

## Small scale gradient effects on isopods (Crustacea: Oniscidea) in karstic sinkholes

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**Abstract:** We studied abundance and diversity patterns of terrestrial isopod assemblages along a ‘micro-scale’ vertical gradient in sinkholes in the Aggtelek National Park, Hungary. Time restricted manual sampling yielded ten native species, including endemic and rare ones. Along the gradient we found no major differences in species richness and -composition, and abundance decreased from the bottoms to the upper zones of the sinkholes. Species specific habitat preference on a vertical gradient showed two distinct groups by indicator species analysis: occurrence of habitat “generalists” was irrespective of vertical zones while “specialists” were restricted to the bottoms of the dolines. The latter group is formed mainly by rare species. We found that both diversity and evenness of isopod assemblages were highest in the bottom zone. Our results draw the attention to the significance of such common, yet undiscovered surficial depressions that can provide shelters for rare and specialist species and can provide shelter for survival of populations under changing climatic conditions.

**Key words:** diversity; woodlice; zonation; biodiversity assessment; abundance; species richness; Aggtelek National Park

### Introduction

Biotic surveys of isopods most often focus on large scale correlative relationships between occurrences/abundances of species and environmental variables. Geographic location and elevation are often used as proxies for climatic gradients and variability (Lawton et al. 1987; Lymberakis et al. 2003; Sfenthourakis et al. 2005). As large scale changes in the biota might be coarsely predicted using models built for large scale observations, it is likely that small scale realization of these scenarios will ultimately depend on future colonization/establishment and survival of populations determined by local factors.

Sinkholes (also known as dolines) are depressions in the bedrock in karstic regions possessing various shapes and sizes, reaching up to more than hundred metres in depth and diameter. They are characterized by a marked vertical climatic gradient. As cold air fills the lower layers of dolines at night, the bottom of the sinkholes is usually wetter and cooler than slopes and edges (Bárány 1985; Bárány-Kevei 1999; Nagy & Sóllymos 2002).

Recent studies (Raschmanová et al. 2008) from the Slovak Karst revealed significant relationships between Collembola diversity and meso/-microclimatic gradient of a deep valley. Sóllymos et al. (2009) described how

mollusc species respond to micro-scale variations in sinkhole morphology and microhabitat structure. Dolines, as typical karstic depressions also provide opportunities for soil zoologists to do repeated observations on the local and landscape-wide effects, to observe species distributions with special respect to exposure and doline depth. Background factors combined with effects mentioned above may provide essential knowledge on habitat preferences and shelter use of epigeic macroinvertebrates, like isopods.

Isopods are important representatives of the soil and litter dwelling macro-decomposer guild (e.g., Sutton 1980). Although there is an expanding knowledge on Hungarian woodlice (e.g., Forró & Farkas 1998; Horning et al. 2008), our understanding on the ecology of these crustaceans is still incomplete. Here we present results on how the vertical temperature and moisture gradient affect composition of isopod assemblages. We show that microclimatic differences along the vertical gradient in these dolines have profound effect on isopod assemblages, which in turn has implications for the conservation of rare and sensitive species.

### Material and methods

#### *Hypotheses*

We established three hypotheses to get a better understand-



Fig. 1. A forested doline of Alsó-hegy at the Aggtelek Karst region (cca. 20 metres of depth). Note the accumulated dead wood on the bottom. (Photo: Z. Kemencei).

ing of ecological patterns and associated ecological mechanisms: (1) We predict discrete assemblages (species composition), driven by great differences of microclimate between depressions and the surrounding area. We assume several forest specialist species to be distributed outside of dolines, while others to be restricted to the depressions, resulting in great differences in species composition. This hypothesis applies to landscapes under various levels of human impact resulting in a patchwork of various disturbances where species of different tolerances find suitable “shelters”. This also implies large species turnover along the gradient, but not necessarily a change in species richness. In this case, species prioritization should take into account the high level of complementarity along the gradient. (2) Our second hypothesis predicts the partial overlap of two main assemblages along the depth/temperature/moisture gradient resulting in a peak of species richness at the transitional zone. This kind of turnover combined with the hump-shaped species richness pattern imply that species protection can be maximized by focusing on transitional areas, but at the same time these conditions might be suboptimal for many species. (3) The third hypothesis predicts an overall presence of habitat generalist species within and outside the karstic depressions, while several habitat specialists remain restricted to inner zones of dolines, resulting in a higher species richness within dolines (more favourable) compared to the surrounding environment (less preferred by most species). This nested species occurrence pattern and the monotonic change in species richness imply that the highest efficiency can be achieved by focusing on protection of favourable habitats, where sensitive and tolerant species can be saved alike.

