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## Duality of terrestrial subterranean fauna

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### Abstract:

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Terrestrial animals in subterranean habitats are often classified according to their degree of morphological or ecological specialization to the subterranean environment. The commonly held view is that, as distance into a cave increases, the frequency of morphologically specialized, i.e., troglomorphic, species or ecological specialization will increase. We tested this hypothesis for the fauna in 54 caves in Slovenia—the classical land for subterranean biology. We found that there exist two ecologically well separated terrestrial subsurface faunas: one shallow and one deep. 1) The shallow subterranean fauna, adapted to the terrestrial shallow subterranean habitats (SSHs) in the upper 10 m of subsurface strata, is most diverse. It consists of randomly distributed non-troglobionts and a major group of troglobionts adapted to the soil root zone. 2) The deep subterranean fauna is represented by a minor group of troglobionts, adapted to caves. Troglobionts are strictly divided between the two faunas. There is strong evidence that in karstic ecosystems with deep-rooted vegetation this might be a global pattern, or that in these locations only the shallow subterranean fauna exist.

**Keywords:** endemites; superficial subterranean habitats (SSHs); troglonexes; troglaphiles; troglobionts

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### INTRODUCTION

There are two time frames in considering terrestrial subterranean ecology, the classical period of 1832–1980 dealing with caves, and the modern period after the 1980s when a wide range of other subterranean habitats were also considered. After Schmidt (1832) published the first scientific description of an invertebrate well adapted for living in hypogean habitats, the beetle *Leptodirus hochenwartii* from the cave Postojnska jama in Slovenia, interest in studying subterranean biology and ecology increased enormously. Evidence of eyelessness, depigmentation, relatively long appendages and other convergent characteristics of subterranean animals launched the need for their ecological and morphological classification (Schiödte, 1849, 1851; Schiner, 1854; Racovitza, 1907). Since then, many modifications and refinements have been

suggested (reviewed by Sket, 2008), among which Christiansen's (1962) introduction of the term troglomorphism to denote the typical appearance of well-adapted subterranean species has been widely accepted. There are three main ecological groups of animals in habitats beneath the surface (Boutin, 2004; Sket, 2008). 1) Troglonexes are taxa that enter caves for shelter or feeding opportunities, but which exhibit no morphological adaptation to the hypogean environment and do not complete their life cycle there. 2) Troglaphiles (terrestrial) and stygophiles (aquatic animals) alternate between the epigeal and hypogean habitats or live permanently in subterranean habitats, and show some moderate adaptation to subterranean conditions, such as reduced eyes and adaptations to compensate for the lack of visual orientation. Some among these do not complete their life cycle underground (subtroglaphiles), while others (eutroglaphiles) do. 3) Troglobionts and stygobionts complete their life cycle in a completely dark, humid/water and thermally stable hypogean environment. Most of these clearly show troglomorphism. For the purpose of simplification, troglonexes and troglaphiles together are treated here as non-troglobionts.

In caves, according to the classical understanding, troglonexes have been expected in the entrance zone, troglaphiles in the twilight zone, and troglobionts in the totally dark zone, deep inside the cave. In prac-

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tice, ranking among both troglloxenes and trogllophiles is often confusing because of the lack of generally accepted criteria for delimiting the two groups or impossible because of the unresolved status of many of these species. Besides, many trogllobionts are not consistent with this distributional range and are recorded rarely or sparsely in deep cave sections, but are abundant in terrestrial superficial subterranean habitats (SSHs), like in talus slopes (Juberthie et al., 1980; G. Racovitza, 1983; Juberthie, 2000; Juberthie & Decu, 1994; Růžička, 1999; Culver & Pipan, 2009a, b) or, especially in the tropics, near cave entrances (Prous et al., 2004). The terrestrial SSHs are difficult to investigate directly (Růžička & Klimeš, 2005) and have been much more poorly researched than those in water habitats (Culver & Pipan, 2009a). They are physically similar to caves within the same area, but with larger annual temperature variation and much more abundant and diverse food supply from the surface and soils. These may be in close contact with caves, and therefore considered a gateway to the deep subterranean habitats (Juberthie & Decu, 1994; Růžička, 1999; Culver & Pipan, 2009a, b; Pipan et al., 2011).

