Unveiling the unusual bat distribution in threatened montane environments: the Valbona River Valley (Albanian Alps) case study

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Abstract:
This study provides new insights into bat diversity and ecology in high-mountain environments of southern Europe, focusing on the Valbona River Valley in the Albanian Alps, a recognised biodiversity hotspot that remains poorly studied, despite its significant natural value. Using mist-netting and acoustic monitoring conducted between 2021 and 2025 across an altitudinal gradient, we found 24 species of bats, including 13 species previously unreported from the region. Bat assemblages varied with elevation: species richness and activity peaked at the valley floor (700-800 m a.s.l.) and mid-altitude sites (1000-1700 m a.s.l.), whereas high-altitude habitats (>2000 m a.s.l.) exhibited lower activity but higher diversity (S-W index 2.223 comparing to 1.574) due to a more even species distribution. A strong male bias across all studied sites provides robust evidence for vertical sex segregation, extending previous published data by demonstrating its persistence above 2000 m a.s.l. in the Mediterranean region. High-altitude caves use was severely limited, likely due to microclimatic constraints, indicating that such sites do not function as summer roosts. Differences in species composition between sites highlight the importance of habitat structure, particularly woody vegetation and water bodies, in shaping bat communities. Species-specific observations reveal greater ecological plasticity than previously recognised and suggest that high-altitude habitats are used opportunistically for foraging and swarming, probably influenced by cave entrance exposure to sunlight.
These results demonstrate that alpine environments, although suboptimal, play a previously underestimated role in bat spatial ecology and provide essential baseline data for conservation planning under increasing anthropogenic pressure.

Keywords: biodiversity, bats, caves, anthropogenic pressure, alpine environment.

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This study provides new insights into bat diversity and ecology in high-mountain environments of southern Europe, focusing on the Valbona River Valley in the Albanian Alps, a recognised biodiversity hotspot that remains poorly studied, despite its significant natural value. Using mist-netting and acoustic monitoring conducted between 2021 and 2025 across an altitudinal gradient, we found 24 species of bats, including 13 species previously unreported from the region. Bat assemblages varied with elevation: species richness and activity peaked at the valley floor (700-800 m a.s.l.) and mid-altitude sites (1000-1700 m a.s.l.), whereas high-altitude habitats (>2000 m a.s.l.) exhibited lower activity but higher diversity (S-W index 2.223 comparing to 1.574) due to a more even species distribution. A strong male bias across all studied sites provides robust evidence for vertical sex segregation, extending previous published data by demonstrating its persistence above 2000 m a.s.l. in the Mediterranean region. High-altitude caves use was severely limited, likely due to microclimatic constraints, indicating that such sites do not function as summer roosts. Differences in species composition between sites highlight the importance of habitat structure, particularly woody vegetation and water bodies, in shaping bat communities. Species-specific observations reveal greater ecological plasticity than previously recognised and suggest that high-altitude habitats are used opportunistically for foraging and swarming, probably influenced by cave entrance exposure to sunlight.

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1. Introduction

The natural habitats of Southern Europe are characterised by a particularly high level of biological diversity, due to its complex topography, climatic heterogeneity, and despite (or because of) a long history of anthropogenic pressure (Hughes 2005). The Mediterranean Basin, recognised as a global biodiversity hotspot, is characterised by remarkable species richness and level of endemism, particularly in mountainous and island systems (Myers et al., 2000; Médail & Quézel, 1999). Environmental gradients and refugial dynamics have promoted diversification and persistence of taxa (Hewitt, 2011). However, this diversity is increasingly threatened by land-use change (including tourism, which is a known factor of influence in the Mediterranean basin), habitat fragmentation, and climate change (Cramer et al., 2018; Blondel et al., 2010). Taking this into account, Southern Europe remains a key region for studying biodiversity patterns and for developing conservation strategies.

Albania is recognised as one of the biodiversity hotspots within the Mediterranean region and as a post-glacial refugium (Hewitt 1999; Ridush et al 2024). Consequently, its bat fauna is also potentially among the richest in Europe (Ulrich et al. 2007; Sachanowicz et al. 2015). The earliest scientific records of bats in Albania are based on museum specimens of *Plecotus auritus* (Linnaeus, 1758) and *Pipistrellus kuhlii* (Kuhl, 1817), collected during the first half of the twentieth century (Ticehurst & Whistler 1932; Whistler 1936; Spitzenberger et al. 2001; Sachanowicz & Ciechanowski 2018). The first studies reporting 13 bat species were published in the 1960s, following field surveys conducted by Czechoslovak and Albanian zoologists (Hanák et al. 1961; Hanák 1964). Nevertheless, by the end of the twentieth century, Albania remained one of the least studied countries in Europe with respect to bat fauna (Uhrin et al. 1996), particularly in mountainous regions such as the Albanian Alps, including the Valbona River Valley - one of the most valuable natural areas in the country (Keçi & Krog 2014; Barina 2017).

