Terrestrial isopods and myriapods in a forested scree slope: subterranean biodiversity, depth gradient and annual dynamics

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ABSTRACT
Diversity, depth distribution and seasonal activity of isopods and myriapods were studied using subterranean traps buried in a forested limestone scree slope in the Čierna Hora Mts, Western Carpathians, Slovakia, throughout the depth gradient from 5 to 95 cm. A total of five isopod, 13 diplopod and 11 chilopod species were identified. Most edaphic species strongly preferred the uppermost organic soil layers. Among the species captured, some represented rare stenoecous Carpathian endemics, namely the isopod Trichoniscus carpaticus, and diplopods Julus curvicornis and Leptoiulus mariae. Others were subterranean forms, partly adapted to hypogean conditions: the isopod Mesoniscus graniger, and diplopods Mecogonopodium carpathicum and Trachysphaera costata. The annual activity in the vast majority of the species ceased completely in winter, and was gradually relaunched in spring. In evaluating the age structure of two predominant diplopods Polydesmus denticulatus and Mecogonopodium carpathicum, both widespread across the depth gradient, a vertical segregation of early post-embryonic stages was found. While P. denticulatus tended to undergo the early stages of development in the soil-filled topmost levels, the early juvenile stage of M. carpathicum was distributed deep in the scree slope profile.

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Introduction
Underneath the ground surface, there are a variety of subterranean habitats differing in depth and size of space. In general, we can distinguish soil interstices with dimensions comparable to the body size of organisms and spacious caves extending to a depth of several tens of metres (Vandel 1965; Culver and Pipan 2009). In addition, there is another category of intermediate subterranean habitats with a depth of less than 10 m and spaces large enough for inhabiting fauna not to be in contact with a solid surface. They have the common name of shallow subterranean habitats (SSH) and include epikarstic crevices, fissured rocks, alluvial sediments and scree slopes (Culver and Pipan 2014). Like caves, SSH are aphotic and they may be colonised by fauna adapted to subterranean life.
(troglobionts and troglophiles). The SSH share with soil the occurrence of edaphobionts and have a better availability of nutrients (Culver and Pipan 2008).

In central Europe, scree slopes represent mostly isolated ‘island’ formations resulting, in most cases, from frost weathering of originally compact rocks. The living conditions inside stony accumulations strongly depend on exposure, stabilisation by soil, and the above-growing vegetation (Růžička 1993; Růžička et al. 2012). Forested scree slopes are characterised by a favourable microclimate throughout the whole profile (Růžička 1990) and their inner spaces represent a peculiar type of subterranean habitat known as mesovoid shallow substratum (MSS) (Juberthie et al. 1980). The MSS comprises a network of heterogeneous voids within the rocky accumulation between the base of the soil and bedrock, and is generally situated in the lower levels of scree slopes. The soil cover on scree acts as a buffer of external variations, resulting in low temperature extremes and high relative humidity (Juberthie 2000; Juberthie and Decu 2004; Giachino and Vailati 2010).

Most of what we know about isopods and myriapods in the scree habitats comes from ecological and taxonomic studies. Borges (1993) referred to the occurrence of diplopods and chilopods in the volcanic MSS in the Azores at a depth of 80 cm. A series of studies was later conducted in the Romanian Carpathians to compare species diversity among various types of MSS as well as the adjacent habitats. The MSS sites covered with a thick layer of soil and decaying remnants of vegetation were characterised by a considerable abundance of Chilopoda. At the same time, this type of MSS harboured several large edaphic species and strictly subterranean species recorded before only in the caves (Ilie 2003a, 2003b). Several species of Isopoda and Diplopoda were common to both ‘colluvial’ (rock material accumulated at the base of a cliff or slope) and ‘cletric’ (fr. clétrique = system of fissures and cracks in the bedrock) MSS while others proved to be constant in a particular type (Nitzu et al. 2010). Similarly, some isopods and diplopods showed a high affinity to MSS when comparing the species richness with that of the soil layer above (Nitzu et al. 2011). Vertical distribution of Diplopoda and Chilopoda was investigated in several scree habitats in the Austrian Alps, with both taxa being most abundant near the soil surface (Querner and Greben-Krenn 2005). Tuf et al. (2008) found that isopod assemblages differed considerably among a cave system, surrounding scree slope, and above-ground karst habitats in north-eastern Moravia (Czech Republic). Recent studies have pointed to the exceptional diversity of diplopods at several MSS sites in the Iberian Peninsula, associated not only with the discovery of new species, but also with the findings of previously poorly known taxa often limited to specific caves (Enghoff and Reboleira 2013; Gilgado et al. 2015a, 2015b).

