Species Composition and Structure of Beetle Associations in Caves of the Częstochowa Upland, Poland

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Abstract: This paper presents the study's results on beetles (Insecta: Coleoptera) inhabiting caves in the Częstochowa Upland, southern Poland. During two years of research, 2084 specimens, representing 105 species from 19 beetle families, were collected. The obtained results indicate that many beetle species choose to inhabit caves despite lacking specific adaptations for living in such environments. The cave entrance zone is the most attractive place for surface species to inhabit because its climatic conditions are more stable than outside the cave, some sunlight is present, and the availability of organic matter is high. In the deeper parts of the studied caves, the number of occurring species rapidly decreased. Three species were recognised as troglobionts, four as troglophiles and 32 as subtroglophiles. *Speonomus normandi hydrophilus*, *Choleva lederiana gracilenta* and *Quedius mesomelinus mesomelinus* were identified as the most frequent in the studied caves. *Speonomus normandi hydrophilus* is endemic to the Arize massif in the Central Pyrenees (France) and was experimentally introduced into the Dzwonnica cave (Poland) in 1982, while *Ch. lederiana gracilenta* is one of two troglobitic beetles native to Polish caves and *Q. imesomelinus mesomelinus* is a widespread, very common troglophile.

Keywords: troglobiont; troglophile; eutroglophile; subtroglophile; trogloxenes; round fungus beetles; rove beetles; cave; Poland

1. Introduction

Beetles (Coleoptera) are the most species-rich order of insects, inhabiting various terrestrial and aquatic environments and occurring in almost all climatic zones [1,2]. Beetles can be herbivorous, carnivorous, necrophagous, saprophagous, and mixophagous, and because of this versatility, they have also colonised subterranean environments [1,2]. Some, named troglobionts, are closely associated with caves, while others prefer caves but live in different subterranean habitats (troglophiles) and some temporarily inhabit caves (trogloxenes) [3,4]. Beetles are also found in shallow subterranean habitats, termed the Mesovoid Shallow Substratum (MSS) [5–10]. The MSS comprises small crevices and scree slopes in rock debris [8–10]. The uniqueness of this environment relies on a connection between subterranean conditions—such as lack of light—with a direct inflow of organic matter from the surface [7,9,10].

Beetles also dwell in caves in Poland, and several species are known from previous research conducted in recent years [11,12]. However, a lack of comprehensive data about beetles inhabiting the subterranean environment in Poland was the main impetus for the authors to undertake this research. In Poland, caves occur in several of its southern regions, such as the Sudety Mountains, Tatra Mountains, Kraków-Częstochowa Upland, Carpathian Flysch Belt, Nidziańska Basin and Świętokrzyskie Mountains. The total number of caves is over 5000; the majority (about 1500) are located in the Kraków-Częstochowa Upland [13].

The purpose of the present research was to observe the species communities of beetles from caves of the Częstochowa Upland, which is a part of the Kraków-Częstochowa Upland.

Special attention was paid to the degree of certain species' relations with the subterranean habitat. Moreover, the particular beetle association structure was also analysed.

2. Materials and Methods

2.1. Study Area

Six caves in the Częstochowa Upland were investigated (Figure 1); these were previously described in detail by Kocot-Zalewska and Woźnica [14]. Graphic diagrams of the studied caves have been taken from the public website of the Polish Geological Institute—National Research Institute [15]. All these caves are horizontal, with similar lengths and altitude a.s.l., but with slight height differences [16,17]. The size and exposure of the entrance, shape, configuration of passages and vegetation around the cave entrance vary for each cave (Figures 2–4). The caves are situated in forest zones except for the Towarna cave, which lies in an area with xerothermic grassland. Five of the six studied caves have one entrance; only the Kroczycka cave has two, but both are much smaller than the entrances of other caves.

2.2. Sampling Design

The specimens were sampled from December 2014 to February 2017 using 5 cm-diameter Barber's traps with 30% propylene glycol (as a preservative liquid). From December 2014 to January 2016, the material was sampled constantly (12 samples from every site per year). The following year, samples were gathered every two months (thus, six times per year). The direct-search method was also used for collecting the insects. However, individuals sampled in such a way were used only for the qualitative analysis and were not included in the quantitative evaluation.
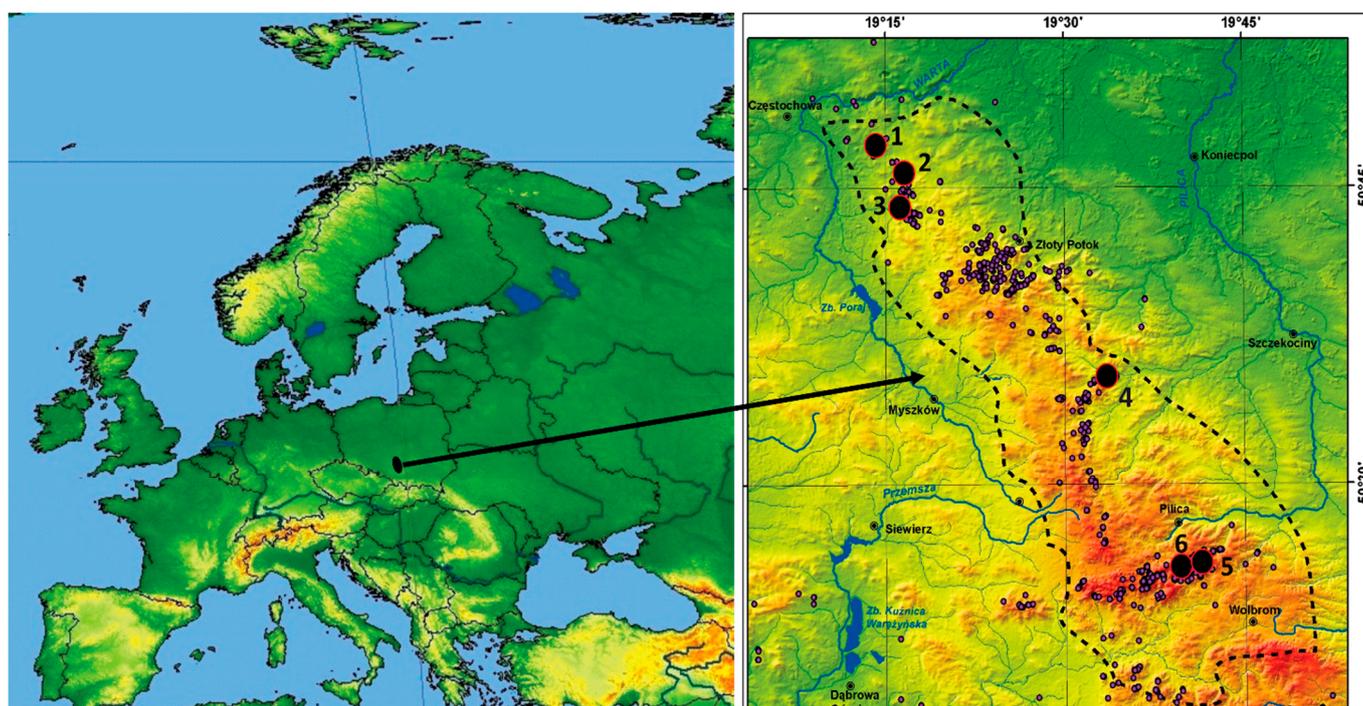

