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Mesofauna at the Soil-Scree Interface in a Deep Karst Environment

Nikola Jureková [1,*], Natália Raschmanová [1], Dana Miklisová [2] and Ľubomír Kováč [1]

[1] Department of Zoology, Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Šrobárova 2, SK-04180 Košice, Slovakia; natalia.raschmanova@upjs.sk (N.R.); lubomir.kovac@upjs.sk (Ľ.K.)

[2] Institute of Parasitology, Slovak Academy of Sciences, Hlinkova 3, SK-04001 Košice, Slovakia; miklis@saske.sk

* Correspondence: nikola.jurekova@student.upjs.sk

Abstract: The community patterns of Collembola (Hexapoda) were studied at two sites along a microclimatically inversed scree slope in a deep karst valley in the Western Carpathians, Slovakia, in warm and cold periods of the year, respectively. Significantly lower average temperatures in the scree profile were noted at the gorge bottom in both periods, meaning that the site in the lower part of the scree, near the bank of creek, was considerably colder and wetter compared to the warmer and drier site at upper part of the scree slope. Relatively high diversity of Collembola was observed at two fieldwork scree sites, where cold-adapted species, considered climatic relicts, showed considerable abundance. The gorge bottom, with a cold and wet microclimate and high carbon content even in the deeper MSS horizons, provided suitable environmental conditions for numerous psychrophilic and subterranean species. Ecological groups such as trogloxenes and subtroglophiles showed decreasing trends of abundance with depth, in contrast to eutroglophiles and a troglobiont showing an opposite distributional pattern at scree sites in both periods. Our study documented that in terms of soil and subterranean mesofauna, colluvial screes of deep karst gorges represent (1) a transition zone between the surface and the deep subterranean environment, and (2) important climate change refugia.

Keywords: inversed scree slope; vertical distribution; microclimate; psychrophilic species; climatic relicts

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1. Introduction

A mesovoid shallow substratum—MSS [1,2]—represents an extensive underground ecosystem formed by a widespread network of air-filled voids and open spaces inside multiple layers of rock fragments [3,4]. Like caves, MSSs are characterized by perpetual darkness, low energy inputs and buffered microclimatic conditions. These habitats include rocky debris and screes of varying size ranging from low to high altitudes of the temperate zone, in both calcareous and non-calcareous rocks [3,5].

In Europe, some scree accumulations with perennially cold microclimates are commonly known as ice-bearing taluses or cold/freezing screes. This phenomenon has been documented on hills and mountain slopes [6–9]. Analogous conditions may be found in limestone deposits spread across low to middle altitude karst landforms, such as collapse dolines of ice caves or the cold bottoms of deep gorges and valleys that have historically experienced a periglacial climate and thus can serve as unique refugia for cryophylic (psychrophilic) invertebrates, especially in terms of the ongoing climate change [10–17]. The climatic conditions inside cold screes are often characterized by a strong thermal inversion [4]. The specific air flow passing through the interstitial voids leads to the development of a highly conservative and stable cold microclimatic regime in the lower parts of the scree slope, potentially resulting in the formation of solid ice or sporadic permafrost [12,15,18–23]. In the winter months, the thermal contrast between the internal scree accumulation and the external air creates a "chimney effect" that leads to the warming of the scree top, while the bottom remains constantly and strongly subcooled and shows high values of soil moisture throughout the year [19,22]. Moreover, many other factors, such as topography, altitude, sun exposure and vegetation cover, contribute to the differences in the microclimate between the bottom and the top of the scree slope [16,24].

It is known that periods of the year affect the basic ecological attributes of arthropod assemblages in scree slope habitats, such as richness and abundance, which often positively correlate with temperature [9,11,25–33]. Furthermore, the scree microclimate has also been suggested as being an important factor affecting the vertical migration of invertebrates from the surface deeper into MSS habitats with microclimatically stable conditions to avoid a harsh external climate, resulting in the formation of specific community patterns and their dynamics along a depth gradient in scree slopes [9,11,27–31]. The availability of organic carbon content along the depth gradient is another crucial limiting factor in an MSS [30,34]. The presence of vegetation and the amount of leaf litter and humus on the surface contributes to nutrient resources in the MSS and may significantly influence the biodiversity patterns in this habitat [9,30,35].

Habitats that remain humid during the whole year, such as protected gorges, dolines or cold scree deposits, may experience the greatest thermal stability and resilience to climate changes [36,37] and thus can provide long-term shelters (refugia) for arthropods sensitive to temperature fluctuations, especially cold-adapted/psychrophilic taxa [16,38–40]. Therefore, it is important to identify such refugia within MSS habitats that may sustain high levels of underground biodiversity [9,24,27,41–43].

Several studies focused on Collembola along inversed scree habitats have been conducted by authors of the present study. Among others, [33,42,44] concluded that microclimate is a major driver of diversity for Collembola occupying superficial scree layers along microclimatic gradients on karstic slopes. In the present study, we focused on a long slope scree in a deep karstic gorge, unique in Central Europe. We hypothesized that the diversity, vertical distribution and community composition of Collembola along this microclimatically inversed scree slope would markedly differ as a result of the primary role of the thermal regime. We also hypothesized that the period of the year (warm vs. cold) would substantially affect these community patterns at both scree sites. Since MSS habitats are considered as an ecotonal zone between the epigean and deep hypogean domain [3,45,46], we also expected the occurrence of obligate cave-dwellers (troglobionts) in the deeper levels of the scree sites. Moreover, scree slopes are often inhabited by specialized cold-adapted species, most of them considered as unique climatic relicts, which may significantly contribute to MSS biodiversity. We expected their predominance at the cold scree site at the gorge bottom. Finally, scree habitats with inversed microclimatic conditions are vulnerable environments, where global warming may lead to the loss of relict forms of invertebrates and consequently to the reduction of biodiversity in these unique natural habitats. Thus, preservation of these karst landforms and their sensitive soil biota should be a central part of biodiversity conservation programs.

The objectives of the present study were: (1) to compare diversity, vertical distribution and community structure of Collembola at two sites on a microclimatically inversed scree slope in two different periods of the year, (2) to analyse the responses of ecological groups of Collembola regarding their affinities to subterranean habitats and to climatic conditions in the given periods, and (3) to assess the function of scree slopes in deep karst valleys as potential climate refugia for psychrophilic forms of soil and subterranean fauna.

2. Materials and Methods

2.1. Study Area and Site Description

The Slovak Karst National Park, as a part of the Slovak and Aggtelek Karst region, is situated in the Western Carpathians, in south-eastern Slovakia (Figure 1A). The region is characterized by typical karst landform features, such as dolines, sinkholes, deep valleys and gorges, and a series of karst plateaus in a mid-latitude karst terrain between 400 to 900 m above sea level. It is located at the junction between the oceanic and continental climatic zones, with the mean annual temperature ranging from 5.7 to 8.5 °C, annual average precipitation from 630 to 990 mm, and average height of snow cover ranging from 50 to 100 mm [47,48].

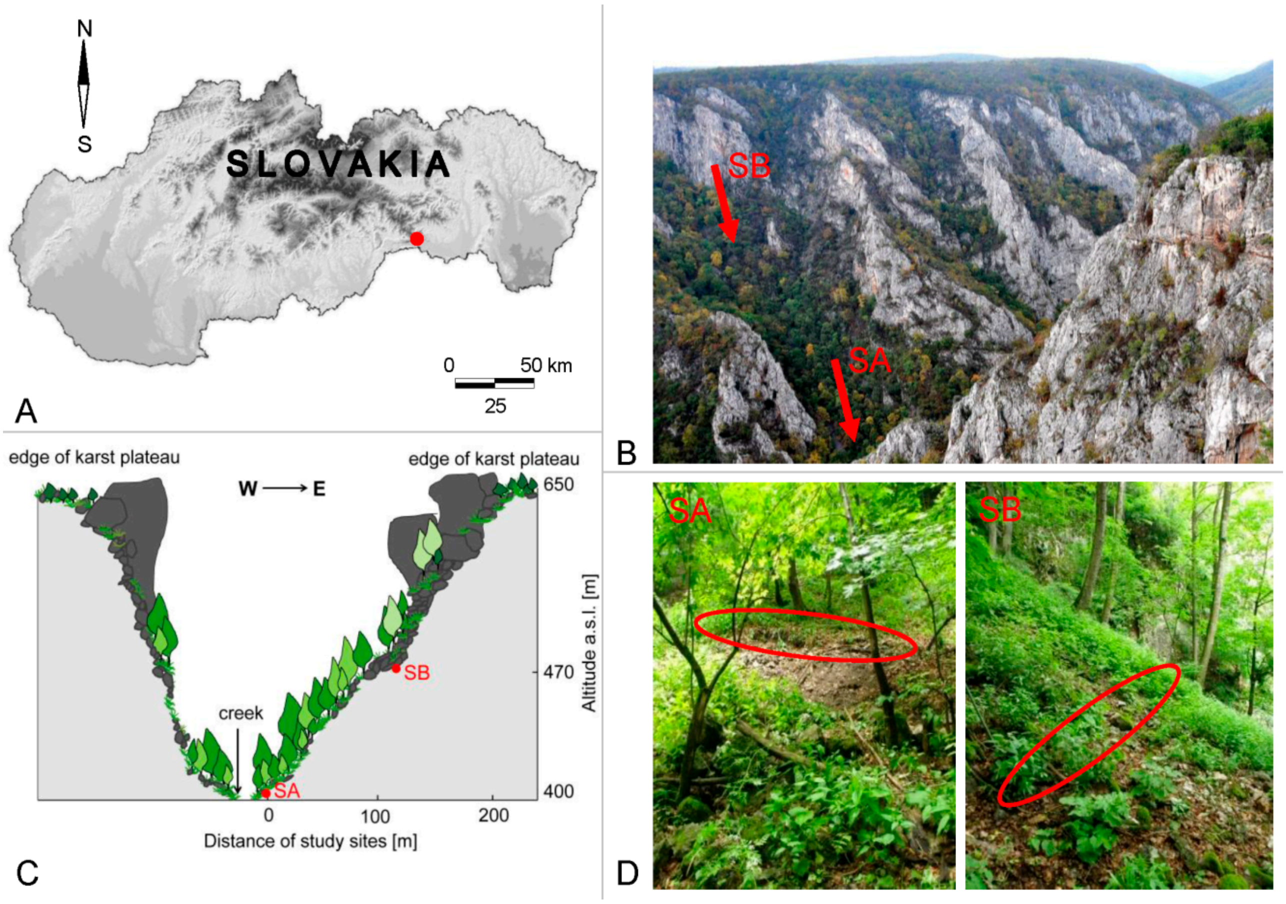

Figure 1. (**A**) Location of the Zádiel Valley; (**B**) Scree slope in the Zádiel Valley with the position of the study sites SA and SB (Photo: Ľ. Kováč); (**C**) Schematic cross-section of the valley with the position of the study sites on the scree slope; (**D**) Red ellipse—position of subterranean traps at sites on the slope (Photo: P. Ľuptáčik).