The objectives of the present study were as follows: (1) to reveal the diversity and distribution patterns of Isopoda, Diplopoda and Chilopoda along the depth profile of a forested scree slope in the Western Carpathians; (2) to assess the annual activity of dominant species; and (3) to characterise the age structure and depth distribution of two predominant diplopods, *Mecogonopodium carpathicum* and *Polydesmus denticulatus*.

**Material and methods**

**Study site**

The study was carried out in the approximately 5-km-long Malý Ružínok Valley (Sivec National Reserve), forming a part of the Čierna Hora Mts, a small karst area
situated in the Western Carpathians (Slovakia). An extensive massif of Mesozoic limestones with several shallow caves and steep forested scree slopes are peculiar to this site. The study stand (48°50′31″N, 21°06′34″E) was selected in the foothill of the rock cliff, a few metres below the top of the scree slope, with *Tilio-Aceretum* forest association, on a 10–25° slope facing northeast at an altitude 530 m above sea level. The scree material was covered with Holocene rendzina (classification of soil type after Food and Agriculture Organization of the United Nations – FAO), and the herbal growth formed by *Asplenium alternifolium*, *Dentaria* sp., *Lamium* sp., *Mercurialis perennis*, *Urtica dioica*, young seedlings of *Sambucus* sp. and ferns. There were three distinct layers in the scree slope profile: leaf litter and humus (0–15 cm), and organo-mineral layer (15–45 cm) clearly separated from scree (45–110 cm). The scree with spaces slightly filled up with soil was composed of rocks varying from 10 to 15 cm in diameter. The temperature regime inside the slope was characterised by thermal fluctuations synchronised with microclimate dynamics on the soil surface. The average annual temperature (measured from October 2008 to November 2009) on the soil surface was 7.9°C. It increased with depth and at 95 cm reached a value of 9.3°C (Rendoš et al. 2012).

**Sampling and species identification**

The specimens were collected with a set of three subterranean traps (Schlick-Steiner and Steiner 2000). Each trap consisted of a plastic cylinder (length 110 cm, diameter 10.5 cm) with openings (diameter 0.8 cm) drilled around at 10 horizontal levels (5, 15, 25–95 cm), and a system of 10 plastic cups (volume 500 ml) attached to each other by a central helical rod and nuts. A pit, approximately 200 × 40 cm in size and over 100 cm deep, was dug at the study site, and the soil and stones of the particular layers were carefully separated. Three plastic cylinders were vertically placed into the pit (50 cm apart) and filled with the dug-out material in the original order of the layers. Subsequently, the system of plastic cups was inserted in each of the buried cylinders; the position of the cups corresponded to the openings on the cylinder parameter. The top of the buried subterranean trap was covered with a plastic lid. During the investigation, two types of preservatives were used: 4% formaldehyde (November 2008–November 2009) and 50% ethylene glycol (November 2009–July 2010). The formaldehyde traps were emptied monthly so that changes in locomotory activity could be recorded. The ethylene glycol traps were emptied twice, in May and July 2010. To remove the captured specimens, the system of plastic cups was pulled out of the cylinder and the individual cups were gradually dismounted from one another. The contents of the cups were then poured into plastic bottles, transported to the laboratory and fixed in 75% ethyl-alcohol. The specimens of Isopoda, Diplopoda and Chilopoda were identified to the species using a stereo microscope and determination keys on European fauna. The nomenclature follows Schmalfuss (2003), Enghoff and Kime (2013) and Bonato et al. (2016). The determination of the post-embryonic development stage of the two predominant diplopods *Mecogonopodium carpathicum* and *Polydesmus denticulatus*, used for analysis of the population age structure, was performed by counting limb pairs and pleurotergites following the typical formula for the millipede orders Chordeumatida and Polydesmida (Enghoff et al. 1993): *M. carpathicum* matures at stage
IX after eight cuticle moultings, while *P. denticulatus* undergoes seven moultings and reaches maturity at the stage VIII.