Figure 1. Location of the Częstochowska Upland in Poland; studied caves marked with numbers: 1—W Zielonej Górze cave; 2—Towarna cave; 3—Pod Sokolą cave; 4—Kroczycka cave; 5—Psia cave; 6—Zegar cave.
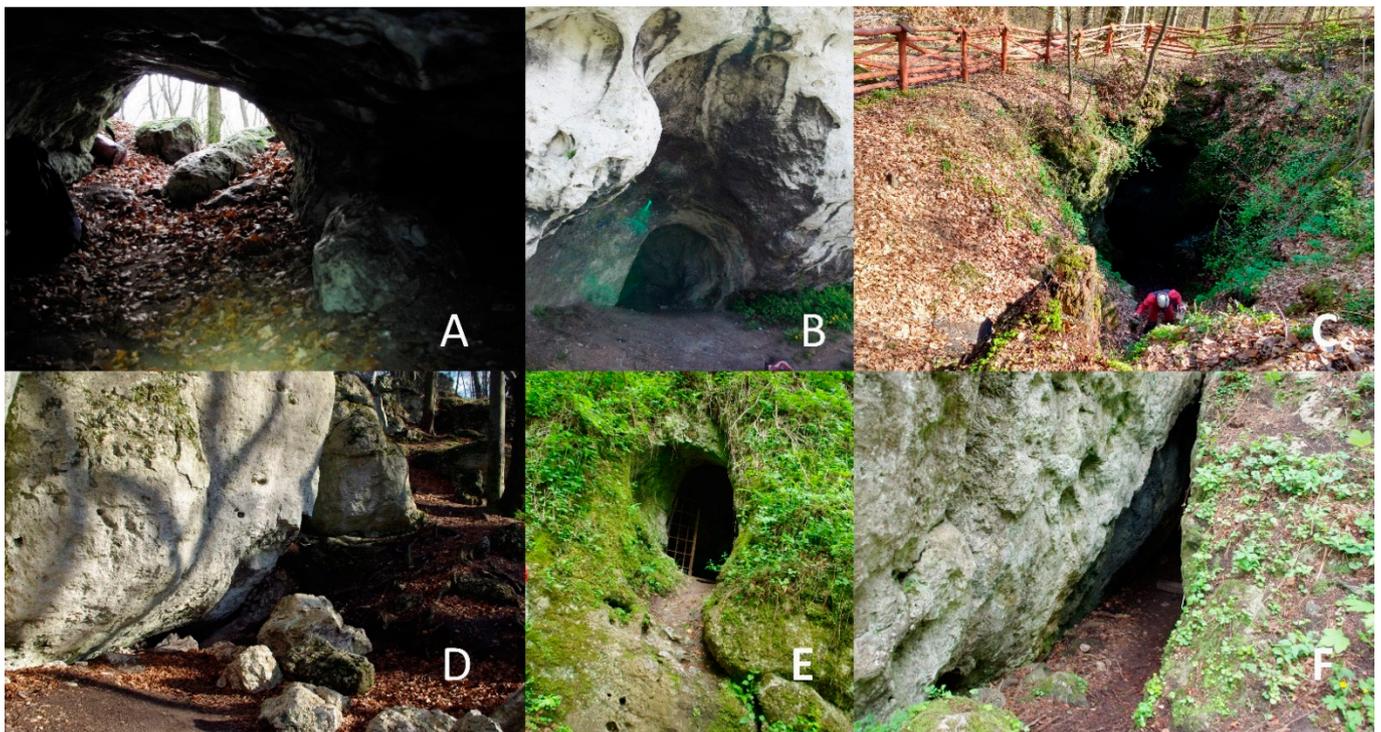
Figure 2. Entrances of studied caves. (**A**)—W Zielonej Górze cave; (**B**)—Towarna cave; (**C**)—Pod Sokolą cave; (**D**)—Kroczycka cave; (**E**)—Psia cave; (**F**)—Zegar cave.
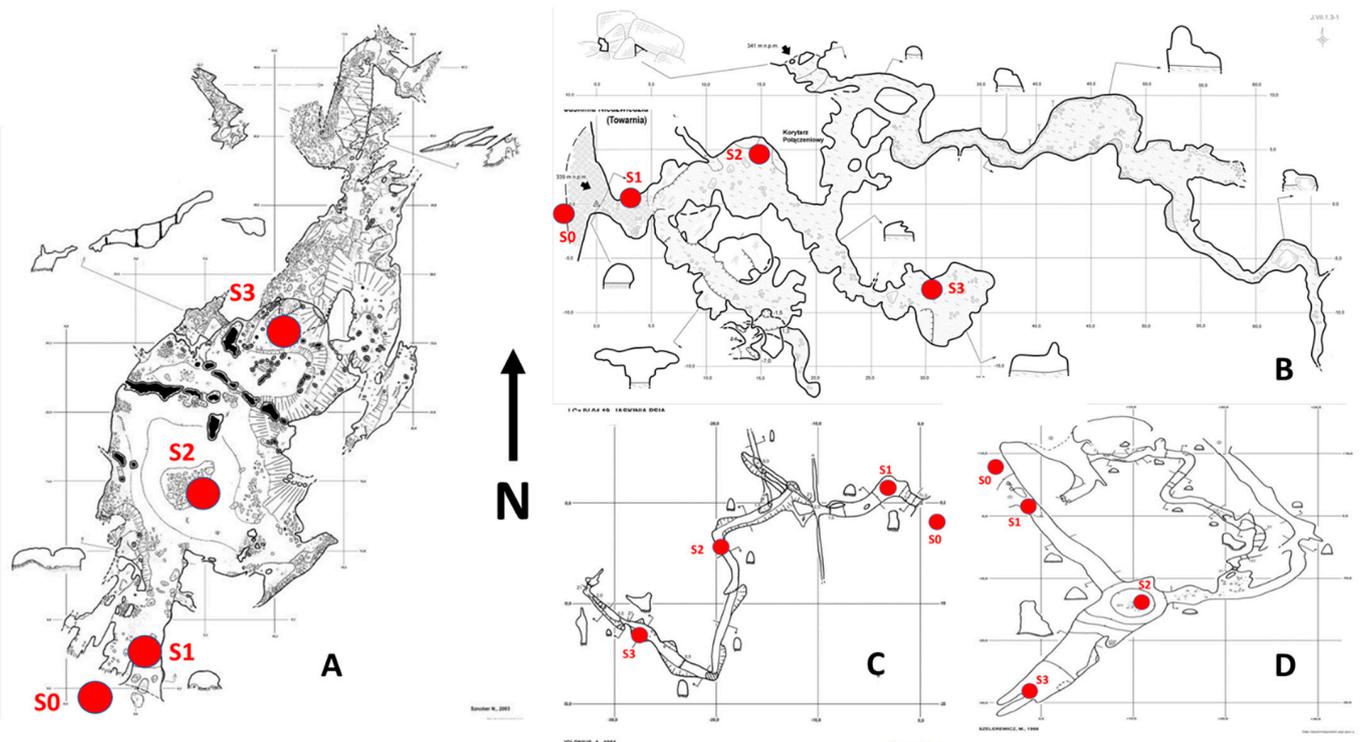