The Zádiel Valley National Nature Reserve (48°37′4″ N and 20°49′56″ E) is a 3-km long karst valley created by intense erosion of the Middle Triassic Wetterstein limestones by the Blatnica Creek (Figure 1B). The lower part of the valley is a gorge that has a distinctly rocky character, with the narrowest section only 10 m wide. The gorge is also characteristic with a series of limestone cliffs reaching an overall height of more than 300 m, vertically divided by long and narrow gullies filled by stony deposits-screes. The locality is well-known for its microclimatic and vegetation inversion, the microclimate at the gorge bottom is markedly colder than that of the karstic plateau situated above (e.g., [32,41,49]).

The studied scree slope was 150 m long and 30 m wide at the base of the gorge. Two sites, one at the bottom and the other at the top of the steep scree slope, were selected at a distance of 120 m apart and 70 m in elevation. The depth of the valley in this section is around 250 m (Figure 1B–D):

SA—The lower site of the slope near the bank of the Blatnica Creek (~10 m), 400 m a.s.l., E exposure, slope 35°, dense maple-lime wood (association *Aceri-Tilietum*) and sparse herbal cover (*Urtica dioica* and *Lunaria rediviva* dominated) with mosses, soil type rendzina. The scree profile comprised of three well-defined layers: (1) 0–15 cm—leaf litter and humus, (2) 15–45 cm—organo-mineral layer formed by fist-size rocks and dark soft soil, rhizosphere less-developed, and (3) 45–100 cm—a scree formed by larger rocks (30–40 cm in diameter) with spaces partially filled with the soil and tree roots.

SB—The upper site of the slope below the rock cliff, 470 m a.s.l, E exposure, slope 35°, dense maple-ash wood (association *Aceri-Fraxinetum*), herbal cover and soil type as in SA. Three distinct layers were observed in the scree profile: (1) 0–5 cm leaf litter and humus, (2) 5–40 cm—an organo-mineral layer with well-developed rhizosphere and spaces between small stones (10–15 cm in diameter) largely filled with soil, and (3) 40–100 cm—a layer with aggregations of small stones with spaces between them partially filled with soil and tree roots.

2.2. Field Sampling

Collembola communities were studied in two climatically different periods of the year: (1) a "warm" period—W: 21 May–19 October 2018 (including three summer months)—and (2) a "cold" period—C: 19 October 2018–15 April 2019 (including three winter months)—and were collected twice, on 19 October 2018 and 15 April 2019 (i.e., one sampling per each period at the given site). The invertebrate sampling was performed roughly 12 months after the burying of subterranean traps, since their installation temporarily disrupts the structure of scree slope layers and thus affects the abundance of some sensitive invertebrate species [30,31,35,50].

Collembola were collected using the method of subterranean traps designed after Schlick-Steiner and Steiner [51]. The traps consisted of 1-m long plastic pipes (Ø 10.5 cm) with small perforations (Ø 0.8 cm) allowing invertebrates to enter the tubes at ten horizontal levels (5, 15, 25, 35, 45, 55, 65, 75, 85 and 95 cm) and a set of 10 plastic cups (volume 500 mL) fixed on a moving metal rod, which were place inside each pipe. At both sites, five traps were buried vertically up to 1 m deep, at a distance of 50 cm from each other, filled with propylene glycol fixative solution and covered up with a plastic lid. Altogether, 200 samples were taken by subterranean pitfall traps (2 periods × 2 scree sites × 5 trap pipes × 10 depth horizons). The collected material was poured into plastic bottles and transported to the laboratory.

Collembola were mounted on permanent slides according to Rusek [52] and identified to the species level using a Leica DM1000 phase-contrast microscope (Leica Microsystems GmbH, Wetzlar, Germany) and multiple taxonomic keys (e.g., [53–58]). Juveniles belonging to the families Entomobryidae and Tomoceridae could not be determined to the species level and therefore were not included in the total species number (Appendices A and B). The specimens are deposited in the collection of the Department of Zoology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Slovakia.

2.3. Soil Microclimatic and Soil-Chemical Data

Soil temperature was measured periodically at four-hour intervals in the two periods at both sites, using two series of thermo-data loggers (iButton DS1921G, Maxim Integrated, San José, CA, U.S.), which were part of the marginal cups (first and fifth set of traps) at four depths of 5, 35, 65 and 95 cm and calculated as daily averages. For both sites, the mean, maximum and minimum soil temperatures (T) for the warm (W) and cold (C) period (T_W/T_C, $T_{W\,max}/T_{C\,max}$ and $T_{W\,min}/T_{C\,min}$) were separately calculated. Differences in average soil temperatures for the warm and cold periods between the two sites at four depths were tested by Wilcoxon signed-rank test in Statistica for Windows, version 12 [59].

Soil samples for additional edaphic variables were taken at four scree depths of 5, 35, 65 and 95 cm per site excavations before the installation of traps in June 2017. Organic carbon content (C_{org}) and soil pH_{H_2O} were analysed at the Soil Science and Conservation Research Institute, Bratislava, Slovakia. Carbon content was analysed using a "dry" method, according to Kobza [60] and soil pH_{H_2O} was measured potentiometrically at the rate of 1:5 (soil:deionised water suspension). Three samples were taken for the gravimetric content of soil moisture (W) from each of the same four depths per site to document the actual soil microclimate.

2.4. Collembola Diversity, Abundance and Vertical Distribution

Species richness (number of species) (S) and abundance (number of specimens) (N) of the collembolan communities were evaluated at both study sites (SA and SB) at individual depths (5–95 cm) separately for the two sampling periods (warm and cold). For a comparison of Collembola abundance in the two sampling periods, the total numbers of specimens out of five samples per each depth were used.

Species dominance (D) at both sites was calculated for both sampling periods (warm, cold); species with $D > 7\%$ were considered as numerically dominant [61].

2.5. Ecological Groups of Collembola

The cold-adapted (psychrophilic) species were distinguished based on our own (unpublished) data and literature data (Appendices A and B). The vertical distribution of ecological groups during the studied periods at both sites was depicted graphically.

Four troglogroups of Collembola were distinguished based on their affinity to the subterranean (cave) environment, after Sket [62]: (1) trogloxenes − epigean species occurring sporadically in subterranean habitats, unable to establish a subterranean population; (2) subtroglophiles − species occurring subterranean habitats perpetually or temporarily, intimately associated with the surface in some biological functions; (3) eutroglophiles − epigean species able to inhabit underground habitats permanently; and (4) troglobionts − species strictly bound to subterranean habitats. The individual species were assigned to these categories basically after Kováč [63].

2.6. Statistical Analyses

Differences in species composition between the sites and sampling periods were examined using non-metric multidimensional scaling (NMS) with Sörensen (Bray-Curtis) distance recommended for community data [64]. This unconstrained analysis was run with Collembola abundance at individual sites using PC-ORD software [65].

The Pearson correlation coefficient was used to evaluate the impact of environmental parameters on species richness and abundance of Collembola, ecological groups and selected dominant species, together for sites and sample periods. Only cases with an absolute value of the coefficient >0.5 are presented without formal testing of its statistical significance due to the low amount of data (soil-chemical parameters were measured at each site only at four depths). Correlation analysis was performed using Statistica for Windows, version 12 [59].

3. Results

3.1. Soil Microclimatic and Soil-Chemical Data

Both sites differed considerably in temperature regime, with site SA markedly colder than site SB throughout the year (Table 1 and Figure 2). At both sites, minimum daily temperatures on the scree surface (5 cm depth) were recorded during January and February and occurred only shortly (1–1.5 or 2 days). Maximum daily temperatures on the surface occurred at intervals of 2–4 and 1–2 days during August and early September. T_W and T_C were significantly different between the two sites at $p < 0.05$. (Table 1 and Figure 2).

Table 1. Microclimatic and soil-chemical characteristics (mean ± standard deviation) at two scree slope sites in the Zádiel Valley.

Site	SA	SB		SA	SB
T_W [°C]			W [%]		
5 cm	8.9 ± 1.9 ^{a}	16.5 ± 3.1 ^{b}	5 cm	75.6 ± 2.9	71.1 ± 13.0
35 cm	6.2 ± 2.2 ^{a}	16.7 ± 2.3 ^{b}	35 cm	53.8 ± 4.3	68.4 ± 3.4
65 cm	5.8 ± 2.2 ^{a}	16.7 ± 2.1 ^{b}	65 cm	47.1 ± 2.8	65.4 ± 8.5
95 cm	5.4 ± 2.1 ^{a}	16.6 ± 2.1 ^{b}	95 cm	54.2 ± 10.3	21.1 ± 3.1
T_C [°C]			pH_{H_2O}		
5 cm	1.1 ± 4.3 ^{a}	6.4 ± 3.7 ^{b}	5 cm	6.9	7.2
35 cm	0.7 ± 3.8 ^{a}	8.5 ± 3.2 ^{b}	35 cm	7.7	7.3
65 cm	0.7 ± 3.7 ^{a}	8.7 ± 3.1 ^{b}	65 cm	7.7	7.7
95 cm	0.6 ± 3.6 ^{a}	8.7 ± 3.1 ^{b}	95 cm	7.6	7.0
			C_{org} [%]		
$T_{W\,min}$ [°C]	−0.1	9.1	5 cm	52.5	47.0
$T_{W\,max}$ [°C]	12.0	23.0	35 cm	31.3	46.0
$T_{C\,min}$ [°C]	−8.4	−0.5	65 cm	28.6	24.3
$T_{C\,max}$ [°C]	9.9	16.0	95 cm	29.4	13.8

T_W—average temperature in the warm period (average value from daily temperature means, May 2018–October 2018), T_C—average temperature in the cold period (average value from daily temperature means, October 2018–April 2019), $T_{W\,min}$—daily minimum temperature in the warm period, $T_{W\,max}$—daily maximum temperature in the warm period, $T_{C\,min}$—daily minimum temperature in the cold period, $T_{C\,max}$—daily maximum temperature in the cold period, W—average soil moisture, soil pH_{H_2O}, C_{org}—organic carbon content, (for site abbreviations, see the section "Material and Methods"), Significant differences between temperature means are indicated by superscript letters (a,b).