**Statistical analysis**

Nonparametric Spearman’s correlation coefficient \((r_s)\) with a level of significance of \(p = 0.05\) was applied to test the relationship between the depth gradient and quantity (expressed as the number of individuals captured) of particular taxa. The STATISTICA 12.0 software package (StatSoft, Inc. 2013) was used for the analysis. Non-metric multi-dimensional scaling ordination analysis (NMS) using PC-ORD software (McCune and Mefford 2011) was performed to examine the similarity of species communities for the investigated arthropod taxa at different depths. In the NMS analysis, only individuals collected in the periods November 2008 to July 2009 (formaldehyde traps) and November 2009 to July 2010 (ethylene glycol traps) are included. To minimise outlier influence, the means per pitfall trap were logarithmically transformed [\(\ln(x + 1)\)]. Species with total occurrence \(\leq 3\) specimens were arbitrarily excluded from the analysis. For the community data, an autopilot with slow and thorough mode and Sørensen (Bray-Curtis) distance was used. After randomisation runs, a two-dimensional solution was accepted as optimal.

**Results**

**Diversity and depth distribution**

A total of 95 individuals of terrestrial Isopoda, two individuals of Symphyla, four individuals of Pauropoda, 979 individuals of Diplopoda and 123 individuals of Chilopoda were captured along the depth gradient. Altogether, five species of isopods, 13 species of diploponds and 11 species of chilopods were identified (Table 1).

The vertical distribution varied considerably among the taxa investigated. There was no significant correlation between activity of Isopoda and depth \((r_s = -0.55, N = 10, p > 0.05)\). Three vertical zones were typical of the distribution of this group: depth 5 cm (the level with the highest number of isopods), depth range 25 to 45 cm, and depth 65 cm. In other levels, solitary individuals were observed (Figure 1). On the other hand, the numbers of Diplopoda and Chilopoda correlated negatively with increasing depth \((r_s = -0.81, p = 0.05, N = 10\) and \(r_s = -0.77, p = 0.05, N = 10\), respectively). Diplopods were the most numerous at a depth of 35 cm below the surface. This was particularly due to the high aggregation of juveniles of *Polydesmus denticulatus* (417 ind.) captured in the ethylene glycol traps during the second collecting period. Apart from this extreme value, the activity of Diplopoda gradually declined with depth, except at 65 and 85 cm where a slight increase was observed. The chilopods were most abundant at a depth of 5 cm. Deeper, the numbers declined sharply. The decrease continued up to 45 cm, and, at the bottom of the vertical gradient, a slight fluctuation in the number of individuals was noticeable.

No significant correlation was found between particular species and depth. The data were subsequently analysed by NMS ordination (Figure 2). A two-dimensional solution was recommended by Autopilot and confirmed by the Monte Carlo permutation test,
Table 1. Terrestrial isopods and myriapods captured in the subterranean traps; I – first sampling period (November 2008–November 2009), II – second sampling period (November 2009–July 2010), ♂ – male, ♀ – female, nd – not indentified. The specimen numbers stated for a particular depth are the sum of the two sampling periods. “Lithobius sp. juv.” was not included in total species richness (due to immaturity of individuals, we were unable to identify to which particular species of the genus they belonged).