Figure 3. Diagrams of the studied caves with marked sampling points (for explanations, see the text). (**A**)—W Zielonej Górze cave; (**B**)—Towarna cave; (**C**)—Psia cave; (**D**)—Zegar cave.
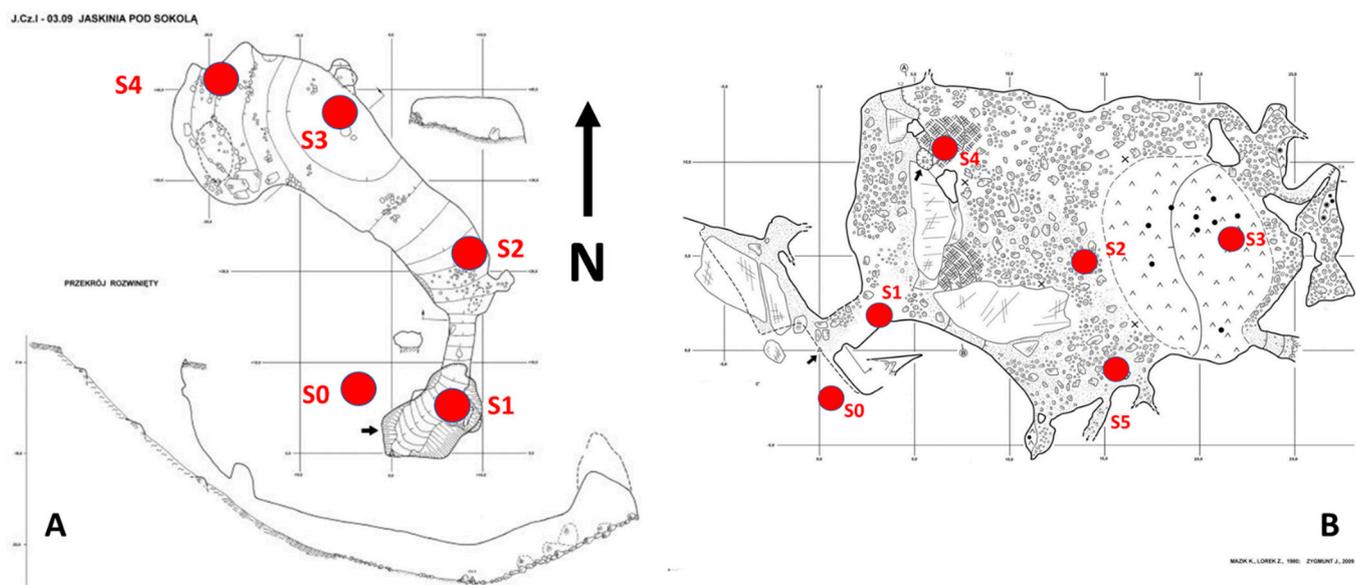
Figure 4. Diagrams of the studied caves with marked sampling points (for explanations, see the text). (**A**)—Pod Sokolą cave; (**B**)—Kroczycka cave.

The traps were always situated in the same area in each cave. The first was placed in the entrance zone of the cave (S1), the second in the middle of the passage (S2) and the third at the end of the passage (S3) (Figure 3). Additionally, one trap was always placed in the direct surroundings of each cave entrance (S0) (Figure 3).

Because of the enormous entrance of the Pod Sokolą cave, the entrance zone (ca 3–4 m inside the cave) was not characterised by specific features. Therefore, an additional trap was used there. In this cave, for the statistical analyses, the trap in S2 was treated as the entrance zone trap, the trap in S3 as a transition zone trap, and that in S4 as a deep zone trap (Figure 4A).

In the Kroczycka cave, four traps were also used, due to the cave morphology resembling a rectangle with two entrances (Figure 4B). Traps S1 and S4 were located near the entrances, and, in the statistical analyses, they were used collectively as the entrance zone traps. Trap S5 was placed approximately in the middle of the cave length, and was thus treated as a trap appropriate for the transition zone. Trap S3 was placed at the end of the cave and represented a deeper part of the cave. Trap S2 marked a microclimate measurement point.

2.3. Microclimate Measurements

The temperature and humidity were measured from December 2014 to February 2017 in the studied caves. The Assmann psychrometer was set up monthly at the same points (S1 to S3 in every cave, and S4 in the Pod Sokolą cave). The psychrometer consisted of two thermometers (wet and dry) and an electric fan. In situ, the temperature was measured on both thermometers, and then, using psychrometric tables, the relative humidity was estimated. It was not possible to use automatic data loggers.

2.4. Data Analysis

In order to identify species associated with the subterranean environment, the dominance was calculated, and habitat and food preferences were analysed. Additionally, species richness for each cave was estimated using Hill numbers (^qD, sensu Jost [18]). It was parameterised with q values of 1 and 2 to obtain the Shannon–Wiener diversity ($q = 1$) and Simpson diversity ($q = 2$) [19,20] (Appendix A, Formulas (A1) and (A2)). Both formulas are modified versions of the Shannon–Wiener and Simpson indices, respectively [18–20]. However, modification of the first index enables the elimination of favouritism of rare or

common species, while Simpson diversity puts more weight on the frequencies of species and discounts rare species [19,20]. The analyses were performed using the PAST3 software ver. 4.03 [21].