Current data on bat species richness (Bego and Griffiths 1994; Sachanowicz et al. 2006; Sachanowicz and Ciechanowski 2006; Niermann et al. 2007; Théou et al. 2015a, 2015b; Sachanowicz et al. 2015; Sachanowicz et al. 2016; Théou and Loçe 2017; Sachanowicz & Ciechanowski 2018; Théou and Bego 2018) indicates that, despite considerable progress in recent decades, knowledge of bat distribution in mountainous and high-altitude areas of Albania remains limited. Although the bat fauna of Albania is currently estimated at 32 species (Sachanowicz et al. 2015), 13 species have thus far been recorded in the Valbona Valley (Sachanowicz & Ciechanowski 2018; Théou & Bego 2018). These were: Bechstein's bat *Myotis bechsteinii* (Kuhl, 1817), parti-coloured bat *Vespertilio murinus* Linnaeus, 1758, greater

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horse-shoe bat *Rhinolophus ferrumequinum* (Schreber, 1774), lesser horse-shoe bat *R. hipposideros* (André, 1797), Geoffroy's bat *M. emarginatus* (É. Geoffroy Saint-Hilaire, 1806), whiskered bat *M. mystacinus* (Kuhl, 1817) (complex), common noctule *Nyctalus noctula* (Schreber, 1774), Leisler's bat *N. leisleri* (Kuhl, 1817), serotine *Cnephaeus serotinus* (Schreber, 1774), Savi's bat *Hypsugo savii* Bonaparte, 1837, common pipistrelle *P. pipistrellus* (Schreber, 1774), soprano pipistrelle *P. pygmaeus* (Leach, 1825), and European free-tailed bat *Tadarida teniotis* (Rafinesque, 1814). A certain number of them were caught in this area (7 species), and some were identified based on ultrasonic recordings (remaining).

Bats are major consumers of arthropods of agricultural importance, particularly herbivorous insects, thereby significantly reducing crop damage (Tuneu-Corral et al. 2024; Ancillotto et al. 2024). They also play a stabilising role in forest ecosystems (Kunz et al. 2011) and serve as valuable indicators of environmental condition (Russo & Jones 2015; Rachwald 2019; Russo et al. 2025). During the active season (approximately from April to October in the temperate zone), insectivorous bats consume between 30% and 100% of their body mass per night (Kolkert et al. 2020), providing an ecosystem service valued at billions of euros annually to global agriculture (Cleveland et al. 2006; Boyles et al. 2011). Consequently, studies on bat ecology offer important insights into their interactions with the environment as consumers (Stephens & Krebs 1986; Hagen & Sabo 2011; Salvarina et al. 2018), while knowledge of diet composition and habitat preferences is essential for effective management and conservation (Kunz et al. 2011).

In alpine environments, food availability for bats varies with elevation, habitat type, seasonality, and the degree of anthropogenic pressure (McCain 2007; Weier et al. 2016), which in turn influences their altitudinal distribution (Nardone et al. 2015). However, bat ecology in such regions remains poorly understood compared with that of other mammalian taxa.

To address this gap and expand current knowledge of bat ecology in mountainous areas of the Mediterranean region, field studies have been conducted since 2021 during four summer seasons in the Valbona River Valley and the surrounding mountains.

The aims of the study were to:

- determine whether the higher elevations of the Albanian Alps represent the upper distributional limits of certain bat species, and to investigate whether the elevational difference between the valley floor and mountain passes affects bat abundance at these elevations;
- examine the sex ratio of bats and, in this context, assess the possibility of bats breeding within the study area;

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- expand the list of species known to occur in the area by applying a comprehensive methodological approach and conducting more extensive surveys, including along the altitudinal gradient;
- conduct a preliminary assessment of ongoing anthropogenic changes in the Valbona Valley and identify their potential impacts on local bat populations.

This study provides new insights into bat ecology, compares assemblages between high-altitude sites and the valley floor, and discusses selected ecological aspects in the context of the current knowledge of Albanian bat fauna.

2. Materials and Methods

2.1 Study area

The Valbona River is a well-preserved mountain watercourse located in the Albanian Alps. The Valbona River Valley, through which the river flows, is regarded as one of the most valuable natural areas in Albania (Keçi & Krog 2014; Barina 2017). Part of the valley is currently included in the Albanian Alps National Park (established in 2022), while previously (since 1966) it formed part of the Valbona Valley National Park. Although Albania remains relatively underexplored from a natural history perspective, available data from the Valbona River Valley highlight its importance for regional biodiversity (Bego 2005; Mizsei et al. 2017; Szabolcs et al. 2017; Bego et al. 2018; de Bree 2022).

The study area comprises a mosaic of habitats, including riverine systems, montane forests dominated by European beech (*Fagus sylvatica* L.) and Bosnian pine (*Pinus heldreichii* Christ.) (hereafter referred to as beech and pine), as well as alpine and subalpine habitats characterised by diverse flora (Rakaj 2009; Barina 2017; Shuka et al. 2017). In 2021, the deepest cave currently known in Albania was discovered in this area at an altitude of 2,180 m a.s.l. (Słupińska et al. 2025). Several caves exceeding 100 m in depth and length are located in the surrounding mountains, with internal temperatures ranging from approximately −5 to +10 °C (Słupińska et al. 2025).

Due to its high nature conservation value, the Valbona Valley is expected to be proposed as a Natura 2000 site in the event of Albania's accession to the European Union, with numerous species listed under Annex II of the EU Habitats Directive, including rare and threatened bat species (Théou & Bego 2018).

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Tourism in the Valbona River Valley has increased markedly over the past two decades (Lushaj and Malsia 2008; Byberaj et al. 2014; Kortoci & Kortoci 2017), leading to the expansion of infrastructure and increased anthropogenic pressure, particularly on the valley floor. In contrast, higher elevations remain relatively less accessible. Additional threats include ongoing development pressures associated with economic growth, such as hydropower expansion (Diku et al. 2017) and light pollution. These factors should be considered when interpreting biodiversity patterns, as they may influence habitat condition and species occurrence and activity.