| Species | Depth (cm) | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | I | II | I+II | Adults (%) | ♀ (% of adults) |
|---------|------------|---|----|----|----|----|----|----|----|----|----|----|----|-----|-----------|----------------|
| **Isopoda** | Lepidoniscus minutus (Koch) | 1 | 1 | 2 | 2 | 2 | 50 | 100 | 36 | 1 | 1 | 1 | 1 | 1 | 100 | 100 |
| | Ligidium germanicum Verhoeff | 36 | 1 | 10 | 27 | 37 | 87 | 22 | 25 | 1 | 1 | 1 | 1 | 1 | 22 | 22 |
| | Ligidium hypnorum (Cuvier) | 2 | 2 | 2 | 2 | 100 | 100 | 27 | 27 | 27 | 27 | 27 | 27 | 27 | 27 |
| | Mesoniscus graniger (Frivaldszky) | 6 | 21 | 7 | 8 | 1 | 1 | 1 | 2 | 43 | 45 | 73 | 63 | 73 | 73 |
| | Trichonisca carpatica Tabacaru | 9 | 8 | 1 | 9 | 89 | 63 | 63 | 63 | 63 | 63 | 63 | 63 | 63 | 63 |
| **Pauropoda** (indet.) | 2 | 1 | 1 | 4 | 4 | nd | nd | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| **Symphyla** (indet.) | 2 | 1 | 1 | 2 | 2 | nd | nd | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| **Diplopoda** | Julius curvicornis Verhoeff | 7 | 5 | 2 | 4 | 10 | 14 | 100 | 36 | 1 | 1 | 1 | 1 | 1 | 100 | 100 |
| | Leptoiulus cf. proximus (Němec) | 8 | 5 | 12 | 13 | 62 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 |
| | Leptoiulus mariae Gulička | 2 | 2 | 4 | 4 | 100 | 77 | 77 | 77 | 77 | 77 | 77 | 77 | 77 | 77 |
| | Mecogonopodium carpathicum Mock et Tajovsky | 29 | 12 | 7 | 6 | 11 | 3 | 16 | 5 | 5 | 8 | 27 | 76 | 103 | 20 | 77 |
| | Polydesmus complanatus (Linnaeus) | 1 | 4 | 1 | 1 | 5 | 6 | 83 | 59 | 59 | 59 | 59 | 59 | 59 | 59 |
| | Polydesmus denticulatus C.L. Koch | 29 | 65 | 41 | 425 | 41 | 37 | 42 | 22 | 26 | 14 | 32 | 710 | 742 | 32 | 34 |
| | Polyxenus lagurus (Linnaeus) | 1 | 1 | 1 | 1 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | Strongylosoma stigmatosum (Eichwald) | 17 | 3 | 2 | 1 | 3 | 20 | 23 | 29 | 29 | 29 | 29 | 29 | 29 | 29 |
| | Trachysphaera acutula (Latzel) | 40 | 9 | 1 | 1 | 2 | 1 | 4 | 1 | 5 | 1 | 26 | 39 | 65 | 95 | 26 |
| | Trachysphaera costata (Waga) | 1 | 1 | 1 | 1 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | Trachysphaera gilbula (Latzel) | 1 | 1 | 1 | 1 | 100 | 33 | 33 | 33 | 33 | 33 | 33 | 33 | 33 | 33 |
| | Xestoiulus carpathicus (Verhoeff) | 2 | 2 | 2 | 2 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| **Chilopoda** | Cryptops parisi Brolemann | 2 | 2 | 2 | 2 | nd | nd | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| | Geophilus alpinus Meinert | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| | Harpolithobius anodus (Latzel) | 27 | 3 | 1 | 1 | 13 | 19 | 32 | 63 | 77 | 77 | 77 | 77 | 77 | 77 |
| | Lithobius sp. juv. | 8 | 1 | 1 | 2 | 5 | 1 | 1 | 2 | 15 | 7 | 22 | nd | nd | nd |
| | Lithobius erythrocephalus C.L. Koch | 1 | 1 | 1 | 1 | 100 | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| | Lithobius forficatus (Linnaeus) | 17 | 4 | 5 | 2 | 2 | 1 | 4 | 1 | 25 | 11 | 36 | 67 | 50 | 50 |
| | Lithobius lucifugus L. Koch | 5 | 1 | 1 | 3 | 4 | 7 | 86 | 67 | 67 | 67 | 67 | 67 | 67 | 67 |
| | Lithobius mutabilis L. Koch | 1 | 1 | 1 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Lithobius piceus L. Koch | 1 | 1 | 1 | 1 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Strigamia acuminata (Leach) | 7 | 1 | 8 | 8 | 75 | 83 | 83 | 83 | 83 | 83 | 83 | 83 | 83 | 83 |
| | Strigamia crassipes (C.L.Koch) | 2 | 1 | 1 | 2 | 3 | nd | nd | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| | Strigamia transsilvanica (Verhoeff) | 6 | 1 | 1 | 1 | 7 | 8 | nd | nd | 2 | 2 | 2 | 2 | 2 | 2 |
| **Number of individuals** | 262 | 120 | 66 | 460 | 67 | 50 | 76 | 33 | 41 | 28 | 196 | 1007 | 1203 | 1203 |
| **Species richness** | 25 | 15 | 8 | 8 | 8 | 4 | 7 | 6 | 5 | 6 | 24 | 20 | 29 | 29 |
Figure 1. Distribution of Isopoda, Diplopoda and Chilopoda along the depth gradient of the scree slope expressed as the total number of individuals trapped in two sampling periods (November 2008–November 2009; November 2009–July 2010).
with a significance of $p = 0.004$ and a mean stress of 6.0 for real data, and 250 runs for both real and randomised data. The best two-dimensional solution had a final stress of 4.1, $p < 0.00001$, after 53 iterations. Variance explained by the first two axes was 87.0% and 8.7%, respectively. The NMS ordination diagram separated depths into two distinct clusters. The cluster ‘subsurface’ contains the two uppermost levels, with typical representatives such as isopod *Ligidium germanicum*; diplopods *Julus curvicornis*, *Leptoilulus mariae*, *L. trilobatus*, *Mecogonopodium carpathicum*, *Polydesmus complanatus*, *Polydesmus denticulatus*, *Trachysphaera acutula*, *STST* – *Strongylsoma stigmatosum*; chilopod: *HAAN* – *Harpolithobius anodus*, *LI* – *Lithobius* sp. juv., *LIFO* – *Lithobius forficatus*, *LILU* – *Lithobius lucifugus*; *STAC* – *Strigamia acuminata*, *STTR* – *Strigamia transsilvanica*. 