The dominance index was calculated to detect the dominant species in particular caves (Formula (A3)). All species were classified within four groups, namely, eudominants (above 10.0%), dominants (5.1–10.0%), subdominants (2.1–5.0%) and recedents (1.0–2.0%) [22,23].

The analyses of species habitat and food preferences were based on the literature data [24–54]. According to the habitat, species were assigned to the proper environment groups, e.g., species living in the forest, grasslands, MSS (inhabiting mammal burrows and nests, living under moss, stones, in cave entrances) and others. Regarding diet, the studied beetle species were divided into five groups: herbivores, predators, fungivores, detritivores and omnivores. The group of detritivores includes all the phytosaprophages, zoosaprophages, coprophages and necrophages.

For subterranean species, we used four categories of ecological classification based on Sket's concept [55], i.e., the group of troglobionts consists of species exclusively found in caves and, in the literature, considered as this form. The group of eutroglophiles is formed by species consistently found in caves throughout the year. However, they are generally epigean species. The group of subtroglophiles is composed of species that temporarily occur in caves; however, they were collected several times in many caves. Those species prefer living in mesovoid shallow substratum. The trogloxenes group includes accidental species for which caves and other subterranean shelters are not a typical habitat.

Moreover, a different group found in shallow subterranean habitats—MSS—was recognised [5–7]. In order to assign each of the analysed beetle species to the appropriate ecological category, we used previously published data [56–61]. All usable information was involved, i.e., the presence of species throughout the year, food and habitat preference, the area of the cave in which the species was most frequently caught.

3. Results

3.1. Species Dispersal

A total of 2084 specimens of Coleoptera were collected from the traps (Table S1). These individuals represented 105 species in 61 genera and 19 families (Table S2). Three families accounted for over 96% of total individuals, i.e., Leiodidae (74%), Staphylinidae (12.6%) and Cryptophagidae (9.7%).

Additionally, we compared the frequency of particular species collected from caves with results obtained from the traps outside the studied caves (especially those species considered eutroglophiles and troglobionts). None of the troglobionts and eutroglophiles, was sampled outside the cave, with one exception. Several specimens of *Catops picipes* (Fabricius, 1787) were collected from traps located outside the caves. However, sample sites S0 were still situated among rocks and debris near the cave entrances. The presence of the beetles inside the caves varied and depended on the zones within the caves (Figure 5). Many collected specimens for each family were also correlated with the cave zones (Figure 6). When certain zones of the caves were considered, the entrance zone (S1) was the most numerous in species (10 to 35 species). Five to eleven species were collected in the middle of the passages (S2), whereas at the end of the caves (S3), one to eleven species were recorded. The results presenting the number of recorded species in particular parts of each cave are provided in Table 1, and the total number of species in each cave is presented in Table 2.

3.2. Species Richness

The number of species in particular caves differed (Table 2). The highest numbers were observed in the Pod Sokolą cave, while the lowest were observed in the Psia and Kroczycka caves. The highest species richness was calculated for the Zegar and Kroczycka caves, and the lowest in the Towarna cave (Table 2).
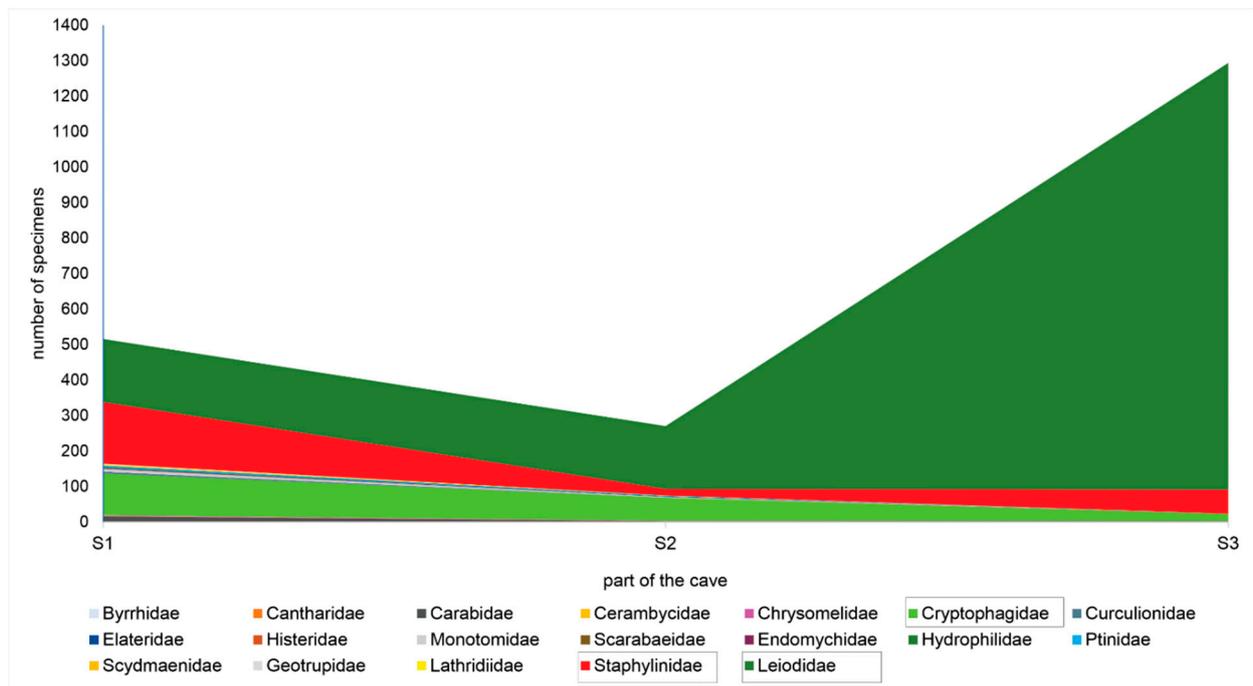
Figure 5. Distribution of beetles inside the caves; richness in particular parts of the caves is shown for all beetle families.
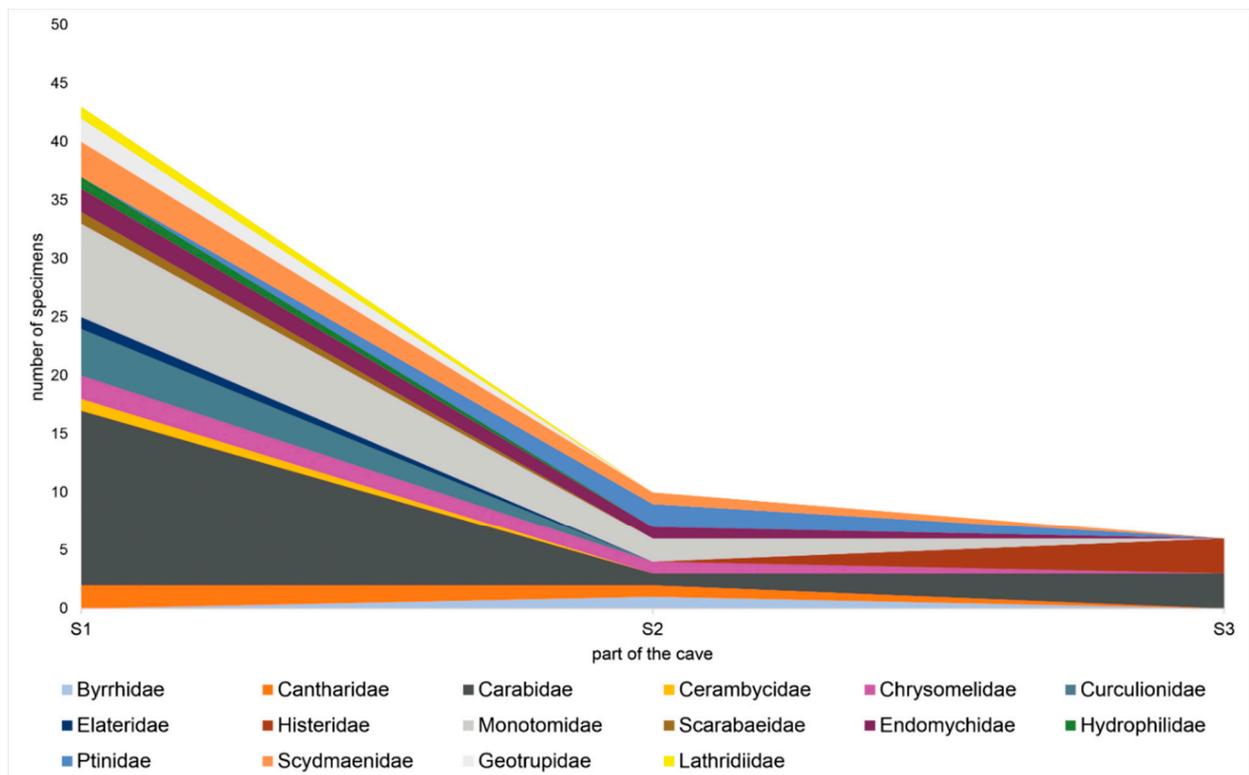