The study was conducted in the north-eastern upper part of the Valbona River Valley and in the surrounding mountains. The valley floor ranges in altitude from 700 to 1200 m a.s.l.. The valley has a general SSE-NNW course, locally in the study area it bypasses the Maja e Pečmares massif, changing its course to the NW and then to the SW, and then returns to the main course direction where the valley is enclosed by a mountain range with altitudes of 1800–2400 m a.s.l. Sampling was carried out in forest and rocky habitats, along watercourses, at cave entrances, and at two small ponds located at different altitudes above sea level, in order to cover at least the basic types of natural habitats occurring in this area with research. (Fig. 1).

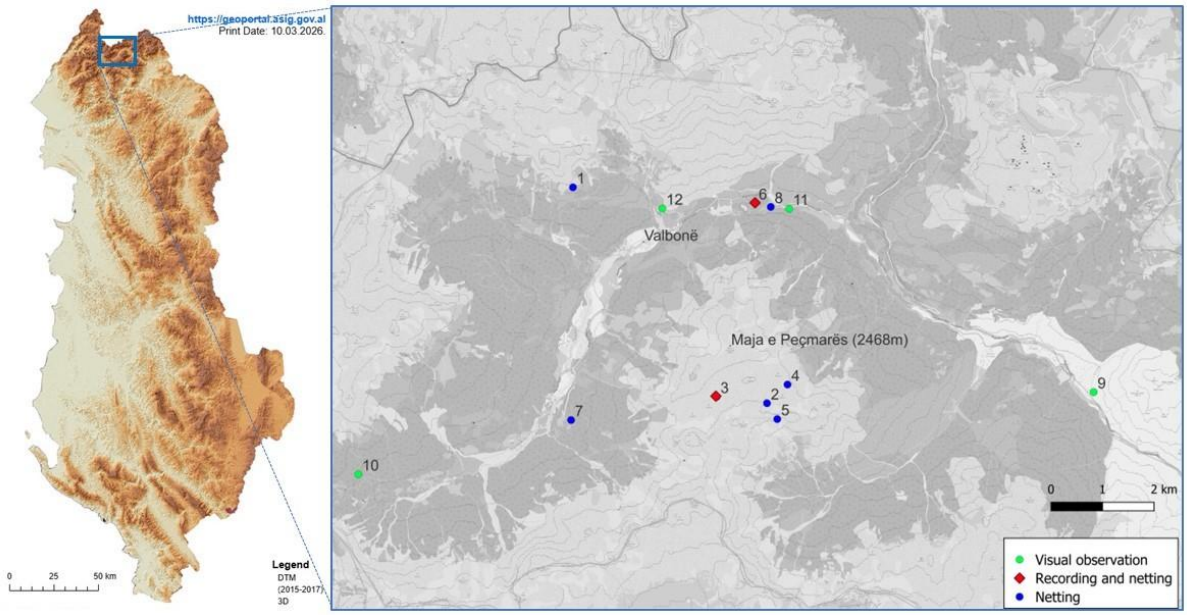


Figure 1. The study area is located in northern Albania (left panel). Study points are marked in color (right panel). Numbering descriptions are in Appendix 1.

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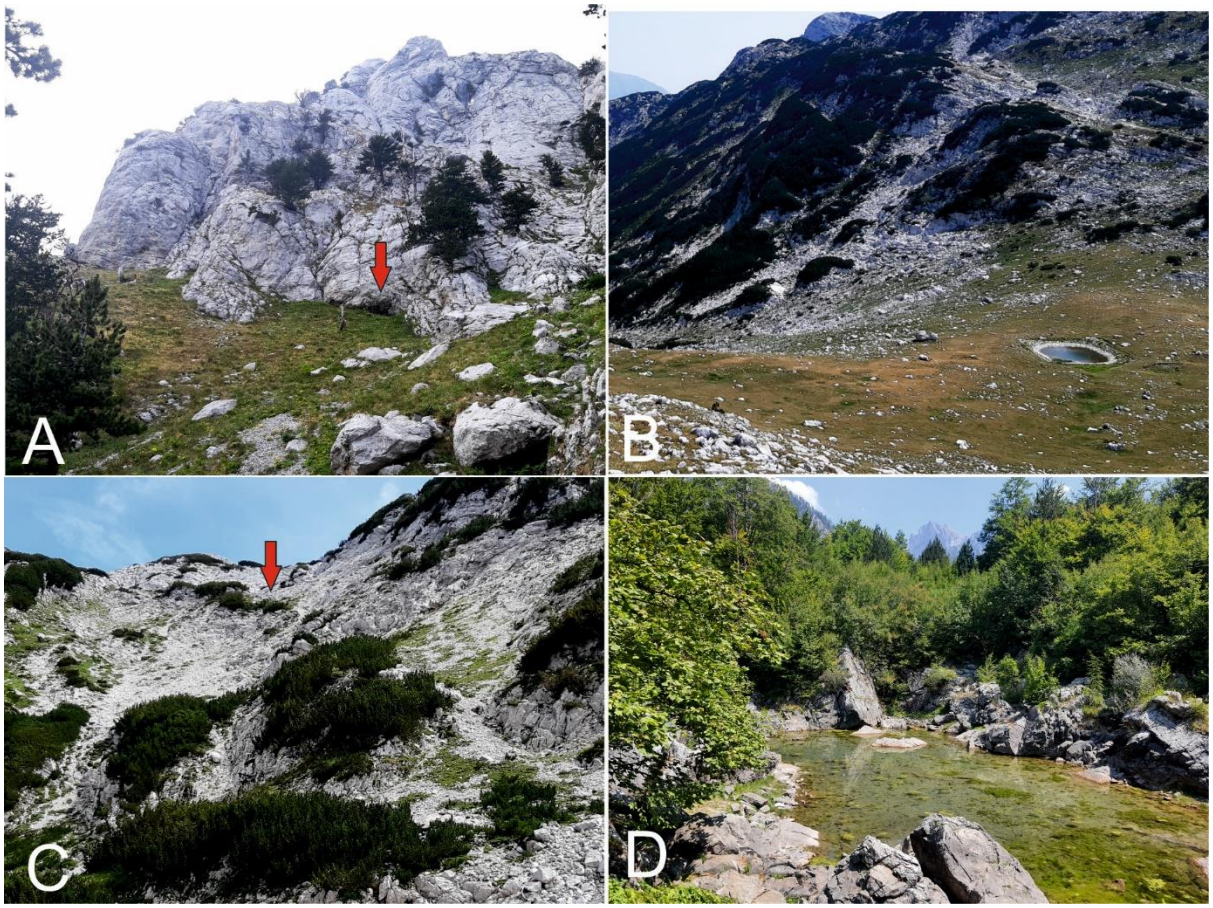