![Figure 2. The non-metric multidimensional scaling ordination analysis (NMS) diagram of Isopoda and Myriapoda collected during both sampling periods; variance explained by axes 1 and 2 as 87.0% and 8.7%, respectively (triangles – depths, dots – species). Abbreviations: i – Isopoda: LIGE – *Ligidium germanicum*, MEGR – *Mesoniscus graniger*, TRCA – *Trichoniscus carpaticus*; d – Diplopoda: JUCU – *Julus curvicornis*, LEMA – *Leptoilulus mariae*, LETR – *L. trilobatus*, MECA – *Mecogonopodium carpathicum*, POCO – *Polydesmus complanatus*, PODE – *Polydesmus denticulatus*, TRAC – *Trachysphaera acutula*, STST – *Strongylsoma stigmatosum*; c – Chilopoda: HAAN – *Harpolithobius anodus*, LI - *Lithobius* sp. juv., LIFO – *Lithobius forficatus*, LILU – *Lithobius lucifugus*; STAC – *Strigamia acuminata*, STTR – *Strigamia transsilvanica*.](image-url)
curvicornis, Polydesmus denticulatus, Strongylosoma stigmatosum and Trachysphaera acutula. The chilopod Lithobius forficatus was the only species with an equal sex ratio (Table 1). There was no evident pattern regarding the preferences of a particular sex for depth or season.

**Seasonal activity of dominant species**

Monthly trends in activity were evaluated in dominant species collected in the first sampling period (Figure 3). In winter, the activity of all species ceased completely, aside from the isopod Ligidium germanicum and diplopod Mecogonopodium carpathicum, which exceptionally appeared in the traps in this season. The activity of both L. germanicum and M. carpathicum started in April and peaked at the turn of spring and summer. The activity of L. germanicum juveniles was concentrated in spring and summer whereas M. carpathicum juveniles occurred in traps throughout the year. Most other species appeared in early summer. The activity of diplopod Polydesmus denticulatus culminated in July. The occurrence of Trachysphaera acutula was predominantly limited to autumn. Chilopods Harpolithobius anodus and Lithobius forficatus were continuously present in the traps during summer and autumn. The juveniles of P. denticulatus and H. anodus showed activity in summer and autumn. On the other hand, the juveniles of T. acutula and L. forficatus were active only during autumn.

**Age structure of Mecogonopodium carpathicum and Polydesmus denticulatus**

Taking a closer look at the particular developmental stages of the two predominant diplopod species, we found a partial dependence of their life cycles on depth (Table 2).

![Figure 3. Activity dynamics of isopod Ligidium germanicum (LIGE); diplopods Mecogonopodium carpathicum (MECA), Polydesmus denticulatus (PODE), Trachysphaera acutula (TRAC); and centipedes Harpolithobius anodus (HAAN), Lithobius forficatus (LIFO), during the period November 2008–November 2009.](image-url)
Seven developmental stages were recorded in both *P. denticulatus* (stages II–VIII) and *M. carpathicum* (stages III–IX). In *P. denticulatus*, stages II and VIII prevailed considerably over the others. *M. carpathicum* was numerously represented by stages IV–V, and VIII–IX.