#### Sampling

Alsó-hegy (“Alsó Hill”, UTM – Universal Transverse Mercator – coordinate: DU78, coordinates: 48°33′37″ N, 20°44′00″

E) – is the eastern part of Aggtelek Karst area which is geologically connected to Slovak Karst and is the southern (Hungarian) part of Gömör-Torna Karst Region, connected to the northern Carpathians. Triassic limestone is the typical bedrock of the area, characterised by numerous depressions (sinkholes a.k.a dolines), caves and other karstic formations belonging to the UNESCO World Heritage. The area is covered by forests dominated by oak (*Quercus* spp.), beech (*Fagus sylvatica* L.) and hornbeam (*Carpinus betulus* L.). We chose 16 adjacent dolines of an average size of 1.25 hectares (min = 0.53 ha; max = 2.52 ha) and an average depth of 19.6 metres (min = 10 m; max = 30 m). Due to their arboreal vegetation, effects of exposure is radically decreased (Fig. 1).

To observe the spatial distribution of isopods we distinguished three zones in each doline along a vertical gradient: bottom, middle and upper area that contained the headwall as well. The upper zone represent the surrounding matrix of the plateau covered by oak-hornbeam forests. The bottom category stood for the bottom and lower zones of dolines characterized by cooler microclimate, higher humidity and differing vegetation (*Fagus sylvatica*, *Fraxinus excelsior* L.), while the middle zone serves as a supposed transition zone. Time restricted direct search took place from 16 to 18 August, 2007. Our preliminary studies have proved that isopod species are available for faunistic surveys from early spring (March) to autumn (October). Dolines, even in summer droughts, provide a more constant humidity than the outside karstic areas (Bárány 1985).

During time sampling, two samplers (F.V. and A.N.) collected isopods for 20–20 minutes in each zone, spending 120 person-minutes with sampling in each doline. Time sampling provided data eligible in respect to quantitative data analyses, and resulted in a total of 96 samples (16 dolines × 3 zones × 2 collectors). Nomenclature follows Schmalzfuss (2003).

Table 1. Abundance of isopod species, and diversity of assemblages along the vertical gradient of dolines of the Alsó-hegy.

No.	Species	Doline zones			Total
		Bottom	Middle	Upper	
1.	<i>Trachelipus difficilis</i> (Radu, 1950)	100	48	32	180
2.	<i>Protracheoniscus politus</i> (C. Koch, 1841)	41	49	49	139
3.	<i>Lepidoniscus minutus</i> (C. Koch, 1838)	20	23	20	63
4.	<i>Haplophthalmus hungaricus</i> Kesselyák, 1930	25	2	4	31
5.	<i>Porcellium conspersum</i> (C. Koch, 1841)	19	2	0	21
6.	<i>Trichoniscus provisorius</i> Racovitza, 1908	17	4	0	21
7.	<i>Ligidium hypnorum</i> (Cuvier, 1792)	15	4	1	20
8.	<i>Orthometopon planum</i> (Budde-Lund, 1885)	5	5	9	19
9.	<i>Trachelipus ratzeburgii</i> (Brandt, 1833)	5	0	5	10
10.	<i>Mesoniscus graniger</i> Frivaldszky, 1875	0	1	0	1
Diversity					
1.	Shannon $H'$	1.80	1.52	1.49	
2.	Shannon $J'$	0.78	0.66	0.65	
3.	Simpson $D$	0.22	0.27	0.27	
4.	Berger-Parker $d$	0.16	0.35	0.40	

### Data analyses

Due to excess zeros, we used zero-inflated Poisson (ZIP) model to test for differences in total abundance among the strata. The ZIP model is a mixture of a Bernoulli and a Poisson distribution, where the Bernoulli part described the probability of zero observations (with logistic link function), and the Poisson was for the counts (including zeros due to Poisson variation, with log link function). Zeros can arise as part of both distributions. We used strata as covariate for the count part of the model, while only the intercept was used only for the Bernoulli model corresponding to constant probability of excess zeros. Similarities between species assemblages were calculated with Sørensen index of similarity. Redundancy analysis (RDA) was applied to assess the effects of the three vertical zones of 16 dolines in the distribution of isopod species.