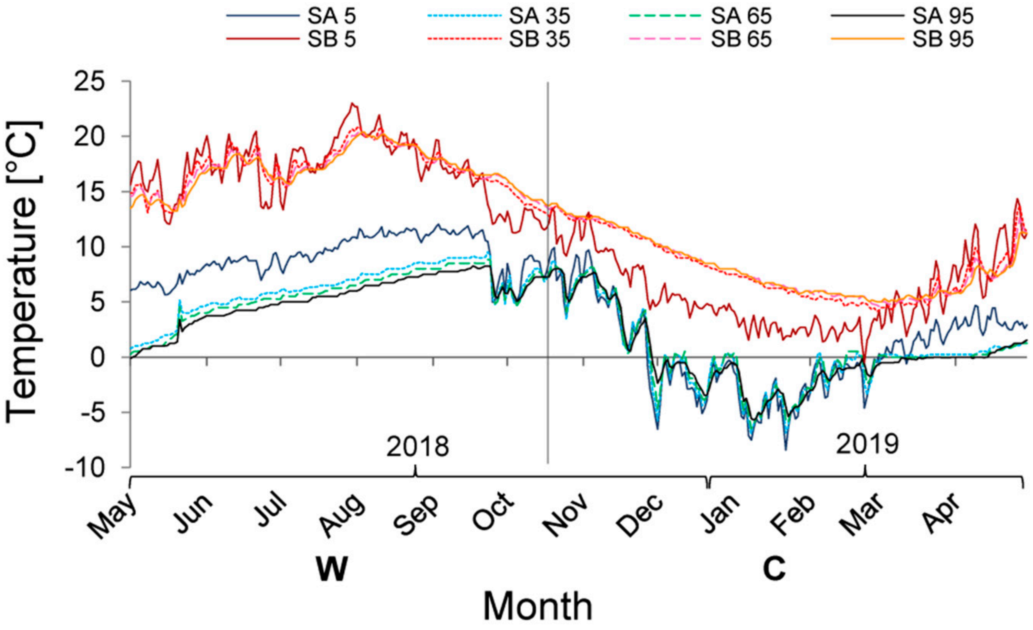

Figure 2. Temperature regime based on daily temperature means along the depth gradient at both sites in two different periods; W—warm period (May 2018–October 2018), C—cold period (October 2018–April 2019), 5, 35, 65, 95—soil/scree depth [cm].

The middle and deeper layers (35–95 cm) showed considerably smaller temperature fluctuations; however, at site SA during the cold period the variation was relatively high across the whole depth profile.

Regarding depth patterns of the soil temperature (Figure 2), in the warm period the average temperature gradually decreased with depth at site SA, with the occurrence of ice crystals in its deeper levels (75–95 cm) in the beginning of the period (May 2018). On the other hand, at site SB a less marked pattern in temperature means was recorded along the whole depth profile in the warm period. In the cold period, an increasing temperature trend with depth was observed at site SB, while at SA it slightly decreased with depth.

The soil moisture content showed a declining trend with increasing depth at both sites, with markedly higher content in the deeper layer (95 cm) recorded at site SA compared to SB (Table 1). At both sites, soil pH_{H_2O} increased with increasing depth, with the exception of the depth 95 cm at SB, where a noticeable lower pH value was measured (Table 1). The organic carbon content showed a declining trend with increasing depth at both sites, with noticeable higher contents in deeper layers (65–95 cm) recorded at site SA compared to SB.

3.2. Collembola Diversity, Abundance and Vertical Distribution

A total of 32,155 specimens of Collembola comprising 58 species were captured in subterranean traps at both sites of the scree slope during the two climatic periods (Appendices A and B). The number of specimens varied considerably among the the five subterranean traps at the given site, ranging from 18 to 819 at site SA and from 11 to 249 at site SB. Regarding the number of species captured, at site SA the species number ranged from 6 to 21 and at site SB from 3 to 20.

Both sites differed in the diversity and vertical distribution of Collembola (Appendices A and B). Overall, higher abundance (21,330 specimens) and species richness (50 species) were recorded at scree site near the valley bottom (SA) compared to the upper slope site (SB), with 10,825 specimens and 44 species. Regarding the studied periods, at site SA the same species number was recorded in vertical profile in both periods (41 species), but the abundance was more than twice as high in the warm period (14,681 specimens) compared to the cold one (6649 specimens). In contrast, site SB showed a higher species diversity (37 species) and abundance (6176 specimens) in the cold period compared to the warm one (32 species, 4649 specimens).

At site SA, a decreasing trend in abundance to the depth of 45 cm and significantly high values of this parameter were recorded in the middle and especially in the deeper levels of the scree profile (55–95 cm) in the warm period, with a high abundance of adults of *Ceratophysella granulata*, *Plutomurus carpaticus*, *Protaphorura armata* and *Pygmarrhopalites pygmaeus* (Figure 3A). The species richness declined to depth 35 cm and an unclear trend was observed in the deeper scree layers. In the cold period, both abundance and species richness showed an identical trend (decreasing between 45–95 cm), with peaks at 15–25 and 45–55 cm (Figure 3B). At the second site (SB), relatively balanced trends in the number of species and specimens across the scree depth were recorded in the warm period (Figure 3C), and principally declining trends in collembolan species richness and abundance with increasing depth were recorded in the cold period, showing higher abundances of *Neelus koseli* and *Plutomurus carpaticus* in the deeper scree layers (Figure 3D).

Ceratophysella granulata was among the dominant species at site SA in the warm period. At site SB, two species, *Pseudosinella horaki* and *Pygmarrhopalites principalis* were dominant along the entire scree profile in the warm period. *Pygmarrhopalites pygmaeus* showed different patterns, being numerous along the entire vertical gradient at site SA in the warm period and at site SB in the cold period. The species *Lepidocyrtus lignorum* was abundant in both periods at both sites.

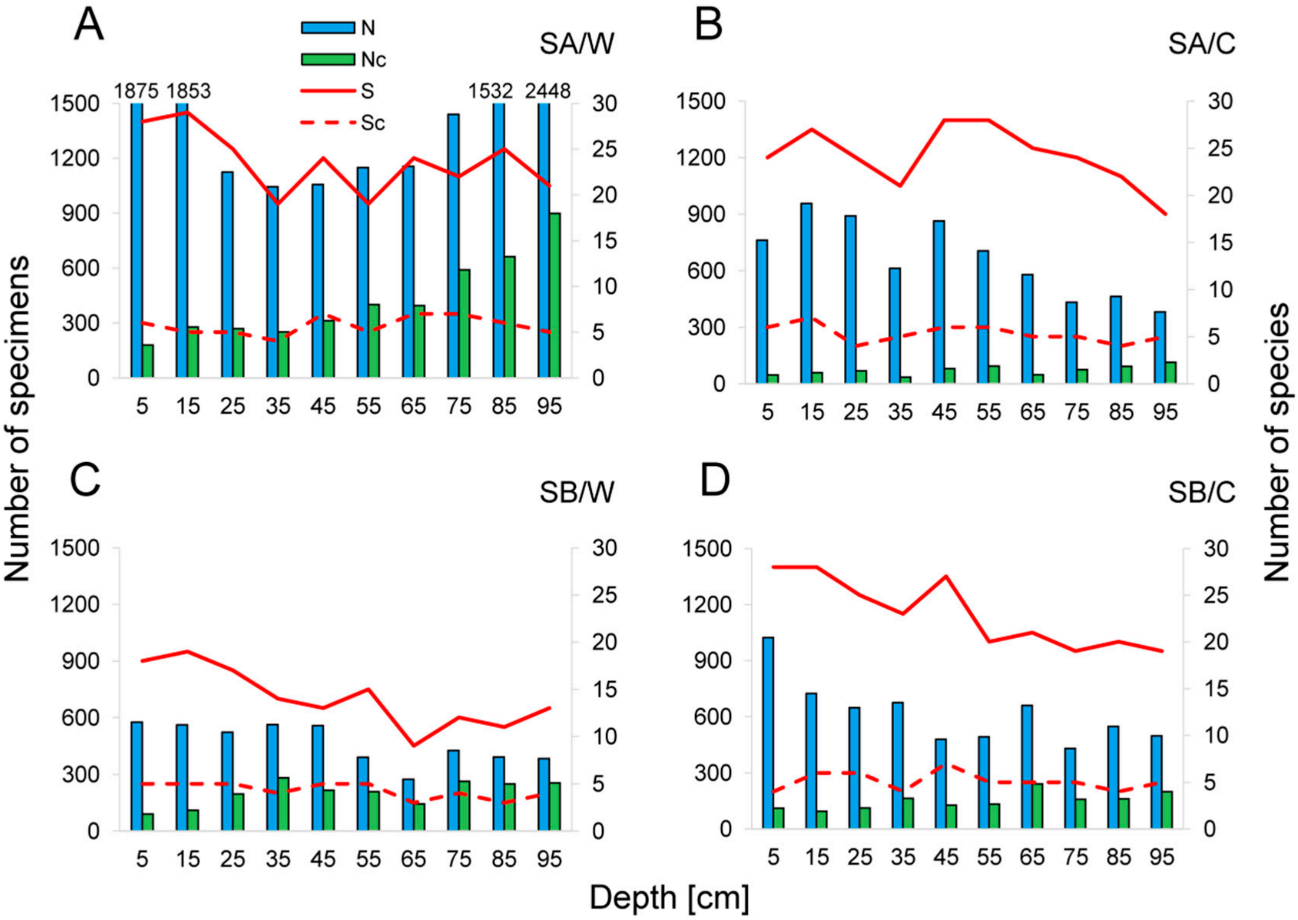

Figure 3. (**A**–**D**) Vertical distribution of Collembola and separately cold-adapted species along the depth profile (5–95 cm) at two scree sites (SA, SB) in two periods; W—warm period, C—cold period, N—total number of Collembola specimens, Nc—number of specimens of cold-adapted species, S—total number of Collembola species, Sc—number of cold-adapted species.