Caves adjacent to other subsurface habitats enable indirect study of these habitats as well. Although caves are much easier to investigate than SSHs, the ecological interpretation of biota in caves is skewed for several reasons. Caves vary considerably in shape, length, altitude and other characteristics, resulting in a wide range of environmentally dissimilar combinations. The usual sampling methods, such as visual inspection, pitfall trapping and Berlese extraction deserve careful interpretation (e.g., Kuštor & Novak, 1980a; Sabu & Shiju, 2010; Gotelli & Collwell, 2011). Most trogllobionts are rare in caves, indicating that this is not their preferred habitat (Novak 1989). Some of them show a preference for narrow spaces (e.g., *Aphaenops* – Juberthie, 1969; Juberthie & Bouillon, 1983; *Speonomus* – Delay, 1978; *Leptodirus*, *Anophthalmus* – Kuštor & Novak, 1980a, b), and some have been reported from SSHs (e.g., *Tylogonium* – Christian, 1987; *Eukoenenia* – Christian, 2004; *Anophthalmus*, *Aphaenopidius*, *Orotrechus* – Drovenik et al., 2007). Species may vary considerably in abundance from year to year. According to the modern understanding of adaptive processes, a wide range of adaptations and niches can be expected in the subterranean environment, as shown, e.g., among fishes (Riesch et al., 2010; Romero, 2011).

Considering all these facts, the classical understanding of the distribution does not conform to recent knowledge and should be revised on the general level. Here we focus on two points: 1) how the proportion between non-trogllobionts and trogllobionts changes with distance from the entrance inward and 2) whether the trogllobionts represent a unique ecological group or not. We hypothesized that, in territories providing a continuous range of shallow to deep subterranean habitats, such as karst territories, non-trogllobionts and trogllobionts are evenly distributed within the SSHs. We also hypothesized that there are two ecologically well defined subgroups of trogllobionts: 1) species adapted to the SSHs, i.e., the deep soil root zone, and 2) species adapted to caves

*sensu* Culver & Pipan (2009a). They argue that from the biological/ecological point of view, a “cave” represents a natural space in the solid rock with areas of complete darkness and is larger than a few millimeters in diameter.

## MATERIALS AND METHODS

### Terminological notes

Speleobiological classifications themselves are not the subject of this contribution and do not influence its outcome, but they deserve a brief comment. Most European authors dealing with terrestrial fauna traditionally use “troglloxenes” (see references, e.g., in Juberthie & Decu, 1994) in place of “subtrogllophiles” in the resurrected Pavan-Ruffo classification (Sket, 2008), but not all traditional “trogllophiles” rank among “eutrogllophiles”. To avoid confusion, we pragmatically apply the term “non-trogllobionts” – without any intention of introducing a new category – as a group which includes two ecologically different entities: troglloxenes and trogllophiles (traditional classification), or subtrogllophiles and eutrogllophiles (Pavan-Ruffo classification). We understand “trogllobionts” in the sense of species confined to subterranean habitats.

### Study area and sampling

In the study area in central and northern Slovenia, using a 10x10 km<sup>2</sup> UTM grid, we selected 54 natural caves and artificial galleries (in the following: caves, mapped in Novak, 2005) at altitudes of 260–2450 m that were morphologically and meteorologically varied for the investigation. As far as possible, these were homogeneously scattered within a territory of 7,500 km<sup>2</sup> in carbonate and non-carbonate rocks. For the investigation, we chose caves at least 30 m long, or the longest ones available. The caves were investigated between 1977 and 2001. We sampled in January, April, July and October in a total of 617 sampling sections, every 3.5 m, on average. Besides measuring various environmental parameters, faunal records were provided on two visits within 45–48 hrs by observing cave walls, ceiling and floor, and applying standardized baited pit-fall trapping and Berlese funnels. Such sampling ensured avoiding autocorrelation (cf. Beale et al., 2010) to the highest possible degree. Altogether, 2,468 records were provided, referring to 173,008 individuals of 600 estimated species in total, of which 456 were determined (details in Novak et al., 2004; Novak, 2005).

