



Biodiversity of Fungi in the photic and aphotic zones of Montenegro caves

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Abstract For the first time, the composition of micromycetes communities was investigated in both photic and aphotic entrance zones of seven caves in Montenegro: Obodska Pećina, Golubinja Pećina, Veluštica Pećina, Vrbicka jama, Jama ER-1, Njegoš Pećina, and an unnamed cave. In total, 72 species of micromycetes were identified: 46 species from illuminated photic zones of the caves, including 43 species on phototrophs, 10 species from the air, 15 species on substrates, and 50 species from unlit aphotic zones, including 35 species from the air and 37 species on substrates. The most frequently isolated species were *Acrodontium salmoneum*, *Aureobasidium pullulans*, *Cladosporium oxysporum*, *Mucor racemosus* f. *racemosus*, *Penicillium chrysogenum*, and *Rhizopus stolonifer*. The similarity between micromycetes composition of different biotopes was evaluated using the Jaccard index and cluster analysis. The greatest similarity was observed in the

communities isolated from the air of the photic zones of the caves.

Keywords Ecotones · Micromycetes · Karst caves · Montenegro

1 Introduction

Fungal biodiversity in karst ecosystems is of great interest for the study: Allochthonous microbiota with unique antibacterial properties is important for solving biomedical problems and discovering new antibiotics (Bhullar et al. 2012; Cheeptham and Saiz-Jimenez 2015). The microclimate conditions of karst caves are favorable for the development of microscopic fungi, which play an important role in cave microbiota as decomposers or parasites and probably the major food source for other organisms (Burford et al. 2003; Šustr et al. 2005; Gorbushina 2007). Generally, they are widespread soil species transferred into caves by wind, water, vertebrates or invertebrates, in the form of propagules and settle on various substrates specific for underground ecosystems: bat droppings and guano deposits, corpses of troglobionts and troglodhils, speleothemes, vermiculation, rocks and mineral deposits, plant debris from the surface (Novakova 2009; Souza-Silva et al. 2012; Vanderwolf et al. 2013; Prous et al. 2015; Pfendler et al. 2019). The number of species and species diversity of micromycetes of karst ecosystems directly depends on the abundance and

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diversity of substrate (Novakova 2009). Bat guano is noted to be the most suitable substrate for the development of micromycetes in caves (Nieves-Rivera et al. 2009), with the highest species diversity (Novakova 2009) and the greatest biomass observed (Šustr et al. 2005).

The distribution of micromycetes inside the cave is uneven and depends on biotope characteristics: presence of water streams, humidity, temperature, pH of substrates, availability of nutrients, mineral composition, speleothems, porosity, and permeability of rocks (Gorbushina 2007). Tourist visits increase the content of air microflora, including microscopic fungi (Vaughan-Martini et al. 2000; Wang et al. 2010; Fernandez-Cortes et al. 2001; Adetutu et al. 2011).

Many regions are characterized by a lack of moisture in certain seasons, and this deficiency is especially characteristic on karst territories, in conditions of uncovered karst. The transitional zone between the surface and the unlit environment of the caves is the entrance area where a large number of species can develop and survive due to high humidity and low temperatures (Pentecost and Zhaohui 2001) and where decomposition is not limited to dry periods (Nováková et al. 2018). In such conditions, one can expect the appearance of non-specific biota and native species (Prous et al. 2004, 2015; Culver 2005). The analysis of the micromycetes species composition of the entrance zones of the caves is extremely rare (Mazina and Kozlova 2018; Kozlova et al. 2019) and does not take into account the investigation of different biotopes. Given the importance of micromycetes for community functioning as a trophic level in the decomposer food chain, it is necessary to assess biodiversity of micromycetes, and by assessing the biodiversity of various biotopes, we can track the paths of species introduction.

The goal of this study was to identify the composition and perform a comparative analysis of microscopic fungi in the photic and aphotic areas of the entrance zone: in the air, on substrates, in the composition of phototrophs.

2 Materials and methods

2.1 Study area

Seven caves in Montenegro were the objects of the study (Fig. 1). An unnamed cave (42° 17' 32.46" N,

18° 52' 26.03" E) is located near the Bečići town, close to the natural monument of Olive tree. The cave may be of artificial origin, has a large number of calcite sludge deposits in the entrance zone, and functions as a seasonal vauculian spring. Obodska Pećina (42.352113° N, 19.005209° E) is located west of the Rijeka Crnojevića, Cetinje. The cave has a large grotto-type entrance, and unlike other caves, Obodska Pećina has a large deep dark zone. Bats live in the entrance zone full of nutrient-rich bat guano. The cave functions as a seasonal vauculian spring.