Twelve species were exclusively captured at site SA, e.g., the abundant species *Ceratophysella granulata*, and three species at site SB, e.g., the abundant *Neelus koseli*.

Three species were Carpathian/Western Carpathian endemics, namely *Neelus koseli*, which occurred in the middle and deeper parts of the scree exclusively at site SB and in both periods; *Plutomurus carpaticus*, whose abundance increased with depth at both sites and in both periods; and *Morulina verrucosa*, collected only in small numbers on the surface layer of site SA in the cold period (Appendices A and B).

3.3. Vertical Distribution of Ecological Groups

A total of 14 cold-adapted species (24.1%) were recorded at both sites (mainly sub- and eutroglophiles). The number of species ranged between the warm (W) and cold (C) periods: at SA from 8 (W) to 9 (C) and at SB from 5 (W) to 8 (C). At site SA the number of specimens of cold-adapted species ranged from 711 (C) to 4238 (W), and at site SB from 1503 (C) to 2019 (W), respectively. At site SA, a higher number of cold-adapted species was observed at deeper layers in both periods. While high abundance of specimens markedly increased with depth in the warm period (Figure 3A), very low and balanced values of this parameter were observed along the depth gradient in the cold period (Figure 3B). At site SB, the number of cold-adapted species showed a relatively balanced trend along the whole scree profile in both periods. High abundance of these forms was recorded at a depth of 35 cm and at greater depths (75–95 cm) in the warm period (Figure 3C); in cold months, their abundance increased slightly to a depth of 65 cm with the balanced parameter in the deeper horizons of the scree profile (75–95 cm) (Figure 3D).

The species richness of troglogroups associated with subterranean habitats differed at both sites between the warm and cold period, respectively (Appendices A and B): trogloxenes 15 vs. 15 at site SA and 12 vs. 9 at site SB; subtroglophiles 14 vs. 15 at SA and 12 vs. 14 at SB; and eutroglophiles 12 vs. 11 at SA and 7 vs. 13 at SB. One troglobiont (*Neelus koseli*) was captured at site SB in both periods. Regarding the abundance of these ecological groups per trap, the differences between the warm and cold periods were the following: trogloxenes 363 vs. 335 at SA and 189 vs. 268 at SB; subtroglophiles 7866 vs. 5015 at SA and 2071 vs. 2850 at SB; eutroglophiles ranged from 6436 vs. 1045 at SA and 2256 vs. 2650 at SB; and finally abundance of the troglobiont 128 vs. 170 (site SB).

At both sites and in both periods, trogloxenes and subtroglophiles showed decreasing trends of abundance with increasing depth, with especially steep trend lines at site SA in the warm period (Figure 4A,B). On the other hand, eutroglophiles and troglobionts showed the opposite, i.e., increasing trends of abundance with depth (Figure 4C,D). In detail, the abundance of eutroglophiles slightly increased with depth at site SA in the cold period and at site SB in both periods. A notable increase in the abundance of eutroglophiles with depth was recorded at site SA in the warm period, associated with several species, such as *Ceratophysella granulata*, *Plutomurus carpaticus* and *Pygmarrhopalites pygmaeus*. The troglobiont *Neelus koseli* showed an increasing trend of abundance with depth at site SB in both periods.

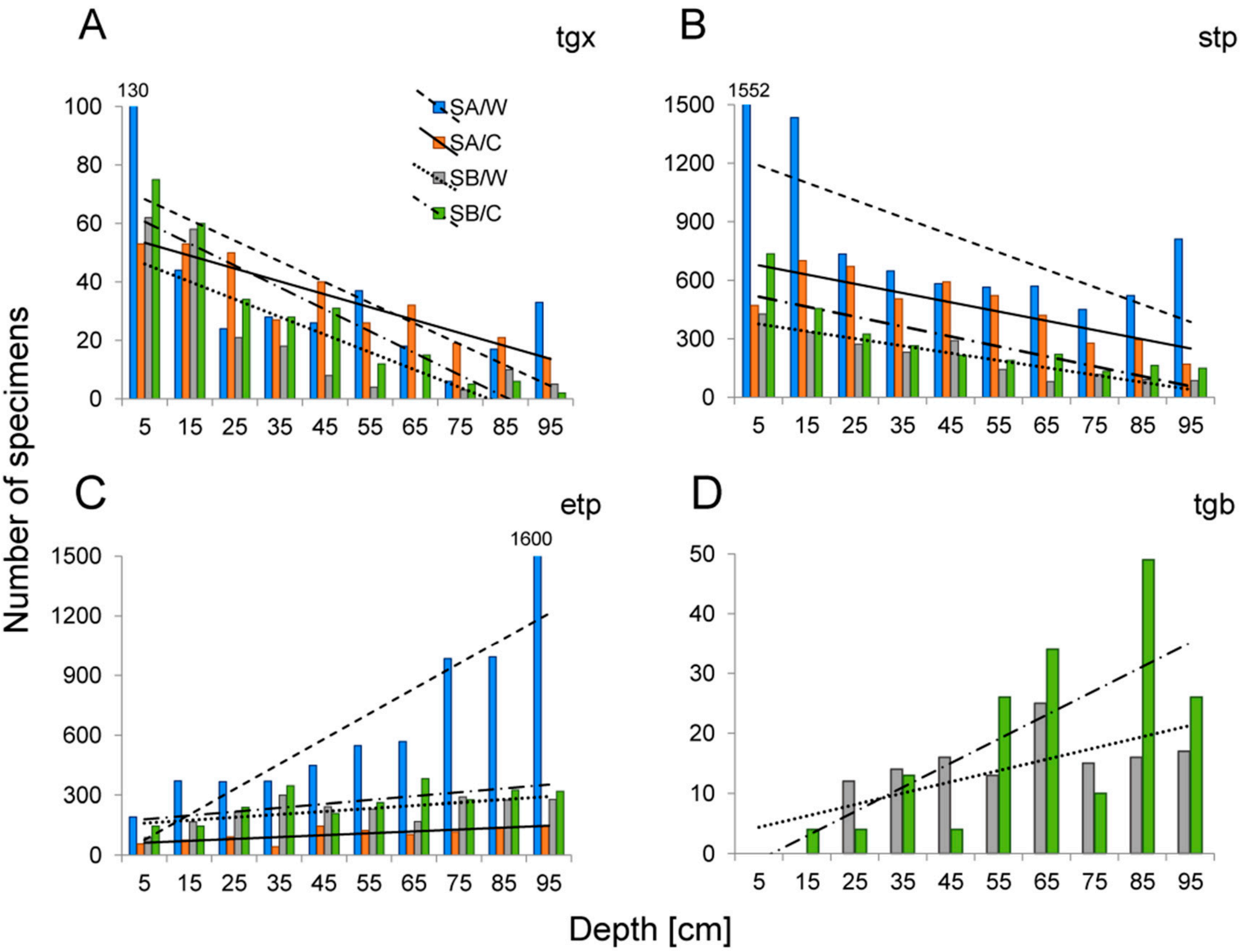

Figure 4. Vertical distribution of troglogroups along the depth gradient at both sites (SA, SB) in two periods; W—warm period, C—cold period, (**A**) tgx—trogloxenes, (**B**) stp—subtroglophiles, (**C**) etp—eutroglophiles, (**D**) tgb—troglobionts, Notice the different scaling of the second axis in the individual graphs.

3.4. Community Composition

Community composition of Collembola in two climatic periods was analysed using NMS ordination. A two-dimensional solution (Figure 5A,B) was recommended by Autopilot with slow and thorough mode, and Sörensen (Bray-Curtis) distance recommended for community data [64] for both the cold and warm period. The best two-dimensional solutions for the cold/warm period had a final stress of 4.56/5.04, $p < 0.00001$ after 73/45 iterations, which was confirmed by a Monte Carlo permutation test with $p = 0.004$ and a mean stress of 6.00/7.38 for real data and 250 runs for both real and randomized data. The first and second axis explained 86.0%/77.1% and 11.6%/19.1% of the variance for the cold and warm period, respectively. Both NMS diagrams of the two study periods showed two clearly bordered clusters related to study sites SA and SB.

In the ordination diagram of the warm period (Figure 5A), the first cluster, representing site SA, consisted of characteristic species, such as *Ceratophysella granulata*, *Plutomurus carpaticus*, *Protaphorura armata* and *Pygmarrhopalites pygmaeus*, linked to the upper and middle levels of the depth gradient (5–45 cm). The second cluster, representing site SB, consisted of a few abundant species, e.g., *Pygmarrhopalites principalis* and *Neelus koseli*, occupying the depths 45–55 cm, and two species with very low abundance, namely *Protaphorura campata* and *Tomocerus vulgaris*, associated with the deeper scree layers (85–95 cm).

In the diagram of the cold period (Figure 5B), the first cluster, representing site SA, consisted of species *Lepidocyrtus lignorum* and *Pogonognathellus flavescens* associated with uppermost and middle layers of the scree profile, while *Ceratophysella granulata* was associated with deeper levels (65–95 cm) of the scree profile. The second cluster represented the community of site SB consisted of *Dicyrtoma fusca* and *Dicyrtomina minuta*, which were associated with the surface horizons (5–25 cm) of the scree, and several other species, such as *Plutomurus carpaticus*, *Pygmarrhopalites pygmaeus* and *Neelus koseli*, which occupied the medium and deeper scree levels (35–95 cm).