### Statistical Analyses

In the analysis, presence was used as the most reliable information on biota. We selected ecologically key taxa: the most abundant non-trogllobionts, arbitrarily defined as those recorded in  $N \geq 2$  individuals/cave, on average, and all the trogllobiotic taxa. Non-trogllobionts were unified in the same dataset and trogllobionts in the other one. In this way, the non-trogllobionts were represented by 19 species and the trogllobionts by 15 species – two of them undetermined – plus 4 subspecies. The basic statistical item was the presence of a taxon within a sampling section per season. We observed the frequencies in repetitive presence of the taxon with respect to dis-

tance from the cave entrance and from the surface, the last referring to the surface vertically above the sampling place within the cave. We first checked the distribution of presence frequencies for normality. The Mann-Whitney U test was used in testing the adequacy of presence frequencies within and between the groups. The spatial distribution of species was evaluated by means of spatial density maps, the density referring to the normalized presence frequencies at any given distance from the entrance or the surface. The normalization was such that for each taxon the sum of densities over the whole distance range was equal to one. The overall similarity between different density maps was compared with the normalized spatial cross-correlation function,  $\chi \in [0,1]$  (Kantz & Schreiber, 2004). The best border between two identified subgroups of the troglonites was obtained by determination of the smallest relative difference between the cumulative occupancies,  $\kappa \in [0,1]$ , where 1 means no, and 0 full separation.

**RESULTS**

Within the 54 caves, there were 51,162 individuals of the most abundant non-troglonites recorded in 2–53 caves, and 3,086 individuals of the troglonitic taxa in 1–14 caves up to 96 m from the entrance and 80 m from the surface (Table 1). Most representatives of the non-troglonites are Central-European, Alpine, European or more widely distributed species, such as the Holarctic *Scoliopteryx libatrix*, while *Troglolyphantes diabolicus* is a local endemite. Among the troglonites, except for *Androniscus stygius*, all the others are endemic to an area from a few tens of to a few hundred km<sup>2</sup>. Only two troglonitic species: *A. stygius* and *Ceuthmonocharis robici*—with two subspecies—were represented by  $\geq 2$  individuals/cave, on average, while the others were rare. The spatial density maps of the 19 most abundant non-troglonites (Fig. 1) and 19 troglonites (Fig. 2) reveal that the majority of species were most frequently present either about 8 m equidistant, or 8 m distant from the entrance and 32 m from the

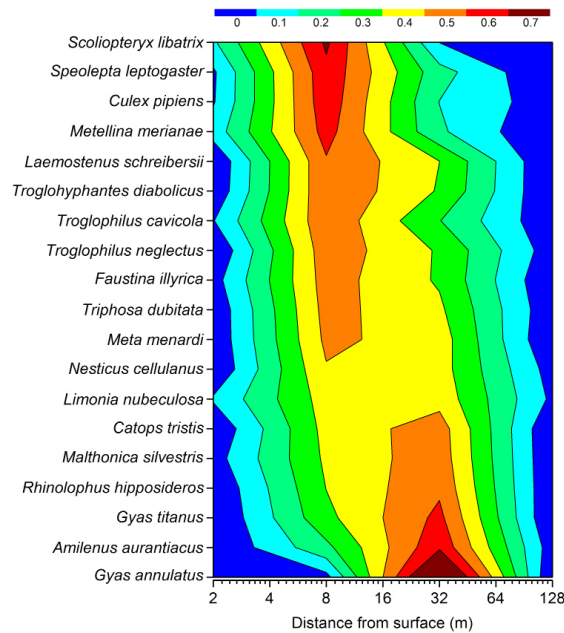
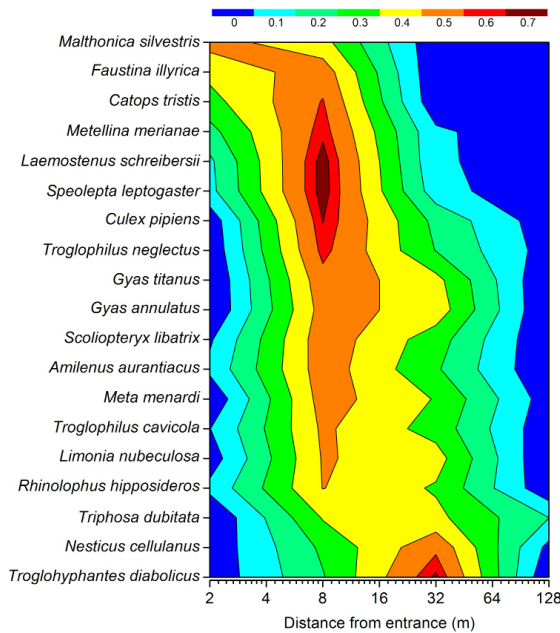


Fig. 1. Comparative normalized spatial density map of the 19 most abundant non-troglonites in cavities of central and eastern Slovenia. See text for comments.