Golubinja Pećina (42° 21' 07.61" N, 19° 00' 18.75" E) is located on the territory of Lovćen National Park. The cave has a large grotto-type entrance with a small slit-like fracture on the arch connecting the cavity with the surface. A colony of bats and pigeons lives in the cave, guano and droppings are located on the arches and at the bottom of the cavity. The remaining caves are located near Lovćen National Park, in the village of Njeguši or near it: Veluštica Pećina (42° 25' 58.32" N, 18° 48' 13.62" E), Njegoš Pećina (42° 25' 58.84" N, 18° 49' 53.72" E), Vrbacka jama (42° 25' 58.98" N, 18° 48' 38" E), and Jama ER-1 (42° 25' 56" N, 18° 49' 55.02" E). Veluštica Pećina lies 1062 m above sea level, located on the slope of Mrajanik Mountain. A particularity of the cave is the second slit-like exit on the other side of the conical top of the mountain. Njegoš Pećina is a small cavity about 120 cm high with clayey arches. Vrbačka jama is a vertical cavity with ledges. Jama ER-1 is a vertical well with practically no ledges.

Fieldwork for the study was carried out during July 2017. The study included 15 sites from each cave. Sampling was carried out in the photic and aphotic zones of caves entrances, the allocation of zones with different entrance types is shown in Fig. 2.

2.2 Sampling methods

Samples were taken in the following habitats in the photic zones: from the air, on substrates without visible phototrophs (calcite, limestone, clay deposits) and on the communities of phototrophs. Sampling of substrates and from the air was performed in the aphotic zones. Samples were collected into sterile sealed vials which were stored in the dark at the temperature of the caves. The assessment of habitat parameters (air temperature, relative humidity, pH of substrates) at the sampling sites was performed using



Fig. 1 Location of the studied caves in Montenegro: 1—unnamed cave; 2—Golubinja Pećina; 3—Veluštica Pećina; 4—Vrbačka jama; 5—Jama ER-1; 6—Njegoš Pećina; 7—Obodska Pećina

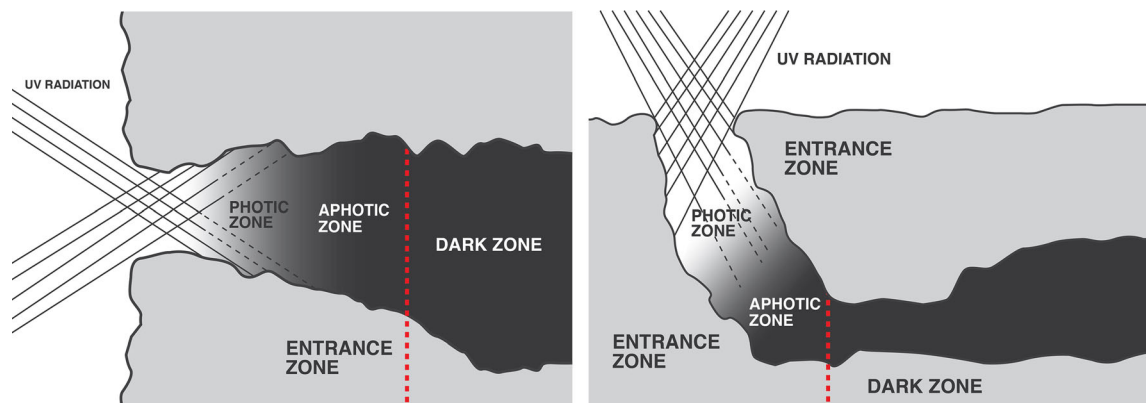


Fig. 2 Schematic zoning of horizontal grotto-type cave (left) and vertical well-type cave (right)

electronic devices Elin Complex iBDLR-L-U (thermochron) with an error of 0.5 °C and 1%, pH meters PH013 (accuracy ± 0.01 pH) and HI99121 (Table 1). Samples were taken from 12 pm to 4 pm.

Sampling methods varies in different habitats.

2.3 Substrates

Clay deposits, limestone on the floor, and arches in the photic zone were collected from the areas with no visual phototrophs starting from 1 to 2 m from the entrance every meter from a depth of 1–10 cm

(depending on the thickness of deposits). Similarly, substrates were selected in the aphotic zone. Samples of rock chips and limestone were taken.

Samples of clay deposits and limestone gruss were analyzed by the soil dilution method of Vaksman in the modification of Zvyagintsev with seeding and counting on solid agar nutrient media and release into pure cultures (Zvyagintsev 1991). Soil samples were treated with a standard method of sowing aliquots from serial dilutions of the suspension onto the surface of nutrient agar and the method of fouling glasses was applied to isolate micromycetes (Lund 1945). The

Table 1 The number of samples and microbiological parameters of sampling sites

Cave	The sample size	Temperature $\pm$ 0.5/relative humidity $\pm$ 1%		PH of clay deposits
		Photic zone	Aphotic zone	
Obodska Pećina	43	20–16/48–78	16–12/80–90	7.4–8.5
Unnamed cave	28	18–14/56–82	14–12/80–86	7.8–8.2
Golubinja Pećina	32	22–18/35–60	20–18/45–65	6.9–8.1
Veluštica Pećina	36	18–12/65–74	14–12/72–96	7.2–7.4
Vrbačka jama	28	14–12/67–72	14–12/70–96	7.3–7.9
Jama ER-1	24	16–12/42–65	13–12/60–96	7.2–7.8
Njegoš Pećina	16	16–14/54–72	14/86–88	7.2–7.5

Czapek–Dox agar medium (sucrose concentrations of 0.3% and 3%), potato–glucose agar, soil extract and starvation agar were used (Netrusov et al. 2005).