The early juvenile stages (II–IV) of *P. denticulatus* occurred exclusively at depths close to the soil surface (5–35 cm) while the later ones were active across the entire depth profile. In *M. carpathicum*, stage III was unique to deeper levels (65–95 cm).

**Discussion**

Interior spaces of forested scree slopes form a confluence habitat in which both edaphic and truly subterranean species thrive equally (Juberthie 2000; Nitzu et al. 2014; Jiménez-Valverde et al. 2015). As pointed out by Gers (1998), there is a continuum of life established from the soil surface to the deep subterranean environment, with the rock accumulation as the zone where the food webs of the two environments overlap. This study shows that there are some differences in distribution of the isopod and myriapod assemblages along the depth profile investigated. The vast majority of the edaphic species were strictly bounded to the nutrient-rich uppermost soil layers, and their occurrence deeper in the scree was transient or rather incidental. Among the edaphic species collected, three rare stenoecous forms peculiar to the native undisturbed woodlands were recognised, namely *Trichoniscus carpaticus*, an isopod endemic to the Carpathians; and diplopods *Julus curvicornis* and *Leptoiulus mariae*, both with a distribution range limited to some parts of the Western Carpathians (Košel 2012; Tabacaru and Giurginca 2013). Going down the scree slope profile, we found lower levels to be largely populated by three species: isopod *Mesoniscus graniger*, which tended to aggregate between the depths of 25 and 65 cm; and diplopods *Mecogonopodium carpathicum* and *Polydesmus denticulatus*, both abundant along the depth profile. *M. graniger* is considered a eutroglophile, with depigmentated body and missing ocelli. This species is distributed in the Carpathians and Dinarides, inhabiting various subterranean habitats (Mlejnek and Ducháč 2001). *M. carpathicum* is another eutroglophile found in this study. Like most of the representatives of the Attemsiiidae family, it has no specific morphological adaptations to life underground. Nevertheless, this species strongly prefers
subterranean habitats where it presumably survived in situ climatic changes during its long history as proposed by Bosák et al. (2014). *M. carpathicum* is the easternmost representative of the Attemsiidae family with the range limited to the small karst area of the Ružínsky kras (Mock and Tajovský 2008). On the contrary, *P. denticulatus* represents a recently expanding and highly adaptive diplopod (Kime and Enghoff 2011), with several local cave populations in the Western Carpathians (Kováč et al. 2014).

Among all species captured, diplopods *M. carpathicum* and *P. denticulatus* were the only species characterised by a considerable prevalence of immature stages. This finding might suggest that both species reproduce and undergo their life cycles within the forested scree slope. Both *M. carpathicum* and *P. denticulatus* are considered to be semelparous. While the adult females of *M. carpathicum* produce only a few eggs during their sexual maturity, having a separate oviposition (Minelli and Michalik 2015), the females of *P. denticulatus* oviposit several times during the season in very high numbers into individual separated hollows created in the soil (Blower 1970; Minelli 2015). This probably resulted in a mass capture of the first motile juvenile stages of *P. denticulatus* in a single trap at a depth of 35 cm. The more detailed evaluation of the distribution of the particular developmental stages of diplopods *M. carpathicum* and *P. denticulatus* along the scree slope profile revealed an evident vertical segregation of very early post-embryonic stages. *P. denticulatus* seems to undergo the first stages of the life cycle in the uppermost levels filled with soil, and then, more moveable later stages expand deeper. In contrast to this, very early juvenile stages of *M. carpathicum* remain deep inside the scree slope before being spread to the upper parts.

The present study aimed also to bring more light to the monthly dynamics of isopod and myriapod assemblages inside the forested scree slope during the first year of sampling. In most species, however, activity ceased completely in winter, and although it was re-launched in spring, the collected species were represented by only a small number of individuals in the following months. Continuing with sampling using ethylene glycol preservative solution in the second year of the study, there was a severalfold increase in the number of captured isopods and myriapods. We assume the strong decline of activity in the first year might be caused by two factors: (1) formaldehyde solution had a repellent effect on some species, an effect observed by several authors (e.g. Greenslade and Greenslade 1971; Renner 1982; Gerlach et al. 2009); and (2) dry weather conditions during the first year of the study. In analogous studies on seasonal activity of terrestrial isopods and myriapods, it is therefore appropriate to limit the use of formaldehyde and carry out the sampling for at least two successive years.