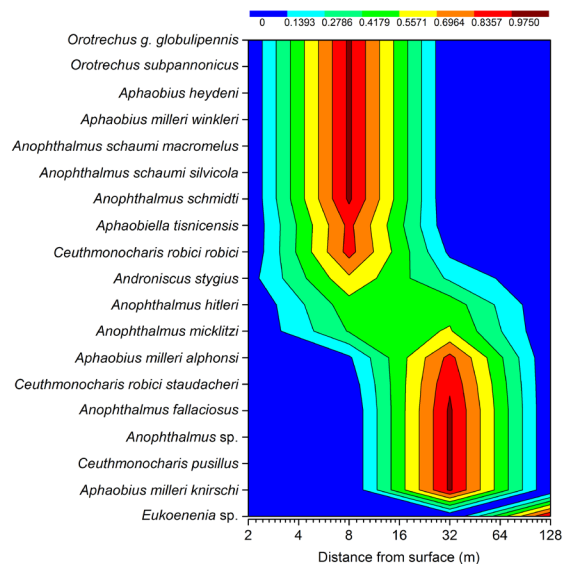
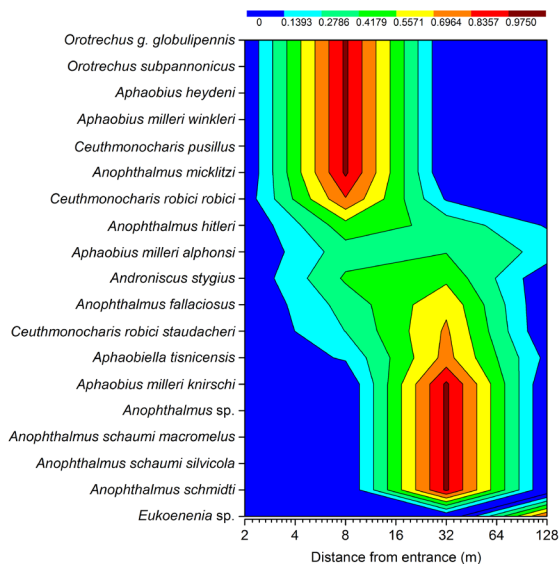


Fig. 2. Comparative normalized spatial density map of 19 troglonites in cavities of central and eastern Slovenia.



Table 1. List of species, their presence and abundance in investigated caves with respect to distance from the entrance and the surface. Traditional European classification (e.g., Juberthie & Decu, 1994): x troglone, f troglophile, b troglobionts, and Pavan-Ruffo classification (Sket, 2008): (s) subtroglophile, (e) eutroglophile.