Chipped rocks and large debris were placed in sterile isotonic NaCl solution and sonicated (1–3 min, 0.4 A, 15 kHz) to separate micromycetes from the rock, after which 1 ml samples were seeded on the selective medium (Netrusov et al. 2005). In addition, imprints were made from the surface of the rocks and sinter formations on the Czapek–Dox agar medium.

2.4 Air

To study air microflora, a sample pump was applied (Dyakonov's method): A volume of air of 200 ml was pumped through water, after which 1 ml of the suspension was seeded on Czapek–Dox agar medium with 0.3% sucrose concentrations (Netrusov et al. 2005). Samples were collected approximately 0.5 m from the floor of the cave.

2.5 Phototrophs

Samples of fouling communities were taken from each visually distinguishable parcel along with the substrate on which the community developed. Mosses were separated from the surface manually maintaining a sterile field; cyanobacterial mats were scraped off the substrate with the edge of the tube; algae biofilms were cleaned with a sterile instrument. The substrates were separated from the mosses and mats by shaking off the soil from the underneath communities.

The obtained substrates and scrapings of algae were analyzed analogically to clay deposits, with addition of tetracycline (0.001 g/l) into cultivation media.

Additionally, imprints on the nutrient medium were made from bryophytes component of phototrophic communities, and the method of fouling glasses was applied. Czapek–Dox agar medium with 0.3% sucrose concentrations were used.

Cultivation of micromycetes was carried out at a temperature of 12 °C and 24 °C, calculation of the grown colonies and isolation of pure cultures was carried out every week, the cultivation time was at least 4 weeks (maximum 12 weeks) at low temperature. Samples were stored and grown in the dark.

Isolates were purified on Czapek–Dox agar medium and incubated at the temperature of the caves during 7–14 days depending on the temperature. Samples were examined under a light microscopes Leica DMLS (Germany) and Biolam MBS-9 (Russia). Identifications of micromycetes were performed using the following identification keys: Booth (1971), Domsch et al. (2007), Ellis (1971, 1976), de Hoog et al. (2001), Pitt (1991), Ramirez (1982) and Raper and Thom (1968). The names of species are given according to the <http://www.mycobank.org> database (Robert and Stalpers 2005).

2.6 Statistical analysis

The similarity of the species composition of micromycetes in different clusters of the photic and aphotic zones of the caves was evaluated using the Jaccard index (Jaccard similarity coefficient), which is the simplest and most effective for comparing β -

diversity. Similarity is defined as the size of the intersection of set *A* and set *B* (i.e., the number of common elements) over the size of the union of set *A* and set *B* (i.e., the number of unique elements):

$$J(A, B) = \frac{|A \cap B|}{|A \cup B|} = \frac{|A \cap B|}{|A| + |B| - |A \cap B|}.$$

Cluster analysis was carried out and tree diagrams were constructed using the Euclidean distance in the STATISTICA 7.0 program.

3 Results and discussion

In total, 72 species of micromycetes were identified: 46 species were identified in the entrance zones of the caves (43 species in the phototrophic communities, 10 species in the air, 15 species on substrates), 51 species identified in the dark zones (34 species in the air and 36 species on the substrates). Representatives of phylum Ascomycota prevailed, mainly anamorphs. The following genera showed the greatest species diversity: *Penicillium*—21 species (29%), *Aspergillus*—10 species (14%), *Mucor*—7 species (10%), *Trichoderma*—6 species (8%), *Cladosporium*—4 species (6%), *Alternaria* and *Fusarium*—two of each (3%).

The greatest biodiversity of micromycetes was documented on substrates in the aphotic zones of the caves (Table 2). In the photic zones, the number of micromycetes isolated from fouling communities exceeded the number in the air and on substrates. This can be explained by the predominant survival of micromycetes propagules on clumps of mosses. The

conditions for survival on illuminated substrates and in the aerosol of the photic zone are less favorable for micromycetes due to low humidity and increased insolation.