We used IndVal analysis (Dufrêne & Legendre 1997) to highlight characteristic species of different doline zones. This method combines the specificity and fidelity of a given species in each hierarchical level of an a priori hierarchical cluster of studied habitats (i.e., doline zones). The indicator species were defined as the most characteristic species of each group, found mostly in a single group of the typology (specificity) and present in the majority of the sites or samples belonging to that group (fidelity). The indicator value ( $\text{IndVal}_{ij}$ ) of a given species ( $i$ ) for a given group of sites ( $j$ ) combine specificity ( $A_i$ ) and fidelity ( $B_i$ ) of the certain species ( $\text{IndVal}_{ij} = A_{ij} * B_{ij} * 100$ ). The indicator value of a given species ( $\text{IndVal}_i$ ) for a typology of sites is the largest value of  $\text{IndVal}_{ij}$  observed over all groups of the typology.

In order to test significance of IndVal, random reallocation of procedure of sites among site groups was used with 1000 permutations (Dufrêne & Legendre 1997). For the analysis we used the sample pairs in every vertical zones (bottom, middle, upper zone) that were selected in each doline.

In the a priori typology of sites the similarity of middle and upper zones of sinkholes, as well as the divergence of the bottom zone were assessed.

Diversity was analysed by rank-abundance curves and diversity indices sensitive to various attributes of assemblages (Shannon  $H'$ , Shannon  $J'$ , Simpson and Berger-Parker). We visualized diversities by using the Rényi diversity profiles, that offered a comprehensive way to investigate differences in diversity (Tóthmérész 1995, 1998). For

Table 2. Total abundance of isopods increase towards the bottoms of the dolines, while the probability of zero values is high (0.5) according to the results of the zero-inflated Poisson model.

	Estimate	Std. Error	z value	P value
Count model				
Intercept	2.737	0.064	43.012	<0.001
Middle zone	-0.582	0.106	-5.476	<0.001
Upper zone	-0.721	0.111	-6.483	<0.001
Zero model				
Intercept	-0.0005	0.204	-0.002	0.998

Explanations: Zones of the dolines were used as independent categorical covariate in the Poisson (count) model part with log link function, the bottom zone served as reference category (intercept). Zero model with logistic link function describes the probabilities of zero observations, we used a constant (intercept only) model.

RDA, cluster analysis and Rényi diversity profiles we used the vegan package (Oksanen et al. 2010) in R software environment (R Development Core Team 2010).

## Results

Time sampling resulted a total of 505 individuals and ten species of Isopoda in dolines surveyed (Table 1). The highest overall abundance was found at the bottom zone (247), followed by the middle (138) and the upper zone (120). According to the ZIP model (Table 2), total abundance increased from the bottoms towards the edges of the dolines. Expected abundance was 15.4 in the bottoms, 8.6 in the middle zones and 7.5 at the edges. The probability of zero observations was 0.5.

Among the ten species found, the Hungarian endemic isopod *Haplophthalmus hungaricus*, the cavernicolous *Mesoniscus graniger* and the rare Carpathian endemic *Trachelipus difficilis* deserve special attention. The most abundant species were *T. difficilis* (35.6%), *Protracheoniscus politus* (27.5%) and *Lepidoniscus minutus* (12.5%).