Higher taxon	Family	Species	N of individuals	N of inhabited caves	N of presence observations	Distance from the entrance [m]	Distance from the surface [m]	
Gastropoda	Helicidae	x (s) <i>Faustina illyrica</i> (Stabile, 1864)	949	44	247	0–28	0–45	
Oniscoidea	Trichoniscidae	b <i>Androniscus stygius</i> Nemeč, 1897	104	14	70	2–77	2–80	
Opiliones	Phalangidae	x (s) <i>Amilenus aurantiacus</i> (Simon, 1881)	12,570	53	701	0–77	0–65	
		x (s) <i>Gyas annulatus</i> (Olivier, 1791)	120	4	14	3–55	12–30	
		x (s) <i>Gyas titanus</i> Simon, 1879	139	6	25	4–30	9–37	
Araneae	Agelenidae	x (s) <i>Malthonica silvestris</i> (L. Koch, 1872)	180	24	108	0–24	0–27	
	Linyphiidae	f (e) <i>Troglohyphantes diabolicus</i> Deeleman-Reinhold, 1978	100	15	72	0–66	2–37	
	Nesticidae	x (s) <i>Nesticus cellulanus</i> (Latreille, 1804)	282	21	132	0–65	0–65	
	Tetragnathidae	f (e) <i>Meta menardi</i> (Latreille, 1804)	3,107	48	555	0–69	0–65	
		x (s) <i>Metellina merianae</i> (Scopoli, 1763)	883	39	221	0–69	0–65	
Palpigradi	Eukoeneiidae	b <i>Eukoeneia</i> sp.	2	1	2	100	80	
Coleoptera	Carabidae	b <i>Anophthalmus hitleri</i> Scheibel, 1937	8	1	7	11–66	8–25	
		b <i>A. fallaciosus</i> (J. Müller, 1914)	3	2	3	10–30	18–24	
		b <i>A. micklitzii</i> (Ganglbauer in G. Müller, 1913)	7	2	4	9–13	3–16	
		b <i>A. schaumii macromelus</i> Jeannel, 1926	4	1	3	21–29	4–10	
		b <i>A. s. silvicola</i> Jeannel, 1928	1	1	1	41	11	
		b <i>A. schmidti</i> Sturm, 1844	3	1	3	30–41	9–11	
		b <i>Anophthalmus</i> sp.	1	1	1	25	32	
		f (e) <i>Laemostenus schreibersii</i> (Küster, 1846)	328	30	124	0–75	0–80	
		b <i>Orotrechus g. globulipennis</i> (Schaum, 1860)	2	1	1	8	9	
		b <i>O. subpannonicus</i> Daffner, 1994	4	1	2	6–11	8–11	
		Leiodidae	b <i>Aphaobiella tisnicensis</i> Pretner, 1949	63	4	18	9–90	7–65
			b <i>Aphaobius heydeni</i> Reitter, 1882	1	1	1	9	13
			b <i>A. milleri alphonsi</i> G. Müller, 1914	17	4	10	10–77	9–46
			b <i>A. m. knirschi</i> G. Müller, 1913	34	1	8	20–55	34–54
b <i>A. m. winkleri</i> Mandl, 1944	2		2	2	3–12	5–10		
x (s) <i>Catops tristis</i> (Panzer, 1794)	106		12	28	0–15	2–43		
b <i>Ceuthmonocharis pusillus</i> Jeannel, 1924	64		1	79	0–42	0–29		
b <i>C. robici robici</i> Ganglbauer, 1899	2,579		4	19	5–33	13–25		
	b <i>C. r. staudacheri</i> Müller, 1919	188	1	9	6–13	24–26		
Diptera	Culicidae	x (s) <i>Culex pipiens</i> (Linnaeus, 1758)	5,373	50	441	0–96	0–80	
		Limoniidae	x (s) <i>Limonia nubeculosa</i> Meigen, 1804	3,544	50	315	0–84	0–65
			f (e) <i>Speolepta leptogaster</i> (Winnertz, 1863)	575	31	235	0–68	0–64
Lepidoptera	Geometridae	x (s) <i>Triphosa dubitata</i> (Linnaeus, 1758)	539	32	187	0–75	2–65	
	Noctuidae	x (s) <i>Scoliopteryx libatrix</i> (Linnaeus, 1758)	836	50	265	0–84	2–65	
Orthoptera	Rhaphidophoridae	f (s) <i>Troglophilus cavicola</i> (Kollar, 1833)	15,730	48	1565	0–92	0–67	
		f (s) <i>Troglophilus neglectus</i> Krauss, 1879	5,673	44	1203	0–88	0–65	
Mammalia	Rhinolophidae	x (s) <i>Rhinolophus hipposideros</i> (Bechstein, 1800)	128	39	95	1–84	2–65	

surface or vice versa, while only six of them were 32 m, or deeper inside, equidistant from both (Tables 1, 2). With respect to distance from the entrance and from the surface, there were no statistical differences in any taxon (Mann-Whitney,  $0.069 > p > 0.953$  for the non-troglobiont, and  $0.754 > p > 0.981$  for the troglobionts) or within any group (Mann-Whitney,  $p = 0.454$  for the whole non-troglobiont group, and  $p = 0.427$  for the troglobiont group). This indicates that each species and each group as a whole inhabited hypogean habitats proportionally distant from the epigean en-

vironment, irrespective of the way of measuring the distance. The correlations between the density maps were nearly perfect within each group (entrance vs. surface, the non-troglobiont group,  $r = 0.951$ ; the troglobiont group,  $r = 0.972$ ), and high between the two groups (entrance vs. entrance,  $r = 0.721$ ; surface vs. surface,  $r = 0.770$ ). The troglobiont group was bimodal with two clearly separated subgroups (Fig. 2), and such a trend is also evident in non-troglobionts (Fig. 1). There was a highly significant difference in distribution between the non-troglobionts vs. the troglo-