The species richness of Collembola and trogloxenes, as well as the numbers of total Collembola, subtroglophiles and several dominant species, had a negative relationship with the temperature (Table 2). In contrast, the abundance of *Plutomurus carpaticus* showed a positive correlation with the temperature ($T_{C\ min}$) and the species richness of subtroglophiles with the all temperature measures (T_W, $T_{W\ min}$, $T_{W\ max}$, T_C, $T_{C\ min}$, $T_{C\ max}$). Furthermore, the species richness of Collembola and trogloxenes and the abundance of trogloxenes, subtroglophiles, *Lepidocyrtus lignorum* and *Pogonognathellus flavescens* correlated positively with the organic carbon content (C_{org}) in the soil.

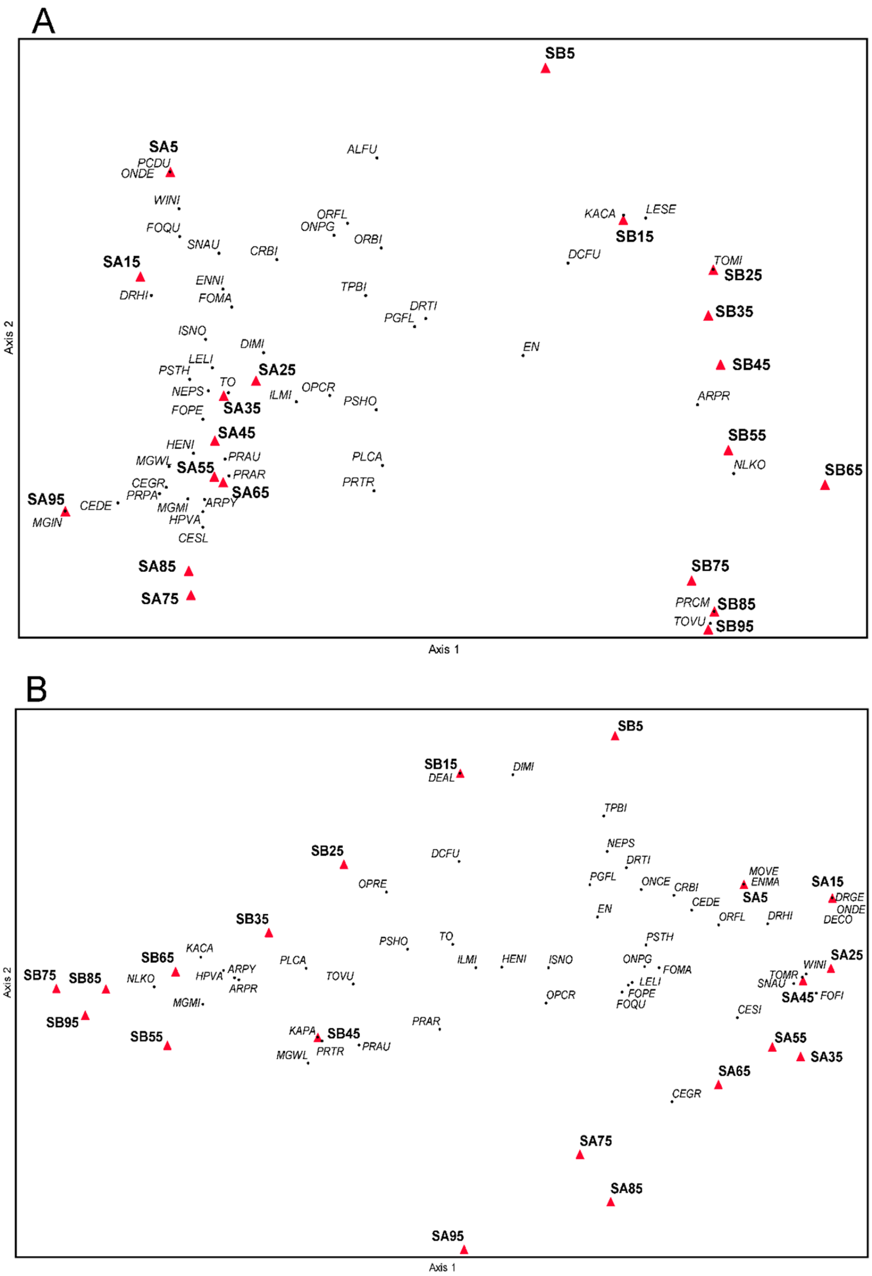

Figure 5. NMS ordination of collembolan communities at sites of a forested scree slope in the Zádiel Valley in two periods; (**A**) warm period, (**B**) cold period; 5–95—soil/scree depth [cm], ALFU—*Allacma fusca*, ARPR—*Pygmarrhopalites principalis*, ARPY—*P. pygmaeus*, CEDE—*Ceratophysella denticulata*, CEGR—*C. granulata*, CESI—*C. sigillata*, CESL—*C. silvatica*, CRBI—*Proisotomodes bipunctatus*, DCFU—*Dicyrtoma fusca*, DEAL—*Deutonura albella*, DECO—*D. conjuncta*, DIMI—*Dicyrtomina minuta*, DRGE—*Desoria germanica*, DRHI—*D. hiemalis*, DRTI—*D. tigrina*, EN—*Entomobryidae* juv., ENMA—*Entomobrya marginata*, ENNI—*E. nivalis*, FOFI—*Folsomia fimetaria*, FOMA—*F. manolachei*, FOPE—*F. penicula*, FOQU—*F. quadrioculata*, HENI—*Heteromurus nitidus*, HPVA—*Heteraphorura variotuberculata*, ILMI—*Isotomiella minor*, ISNO—*Parisotoma notabilis*, KACA—*Kalaphorura carpenteri*, KAPA—*K. paradoxa*, LELI—*Lepidocyrtus lignorum*, LESE—*L. serbicus*, MGIN—*Megalothorax incertus*, MGMI—*M. minimus*, MGWL—*M. willemi*, MOVE—*Morulina verrucosa*, NEPS—*Neanura pseudoparva*, NLKO—*Neelus koseli*, ONCE—*Deuteraphorura cebennaria*, ONDE—*Deharvengiurus denisi*, ONPG—*Onychiuroides pseudogranulosus*, OPCR—*Oncopodura crassicornis*, OPRE—*O. reyersdorfensis*, ORBI—*Orchesella bifasciata*, ORFL—*O. flavescens*, PCDU—*Pseudachorutes dubius*, PGFL—*Pogonognathellus flavescens*, PLCA—*Plutomurus carpaticus*, PRAR—*Protaphorura armata*, PRAU—*P. aurantiaca*, PRCM—*P. campata*, PRPA—*P. pannonica*, PRTR—*P. tricampata*, PSHO—*Pseudosinella horaki*, PSTH—*P. thibaudi*, SNAU—*Sminthurinus aureus*, TO—*Tomoceridae* sp. juv., TOMI—*Tomocerina minuta*, TOMR—*Tomocerus minor*, TOVU—*T. vulgaris*, TPBI—*Tetrodontophora bielanensis*, WINI—*Willowsia nigromaculata*.

Table 2. Pearson correlation between Collembola, their ecological groups, dominant species and environmental parameters (for both periods soil temperature, pH_{H_2O}, organic carbon content, species richness and abundance counted for depths 5, 35, 65 and 95 cm).

	Parameter	Pearson Coefficient
S_Collembola	T_C	−0.56
	$T_{C\ min}$	−0.79
	C_{org}	0.77
N_Collembola	T_W	−0.74
	T_C	−0.81
	$T_{W\ min}$	−0.77
	$T_{W\ max}$	−0.71
	$T_{C\ min}$	−0.61
	$T_{C\ max}$	−0.77
S_trogloxenes	T_C	−0.51
	$T_{W\ min}$	−0.52
	C_{org}	0.61
N_trogloxenes	pH_{H_2O}	−0.65
	C_{org}	0.79
S_subtroglophiles	T_W	0.82
	T_C	0.77
	$T_{W\ min}$	0.75
	$T_{W\ max}$	0.86
	$T_{C\ min}$	0.71
	$T_{C\ max}$	0.81
N_subtroglophiles	T_W	−0.56
	T_C	−0.72
	$T_{C\ max}$	−0.63
	$T_{W\ min}$	−0.63
	$T_{W\ max}$	−0.51
	$T_{C\ min}$	−0.86
	C_{org}	0.69
Lepidocyrtus lignorum	T_W	−0.69
	T_C	−0.81
	$T_{C\ max}$	−0.74
	$T_{W\ min}$	−0.71
	$T_{W\ max}$	−0.67
	$T_{C\ min}$	−0.91
	C_{org}	0.51
Plutomurus carpaticus	$T_{C\ min}$	0.78
	C_{org}	−0.58
Pogonognathellus flavescens	C_{org}	0.86
Pygmarrhopalites pygmaeus	T_W	−0.50
	$T_{W\ max}$	−0.51

T_W—average temperature in the warm period (May–October 2018), T_C—average temperature in the cold period (October 2018–April 2019), $T_{W\ min}$—daily minimum temperature in the warm period, $T_{W\ max}$—daily maximum temperature in the warm period, $T_{C\ min}$—daily minimum temperature in the cold period, $T_{C\ max}$—daily maximum temperature in the cold period, C_{org}—organic carbon content, N—number of specimens, S—number of species.

4. Discussion

Climatic and vegetation inversion is a natural phenomenon characteristic of various karst landscape depressions, such as deep valleys, gorges and deep dolines. Deep karst valleys and gorges introduce great variation in microclimatic conditions, especially during the summer season, with their colder and wetter bottoms compared to the considerably warmer and drier habitats of the surrounding upper plateaus (e.g., [32,41,66]). Habitats at the bottoms of these landforms thus tend to retain higher moisture and lower temperatures due to receiving less solar radiation. In addition, these inversed sites may retain snow cover for a longer time than plateaus, even into early summer [37]. Similarly, screes on inverse slopes in deep karst valleys provide a variety of microhabitats with the unique microclimate regime, which are comprehensively affected by topography (altitude, slope inclination), the nature of the bedrock, scree profiles and the presence of vegetation cover [4,24,35].