Figure 6. Distribution of beetles inside the caves; richness in particular parts of the caves is shown for beetle families, except the three most numerous (Staphylinidae, Leiodidae, Cryptophagidae).

Table 1. Number of species recorded in particular parts of studied caves. S0–S5—sampling sites.

Cave	S0	S1	S2	S3	S4	S5
W Zielonej Górze	22	34	11	7	——	——
Towarna	53	24	9	8	——	——
Pod Sokolą	13	35	11	5	3	——
Kroczycka	17	10	——	5	11	7
Psia	20	10	8	1	——	——
Zegar	23	33	8	11	——	——

Table 2. Number of species collected in the studied caves and the value of the species richness indices.

Cave	Number of Species	Shannon Diversity Index	Simpson Diversity Index
W Zielonej Górze	38	7.614086359	1.375137514
Towarna	27	1.447734615	7.692307692
Pod Sokolą	42	5.053090317	1.497005988
Psia	17	8.758284041	2.949852507
Zegar	37	15.95863401	1.051524711
Kroczycka	21	8.846306259	1.112718371

3.3. Species Dominance

Speonomus normandi hydrophilus (Jeannel, 1907), representing the family Leiodidae, was the most abundant among collected specimens (a total of 1120 individuals, 53% of all sampled specimens). Despite its abundance, all its specimens were exclusively found in the Towarna cave. *Choleva lederiana gracilenta* Szymczakowski, 1957, also from Leiodidae, was the second most abundant beetle, comprising 11% of the total collected specimens. As with *S. normandi hydrophilus*, all its individuals were exclusively sampled in one cave, namely, the Pod Sokolą cave. The third most abundant species found (representing 3.8% of the assemblage) was the staphylinid *Quedius mesomelinus mesomelinus* Marsham, 1802, which was found in each of the studied caves. Moreover, each cave had its own different set of eudominants and dominants (Table 3).

Table 3. Dominant species in the studied caves.

Cave	Eudominant	Dominant
W Zielonej Górze	*Cryptophagus distinguendus* J. Sturm, 1845 (25.76%) *Cryptophagus punctipennis* Ch.N.F. Brisout de Barneville, 1863 (28.46%) *Quedius mesomelinus mesomelinus* Marsham, 1802 (12.30%)	
Towarna	*Speonomus normandi hydrophilus* (Jeannel, 1907) (92.86%)	
Pod Sokolą	*Choleva lederiana gracilenta* Szymczakowski, 1957 (55.6%) *Catops picipes* (Fabricius, 1787) (10.97%)	*Catops tristis infernus* Szymczakowski, 1957 (9%).
Kroczycka	*Quedius mesomelinus mesomelinus* Marsham, 1802 (22.2%) *Othius subuliformis* Stephens, 1833 (16.65%) *Cryptophagus distinguendus* J. Sturm, 1845 (12.5%).	*Choleva paskoviensis* E. Reitter, 1913 (8.3%) *Proteinus brachypterus* (Fabricius, 1792) (6.9%).
Psia	*Omalium caesum* Gravenhorst, 1806 (23.8%) *Choleva cisteloides* (Frölich, 1799) (14.28%).	
Zegar	*Catops picipes* (Fabricius, 1787) (13.56%) *Omalium validum* Kraatz, 1857 (10.17%)	*Omalium caesum* Gravenhorst, 1806 (8.47%), *Choleva glauca* Britten, 1918 (5.1%) *Lesteva longoelytrata* (Goeze, 1777) (5.1%) *Quedius mesomelinus mesolmelinus* Marsham, 1802 (5.1%)

3.4. Habitat and Food Preferences

The forest beetles appeared to be the most numerous group (45 species, 43%), whereas the smallest group comprised species that occur in grasslands (three species, 3%) (Table S3). Beetles that occur in forests and grasslands were represented by eight species (7.5%). Thirty-two species were classified as those inhabiting MSS environments (30.5%). Most importantly, four species were assigned to the group of strict cave-dwellers (4%). Eight per cent of the collected material represented species inhabiting other environments (e.g., *Oxypoda annularis* (Mannerheim, 1830) or *Anotylus sculpturatus* (Gravenhorst, 1806)). Food preferences for 78 species (74% of the collection) were possible to estimate (Table S3). The most numerous groups were the detritivores (36%, 28 species) and predators (33%, 26 species). Fifteen species were classified as fungivores (18%). The minor groups comprised herbivores (three species, 4%), mixophagous and coprophagous (one species in each group, 1.5%).