In spite of the high similarities in species richness within the gradient, rank abundance curves (Fig. 2)

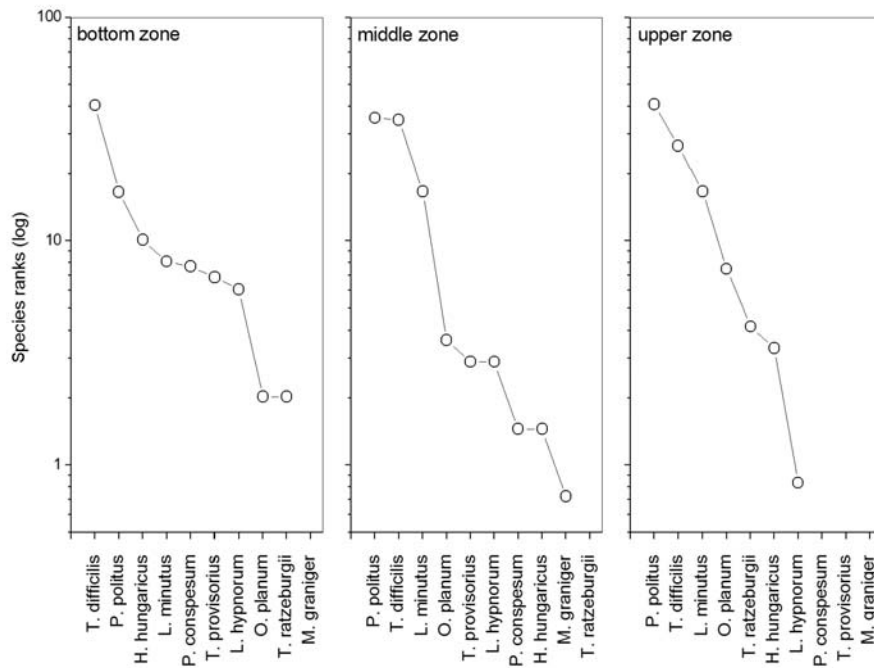


Fig. 2. Rank abundance curves ( $\log_{10}$ ) indicating evenness of assemblages with ranks of isopod species in different zones of dolines.

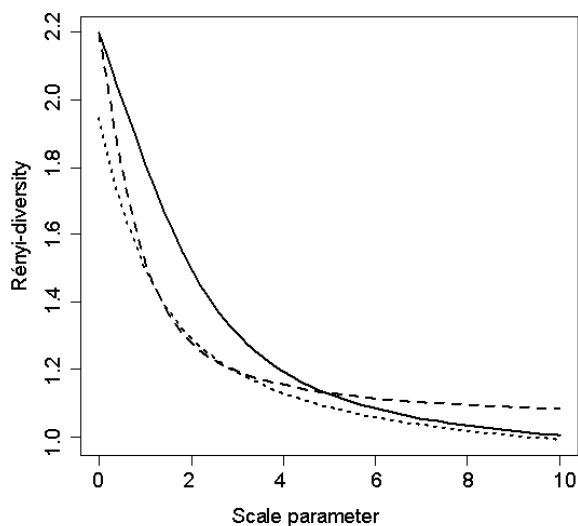


Fig. 3. Rényi diversity profiles of isopod assemblages of dolines in different zones. Legend: solid line – bottom zone; dashed line – middle zone; dotted line – upper zone.

showed differences in evenness of isopod assemblages among the vertical gradient.

Approving this result, Shannon  $H'$  and  $J'$  were found to decline gradually from the bottom to the upper zone (Table 1). Accordingly, indices more sensitive to dominant species were found to be lowest at the bottom zone, indicating evenness and proving that no species gained high dominance at the lowest zone. This was due to the relatively high proportion of species occurring exclusively in the bottom, while the middle and upper zones were dominated by some habitat generalist species with few specialists present, suggesting the validity of our third hypothesis.