Figure 2. Bet mist-netting sites. Shpella e Haxhisë entrance (A), upper pond at mountain pass, (distant shot, B), Shpella e Valbonës entrance (C), lower pond (Liqeni i Xhemës, D). All photos: A. Pereswiet-Soltan.

2.2 Bat mist-netting

Bat captures was conducted along a forest trail connecting the valley floor with parts located at higher elevation, near a small flow-through pond on the valley floor, at two selected ponds located at different altitude (776 m a.s.l. and 2108 m a.s.l.), and at several medium and high-altitude caves: Shpella e Haxhisë (1700 m a.s.l.), cave AVL-R-78 (2078 m a.s.l.), cave AVL-R-51 (2220 m a.s.l.) and Shpella e Valbonës (2180 m a.s.l.) (Fig. 1; Fig. 2; Appendix 1). During cave sampling, mist nets were placed either at the cave entrance (outside) or just inside, close to the entrance, depending on site conditions. All temperature measurements in the caves were made using Hobo U23 Pro v2 loggers (Onset Computer Corporation, Bourne, MA, USA). Bat mist-netting was carried out over four summer field seasons (2021, 2023, 2024, and 2025).

At the forest trail site (1093 m a.s.l.), two mist nets (2.5 m in height) were set up across a forest dirt road, spaced 10–20 m apart. The surrounding stand was dominated by beech with an admixture of pine. At the flow-through pond on the valley floor, two nets were set on land

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directly adjacent to the water body. The pond was bordered by shrubs and low limestone outcrops.

The lower-altitude (forest) pond, at 776 m a.s.l., was located within a montane broadleaf forest dominated by beech, comprising both mature and young trees. The surrounding forest structure varied from slightly open areas to dense patches, while the pond itself remained largely uncovered and was bordered by rocky margins. The high-altitude pond was situated above the tree line on a small plateau at approximately 2100 m a.s.l., characterised by alpine meadow vegetation and surrounded by ridges and rocky peaks. Vegetation consisted primarily of herbaceous communities, with patches of dwarf pine (*Pinus mugo* Turra) occurring on adjacent slopes at some distance from the pond. Rocky habitats were widespread, including numerous small caves with narrow entrances, as well as fissures and boulder fields composed of large stones. At both pond sites, nets were positioned partly over the water surface and partly along the shoreline.

Monofilament mist nets ranging from 3 to 10 m in length (depending on site characteristics) were used. For each captured individual, species identity, sex, age, reproductive status, general condition, and the presence of ectoparasites were recorded. Standard biometric measurements included forearm length and body mass. Species identification followed Dietz and von Helversen (2004) and Sachanowicz et al (2012).

All procedures were conducted in accordance with accepted guidelines for the ethical treatment of animals. Individuals were handled for the minimum time necessary to obtain measurements and were subsequently released at the capture site. The study was carried out under a permit issued by the Albanian National Agency for Protected Areas (Agjencia Kombetare e Zonave Mbjotura) (granted on 07.08.2024 and 01.07.2025) and in cooperation with the Albanian Speleological Scientific Didactic Association (on the basis of their permit, remaining period).

2.3 Acoustic recordings

Bat echolocation calls were recorded using a Dodotronic Ultramic384K BLE microphone (Dodotronic, Rome, Italy) with a 384 kHz sampling rate, an 8 kHz trigger filter, and 40 dB sensitivity, with each recording lasting 5 seconds per activation. Recordings were conducted from sunset to sunrise, with the microphone positioned along the shoreline of both the lower and upper ponds (one detector per pond). For each site, recordings from two nights

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in mid-late August 2021 and two nights in mid-late August 2024 were analysed, yielding a total of 36 hours of recording per site across four nights.

The acoustic analysis method used in this study may overestimate the representation of species with long-range echolocation (LRE) compared to short-range echolocators SRE (Frey-Erhenboldt et al. 2013). Consequently, recordings of Rhinolophidae and bats of the genus *Plecotus* may be underrepresented in the dataset. In addition, the analysis method does not allow all bat passes to be assigned to a species or species group, and some passes therefore remain unrecognized and are excluded from further analyses. As a result, the acoustic activity values obtained in this study may be lower than the actual levels of bat activity, although the relative differences in activity between the study sites are expected to be retained.