The highest biodiversity in the air was revealed in the aphotic zone of Obodska Pečina, which has the largest entrance zone, compared to other caves. Second in biodiversity were grotto-type caves Golubinja Pečina, Veluštica Pečina and an unnamed cave, which located on the flanks with no trees near the entrances. All these cavities were similar to each other in a number of parameters: they actively connected with the surface throughout air flows, which are subjacent in Veluštica Pečina and Golubinja Pečina. Bats live in all caves; bat colonies were found in Golubinja Pečina and Obodska Pečina. Obodska Pečina and an unnamed cave function as a vauclusian spring in rainy seasons.

The contribution of immigration from the photic zone to aphotic one was greatest among Vrbačka jama and Jama ER-1 caves, which are similar in morphological structure and represent the vertical wells where migration is facilitated. Well-shaped caves Vrbačka jama, Jama ER-1 and small grotto-typed Njegoš Pečina with an inclined entrance are poorly communicating with the surface throughout water and air flows, so the number of micromycetes species in these caves is slightly lower.

Ascomycota was the most abundant phylum across the studied clusters, this result is consistent with the world review of fungi, yeasts, and slime molds in caves (Vanderwolf et al. 2013). The genus *Aspergillus* and *Penicillium* were represented in all studied caves.

Table 2 The number of micromycetes in various biotopes of different zones in the studied caves

Cave	Photic zone				Aphotic zone			The proportion of species common to the photic and aphotic zones (%)
	Phototrophic communities	Air	Substrates	All	Air	Substrates	All	
Unnamed cave	4	3	3	7	12	13	22	11
Obodska Pečina	6	3	6	8	14	19	25	22
Golubinja Pečina	12	7	8	15	11	17	21	21
Veluštica Pečina	15	5	4	17	9	16	23	18
Njegoš Pečina	5	2	3	8	10	8	15	21
Vrbačka jama	4	3	4	7	9	11	18	26
Jama ER-1	5	3	5	9	10	9	17	37

Aspergillus spp. were identified in all biotopes, except for the air and substrates of photic zones of the caves. The greatest species diversity of the genus was noted in aphotic zone of Veluštica Pećina. The species *A. ochraceus*, *A. niger*, *A. ustus* were documented in all the studied biotopes. Species of the genus *Penicillium* were identified in all considered biotopes, except for the air of the photic zone of the caves. The greatest species diversity was observed on phototrophs in the photic zone of Veluštica Pećina and on substrates in the aphotic zone of Obodska Pećina. A single species *P. chrysogenum* was documented in all of the studied caves and distributed mainly in the air of the aphotic zone. It is possible that this species was brought in from the deep part of the caves. This species was often noted in the caves worldwide: in Puerto Rico (Nieves-Rivera et al. 2009), in Poland (Ogórek et al. 2014), in Slovakia (Ogórek et al. 2016), in Italy (Mammola 2017), in the Republic of Bashkortostan (Mazina et al. 2018).

The dominance of the genera *Penicillium* and *Aspergillus* is typical for soils, and their ratio varies depending on the region: from the temperate to the tropical zone, the proportion of *Penicillium* decreases and *Aspergillus* increases (Christensen et al. 2000). The low proportion of the genus *Aspergillus* in the underground biotopes of the entrance zone is explained by increased humidity compared with terrestrial habitats. Fungi of the genus *Aspergillus* are characteristic for arid habitats (Mishustin and Pushkinskaya 1960). Despite the fact that *Penicillium* sp. and *Aspergillus* sp. conidia as well as spores of *Rhizopus* and *Mucor* are UV sensitive (Zhdanova and Vasilevskaya 1982), these species are often distinguished in the photic zone of the caves. The species *A. niger*, *A. ustus*, *P. chrysogenum*, *R. solonifer*, which have the greatest occurrence in the studied caves, are recognized as the most common species of cave mycobiota worldwide (Vanderwolf et al. 2013). Taxa from the genera *Aspergillus* and *Rhizopus* are considered to be cosmopolitan species mainly developing on plant debris and animal dung (Chlebicki and Jakus 2019).

The species diversity of the microbiota is unique for each of the studied caves; only a few species were found in more than one cave. Some species were found in different biotopes within the same cave.

The species *Cladosporium oxysporum* had an 100% occurrence in all considered biotopes in the photic and

aphotic zones of Veluštica Pećina, Golubinja Pećina, and Obodska Pećina. *Cladosporium* species are considered as cosmopolitan saprotrophs and dominate in the daytime among spores in the aerotop (Hamilton 1959). According to the previous studies, *Cladosporium* is the most abundant type of spore in the external environment (Fernandez-Cortes et al. 2001; Porca et al. 2011; Ogórek 2014). Other species of this genus are also found in the caves, what is consistent with previous observations of cave microbiota in various regions (Larsen and Gravesen 1991; Stępańska et al. 1999; Pusz et al. 2014; Vanderwolf et al. 2013).