Unfortunately, for all other species (especially those representing the family Staphylinidae), these data were impossible to collect due to inadequate knowledge regarding their biology.

3.5. Ecological Classification

Among the collected beetles, three were classified as troglobionts (*Speonomus normandi hydrophilus*, *Choleva lederiana gracilenta* and *Catops tristis infernus* Szymczakowski, 1957), four as eutroglophiles (*Quedius mesomelinus mesomelinus*, *Tachinus subterraneus* (Linnaeus, 1758), *Omalium validum* Kraatz, 1857, *Catops picipes*), 32 as subtroglophiles or MSS species and 66 as the trogloxenes (Table S2).

3.6. Microclimatic Analyses

The temperature in all studied caves fluctuated, but the greatest temperature changes were detected in the entrance zone (S1). Additionally, it was observed to decrease towards the deeper parts of the cave. The most stable temperatures were observed at the terminal parts of the caves (Figure 7). Humidity in the studied caves was generally high. However, it fluctuated similarly to temperature, especially in the entrance zone (S1). Notably, humidity fluctuations during the summer and winter periods were recorded even in the deeper parts of the caves (Figure 8).
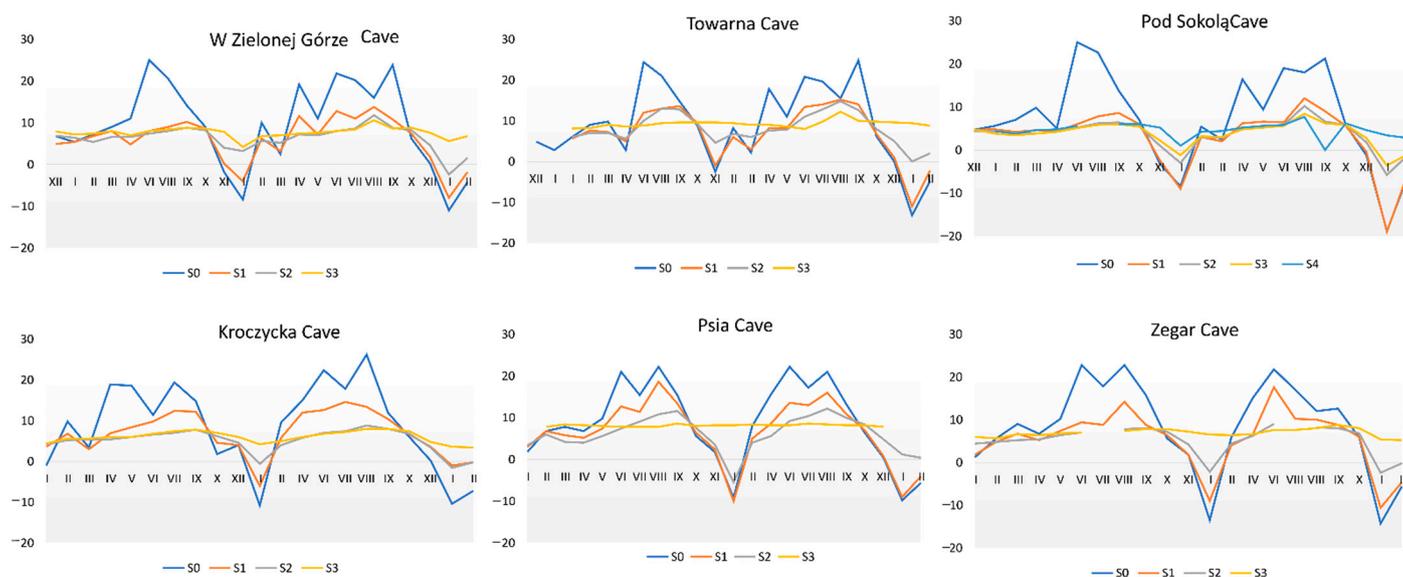

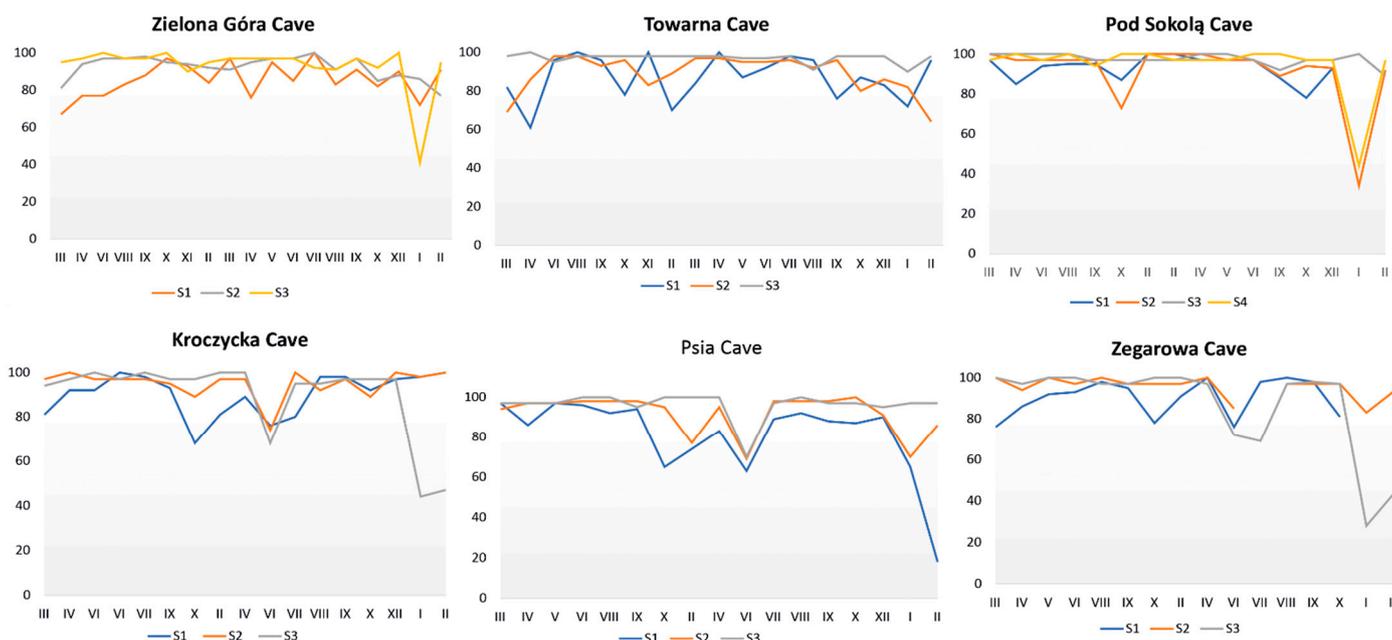**Figure 7.** Temperature fluctuations at the measurement points in the studied caves.