2.4 Bioacoustic analysis

Bioacoustic analysis was performed using Kaleidoscope software (Wildlife Acoustics, Maynard, USA) in batch mode. The analysis employed the Albanian species library provided by Kaleidoscope, supplemented with species already known from Albania but absent from the default library. Analyses were conducted in the most conservative setting (level 3). A species was considered detected if ≥50% of the calls in a given series were identified by the software as that species. Following Furlonger et al. (1987), a “series” was defined as two or more bat calls in sequence. The results concerning species that were particularly similar to each other and therefore difficult to identify using an automatic procedure and unresolved by the manual procedure were combined into groups of species (*N. leisleri/V. murinus*, *Myotis mystacinus/brandtii*) or identified only to the genus level (*Plecotus* spp.). Additional manual identification was performed in possible questionable cases using BatSound 4.4 software (Pettersson Electronic AB, Uppsala, Sweden). This was based on the book by Russ (2021) and the authors' experience.

To assess biological diversity, the Shannon-Wiener index was used (as it is more sensitive to the occurrence of rare species), supported by Hutcheson test and Pielou’s eveness index.

3. Results

3.1 Mist netting and visual observations across habitats and different elevations

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A total of 67 bats representing 13 species were captured: lesser horse-shoe bat *R. hipposideros*, Geoffroy's bat *M. emarginatus*, Natterer's bat *M. nattereri* (Kuhl, 1817), Daubenton's bat *M. daubentonii* (Kuhl, 1817), lesser mouse-eared bat *M. blythii* (Tomes, 1857), Alcathoe bat *M. alcathoe* von Helversen & Heller, 2001, long-fingered bat *M. capaccinii* Bonaparte, 1837, soprano pipistrelle *P. pygmaeus* (Leach, 1825), Savi's bat *H. savii*, common noctule *N. noctula*, parti-coloured bat *V. murinus*, brown long-eared bat *P. auritus*, and Alpine long-eared bat *P. macrobullaris* Kuzjakin, 1965, as well as individuals belonging to the genus *Plecotus* that could not be identified to species level. In addition to captured bats, two greater horse-shoe bats *R. ferrumequinum* and some *R. hipposideros* individuals were visually observed at various locations within the valley during the study period (Appendix 1).

The majority of captured individuals were male, with the exception of two females - one *R. hipposideros* and one *M. alcathoe* - both recorded at Shpella e Haxhisë (Appendix 1). The overall sex ratio indicated a strong male predominance (65 males vs. 2 females). The two females were collected in different years at the same cave site, located at an altitude of 1682 m (Appendix 1). At altitudes above 2,000 m, only sexually active male *Plecotus* bats (*P. auritus*, *P. macrobullaris*, and some unidentified *Plecotus* individuals) were captured at cave entrances. All male *Plecotus* bats were netted upon entering the caves; none were captured exiting. Additionally, a single sexually active male *V. murinus* was captured at this altitude over an open mountain pond rather than at a cave.

The highest species richness was observed at two sites: the valley floor near the small flow-through pond (site 8) and the entrance of Shpella e Haxhisë cave (site 1), with seven bat species recorded at each site (Appendix 1; Fig. 3).

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Bat No.	Species	Sex	Age	Data acquisition	Date	Site (number)	Site type	Altitude[m a.s.l.]	Latitude [°N]	Longitude [°E]	Forearm (mm)	Weight (g)
1	*P. macrobullaris*	m	ad.	C	31.07.2021	Shpella e Haxhisë (1)	cave entrance	1700	42.4626	19.8757	39,25	8,25
2	*M. emarginatus*	m	ad.	C							38,7	7,25
3	*M. emarginatus*	m	ad.	C							40,0	7,5
4	*R. hipposideros*	m	ad.	C							39,2	5,75
5	*M. emarginatus*	m	ad.	C							39,25	9,0
6	*M. emarginatus*	m	ad.	C							38,3	7,25
7	*M. emarginatus*	m	ad.	C							38,6	6,95
8	*R. hipposideros*	f	ad.	C							38,3	6,5
9	*M. emarginatus*	m	ad.	C							39,25	9,0
10	*M. emarginatus*	m	ad.	C							38,6	7,75
11	*M. nattereri*	m	ad.	C							40,0	6,5
12	*R. hipposideros*	m	ad.	C							39,6	6,25
13	*M. emarginatus*	m	ad.	C							37,5	8,75
14	*P. auritus*	m	ad.	C							39,3	7,25
15	*P. macrobullaris*	m	ad.	C							39,1	7,25
16	*P. auritus*	m	ad.	C	19.08.2021	Shpella e Valbonës (2)	cave entrance	2180	42.4250	19.9219	41,0	8,5
17	*Plecotus sp.*	m	ad.	C							38,9	7,25
18	*Plecotus sp.*	m	ad.	C							40,0	7,5
19	*Plecotus sp.*	m	ad.	C							39,3	7,25
20	*Plecotus sp.*	m	ad.	C							38,4	7,0
21	*P. auritus*	m	ad.	C	04.08.2023	Shpella e Valbonës (2)	cave entrance	2180	42.4250	19.9219	39,75	8,5
22	*P. macrobullaris*	m	ad.	C							39,4	8,25
23	*V. murinus*	m	ad.	C	17.08.2024	mountain pass (3)	pond	2108	42.4263	19.9097	44,2	17,25
24	*P. auritus*	m	ad.	C	-	cave AVL-R-78 (4)	cave entrance	2078	42.4284	19.9266	40,5	7,25
25	*P. macrobullaris*	m	ad.	C	-	cave AVL-R-51 (5)	cave entrance	2220	42.4225	19.9241	39,7	8,0
26	*P. auritus*	m	ad.	C	-	cave AVL 51 (5)	cave entrance	2170	42.4225	19.9241	40,0	6,75
27	*Plecotus sp.*	m	ad.	C	21.08.2024	Shpella e Valbonës (2)	cave entrance	2180	42.4250	19.9219	38,8	8,0
28	*Plecotus sp.*	m	ad.	C							38,2	7,5