4.1. Soil Microclimate and Soil-Chemical Parameters

Our study documented the characteristic temperature regime of the screes, i.e., strong temperature variations at the scree surface and only small fluctuations in deeper levels throughout the year. The depth profiles at both sites showed stable temperature regimes in the middle and deeper layers and more variable temperatures at the uppermost horizons in the warm period (including three summer months), and at the warm/upper site also in the cold period (including three winter months). In contrast, at the cold scree site, striking temperature fluctuations along the entire depth gradient were recorded in the cold period.

Generally, carbon content is an indicator of the soil organic matter in a vertical scree profile concentrated predominantly in the uppermost layers [3,30,67]. The organic carbon content clearly showed a declining trend with increasing depth at both sites. The high amount of leaf litter and humus on the surface and the well-developed organo-mineral layer at the gorge bottom site led to the high content of organic carbon in the soil even at greater depths, related to slower decomposition of soil organic matter in cold and wet microclimate conditions [68]. In this study, the soil moisture content declined with the depth at both sites; however, due to method limitations (a single measurement during the trap installation), the effect of this environmental parameter on the collembolan communities was not statistically analysed.

4.2. Species Diversity, Vertical Distribution and Community Structure of Collembola at Scree Sites

It has been documented that temperature and organic matter are the main drivers of diversity and vertical distribution of Collembola in MSS habitats [9,30,35]. Our study showed that cold and wet microclimate and high content of organic carbon in the slope scree deposit at the gorge bottom were more favourable for Collembola, leading to their higher species richness and abundance compared to the upper part of the scree slope with warm and dry conditions. The abundance of Collembola, is strongly negatively correlated with the scree temperature in both periods, thus documenting temperature as one of driving factors for the vertical stratification of Collembola in a scree profile [9,24,27,30,35].

Basic community parameters (species richness, abundance) and community structure varied considerably between the warm and cold periods and also along the depth profile of the scree sites, illustrated by NMS ordination. Warm and dry conditions at the upper scree site diminished the number of species and specimens of Collembola. The warm period at this site was characterised by high and balanced temperature means along the whole depth profile. At the bottom of the gorge, high species richness was recorded in both periods, while high abundance in the warm period only. We conclude that cold, forested scree habitats, such as those at gorge bottoms, play an important role in maintaining the high Collembola α-diversity and abundance, especially in warm climatic periods, due to the more favourable microclimate and usually also high soil carbon content as the food base for the soil and MSS biota.

It is well known that abundance and species richness of invertebrates decrease with increasing depth of the scree profile [3,4,31,34,69]. Moreover, seasonal vertical migrations of fauna have been observed from the surface into the MSS to avoid severe temperatures, as a result of their characteristic response to cold winter conditions on the one hand, and to warm and dry summer conditions on the other [11,27–29]. For instance, arthropod communities inhabiting high-elevation screes, avoid extreme cold surface conditions during the winter and used MSS as a refugium for survival [9]. In our study, temperature had an increasing trend with depth during the winter months. Only short-term low temperature extremes were recorded on the surface, with no strong negative effect on Collembola. In the cold period, their species number and abundance showed declining trends with increasing depth at both sites, except species richness at the gorge bottom, meaning that higher richness was related to deeper scree layers. Moreover, several abundant cold-adapted and eutroglophile species showed an opposite trend, i.e., higher abundances in deeper layers, compared to other Collembola species. These were *Ceratophysella granulata*, *Plutomurus carpaticus*, *Protaphorura armata* and *Pygmarrhopalites principalis* at the gorge bottom, and *Kalaphorura carpenteri*, *Plutomurus carpaticus* and *Protaphorura armata* at upper part of the scree slope. In Central Europe, all these species are known to prefer the cold and thermally stable conditions of MSS habitats [30,31,35,50,70,71]. It is important to note that at the gorge bottom these psychrophilic species were capable of withstanding the extensive temperature fluctuations occurring along the entire depth gradient during the cold period.

In the warm period, clearly declining trends of species richness and abundance of Collembola were observed with increasing depth at the upper scree site. Several species, e.g., the troglobiont *Neelus koseli* and the cold-adapted and eutroglophile *Plutomurus carpaticus*, showed an opposite trend than Collembola overall. The higher abundances of both species in deeper layers of the scree with more stable temperature were noted also by previous studies (e.g., [31,72]). In contrast, at the gorge bottom Collembola had a similar pattern as in the cold period, i.e., markedly high abundances in deeper scree with numerous eutroglophile and cold-adapted species.

4.3. Ecological Groups of Collembola and Climatic Conditions in the Two Periods

We observed typical distribution patterns of Collembola ecological groups (troglogroups) along the vertical profile of the scree sites (e.g., [3,31,50]). Trogloxenes and subtroglophiles, as forms not or weakly associated with subterranean habitats, showed decreasing patterns of abundance with increasing depth at both sites and in both periods. Moreover, the abundance of subtroglophiles negatively correlated with temperature, and the abundance of trogloxenes and subtroglophiles positively correlated with soil organic carbon content. Eutroglophiles showed an opposite trend of vertical distribution at scree sites, similarly as the troglobiont *Neelus koseli*, which was exclusively bound to the middle and deeper scree levels at the upper slope site in both periods.

Small-scale variation in microclimatic conditions across karst landforms affects the distributions of highly specialized invertebrates [40,42,73]. Since the cold scree slopes at low elevations in Central Europe are isolated MSS habitats, their characteristic cold-adapted species have mostly disjunctive distributions [74]. In the present study, almost the same number of psychrophiles was recorded at both sites in the cold period, with their significantly highest abundance observed at the gorge bottom in the warm period, notably in deeper scree layers. It is important to note that the effect of the microclimatic gradient on mesofauna in deep karst valleys and other karst landforms with inversed microclimate in the temperate region is generally more marked in the warm and dry periods of the year [32]. We observed freezing conditions (the presence of ice crystals) in the deeper layers of the cold scree site during the late spring, documenting the analogous conditions of high-elevation screes with specific air circulation along their thermal gradient. Such scree deposits preserve the snow cover and ice lens formations until the mid- or late summer [9,11,15,16,21]. Some psychrophilic species captured by the subterranean traps occurred exclusively in such freezing conditions. For example, *Ceratophysella sigillata*, recorded with low abundance, occurred exclusively at the scree bottom in the cold period. This winter-active species is well-known by its specific adaptations to low temperatures, often occurring in large numbers on snow cover [39,75–77].

4.4. Scree Habitats of Deep Karst Valleys as Climate Refugia

MSS habitats have been identified as refugia of rare subterranean fauna [24,27,30,42,45]. Numerous relict arthropods have been recorded in cold European screes, mostly beetles and spiders, but only a few studies have focused on mesofauna, such as those by [6,9,13,78,79]. *Morulina verrucosa*, considered a glacial relict, was associated with the soil layer of the scree bottom exclusively in the cold period, although in low abundance. This species occurs in the scree habitats of Central European mountains, especially in organic-rich soils [30,80,81]. The troglobiont *Neelus koseli* is considered a Tertiary relict of the subterranean fauna, with distribution restricted to karst areas of eastern Slovakia, both in caves and MSS environments [30,82].

We found that the cold part of a steep forested scree with high organic carbon content across its profile provided suitable environmental conditions for numerous psychrophilic and subterranean species, such as eutroglophiles [30,31,42]. We can thus conclude that cold scree habitats at the bottoms of karst gorges and ravines at low altitudes play an important role as climate refugia in the survival and preservation of psychrophilic fauna occupying these MSS habitats. Moreover, species *Ceratophysella granulata*, *Plutomurus carpaticus*, and *Pygmarrhopalites pygmaeus* are frequent occupants of the Western Carpathians caves [63], which illustrates the important function of MSS habitats as an ecotone between surface and deeper subterranean habitats.

5. Conclusions

In conclusion, the soil temperature regime and nutrient content in the soil considerably affected the species richness and vertical distribution of Collembola at two scree sites with contrasting climatic regimes in both warm and cold periods of the year. These low-altitude scree habitats on a microclimatically inversed slope in a deep karst valley with strong vertical temperature gradients revealed the exceptional diversity of Collembola. The strong effect of the microclimatic regime and depth on community composition within the scree slope was clearly documented in both climatically different periods. Our study confirmed the typical patterns of distribution of individual Collembola troglogroups along the vertical profile of the scree sites. Trogloxenes and subtroglophiles showed decreasing patterns of abundance with increasing depth. Subterranean forms (eutroglophiles, troglobiont) showed an opposite trend of distribution, with increasing abundance towards scree depth, thus documenting that MSS habitats represent a transitional zone between the soil surface and the deep (cave) subterranean environment. We can also conclude that climatically inversed scree slopes in deep karst valleys at low elevation serve as reservoirs of highly specialised fauna, such as endemic and psychrophilic taxa, some of which are considered relicts from former glacial periods. The gorge bottom, with a favourable microclimate (cold and wet) and high organic carbon content even in the deeper horizons of the MSS, provided suitable environmental conditions for numerous psychrophilic and subterranean species. Accordingly, scree slope habitats with inversed microclimatic conditions are vulnerable environments, where global warming may lead to the loss of relict forms of invertebrates and consequently to the reduction of biodiversity in these unique natural sites.

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Appendix A

Table A1. Ecological characteristics of Collembola species and their abundances in vertical profile of 5–95 cm at the base of the scree slope (site SA) in warm and cold periods.