Table 2. Species ranked according to frequency of presence in the 54 cavities with respect to distance from the entrance and the surface. Traditional European classification: x troglaxene, f troglophile, b troglobiont, and Pavan-Ruffo classification: (s) subtroglophile, (e) eutroglophile. Troglobionts adapted to the deep subterranean environment in grey.

Distance from the entrance [m]	Distance from the surface [m]			
	8	16	32	80
4	x (s) <i>Malthonica silvestris</i>			
8	x (s) <i>Faustina illyrica</i> f (e) <i>Meta menardi</i> x (e) <i>Metellina merianae</i> x (e) <i>Nesticus cellulanus</i> b <i>Anophthalmus hitleri</i> f (e) <i>Laemostenus schreibersii</i> b <i>Aphaobius heydeni</i> b <i>A. milleri winkleri</i> b <i>Ceuthmonocharis robici robici</i> b <i>Orotrechus g. globulipennis</i> b <i>O. subpannonicus</i> x (s) <i>Culex pipiens</i> f (e) <i>Speolepta leptogaster</i> x (s) <i>Scoliopteryx libatrix</i> x (s) <i>Troglophilus cavicola</i> x (s) <i>T. neglectus</i> x (s) <i>Rhinolophus hipposideros</i>	x (s) <i>Limonia nubeculosa</i>	x (s) <i>Amilenus aurantiacus</i> x (s) <i>Gyas annulatus</i> x (s) <i>G. titanus</i> b <i>Anophthalmus micklitzii</i> x (s) <i>Catops tristis</i> b <i>Ceuthmonocharis pusillus</i>	
16	x (s) <i>Triphosa dubitata</i>			
32	b <i>Andronuscus stygius</i> f (e) <i>Troglohyphantes diabolicus</i> b <i>Anophthalmus schauumi macromelus</i> b <i>A. schauumi silvicola</i> b <i>A. schmidti</i> b <i>Aphaobiella tisnicensis</i>		b <i>Anophthalmus fallaciosus</i> b <i>Anophthalmus</i> sp. b <i>Aphaobius milleri alphonsi</i> b <i>A. milleri knirschi</i> b <i>Ceuthmonocharis robici staudacheri</i>	
100				b <i>Eukoeneria</i> sp.

biont group with respect to distance from both the entrance and the surface (Mann-Whitney,  $p < 0.001$ ), caused by a bimodal presence of troglobionts. In the maps, the 8 m and 32 m groups represent the most distinctive regions, yielding  $\kappa \approx 10^{-6}$  and indicating nearly-perfect justification of grouping.

## DISCUSSION

The karst in Slovenia is the classical landscape for subterranean biology, often called the cradle of speleobiology. The caves under investigation together with adjacent epikarst, talus slopes and other SSHs form a more or less interconnected frame of subsurface habitats at the disposal of subsurface animals. For troglobionts that are rare in caves, cumulative frequencies of presence help to detect places where their preferred habitats inaccessible to humans are in contact with a cave. These data are even more limited than their low abundance data, rendering impossible the use of most standard statistical methods. Spatial density maps are applicable to abundant data, like studying a species or community dynamics (e.g., Novak et al., 2010b), as well as to such limited datasets.

With respect to their activity in the subterranean environment, the recorded non-troglobionts represent a network of species, showing a range of habitat adaptations, rather than two ecologically clearly separated groups. Most of them belong to the parietal associa-

tion, i.e., animals sojourning especially on the cave walls and ceiling near entrances. Except in a few cases (e.g., Novak et al., 2010a), these assemblages differ in composition and functioning to a limited extent from France to Romania. While these are only exceptionally endemic, troglobionts are highly endemic as reported for many stygobionts and other troglobionts (Gibert & Deharveng, 2002; Christman et al., 2005; Culver & Pipan, 2009a; Reboleira et al., 2011). In this way, a number of widely distributed and locally endemic SSH species co-occur by chance; no characteristic ecological community can be recognized (cf. Ricklefs, 2008). While non-troglobiotic taxa have been ecologically relatively well investigated (Supplement 1), the troglobionts have in principle not been studied or have been understudied.