29	*Plecotus sp.*	m	ad.	C	22.08.2024						39,8	8,0
30	*M. emarginatus*	m	ad.	C	31.07.2024	Shpella e Haxhisë (1)	cave entrance	1700	42.4626	19.8757	39,2	6,5
31	*M. emarginatus*	m	ad.	C							38,5	6,5
32	*M. blythii*	m	ad.	C							56,6	21,25
33	*M. alcathoe*	f	ad.	C							33,2	3,5
34	*M. nattereri*	m	ad.	C							40,7	5,25
35	*R. hipposideros*	m	ad.	C							37,3	4,5
36	*M. emarginatus*	m	ad.	C							38,4	6,2
37	*M. emarginatus*	m	ad.	C							38,7	5,85
38	*M. blythii*	m	ad.	C							57,6	19,25
39	*M. emarginatus*	m	ad.	C							38,3	6,5
40	*M. emarginatus*	m	ad.	C							38,1	7,25
41	*R. hipposideros*	m	ad.	C							39,4	4,75
42	*H. savii*	m	ad.	C							32,5	6,9
43	*R. hipposideros*	m	ad.	C							38,4	4,75
44	*H. savii*	m	ad.	C							32,5	9,5
45	*R. hipposideros*	m	s-ad.	C							38,8	4,5
46	*M. emarginatus*	m	s-ad.	C							38,3	5,5
47	*H. savii*	m	ad.	C	12.08.2025	Liqeni i Xhemës (6)	pond	776	42.4599	19.9189	34,0	8
48	*H. savii*	m	ad.	C							33,6	7,5
49	*H. savii*	m	ad.	C							33,8	6,5
50	*H. savii*	m	ad.	C							33,6	6,5
51	*Plecotus sp.*	m	ad.	C	13.08.2025	mountain forest site (7)	forest trail	1093	42.4222	19.8758	41,4	8,0
52	*M. capaccinii*	m	ad.	C							41,7	8,5
53	*H. savii*	m	ad.	C	19.08.2025	other water body (8)	flow-through pond	739	42.4590	19.9224	35,6	8,0
54	*N. noctula*	m	ad.	C							54,1	32,0
55	*H. savii*	m	ad.	C							33,8	6,5
56	*P. pygmaeus*	m	ad.	C							29,5	6,0
57	*H. savii*	m	ad.	C							32,7	8,5
58	*V. murinus*	m	ad.	C							46,2	16,0

59	*H. savii*	m	ad.	C							35,4	8,0
60	*H. savii*	m	ad.	C							35,0	9,0
61	*H. savii*	m	ad.	C							33,7	8,0
62	*V. murinus*	m	ad.	C							44,5	18,0
63	*P. pygmaeus*	m	ad.	C	20.08.2025	other water body (8)	flow-through pond		42.4590	19.9224	29,5	5,0
64	*M. daubentonii*	m	ad.	C							36,9	8,5
65	*M. alcathoe*	m	ad.	C							31,4	4,5
66	*M. alcathoe*	m	ad.	C							32,2	4,5
67	*H. savii*	m	ad.	C							33,9	7,0
68	*R. ferrumequinum*	-	-	O	20.08.2025	military bunker (9)	ceiling of a concrete room	532	42.4271	19.9987	-	-
69	*R. hipposideros*	-	-	O	12.08.2024	cave AVL-12 (10)	cave ceiling	1319	42.4128	19.8254	-	-
70	*R. hipposideros*	-	-	O	15.08.2024	small rock crevice (11)	flying outside crevice	712	42.4589	19.9269	-	-
71	*R. hipposideros*	-	-	O							-	-
72	*R ferrumequinum*	-	-	O	27.08.2021	mine (12)	Mine tunnel ceiling	998	42.45903	19.89711	-	-
73	*R. hipposideros*	-	-	O							-	-
74	*R. hipposideros*	--	-	O	28.08.2021	Shpella e Haxhisë (1)	cave ceiling	1700	42.4626	19.8757	-	-

Appendix 1. Bats that were caught, as well as observed and visually identified during research in 2021-2025. Ad: adult, s-ad: sub-adult, C: catch, O: visual observation, m: male, f: female. The letter-numerical names of the caves are in accordance with the accepted cave nomenclature (https://grottocenter.org/ui/entrances).