Mucor racemosus f. *racemosus* was found in all biotopes: on phototrophs of the photic zone of Veluštica Pećina, in the air of the photic zone of all studied caves, on substrates of the photic zone of Veluštica Pećina, Golubinja Pećina and Obodska Pećina. *Acrodontium salmoneum* was noted in all the considered clusters of the aphotic areas of Veluštica Pećina, Golubinja Pećina and Obodska Pećina, this species is considered a common air-borne fungus. *Rhizopus stolonifer* was identified in all clusters, except for the soils of the aphotic zone: on phototrophs, on substrates and in the air of both photic zone and aphotic zone of an unnamed cave, Vrbacka jama and Jama ER-1; on phototrophs, on substrates and in the air of the photic zone of Veluštica Pećina and Obodska Pećina; on phototrophs and in the air of the photic zone of Golubinja Pećina; on substrates and in the air of the aphotic zone in Njegoš Pećina. *Rhizopus stolonifer* is commonly presented in the air of underground environment as well as of indoor air (Ogórek et al. 2011). It is a fast-growing saprophyte fungus developing on in wide range of temperatures and relative humidities (Ogórek et al. 2013). *Aureobasidium pullulans* was documented in all considered clusters of the aphotic areas, except for Veluštica Pećina and an unnamed cave. The presence of the species *A. pullulans* on substrates in the photic zone and in the air of the aphotic zone can indicate the transfer of these yeast-like saprotrophic fungi from the surface, the characteristic habitat of which is the flowers and sprout of plants.

Thus, most of the micromycetes taxa found in different zones and biotopes are widespread cosmopolitan saprotrophs (Vanderwolf et al. 2013). Animals harbor many saprotrophic molds and yeasts on their coat (genera *Alternaria*, *Aspergillus*, *Aureobasidium*, *Chrysosporium*, *Cladosporium*, *Mucor*,

Table 3 The results of the cluster analysis of micromycetes species similarity using the Jacquard index

	Photic zone											Aphotic zone	
	G_a	N_a	Vr_a	J_a	O_a	U_s	Ve_s	N_s	Vr_s	J_s	O_s	G_s	Vr_s
<i>Photic zone</i>													
G_p	1												
G_a					1								
U_a			1	1	1		1						
Ve_a		1	1	1	1		1						
N_a			1	1									
Vr_a				1	1		1	1	1				
J_a					1		1	1	1				
O_a						1	1				1		
U_s							1				1		
Ve_s											1		
G_s											1		
N_s									1				
Vr_s										1			
<i>Aphotic zone</i>													
O_s												1	
J_s													1

1—Jacquard similarity index equals 0.4 or higher (the communities species composition is similar) G—Golubinja Pećina; Vr—Vrbacka jama; J—Jama ER-1; O—Obodska Pećina; U—unnamed cave; Ve—Veluštica Pećina; p-phototrophs; a-air; s-substrates

Penicillium and *Rhizopus*), which contributes to the transfer these taxa to the deep zones of the cave (Muller et al. 2001).

Aureobasidium pullulans, *Aspergillus* spp., *Mucor* spp., *Penicillium* spp., and *Rhizopus* spp. are known as opportunistic pathogens in immunocompromised humans, which are able to produce potent mycotoxins, and have allergenic properties (Chan et al. 2011; Docampo et al. 2011; Paterson and Lima 2015). Strains of *A. fumigatus*, *A. niger*, *A. terreus* and *A. nidulans* pose the greatest risk to human health (Köhler et al. 2014). Genus *Fusarium* is known as important plant pathogens that also can infect neutropenic patients (Köhler et al. 2014).

The similarity of the communities of different biotopes of the photic and aphotic zones of the caves was evaluated using the Jaccard index and cluster analysis. The complete similarity was demonstrated by the communities in the air of the photic zones of the Vrbacka jama and Jama ER-1. If we assume that the communities are similar with the Jacquard similarity index equals 0.4 or higher (Maksimov and Kuznetsova 2013), then the similar composition of the communities in the following biotopes is found (Table 3).

In one case, similarities were found between the species composition of micromycetes on phototrophs and in the air of the photic zone in Golubinja Pećina. In 10 cases, a similar species composition on substrates and in the air of the photic zone was noted, and only twice within the same cave—in Obodska Pećina and Vrbacka jama. In 6 cases, the similarity of the species composition on substrates of the photic zone was noted, and in 2 cases, the similarity on substrates of the aphotic zone of different caves was noted. This confirms the introduction of species from the surface into the underground environment.

The cluster analysis using Euclidean distance showed the greatest similarity between species composition in the air of the photic zones in the caves with similar morphological structure in form of a well (Vrbacka jama and Jama ER-1) (Fig. 3).