Rényi diversity plots (Fig. 3) indicated that the

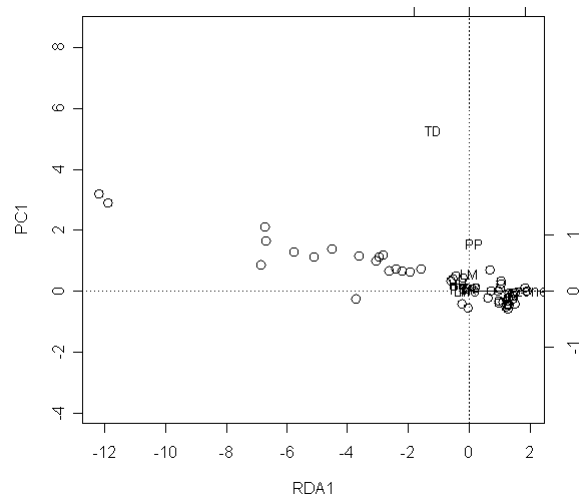


Fig. 4. Redundancy analysis (RDA) biplot showing effects of zonation on species distribution. Legend: Dots – sample sites; PP – *Protracheoniscus politus*; TD – *Trachelipus difficilis*; LM – *Lepidoniscus minutus*; HH – *Haplophthalmus hungaricus*; PC – *Porcellium conspersum*; OP – *Orthometopon planum*; TP – *Trichoniscus provisorius*; TR – *Trachelipus ratzeburgii*; LH – *Ligidium hypnorum*; MG – *Mesoniscus graniger*.

bottom zone had the highest diversity in lower scale parameters. At  $\alpha = 0$  the middle zone shows similar species richness ( $\log S$ ) to the bottom zone, but diversity values decrease at higher scale parameters. This signals the higher diversity of the upper zone in comparison with the middle zone in terms of indices sensitive to abundant species. At higher scale parameters, diversity of the middle zone is the highest while bottom and upper zones (at low diversity values) show similarities.

Sørensen index revealed a high similarity of overall species richness (99%) between bottom and middle

Table 3. The species indicator power for the site clustering hierarchy.

Species	IndVal (%)	Doline zones		
		Bottom	Middle	Upper
Bottom zone of dolines				
<i>Haplophthalmus hungaricus</i>	50.22**	<b>25/9</b>	2/2	4/2
<i>Trichoniscus provisorius</i>	39.14**	<b>17/7</b>	4/3	0/0
<i>Porcellium conspersum</i>	35.62**	<b>19/6</b>	2/1	0/0
<i>Ligidium hypnorum</i>	32.14**	<b>15/6</b>	4/3	1/1
<i>Trachelipus ratzeburgii</i>	16.67	<b>5/4</b>	0/0	5/2
All habitats				
<i>Protracheoniscus politus</i>	83.33	<b>41/12</b>	<b>49/13</b>	<b>49/15</b>
<i>Trachelipus difficilis</i>	62.50	<b>100/11</b>	<b>48/9</b>	<b>32/10</b>
<i>Lepidoniscus minutus</i>	54.17	<b>20/9</b>	<b>23/9</b>	<b>20/8</b>
<i>Orthometopon planum</i>	27.08	<b>5/4</b>	<b>5/3</b>	<b>9/6</b>
Middle zone of dolines				
<i>Mesoniscus graniger</i>	6.25	0/0	<b>1/1</b>	0/0
Middle and upper zone of dolines				
No species		0/0	<b>0/0</b>	<b>0/0</b>
Upper zone of dolines				
No species		0/0	0/0	<b>0/0</b>
Number of sites		16	16	16

Explanations: The IndVal column indicate the species indicator value for the corresponding clustering level, which is the maximum indicator value observed in all the clustering hierarchy. The numbers represent the number of individuals sampled and the number of sites occupied by species in the given group of sites. Boldfaced numbers show the typology of three groups.\*\*  $P < 0.05$ .

zones of dolines, while the lowest similarity was found between the bottom and the upper zones (52%).

Redundancy analysis biplot (Fig. 4) highlights the similarities of species occurrences, but the effects of the vertical gradient gave only 27 percent of the explained variation.

IndVal analyses (Table 3) showed four species (*L. hypnorum*, *H. hungaricus*, *T. provisorius*, *P. conspersum*) to be significantly specific to the bottom area of the sinkholes. Each of them occurred in other zones as well, so these species are regarded as asymmetric character species (IndVal > 55%) of the upper zone assemblages. Four species were present in all zones of sinkholes: *P. politus*, *T. difficilis*, *L. minutus*, *O. planum*. The middle and upper zones have neither their own, nor joint significant characteristic species.

