that most species of forest ground beetles are unable to fly or do not regularly fly. Šustek (2012) state that species of carabids that inhabit unstable riparian habitats are able to fly and successfully colonize anthropogenic ecosystems, such as arable land or vegetation in human settlements. Nevertheless, up to 70% of the species we recorded were able to fly and were present in closed forest stands that were mostly little or unaffected by human activity.

We determined how ground beetle communities vary in the different habitats in floodplain forests in Serbia and Slovakia and found that the total epigeic activity of carabids was significantly positively associated with the number of species of plants in the tree layer and the relative content of N in the leaf litter, and negatively with the cover of the herbaceous plant layer. Species richness was significantly positively associated with the number of species of plants in the tree layer and pH of the leaf litter, while evenness showed the opposite trend. Based on these results (Fig. 3), we selected several species of carabids, which can serve as bioindicators. We conclude that A. micans, A. fuliginosum, P. assimilis, A. flavicollis, D. globosus, P. atrorufus, P. rufus and N. brevicollis, which prefer forest stands with a high number of species of plants in the tree layer, can be used as bioindicators of the presence of high tree species richness in floodplain forests. We also found that T. quadriradiatus, O. azureus, C. melanoecephalus and C. coriaceus preferred stands in which the pH of the leaf litter is low and could be used as bioindicators for assessing changes in landscape structure caused by human activity resulting in soil acidification. Therefore, more information on these associations might be helpful in further elucidating how carabids respond to vegetation, soil and microclimatic conditions, and how these conditions vary in the various types of floodplain forests.

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