4 Conclusion

The micromycetes composition of various biotopes both in illuminated photic and unlit aphotic zones of seven caves of Montenegro was studied. In total, 72 species of micromycetes were identified (“Appendix”), most of the micromycetes taxa found in

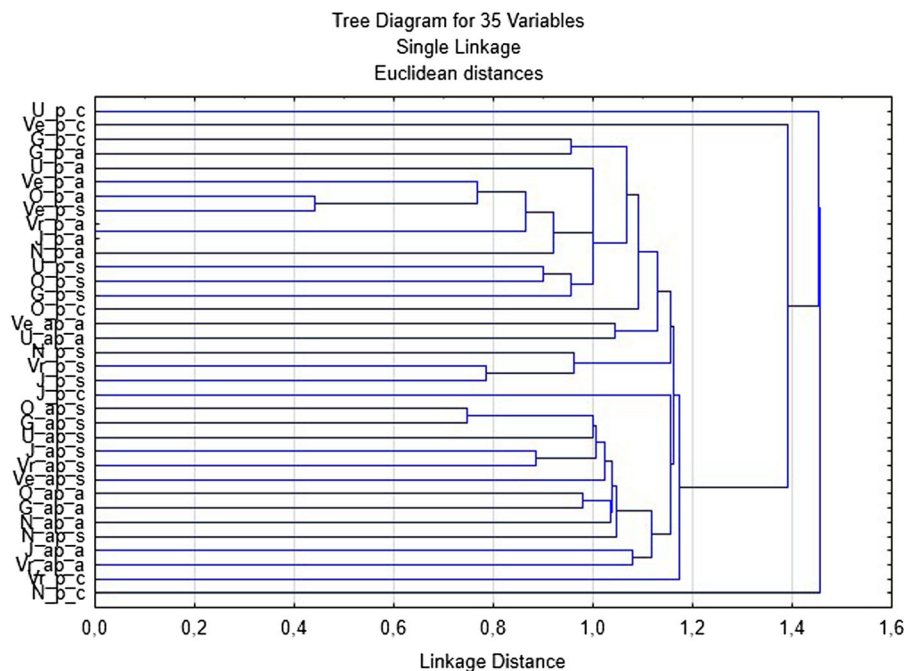


Fig. 3 The dendrogram diagram of micromycetes species similarity in different biotopes of the studied caves. G—Golubinja Pećina; Vr—Vrbacka jama; J—Jama ER-1; O—

Obodska Pećina; U—Unnamed cave; Ve—Veluštica Pećina; c—communities of phototrophs; a—air; s—substrates; p—photic zone; ap—aphotic zone

different zones and biotopes are widespread cosmopolitan saprotrophs. The species diversity was the highest on substrates of aphotic zones, the highest species similarity was demonstrated by the communities isolated from the air of the photic zones of caves with similar morphological structure Vrbacka jama and Jama ER-1. The species composition in illuminated photic zones of various biotopes demonstrated the highest similarity compared to the species composition of the aphotic zones. The species composition in the aphotic zones were unique in each of the cave, the similarity was observed only on substrates in Obodska Pećina and Golubinja Pećina, both characterized by a high abundance of bats and, accordingly, guano sediments, as well as in Vrbacka jama and Jama ER-1 pair.

Considering the fact that micromycetes have not been studied in Montenegró caves, the data of this diagnostic investigation can form the basis for a systematic research of caves and monitoring of their

ecosystems in terms of the safety of human visits as well. Since Lipska cave has recently been equipped in Montenegro, comparing the species composition in the touristic cave with unequipped caves is important for identifying an indicator species for ecosystem under anthropogenic impact. The analysis of the species in entrance zones makes it possible to determine the species that are mainly introduced from the surface. The comparison of species of the entrance and deep zones in the caves with different morphology, as well as different anthropogenic rate, will reveal the preferred migration routes of micromycetes and the significance of different factors for the penetration of species into the underground space.

Appendix

See Table 4.

Table 4 Micromycetes species found in different biotopes of the photic and aphotic zones in Montenegro caves

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Acrodontium salmoneum</i> de Hoog, Studies in Mycology 1: 29 (1972)								a		a	a					a	a	a			
<i>Alternaria alternata</i> (Fr.) Keissl., Beihefte zum Botanischen Centralblatt 29: 433 (1912)															a	a		a			
<i>Alternaria tenuissima</i> (Nees) Wiltshire, Transactions of the British Mycological Society 18 (2): 157 (1933)				p																	
<i>Aspergillus flavipes</i> (Bainier & Sartory) Thom & Church, The Aspergilli: 155 (1926)								a		a	a										
<i>Aspergillus flavus</i> Link, Magazin der Gesellschaft Naturforschenden Freunde Berlin 3 (1): 16 (1809)															a						
<i>Aspergillus flavus</i> var. <i>oryzae</i> (Ahlb.) Kurtzman, M.J. Smiley, Robnett & Wicklow, Mycologia 78 (6): 957 (1986)								a			a			a							
<i>Aspergillus fumigatus</i> Fresen., Beiträge zur Mykologie 3: 81 (1863)						p								a				a		a	
<i>Aspergillus nidulans</i> (Eidam) G. Winter, Rabenhorst's Kryptogamen-Flora, Pilze - Ascomyceten 1(2): 62 (1884)								a													
<i>Aspergillus niger</i> Tiegh., Annales des Sciences Naturelles Botanique 8: 240 (1867)															a	a	a	a			
<i>Aspergillus ochraceus</i> K. Wilh., Beiträge zur Kenntnis der Pilzgattung Aspergillus: 66 (1877)				p				a										a			
<i>Aspergillus phoenicis</i> (Corda) Thom, Journal of Agricultural Research 7: 14 (1916)				p																	