		W											**C**										
Species	**Ech**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_w**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_c**
Allacma fusca (Linnaeus, 1758)	tgx	2	-	-	-	-	-	-	-	-	-	**2**	-	-	-	-	-	-	-	-	-	-	**-**
Ceratophysella denticulata (Bagnall, 1941)	etp	-	-	1	-	-	-	-	1	-	4	**6**	-	-	-	-	4	-	2	1	-	-	**7**
Ceratophysella granulata Stach, 1949	etp, p [a]	37	106	114	134	172	129	176	275	323	531	**1997**	6	18	33	16	43	33	20	30	58	68	**325**
Ceratophysella sigillata (Uzel, 1891)	tgx, p [a]	-	-	-	-	-	-	-	-	-	-	**-**	11	5	8	4	10	3	5	3	5	4	**58**
Ceratophysella silvatica (Rusek, 1964)	stp, p [a]	-	-	-	-	2	-	3	2	4	-	**11**	-	-	-	-	-	-	-	-	-	-	**-**
Deharvengiurus denisi (Stach, 1934)	stp, p [b]	1	-	-	-	-	-	-	-	-	-	**1**	-	2	-	-	-	-	-	-	-	-	**2**
Desoria germanica (Hüther et Winter, 1961)	tgx	-	-	-	-	-	-	-	-	-	-	**-**	-	2	-	-	-	-	-	-	-	-	**2**
Desoria hiemalis (Schött, 1839)	stp	2	18	-	-	2	-	-	1	-	-	**23**	10	10	10	-	6	2	-	1	-	1	**40**
Desoria tigrina Nicolet, 1842	stp	-	-	4	-	-	-	-	-	-	-	**4**	1	-	-	-	4	1	-	-	-	-	**6**
Deuteraphorura cebennaria (Gisin, 1956)	stp	-	-	-	-	-	-	-	-	-	-	**-**	-	-	-	4	2	1	3	-	-	-	**10**
Deutonura conjuncta (Stach, 1926)	tgx	-	-	-	-	-	-	-	-	-	-	**-**	-	1	-	-	-	-	-	-	-	-	**1**
Dicyrtoma fusca (Lubbock, 1873)	tgx	1	1	1	4	2	-	6	-	1	1	**17**	4	-	3	-	3	5	5	2	-	-	**22**
Dicyrtomina minuta (Fabricius, 1783)	stp	5	10	4	8	6	3	13	3	2	-	**54**	-	-	-	-	-	-	-	-	-	-	**-**
Entomobrya marginata (Tullberg, 1871)	tgx	-	-	-	-	-	-	-	-	-	-	**-**	1	-	-	-	-	-	-	-	-	-	**1**
Entomobrya nivalis (Linnaeus, 1758)	tgx	10	-	-	-	-	1	-	-	-	3	**14**	-	-	-	-	-	-	-	-	-	-	**-**
Entomobryidae juv.		1	-	-	-	-	-	-	-	-	-	**1**	28	50	47	16	58	10	2	7	3	26	**247**
Folsomia fimetaria (Linné, 1758)	stp	-	-	-	-	-	-	-	-	-	-	**-**	-	-	2	1	1	-	-	-	-	-	**4**
Folsomia manolachei Bagnall, 1939	tgx	38	10	15	6	6	15	2	2	2	11	**107**	18	25	28	11	18	11	9	8	5	6	**139**
Folsomia penicula Bagnall, 1939	tgx	-	7	1	2	-	5	4	-	1	2	**22**	6	8	4	3	1	1	5	1	6	4	**39**
Folsomia quadrioculata (Tullberg, 1871)	tgx	24	3	1	3	4	-	-	-	-	-	**35**	1	2	1	2	1	1	-	2	1	-	**11**
Heteraphorura variotuberculata (Stach, 1934)	stp, p [b]	1	-	-	-	1	11	10	13	-	1	**37**	-	-	-	-	-	-	-	-	-	-	**-**
Heteromurus nitidus (Templeton, 1835)	etp	-	1	-	-	-	-	2	-	1	-	**4**	11	13	15	4	19	13	15	8	3	7	**108**
Isotomiella minor (Schäffer, 1896)	stp	4	3	10	-	3	5	4	5	12	-	**46**	6	4	4	4	11	6	13	1	2	-	**51**
Lepidocyrtus lignorum (Fabricius, 1775)	stp	1220	1038	461	494	465	396	396	302	350	538	**5660**	431	643	629	484	549	498	377	263	279	154	**4307**
Megalothorax incertus Börner, 1903	etp	-	-	-	-	-	-	-	-	-	1	**1**	-	-	-	-	-	-	-	-	-	-	**-**
Megalothorax minimus Willem, 1900	etp	-	3	7	8	6	15	13	20	13	18	**103**	-	-	-	-	-	-	-	1	5	4	**10**
Megalothorax willemi Schneider et d’Haese, 2013	etp	-	8	4	2	4	-	2	7	8	8	**43**	-	-	-	-	-	-	-	3	5	1	**9**
Morulina verrucosa (Börner, 1903)	tgx, E, p [c,d]	-	-	-	-	-	-	-	-	-	-	**-**	2	-	-	-	-	-	-	-	-	-	**2**

Table A1. *Cont.*

		W											C										
Species	**Ech**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	$\mathbf{N_w}$	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	$\mathbf{N_c}$
Neanura pseudoparva Rusek, 1963	tgx	4	5	4	12	10	11	-	-	-	-	**46**	2	-	-	-	1	-	1	-	-	-	**4**
Oncopodura crassicornis Shoebotham, 1911	etp	3	3	7	5	2	-	-	-	2	-	**22**	11	10	10	4	45	14	41	21	26	11	**193**
Onychiuroides pseudogranulosus (Gisin, 1951)	stp	14	4	5	-	-	3	1	-	1	-	**28**	1	10	9	-	2	5	6	3	5	7	**48**
Orchesella bifasciata Nicolet, 1842	tgx	-	1	-	-	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	**-**
Orchesella flavescens (Bourlet, 1843)	tgx	34	12	-	-	-	-	-	-	11	5	**62**	8	2	1	4	4	2	4	-	1	-	**26**
Parisotoma notabilis (Schäffer, 1896)	stp	16	13	6	2	3	8	4	3	2	-	**57**	9	5	6	-	2	4	14	4	2	-	**46**
Plutomurus carpaticus Rusek et Weiner 1978	etp, E, p [e]	118	122	116	82	96	126	113	213	188	273	**1447**	22	30	23	10	18	22	20	33	21	36	**235**
Pogonognathellus flavescens (Tullberg, 1871)	stp	200	132	174	92	60	62	82	75	81	177	**1135**	150	77	31	22	29	22	21	13	5	24	**394**
Prosisotomodes bipunctatus (Axelson, 1903)	tgx	2	1	-	-	3	-	-	-	-	-	**6**	-	4	3	3	-	1	1	-	-	-	**12**
Protaphorura armata (Tullberg, 1869)	etp, p [f]	18	36	30	33	34	133	90	82	139	91	**686**	4	2	4	3	4	34	2	8	8	4	**73**
Protaphorura aurantiaca (Ridley, 1880)	stp	-	1	-	-	-	-	3	3	1	6	**14**	-	-	-	2	-	1	2	-	-	1	**6**
Protaphorura pannonica (Haybach, 1960)	tgx	-	-	-	-	-	-	3	-	-	2	**5**	-	-	-	-	-	-	-	-	-	-	**-**
Protaphorura tricampata (Gisin, 1956)	tgx	2	-	-	-	1	5	3	4	2	9	**26**	-	1	-	-	-	-	1	3	3	-	**8**
Pseudachorutes dubius Krausbauer, 1898	tgx	3	-	-	-	-	-	-	-	-	-	**3**	-	-	-	-	-	-	-	-	-	-	**-**
Pseudosinella horaki Rusek, 1985	stp	84	209	62	49	39	76	52	42	66	89	**768**	11	24	11	9	10	2	4	4	6	7	**88**
Pseudosinella thibaudi Stomp, 1977	etp	-	4	3	-	-	-	-	1	1	-	**9**	3	3	2	2	1	1	-	-	1	-	**13**
Pygmarrhopalites principalis Stach, 1945	etp, p [g]	-	8	1	-	5	2	2	4	6	3	**31**	-	-	-	-	-	1	-	1	-	2	**4**
Pygmarrhopalites pygmaeus (Wankel, 1860)	etp	15	80	84	105	129	142	170	380	311	671	**2087**	-	-	5	4	11	6	4	10	13	15	**68**
Sminthurinus aureus (Lubbock, 1862)	tgx	5	4	2	-	-	-	-	-	-	-	**11**	-	1	1	-	-	-	1	-	-	-	**3**
Tetrodontophora bielanensis (Waga, 1842)	stp, p [h]	5	6	8	2	2	-	1	1	3	-	**28**	2	1	-	1	2	-	1	-	-	-	**7**
Tomoceridae juv.		1	4	-	-	-	2	2	1	1	4	**15**	3	1	-	-	-	1	-	-	-	-	**5**
Tomocerus minor (Lubbock, 1862)	stp, p [e,i]	-	-	-	-	-	-	-	-	-	-	**-**	-	1	-	-	3	1	-	-	-	-	**5**
Tomocerus vulgaris (Tullberg, 1871)	stp	-	-	-	-	-	-	-	-	-	-	**-**	-	-	-	-	-	1	-	1	1	-	**3**
Willowsia nigromaculata (Lubbock, 1873)	tgx	5	-	-	1	-	-	-	-	-	-	**6**	-	2	1	-	2	2	-	-	-	-	**7**
$\mathbf{N_{total}}$		**1875**	**1853**	**1125**	**1044**	**1057**	**1150**	**1157**	**1440**	**1532**	**2448**	**14,681**	**762**	**957**	**891**	**613**	**864**	**705**	**579**	**432**	**464**	**382**	**6649**
$\mathbf{S_{total}}$		**28**	**29**	**25**	**19**	**24**	**19**	**24**	**22**	**25**	**21**	**41**	**24**	**27**	**24**	**21**	**28**	**28**	**25**	**24**	**22**	**18**	**41**

W—warm period (May–October 2018), C—cold period (October 2018–April 2019), N_{total}—number of specimens, S_{total}—species richness, N_W—number of specimens captured in the warm period, N_C—number of specimens captured in the cold period, Ech—ecological characteristics, tgx—trogloxene, stp—subtroglophile, etp—eutroglophile, E—endemic species, p—psychrophilic species, "sp. juv."—uncertain relationship to the cave environment, 5–95—soil/scree depth [cm], literary sources for selected troglogroups: [53–58], literary sources for selected cold-adapted species: [a] [58], [b] [55], [c] [83], [d] [84], [e] [81], [f] [39], [g] [56], [h] [85], [i] [42].