Many SSH species are dependant on roots (Juberthie et al., 1980; Ashmole, 1994). Rich troglobiotic fauna has been reported from shallow lava tubes (e.g., Medina & Oromi, 1990; Oromi et al., 1990; Howarth, 2004; Howarth et al., 2007) and from shallow Brazilian caves, especially ferruginous ones (Souza-Silva et al., 2011), all of them with extensive tree root systems protruding into the caves and directly or indirectly supporting the cave fauna. The lava and iron ore rocks provide an extensive SSH system of micro- and meso-voids, probably allowing migration of the fauna into macro-caves (Souza-Silva et al., 2011). In the temper-

ate biome, trees grow relatively shallow roots, maximally 4.4–6.3 m deep (Canadell et al., 1996). This is why in the caves from our investigation they rarely grow through the ceiling. Besides, larger fissures and similar habitats connecting caves and adjacent SSHs are mostly as unstable as the cave entrance zone, representing an ecotone between the epigeal and hypogean environments (Prous et al., 2004; Culver, 2005). This is true at least with respect to the air flow, causing troglobionts to avoid such habitats. Consequently, these habitats contribute only occasional SSH individuals to cave biota by hazard. In spite of that, the much larger number of troglolobiotic taxa in the shallow peak of their bimodal distribution indicates that the SSH species are the most diverse group of troglolobionts. This demonstrates the crucial importance of research into this group, adapted to the deep root zone, i.e., the rhizosphere (Cardon & Whitbeck, 2007), for progress in understanding the ecology of the subterranean environment as well as of ecosystems providing the deep rhizosphere. Deep subterranean troglolobionts are much less diverse. Among them, at least a few inhabit the terrestrial phreatic environment – «milieu phreatique terrestre» *sensu* Jeannel (1926), i.e., habitats consisting of tiny water trickles in channels originating in the epikarst and passing into the deep karstic massifs. Such a case is the bathysciid beetle *Aphaobiella tisnicensis*, occurring in mass (more than 1000 individuals per m<sup>2</sup>) in the hardly accessible cave Štravsova luknja near Velenje (not among the 54 investigated caves) on slowly percolated sandy ground (own unpublished data).

Our finding that most non-troglolobionts and troglolobionts are primarily distributed and coexist within the upper 10 m of subsurface strata is, in addition, congruent with the following facts. The belowground communities are usually much more diverse than the corresponding aboveground ones (Wardle, 2006); multiple independent colonization of the subterranean habitat is common in cave-adapted species (Porter, 2007) and in terrestrial species most probably via the SSHs (Růžička, 1999; Culver & Pipan, 2009b); moreover, species diversity generally declines from the shallow towards the deep subterranean habitats (Culver & Pipan, 2009a). To most non-troglolobionts, the entrance cave zone represents either a preferable habitat or merely a conduit from the epigeal habitat to deeper habitats where a daily rest or seasonal inactive hypogean ecophase can unfold and vice versa. To the other non-troglolobionts and all troglolobionts, the entrance cave zone acts as a disturbance, disrupting, or limiting their preferred subsurface habitat within the range from SSHs to deep caves.

In conclusion, the terrestrial fauna in the classical European subterranean environment consists of two well separated faunas: The SSH fauna is represented by non-troglolobionts and a major group of troglolobionts, while the deep subterranean fauna consists of a minor group of troglolobionts. Thus, troglolobionts are strictly divided into the two identified ecological subgroups. Consequently, non-troglolobionts as well as troglolobionts are most diverse and randomly distributed in the upper 10 m of subsurface strata corresponding to the cave entrance zone and the SSHs. Wherever in

the world troglolobionts occur in vegetation landscapes, they most likely inhabit the soil root zone, and, if also present in deep subterranean habitats, they can be expected to be much more diverse in the SSHs.

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**Supplement 1.** Publications, additional to the general references, providing ecological information on the most abundant non-troglobionts in central Europe. – Available on request from the authors.