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Aspergillus terreus</i> Thom, American Journal of Botany 5 (2): 85 (1918)				p			p						a	a	a				a		
<i>Aspergillus ustus</i> (Bainier) Thom & Church, The Aspergilli: 152 (1926)								a		a							a	a		a	a
<i>Aureobasidium pullulans</i> (de Bary) G. Arnaud, Annales de l'École Nationale d'Agriculture de Montpellier 16 (1–4): 39 (1918)									a	a		a	a	a		p, a	p, a		a	p, a	p, a
<i>Botrytis cinerea</i> Pers., Neues Magazin für die Botanik 1: 126, t. 3:9 (1794)			p							p	a		a			a	a				
<i>Candida</i> sp.							p														p
<i>Cladosporium</i> <i>brevicompactum</i> Pidopl. & Deniak, Mykrobiologichnyi Zhurnal Kiev 5 (2): 186, 194 (1938)														a							
<i>Cladosporium</i> <i>cladosporioides</i> (Fresen.) G.A. de Vries, Contribution to the knowledge of the genus <i>Cladosporium</i> : 57 (1952)										a					a	a	a	a			a
<i>Cladosporium herbarum</i> (Pers.) Link, Magazin der Gesellschaft Naturforschenden Freunde Berlin 8: 37 (1816)									a			a						a	a	a	
<i>Cladosporium oxysporum</i> Berk. & M.A. Curtis, Journal of the Linnean Society. Botany 10: 362 (1869)		p	p	p				a	p, a	p, a	p, a	a			p, a	p, a	p, a	p, a			
<i>Cryptococcus albidus</i> (Saito) C.E. Skinner, The American Midland Naturalist 43: 249 (1950)				p					a												
<i>Debaryomyces hansenii</i> (Zopf) Lodder & Kreger, The Yeasts: a taxonomic study: 280 (1952)	p	p							a												

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Fusarium oxysporum</i> Schltdl., Flora Berolinensis, Pars secunda: Cryptogamia: 139 (1824)				p							p										
<i>Fusarium</i> <i>sporotrichioides</i> Sherb., Memoirs of the Cornell University Agricultural Experimental Station 6: 183 (1915)							p			a				a							
<i>Gliocladium roseum</i> Bainier, Bulletin de la Société Mycologique de France 23: 111 (1907)		p													a						
<i>Hyphopichia</i> sp.			p																		
<i>Mucor circinelloides</i> f. <i>circinelloides</i> Tiegh., Annales des Sciences Naturelles Botanique sér. 6, 1: 94 (1875)			p					a		p	a						p				
<i>Mucor hiemalis</i> Wehmer, Annales Mycologici 1 (1): 37 (1903)			p							p							p				
<i>Mucor luteus</i> Linnem. ex Wrzosek, Mycotaxon 111: 81 (2010)					p																
<i>Mucor mucedo</i> L., Species Plantarum: 1185 (1753)		p							a												
<i>Mucor racemosus</i> f. <i>racemosus</i> Fresen. (1850)				p				p	p, a	p, a	p	p, a	p	p	p, a	p, a	p	a			
<i>Mucor ramosissimus</i> Samouts., Materialy po Mikologii i Fitopatologii 6: 210 (1927)	p							p													
<i>Neocosmospora solani</i> (Mart.) L. Lombard & Crous, Studies in Mycology 80: 228 (2015)					p			a	a	a	a				a			a	a		
<i>Paecilomyces variotii</i> Bainier, Bulletin de la Société Mycologique de France 23: 27 (1907)													a					a	a	a	
<i>Penicillium</i> <i>aurantiigriseum</i> var. <i>viridicatum</i> Frisvad, Mycologia 81: 850 (1990)			p																		