In comparison with the isopods and diplopods collected on the soil surface in the same study site by pitfall traps (Mock 2004; Timková 2007), there was a slightly higher representation of Carpathian endemics captured in the scree slope profile. On the other hand, the composition of both endemic and subterranean species (eutroglophiles) in the scree was identical to that previously found in seven nearby shallow caves with a length of several tens of metres (Mock et al. 2009). In terms of the total species number, there was almost no difference among the three compared habitats (Table 3). There are no data on centipedes to compare; however, two species of centipedes scarce in Central Europe, *Harpolithobius anodus* and *Lithobius lucifugus* (Tuf and Tufová 2008), were found to inhabit the scree. In the Western Carpathians, the forested scree slopes have been classified as habitats of European importance as they form the small-scale fragmented
elements of a landscape with the presence of diversified terrestrial fauna with a high proportion of rare species (Viceníková and Polák 2003). Investigations of such habitats are thus crucial to describe the overall biodiversity on a local scale.

**Conclusions**

This is one of the few studies focused on the diversity, distribution and seasonal activity of terrestrial isopods and myriapods along the depth profile of a forested scree slope. It was observed that a remarkable assemblage inhabits this superficial subterranean habitat including rare Carpathian endemics and/or specialised subterranean species. As expected, the edaphic species were strictly bound to the topmost organic soil layers. On the other hand, subterranean species and highly adaptive edaphic species predominated the deeper parts of the scree profile; the development of their very early post-embryonic stages was concentrated in well-separated sections of the depth profile. For further studies on the distribution and seasonal dynamics of arthropod macrofauna

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**Table 3.** Occurrence of terrestrial isopods and diplopods in different habitats in the study area; • – subterranean species, * – Carpathian endemics.

| Species                  | Scree slope | Soil surface | Caves |
|--------------------------|-------------|--------------|-------|
| Isopoda                  |             |              |       |
| Armadillidium versicolor Stein | +           |              |       |
| Lepidoniкус minutus (Koch) | +           |              |       |
| Ligidium germanicum Verhoeff | +           |              |       |
| Ligidium hypnorum (Cuvier) | +           |              |       |
| •Mesoniscus graniger (Frivaldszky) | +           |              |       |
| Protracheonisicus politus (C. L. Koch) | +           |              |       |
| Porcellium conspersum (C. Koch) | +           |              |       |
| Trachelipus nodulosus (C. Koch) | +           |              |       |
| *Trichoniscus carpaticus Tabacaru | +           |              |       |
| Diplopoda                |             |              |       |
| *Cylindroiulus burzenlandicus Verhoeff | +           |              |       |
| Enantiulus nanus (Latzel) | +           |              |       |
| Glomeris hexasticha Brandt | +           |              |       |
| Glomeris tetrasticha Brandt | +           |              |       |
| *Julus curvicornis Verhoeff | +           |              |       |
| *Leptoiulus mariae Gulicka | +           |              |       |
| Leptoiulus proximus (Nemec) | +           |              |       |
| Leptoiulus trilobatus (Verhoeff) | +           |              |       |
| •Mecogonopodium carpathicum Mock et Tajovsky | +           |              |       |
| Nemassoma varicorne C. L. Koch | +           |              |       |
| Polydesmus complanatus (Linnaeus) | +           |              |       |
| Polydesmus denticulatus C. L. Koch | +           |              |       |
| *Polydesmus tatranus Latzel | +           |              |       |
| Polyxenus lagurus (Linnaeus) | +           |              |       |
| Polyzonium germanicum Brandt | +           |              |       |
| Strongylosoma stigmatosum (Eichwald) | +           |              |       |
| Trachysphaera acuta (Latzel) | +           |              |       |
| •Trachysphaera costata (Waga) | +           |              |       |
| Trachysphaera gibbula (Latzel) | +           |              |       |
| Unciger foetidus (C. L. Koch) | +           |              |       |
| *Xestoiulus carpathicus (Verhoeff) | +           |              |       |

| Number of species | 18 | 19 | 20 |
| Number of subterranean species | 3 | 0 | 3 |
| Number of endemics | 5 | 4 | 5 |

(1 present study; *Mock 2004, Timková 2007; Mock et al. 2009).
occupying superficial subterranean habitats, we highly recommend: (1) to limit the use of formaldehyde as the preservation fluid, because of its repellent effect on most arthropods; and (2) to carry out the sampling for at least two successive years after the installation of subterranean traps in SSH.

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