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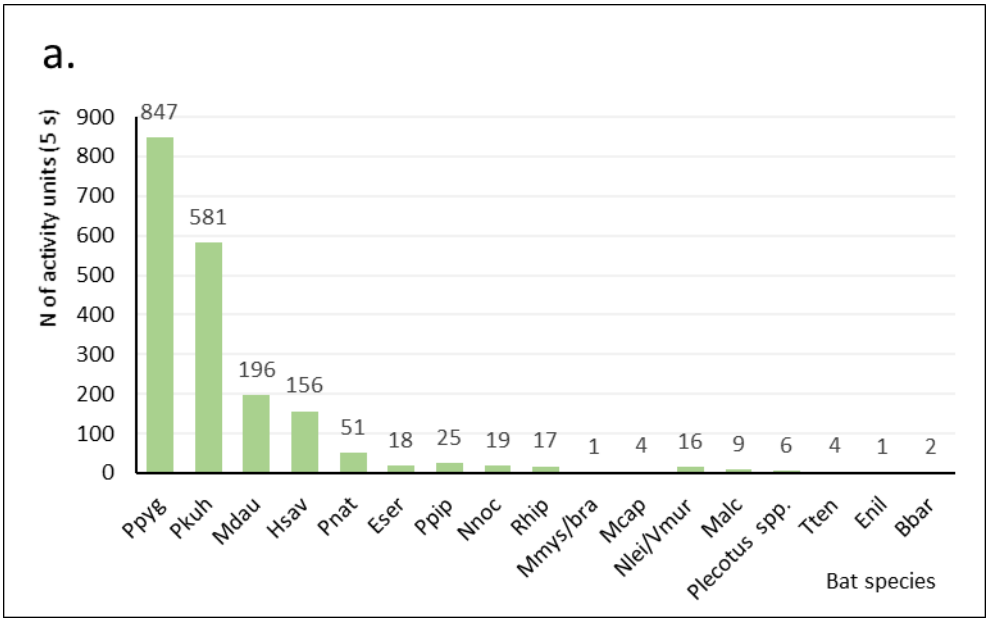
alt. (m)	Hsav	Malc	Mbly	Mcap	Mdau	Mema	Mnat	Nnoc	Ppyg	Paur	Pmac	Pspp.	Rhip	Vmur
739	7	2	2	-	1	-	-	1	2	-	-	-	-	2
776	4	-	-	-	-	-	-	-	-	-	-	-	-	-
1093	-	-	-	1	-	-	-	-	-	-	-	1	-	-
1700	2	1	-	-	-	15	2	-	-	1	2	-	7	-
2078	-	-	-	-	-	-	-	-	-	1	-	-	-	-
2108	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2180	-	-	-	-	-	-	-	-	-	2	1	7	-	-

Table 1. The total abundance of different bat species captured in relation to altitude (alt.) above sea level (in m a.s.l.) of the certain capture sites during study period. Hsav = *Hypsugo savii*, Malc = *Myotis alcathoe*, Mbly = M. *blythii*, Mcap – *M. capaccinii*, Mdau = *M. daubentonii*, Mema = *M. emarginatus*, Mnat = *M. nattereri*, Nnoc = *N. noctula*, Ppyg = *Pipistrellus pygmaeus*, Paur = *Plecotus auritus*, Pmac = *Plecotus macrobullaris*, Pspp. = *Plecotus* species (whole genus, without distinguishing species), Rhip = *Rhinolophus hipposideros*, Vmur = *Vespertilio murinus*. Detailed information regarding the individual capture sites is provided in Appendix 1.

3.2 Bat activity over waterbodies at lower and upper altitudes

Bioacoustic recordings from two pond sites revealed the presence of 17 species or species groups (Fig. 3, Tab. 2), some of which were also captured in mist nets (Appendix 1). The highest species richness was recorded at the valley-floor pond, with 17 species, including forest specialists such as Western barbastelle *Barbastella barbastellus* (Schreber, 1774) and *P. nathusii* (Keyserling & Blasius, 1839), none of which were detected at the high-altitude pond, where 14 species were recorded. Of all species detected, *P. nathusii*, northern bat *Cnephaeus nilssonii* (Keyserling & Blasius, 1839), and *B. barbastellus* were recorded exclusively at the lower pond (Tab. 2, Fig. 3).

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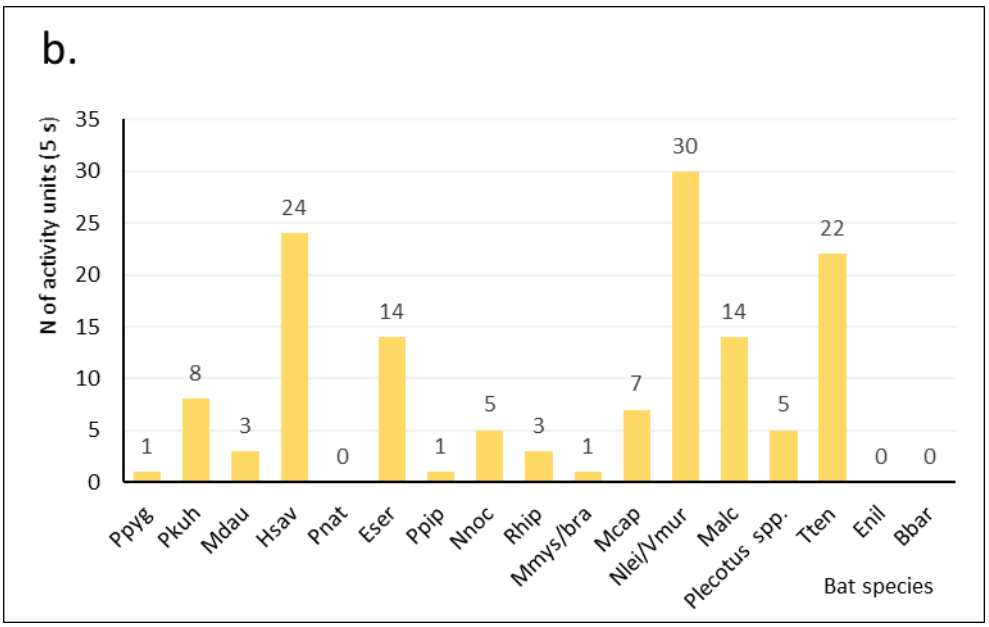


Figure 3. Total recorded activity of bats near lower (**a.**) and upper (**b.**) ponds. One activity unit = 5s. Ppyg = *P. pygmaeus*, Pkuh = *P. kuhlii*, Mdau = *M. daubentonii*, Hsav = *H. savii*, Pnat = *P. nathusii*, Cser = *C. serotinus*, Ppip = *P. pipistrellus*, , Nnoc = *N. noctula*, Rhip = *R. hipposideros*, Mmys/Mbra = *M. mystacinus/M. brandtii*, Mcap – *M. capaccinii*, Nlei/Vmur = *N. leisleri/V. murinus*, Malc = *M. alcathoe*, Plecotus spp. = *Plecotus* species (whole genus, without distinguishing species), Tten = *T. teniotis*, Cnil = *C. nilssonii*, Bbar = *B. barbastellus*.