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Penicillium brevicompactum</i> Dierckx, Annales de la Société Scientifique de Bruxelles 25 (1): 88 (1901)				p																	
<i>Penicillium chrysogenum</i> Thom, U.S.D.A. Bureau of Animal Industry Bulletin 118: 58 (1910)			p					a	a	a	a	a	a	a	a	a	p, a				
<i>Penicillium commune</i> Thom, U.S.D.A. Bureau of Animal Industry Bulletin 118: 56 (1910)				p																	
<i>Penicillium dierckxii</i> Biourge, La Cellule 33: 313 (1923)				p																	
<i>Penicillium funiculosum</i> Thom, U.S.D.A. Bureau of Animal Industry Bulletin 118: 69 (1910)															a	a	a	a			
<i>Penicillium glandicola</i> (Oudem.) Seifert & Samson, Advances in Penicillium and Aspergillus Systematics: 144 (1985)	p														p	p	p				
<i>Penicillium griseofulvum</i> Dierckx, Annales de la Société Scientifique de Bruxelles 25 (1): 88 (1901)				p																	
<i>Penicillium jensenii</i> K.M. Zalessky, Bulletin International de l'Academie Polonaise des Sciences et des Lettres Série B 1927: 494 (1927)								a					a								
<i>Penicillium lanosocoeruleum</i> Thom, The Penicillia: 322 (1930)				p														a			
<i>Penicillium purpurascens</i> (Sopp) Biourge, La Cellule 33: 105 (1923)								a			a										

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Penicillium purpurogenum</i> Stoll, Beiträge zur Morphologischen und Biologischen Charakteristik von Penicillium-Arten: 32 (1904)								a						a	a	a	a				p, a
<i>Penicillium restrictum</i> J.C. Gilman & E.V. Abbott, A summary of the soil fungi: 297 (1927)								a							a			a		a	a
<i>Penicillium roqueforti</i> Thom, U.S.D.A. Bureau of Animal Industry Bulletin 82: 35 (1906)						p															
<i>Penicillium roseopurpureum</i> Dierckx, Annales de la Société Scientifique de Bruxelles 25 (1): 86 (1901)	p																				
<i>Penicillium simplicissimum</i> (Oudem.) Thom, The Penicillia: 335 (1930)				p				a						a							
<i>Penicillium spinulosum</i> Thom, U.S.D.A. Bureau of Animal Industry Bulletin 118: 76 (1910)								a													
<i>Penicillium steckii</i> K.M. Zalessky, Bulletin International de l'Académie Polonaise des Sciences et des Lettres Série B 1927: 469 (1927)			p																		
<i>Penicillium thomii</i> Maire, Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 8: 189 (1917)																		a			
<i>Penicillium velutinum</i> Terui & Shibas. (1948)														a							
<i>Penicillium verrucosum</i> Dierckx, Annales de la Société Scientifique de Bruxelles 25 (1): 88 (1901)				p																	

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Phoma herbarum</i> Westend., Bulletin de l'Académie Royale des Sciences de Belgique Classe des Sciences 19 (3): 118 (1852)											a			a		a	a	a			
<i>Pseudogymnoascus</i> <i>pannorum</i> (Link) Minnis & D.L. Lindner, Fungal Biology 117 (9): 646 (2013)								a							a	a		a		a	a
<i>Purpureocillium</i> <i>lilacinum</i> (Thom) Luangsa-ard, Houbraken, Hywel- Jones & Samson, FEMS Microbiology Letters 321: 144 (2011)											a					a				a	
<i>Rhizopus stolonifer</i> (Ehrenb.) Vuill., Revue Mycologique Toulouse 24: 54 (1902)		p	p			p	p	p, a	p	p, a	p	a	p, a	p, a	p	p		p	p	p	p
<i>Phoma herbarum</i> Westend., Bulletin de l'Académie Royale des Sciences de Belgique Classe des Sciences 19 (3): 118 (1852)														a		a	a	a			
<i>Rhodotorula</i> F.C. Harrison, Transactions of the Royal Society of Canada 21 (2): 349 (1927)		p	p													p	p				
<i>Saccharomyces</i> sp.																	a				
<i>Scopulariopsis</i> sp.			p							p											
<i>Sporothrix</i> sp.					p																
<i>Trichoderma ghanense</i> Yoshim. Doi, Y. Abe & Sugiy., Bulletin of the National Science Museum Tokyo 13: 3 (1987)						p														p, a	
<i>Trichoderma hamatum</i> (Bonord.) Bainier, Bulletin de la Société Mycologique de France 22: 131 (1906)															a		a			a	
<i>Trichoderma harzianum</i> Rifai, Mycological Papers 116: 38 (1969)										a							a				

Table 4 continued

Taxon	Phototrophs							Air							Substrates						
	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J	U	O	G	Ve	N	Vr	J
<i>Trichoderma koningii</i> Oudem., Archives Néerlandaises 7: 291 (1902)				p														p			
<i>Trichoderma polysporum</i> (Link) Rifai, Mycological Papers 116: 18 (1969)					p														p, a		
<i>Trichoderma viride</i> Pers., Neues Magazin für die Botanik 1: 92 (1794)							p		a						a						a
<i>Trichosporon</i> sp.					p											a	a				
<i>Ulocladium chartarum</i> (Preuss) E.G. Simmons, Mycologia 59 (1): 88 (1967)											p	p	p	p	a		a		p, a	p, a	p, a

p photic, *a* aphotic

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