Figure 8. The relative humidity fluctuations at the measurement points in the studied caves.

4. Discussion

4.1. Species Richness

Altogether, 105 Coleoptera species were detected in the studied caves (Table S2). The beetle species number provided in the present study is twice larger than that reported in all previous studies in Polish caves [11,12].

In our study, we confirmed the presence of a beetle species group that commonly inhabits Polish caves [11,12,56,62–65]. These include: *Quedius mesomelinus mesomelinus* (Staphylinidae), occurring in all cave regions of Poland [12,56,62–65]; *Choleva cisteloides* (Frölich, 1799) and *Catops picipes* (Leiodidae), in caves in the Ojców region [12,64]; *Catops fuscus* (Panzer, 1794) (Leiodidae), in caves in the Sudety Mountains [12,62,63,65]; and *Choleva bicolor* Jeannel, 1923 (Leiodidae), *Catops fuliginosus* Erichson, 1837 (Leiodidae), *Tachinus subterraneus* (Staphylinidae), *Omalium rivulare* (Paykull, 1789) and *O. excavatum* Stephens, 1834 (Staphylinidae), and *Otiorhynchus scaber* (Linnaeus, 1758) (Curculionidae) in caves in the Tatra Mountains [12,56].

The highest species frequencies were observed in Leiodidae, Staphylinidae and Cryptophagidae. The occurrence of round fungus beetles (Leiodidae) in the caves was not surprising, because many species of this family are highly associated with subterranean environments [66]. Many rove beetles (Staphylinidae) are also known from subterranean areas [8,66]. However, silken-fungus beetles (Cryptophagidae) are not usually associated with subterranean environments, being closely associated with forest ecosystems and often considered within the ranks of saproxylic and xylobiont Coleoptera [67]. Therefore, the high species frequency of silken-fungus beetles in the studied caves was slightly unexpected. However, most of the Cryptophagidae specimens were collected from the entrance zone of one cave (the W Zielonej Górze cave), and only a few occurred in its deeper zones and in the other caves. Thus, despite collecting about 200 specimens, only two species were classified as subtroglophiles, and five were classified as trogloxenes.

The highest species richness among the studied caves was recorded for the Zegar cave (15.95863401 and 1.051524711 in Shannon diversity and Simpson diversity indices, respectively) (Table 2). The high frequency of those species among the samples may explain such a result. The Towarna cave represented the lowest value of the Shannon diversity (1.447734615), but the highest of the Simpson diversity (7.692307692). It can be explained by the extremal domination of one species (among 1206 specimens in the collection, 1120 belonged to *Speonomus normandi hydrophilus*). The Psia cave represented rather high values of

the abovementioned indices (8.758284041 and 2.949852507, respectively). It was surprising due to the generally poor habitat quality of the cave, which was also confirmed by the low frequency of specimens representing other arthropod groups compared to other studied caves. In addition, we examined the contents of organic carbon in every sampling place of the studied caves only once. The Psia cave is characterised by twice the lower value of organic carbon than other caves. However, this parameter was not elaborated on further due to the small amount of data.

In terms of cave zonation, the highest values of the analysed indices were associated with the entrance zones. This was an expected result because the entrance zones were always characterised by toned temperature fluctuation (in comparison to the surface), a lack of violent weather phenomena, a high accumulation of organic matter, and the presence of direct or indirect sunlight. All these conditions significantly impact cave-dwelling by invertebrate fauna, including beetles. Stable temperatures, high relative humidity and extreme organic matter accumulation were associated with the deepest zones. Despite this, the lowest values of species richness indices resulted from complete darkness, which is not conducive to penetration by surface fauna.

4.2. Species Dominance

The analyses of species dominance indicated the overwhelming contribution of accidental species in the entrance zone (S1), especially in the caves with large entrances. This was evident, for instance, in the Pod Sokolą, Zegar and W Zielonej Górze caves, where the accidental species reached 60% to 80% of the total amount of collected species (Table 3).

Moreover, each studied cave had a different set of eudominant or dominant species (Table 3). In the W Zielonej Górze cave, two species (*Cryptophagus distinguendus* J. Sturm, 1845 and *C. punctipennis* Ch.N.F. Brisout de Barneville, 1863) represented the eudominant class. *Speonomus normandi hydrophilus*, in the Towarna cave, and *Choleva lederiana gracilenta* and *Catops tristis infernus*, in the Pod Sokolą cave, exhibited a spectacular dominance. This reached 98% in the deepest part of Towarna (S3) for *S. normandi hydrophilus* and 87.5% and 20% in the deepest part of Pod Sokolą (S4) for the latter two beetles, respectively.

In the caves of the central and southern part of the investigated area—i.e., the Kroczycka, Psia and Zegar caves—none of the analysed species achieved a high dominance value.

4.3. Habitat and Food Preferences

The examination of food preferences indicated that beetles mostly choose detritus or fungi, and some are predators. Phytophagous species represented only a tiny part of the collected material. Similar results were demonstrated for invertebrates collected in caves in Germany [68]. The analyses of habitat preferences showed that most of the sampled beetle species prefer living in a forest (under rocks, fallen leaves and rotten wood). Beetles preferring open spaces were less abundant (only four per cent of the identified species).

4.4. Ecological Classification

When all data regarding beetle species occurring in Polish caves were taken into consideration, the corroboration in the presently studied caves of three troglobionts (*Choleva lederiana gracilenta*, *Catops tristis infernus* and *Speonomus normandi hydrophilus*) and four eutroglophiles (*Quedius mesomelinus mesomelinus*, *Tachinus subterraneus*, *Omalium validum* and *Catops picipes*) was an expected result.