## Discussion

Nested species distribution patterns of isopods were observed along an environmental gradient represented by vertical position of samples in sinkholes. Apart from several reports from the decomposer invertebrates of surface of karstic areas (e.g., Kováč et al. 2005; Vilisics & Lapanje 2005; Giurginca et al. 2006; Mock et al. 2007; Raschmanová et al. 2008), our study was the first attempt to find fine-scale differences in spatial distribution of woodlice along a vertical gradient of dolines. Hence, besides the essential faunistic publications, no studies have so far emphasized the significance of such depressions in the sense of conservation of native soil fauna.

Woodland Isopoda assemblages in Hungary are rather poor in species, with an average number of four species in the characteristic oak and beech forests (Hornung et al. 2007a, 2008). At our sampling sites, however, an extraordinary high number (10) of species appeared, representing different biogeographical distribution ranges, from endemic to common Central European forest species. In Hungary, all species are regarded as “natural frequent” or “natural rare” by the classification of Hornung et al. (2007b).

Thus, by observing isopods in Aggtelek Karst area, we concluded that dolines might harbour assemblages consisting of numerous rare species, with diversities higher than the surrounding matrix.

Isopod assemblages in each zone were uneven. Studies in Hungary (Hornung et al. 2007a; Végh et al. unpublished), Switzerland (Vilisics et al. unpublished) and Denmark (Vilisics et al. 2007) showed highly uneven isopod assemblages regardless to the naturalness of the observed area. Thus, in contrast to prevailing models (e.g., Magurran 2004), rank/abundance structures of natural isopod assemblages show geometric distributions rather than lognormal or broken stick. However, more data are needed to see whether this is a general pattern, or phenomena that was related to the certain location and environment.

Results on species compositions and species richness showed evidence for the validity of our third hypothesis which predicted generalist species to be present in each zone while specialists dominate the bottom of dolines. Species-specific habitat preference on a vertical gradient revealed two distinct groups of

isopods: several species (e.g., *L. minutus*, *P. politus*, *T. difficilis*) were prevalent within and outside the dolines (“generalists”), and the others (“specialists”) remained in the lower zones (e.g., *H. hungaricus*, *L. hypnorum*).

Evidences for nestedness of isopod assemblages have been found at various scales in Hungary. On a macro-scale, Hornung et al. (2008) showed that species distribution patterns in the western half of Hungary (Transdanubia) were characterized by a few common species [e.g., *Armadillidium vulgare* (Latreille, 1804), *Trachelipus rathkii* (Brandt, 1833), *Porcellium collicola* (Verhoeff, 1907), *P. politus*] co-occurring with sporadically distributed, rare native [e.g., *Hyloniscus vividus* (C. Koch, 1841), *Armadillidium zenckeri* Brandt, 1833] or non-native [(e.g., *Agabiformius lentus* (Budde-Lund, 1885)] ones. Meso-scale studies on the urban isopods of Budapest (Vilisics & Hornung 2009) revealed native generalists and cosmopolitans to be common in each main habitat type of the city while occurrence of forest specialists or tropical non-natives was restricted to areas of special environmental traits (e.g., forest remnants, botanical gardens). On the contrary, meso-scale observations in the Aggtelek National Park (Kontschán 2003; Vilisics et al. 2008) lead to a distinction between assemblages of Alsó-hegy sinkholes and those of the surrounding area.

As a conclusion, isopod assemblages of Alsó-hegy follow a pattern resembling to assemblages observed on larger, regional scales (Hornung et al. 2008): several species possess a wide distribution while others are restricted to certain habitat types. In the present investigation, wide occurrence means that some species are prevalent in all zones (“generalists”) while “specialists” are limited to the dolines’ bottom.

Common European and cosmopolitan isopods (characteristic on human influenced areas in Hungary) are missing. On the contrary, like woodland isopods described from Central Europe and the Carpathians, even the locally common species have a high natural value. The species distribution and dominance structure of isopod assemblages highlight the conservation biological value of the investigated habitat. The low human disturbance around these forests prevent cosmopolitan/invasive species in these local faunas, while the native biota represents species with varying ecological tolerances. These species co-occur in favourable microspots in the bottoms of dolines. So, persistence of rare and sensitive species is dependent on shelters available on small spatial scales. Based on micro-scale evidence from this study and larger scale research results, conservation of isopods can be most efficient by focusing on good quality habitats, where populations of generalist and more restricted species can be protected alike.

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