Appendix B

Table A2. Ecological characteristics of Collembola and their abundances in a vertical profile of 5−95 cm at the upper site of the scree slope (site SB) in warm and cold periods.

		W											C										
Species	**Ech**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_w**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_c**
Allacma fusca (Linnaeus, 1758)	tgx	1	1	-	-	-	-	-	-	-	-	**2**	-	-	-	-	-	-	-	-	-	-	**-**
Ceratophysella denticulata (Bagnall, 1941)	etp	-	-	-	-	-	-	-	-	-	-	**-**	5	-	-	-	-	-	-	-	-	-	**5**
Desoria hiemalis (Schött, 1839)	stp	-	-	-	-	-	-	-	-	-	-	**-**	5	-	-	-	-	-	-	-	-	-	**5**
Desoria tigrina Nicolet, 1842	stp	-	2	1	-	-	-	-	-	-	-	**3**	2	4	1	-	-	-	-	-	-	-	**7**
Deuteraphorura cebennaria (Gisin, 1956)	stp	-	-	-	-	-	-	-	-	-	-	**-**	10	2	-	1	1	-	-	-	-	-	**14**
Deutonura albella (Stach, 1920)	tgx, p ^{h}	-	-	-	-	-	-	-	-	-	-	**-**	-	1	-	-	-	-	-	-	-	-	**1**
Dicyrtoma fusca (Lubbock, 1873)	tgx	16	33	13	13	5	1	-	1	-	-	**82**	42	40	24	20	10	5	7	3	1	-	**152**
Dicyrtomina minuta (Fabricius, 1783)	stp	7	4	-	-	-	-	-	-	-	-	**11**	115	65	24	3	1	-	2	2	1	3	**216**
Entomobrya nivalis (Linnaeus, 1758)	tgx	-	-	-	-	-	2	-	-	-	-	**2**	-	-	-	-	-	-	-	-	-	-	**-**
Entomobryidae juv.		-	-	-	1	-	-	-	1	-	-	**2**	67	59	47	22	19	1	4	5	5	3	**232**
Folsomia manolachei Bagnall, 1939	tgx	13	2	-	-	1	-	-	-	-	-	**16**	14	8	4	5	11	5	6	-	-	-	**53**
Folsomia penicula Bagnall, 1939	tgx	-	-	-	-	-	-	-	-	-	1	**1**	4	3	4	1	5	-	-	-	-	-	**17**
Folsomia quadrioculata (Tullberg, 1871)	tgx	-	-	-	-	-	-	-	-	-	-	**-**	1	1	-	-	2	-	-	1	-	-	**5**
Heteraphorura variotuberculata (Stach, 1934)	stp, p ^{b}	-	-	-	-	-	-	-	-	-	-	**-**	1	-	4	-	2	5	4	1	-	3	**20**
Heteromurus nitidus (Templeton, 1835)	etp	-	-	-	-	-	-	-	-	-	-	**-**	16	15	9	16	10	9	17	4	17	8	**121**
Isotomiella minor (Schäffer, 1896)	stp	5	-	3	3	-	1	-	-	-	-	**12**	8	6	6	6	6	6	11	6	5	8	**68**
Kalaphorura carpenteri (Stach, 1919)	etp, p ^{b}	21	10	2	4	2	1	3	1	-	2	**46**	8	12	1	8	7	7	17	12	18	33	**123**
Kalaphorura paradoxa (Schäffer, 1900)	etp, p ^{b}	-	-	-	-	-	-	-	-	-	-	**-**	-	-	-	-	1	-	-	-	-	-	**1**
Lepidocyrtus lignorum (Fabricius, 1775)	stp	92	87	39	35	39	38	27	29	13	24	**423**	370	210	180	182	158	145	169	97	121	108	**1740**
Lepidocyrtus serbicus Denis, 1936	tgx	3	2	3	-	2	-	-	-	-	-	**10**	-	-	-	-	-	-	-	-	-	-	**-**
Megalothorax minimus Willem, 1900	etp	-	-	-	-	-	-	-	-	-	1	**1**	1	5	1	11	-	30	14	17	18	3	**100**
Megalothorax willemi Schneider et d'Haese, 2013	etp	-	-	-	-	-	-	-	-	-	-	**-**	-	1	-	-	-	6	4	-	4	2	**17**
Neanura pseudoparva Rusek, 1963	tgx	-	-	-	-	-	-	-	-	-	-	**-**	1	4	-	-	-	-	-	-	-	-	**5**
Neelus koseli Kováč et Papáč, 2010	tgb, E	-	-	12	14	16	13	25	15	16	17	**128**	-	4	4	13	4	26	34	10	49	26	**170**
Oncopodura crassicornis Shoebotham, 1911	etp	-	-	-	-	-	1	3	2	-	-	**6**	13	15	20	27	12	5	14	-	12	11	**129**
Oncopodura reyersdorfensis Stach, 1936	etp	-	-	-	-	-	-	-	-	-	-	**-**	1	-	1	1	1	-	-	-	-	-	**4**

Table A2. *Cont.*

		W											**C**										
Species	**Ech**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_w**	**5**	**15**	**25**	**35**	**45**	**55**	**65**	**75**	**85**	**95**	**N_c**
Onychiuroides pseudogranulosus (Gisin, 1951)	stp	7	9	-	-	-	-	-	-	-	-	**16**	8	11	-	3	-	-	-	-	-	-	**22**
Orchesella bifasciata Nicolet, 1842	tgx	-	1	-	-	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	**-**
Orchesella flavescens (Bourlet, 1843)	tgx	27	19	3	-	-	-	-	-	-	-	**49**	8	-	1	-	-	-	-	-	-	-	**9**
Parisotoma notabilis (Schäffer, 1896)	stp	-	-	-	2	-	-	-	-	-	-	**2**	5	5	4	2	2	1	5	4	3	3	**34**
Plutomurus carpaticus Rusek et Weiner 1978	etp, E, p [e]	53	58	55	68	47	75	65	191	152	181	**945**	87	75	95	136	97	107	191	132	126	140	**1186**
Pogonognathellus flavescens (Tullberg, 1871)	stp	288	193	207	158	118	61	30	32	8	10	**1105**	171	119	92	41	29	6	-	-	6	7	**471**
Prosisotomodes bipunctatus (Axelson, 1903)	tgx	2	-	-	-	-	-	-	-	-	-	**2**	5	3	1	-	1	-	-	-	-	-	**10**
Protaphorura armata (Tullberg, 1869)	etp, p [f]	4	16	7	16	1	5	-	3	12	3	**67**	-	2	3	2	8	7	10	7	15	19	**73**
Protaphorura aurantiaca (Ridley, 1880)	stp	-	3	-	-	-	-	-	-	-	-	**3**	-	-	-	-	-	3	1	1	2	2	**9**
Protaphorura campata (Gisin, 1952)	tgx	-	-	-	-	-	-	-	-	6	-	**6**	-	-	-	-	-	-	-	-	-	-	**-**
Protaphorura tricampata (Gisin, 1956)	tgx	-	-	2	4	-	1	-	2	4	4	**17**	-	-	-	2	2	2	2	1	5	2	**16**
Pseudosinella horaki Rusek, 1985	stp	21	30	19	33	132	42	23	56	69	49	**474**	25	26	11	27	11	24	25	22	24	15	**210**
Pseudosinella thibaudi Stomp, 1977	etp	-	-	-	-	-	-	-	-	-	-	**-**	2	-	1	2	2	-	-	-	-	-	**7**
Pygmarrhopalites principalis Stach, 1945	etp, p [g]	6	80	130	194	165	126	76	69	86	69	**1001**	-	1	8	18	12	7	19	7	2	4	**78**
Pygmarrhopalites pygmaeus (Wankel, 1860)	etp	4	3	23	17	27	23	22	24	25	22	**190**	13	20	100	125	59	85	96	97	113	98	**806**
Sminthurinus aureus (Lubbock, 1862)	tgx	-	-	-	1	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	**-**
Tetrodontophora bielanensis (Waga, 1842)	stp, p [h]	7	5	3	-	2	1	-	-	-	-	**18**	15	4	2	-	1	-	-	-	-	-	**22**
Tomoceridae juv.		-	3	-	-	-	-	-	-	-	-	**3**	-	-	-	1	-	-	5	-	-	-	**6**
Tomocerina minuta (Tullberg, 1877)	stp	-	-	1	-	-	-	-	-	-	-	**1**	-	-	-	-	-	-	-	-	-	-	**-**
Tomocerus vulgaris (Tullberg, 1871)	stp	-	-	-	-	-	-	-	-	1	2	**3**	-	3	-	-	4	-	3	1	1	-	**12**
N_{total}		**577**	**561**	**523**	**563**	**557**	**391**	**274**	**426**	**392**	**385**	**4649**	**1023**	**724**	**648**	**675**	**478**	**492**	**660**	**430**	**548**	**498**	**6176**
S_{total}		**18**	**19**	**17**	**14**	**13**	**15**	**9**	**12**	**11**	**13**	**32**	**28**	**28**	**25**	**23**	**27**	**20**	**21**	**19**	**20**	**19**	**37**

W—warm period (May–October 2018), C—cold period (October 2018–April 2019), N_{total}—number of specimens, S_{total}—species richness, N_W—number of specimens captured in the warm period, N_C—number of specimens captured in the cold period, Ech—ecological characteristics, tgx—trogloxene, stp—subtroglophile, etp—eutroglophile, tgb—troglobiont, E—endemic species, p—psychrophilic species, "sp. juv."—uncertain relationship to the cave environment, 5–95—soil/scree depth [cm], literary sources for selected troglogroups: [53–58], literary sources for selected cold–adapted species: [b] [55], [e] [81], [f] [39], [g] [56], [h] [85].

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