Despite *Ch. lederiana gracilenta* and *C. tristis infernus* not presenting particular adaptations for living underground, both species were described from caves [69], and thus far, they have never been found in the epigean environment. In turn, *S. normandi hydrophilus* is a highly specialised subterranean species; however, it can still be found in caves and the MSS environment, such as scree and rock debris [46].

While *Q. mesomelinus mesomelinus* and *T. subterraneus* are commonly accepted as (eu)troglophiles species, *C. picipes* and *O. validum* are not so obviously classified. *C. picipes* is a common, widely distributed European species. It is found in both epigean and hypogean

environments. However, its preference to occur in subterranean environments and high frequency in samples from various caves in Europe influenced considering this species as an (eu)troglophile [61,70].

Similar results concern *O. validum*, which occurs primarily in mountain regions and lives in burrows, rock debris and caves [29,71]. The species was found not only in Polish caves but also in many caves in Czechia [72], Germany [61], and Slovakia [8]. Moreover, it is also known for living in the riparian-sylvan microhabitat [73]. It was considered an (eu)troglophile by both Zaenker et al. [61] and Rendoš et al. [8]. In our investigation, we observed it every season through both years of the study. Burakowski [29] indicated that faint pigmentation, small eyes and more extended feet are an adaptation for subterranean living.

It is worth noting that among all collected species, more than 30 were indicated as subtroglophiles or MSS species, which is approximately 30% of all collected species. It is an interesting result because it proves that many species penetrating caves prefer this habitat. The attractiveness of the MSS environment was already pointed out [8]. On the other hand, more than 50% of collected beetle species were trogloxenes. However, a majority of them were sampled only in the entrance zone. This is not entirely unexpected, since the high ratio of trogloxene diversity (3.560852562–5.640653908 Shannon diversity index value) in the entrance zone was also reported in a temperate marble cave in the Sierra Nevada Range, California, USA [74]. Moreover, the occurrence of many trogloxenes was also observed in the entrance zones of caves in Slovakia [59], Romania [73] and Italy [75], where it was mainly attributed to the contact between subterranean and surface environments and a high accumulation of decomposed organic matter.

The presence of very few species that could be classified as troglobionts and eutroglophiles most probably resulted from the environmental conditions peculiar to caves of the Częstochowa Upland. The temperatures inside the studied caves were unstable and varied throughout the year. Temperature fluctuations were higher in the entrance zones (about several dozen degrees Celsius) than in the depths of the caves (several degrees Celsius). Similarly, relative humidity was inconstant, especially in the entrance zone. Moreover, in some caves, the direct or diffracted light reached even a half-length of the cave passages. Because species strictly associated with subterranean environments prefer stable environmental factors, such as temperature and humidity [76,77], they cannot find such conditions in the investigated caves.

Nevertheless, despite conditions that are not very suitable for dwelling in the analysed caves, two strict troglobionts, *Choleva lederiana gracilenta* and *Catops tristis infernus*, have populations living in the Pod Sokolą cave. This was a slightly unexpected situation, since some diffracted light reaches even the very end of this cave, and a minor fluctuation in air temperature occurs there. In this case, however, stable humidity was a crucial factor for the presence of both these cave-obligated beetles.

In contrast, the deepest terminal part of the Psia cave boasts a very stable temperature (the yearly fluctuation was less than 1 °C), high and stable humidity, and complete darkness. Despite these preferable conditions, this cave zone had outstandingly poor fauna (Tables S1 and S2). Within a two-year study period, a single beetle specimen was sampled in this zone of the Psia cave.

However, there was also a cave in which the climatic conditions appeared to be very dynamic throughout the year, but it still possessed its troglobiont beetle, namely, *Speonomus normandi hydrophilus*. Moreover, this troglobiont was the most abundant beetle in this cave, being extremely dominant (Table 3). It is worth mentioning that *S. n. hydrophilus* is alien to the fauna of Poland. Endemic to the Pyrenees, it is a beetle that was intentionally introduced to the Dzwonnica cave in 1982 [78]. Within 40 years, this species colonised nearby caves (i.e., the Towarna and Cabanowa caves) [79,80].

This case of colonisation success proves that, in Poland, the environmental conditions in caves are sufficient for habitation by troglobionts, but for some reason, are only barely adequate or inadequate for highly specialised dwelling species. As suggested by some authors [56,58,64], this phenomenon can be explained by the geological history of Central

Europe, where, during the Pleistocene, glaciations influenced the entire fauna to such an extent that it could not even survive in the caves, which are normally refugial environments.

There is one more reason for this hypogean environment to be vastly attractive for many beetles. Though the epigean surroundings have their own environmental and climatic conditions, they are not as stable as those in the cave entrances. Additionally, as was suggested in many previous studies, organic matter from the external environment can easily flow into the caves via physical or biological means [4,9,81–84]. Most importantly, the entrance and transition zones of the studied caves exhibit conditions similar to the MSS environment to a greater extent than the deeper cave zones. The MSS, as a specific space [5,6], connects components originating from the underground and the surface environments. Hence, it seems to provide an additional explanation for why so many beetle species live in these caves, albeit being weakly associated with them ecologically.

5. Conclusions

1. Many beetle species choose to dwell in caves, despite lacking specific adaptations for living in such environments.
2. The entrance zone is the most attractive place for surface species to inhabit because the climatic conditions there are more stable than outside the cave (due to the presence of some light and high availability of organic matter).
3. In the deeper parts of the studied caves, the number of occurring species rapidly decreased, though this zone sometimes had a stable environmental condition (namely, humidity).

Appendix A

The Shannon diversity index was calculated as:

$$^1D = \exp(H') = \exp(-\Sigma(p_i \log p_i^2) \tag{A1}$$

where the following are defined:

^{1}D—Shannon diversity;

H′—the Shannon index;

p_i —the proportion (n_i/N) of individuals of ith species found (n_i) divided by the total number of individuals found (N).

The Simpson diversity was calculated as:

$$^2D = 1/\Sigma\, p_i^2 \tag{A2}$$

where the following are defined:

$\Sigma\, p_i^2$—the Simpson index;

p_i—number of specimens of species ith in the community.

The dominance was calculated by using the formula:

$$D_i = n_i/N \times 100\% \tag{A3}$$

where the following are defined:

D_i—dominance index;

n_i—number of individuals in ith species;

N—total number of individuals for all species.

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