Overall bat activity was markedly higher over the lower pond compared with the upper pond (1953 to 138, ie. approximately 14 times). In addition to differences in species richness (17 vs. 14 species), the two sites differed substantially in bat species composition. At the valley-floor pond, *P. pygmaeus* and Kuhl's pipistrelle *P. kuhlii* (Kuhl, 1817) dominated, with

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Daubenton's bat *M. daubentonii* (Kuhl, 1817) and *H. savii* also relatively abundant (Fig. 3); collectively, these four species accounted for 90.9% of recorded activity units. In contrast, at the high-altitude pond, *N. leisleri*, *H. savii*, and *T. teniotis* were dominant, with *E. serotinus* and *M. alcathoe* also contributing substantially (Fig. 3). Together, these five species represented 75.4% of recorded activity. In addition to differences in dominant species, the high-altitude pond exhibited a more even distribution of bat activity among species (Tab. 2, Fig. 3).

Bat species/group	mean n/h	
	Lower pond	Upper pond
P. pygmaeus	23.53	0.03
P. kuhlii	16.14	0.22
M. daubentonii	5.44	0.08
H. savii	4.33	0.67
P. nathusii	1.42	0
C. serotinus	0.5	0.39
P. pipistrellus	0.69	0.03
N. noctula	0.53	0.14
R. hipposideros	0.47	0.08
M. mystacinus/brandtii	0.03	0.03
M. capaccinii	0.11	0.19
N. leisleri/V.murinus	0.44	0.83
M. alcathoe	0.25	0.39
Plecotus spp.	0.17	0.14
T. teniotis	0.11	0.61
C. nilssonii	0.03	0
B. barbastellus	0.06	0
Mean value for whole activity	54.25	3.83

Table 2. Average bat activity (taken from numbers of 5 s activity units per 1 hour) near the lower pond (left) and near the upper pond (right). Mean n/h: mean number of activity units per one hour. Data from recordings in August 2021 and 2024, combined, total 36 hours of night recordings for each point.

Bat assemblage diversity differed significantly between the two studied ponds. Shannon–Wiener diversity was higher at the upper pond ($H' = 2.223$) than at the lower pond ($H' = 1.558$; Hutcheson's t-test: $t = 9.246$, $df = 177.90$, $p < 0.001$). Similarly, Pielou's evenness was considerably higher at the upper pond ($J' = 0.842$) than at the lower pond ($J' = 0.550$), indicating a more even distribution of bat activity among taxa at the higher-elevation site.

3.3 Visual observations of other signs of bat presence

The inspection of underground environments, such as caves, mines, and bunkers, did not reveal the presence of large colonies. Only in Shpella e Haxhisë at high altitude and in the

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mines on the valley floor was a sufficiently widespread quantity of droppings found to suggest that these sites are regularly used as daytime shelters, although only a few individuals were observed during the inspection. A similar situation occurred in other shelters (Appendix 1). In caves above 2,000 meters in altitude, no bat droppings were found in the inspected sites.

4. Discussion

Taking into account the combined data from captures and ultrasonic recordings, our study found 24 species of bats in the Valbona Valley (Tab. 1, 2, Appendix 1), compared to 13 previously reported (Sachanowicz & Ciechanowski 2018; Théou & Bego 2018). *M. bechsteinii*, previously found in this area (Sachanowicz et al. 2015), was not observed during our study. This demonstrates that the Valbona environment, and Albanian Alps in general, are still insufficiently understood. Little is known about high-altitude bat communities in southern Europe, and our results provide new insights into how bats exploit mountainous environments close to their maximum recorded elevation (Benda et al. 2019; Georgiakakis et al. 2023). Overall, our findings indicate that high-altitude habitats are used selectively, primarily by males and non-breeding individuals, and are possibly constrained by habitat conditions

A pronounced male bias was observed across the study area, including at valley bottoms (700–800 m a.s.l.), where almost exclusively adult males were captured (Appendix 1). This pattern suggests the absence of nearby breeding colonies, despite the availability of potential roosting sites such as trees with cavities and loose bark, as well as some artificial underground structures (abandoned military bunkers, commonly present in Albanian landscape, Theou & Bego 2014; Voxhi et al. 2021). Similar male-dominated assemblages have been reported from other mountainous regions, including the Alps and the Apennines (Nardone et al. 2015; Widerin & Reiter 2017). Females are known to avoid high elevations during pregnancy and lactation due to energetic constraints (Grindal et al. 1999; Russo 2002). Our results extend the findings of Nardone et al. (2015), who documented this pattern up to 1000 m a.s.l., by demonstrating that vertical sex segregation persists at altitude exceeding 2000 m a.s.l. in the Mediterranean region.

Cave use by bats at high altitudes appears to be limited by microclimatic conditions. Bat presence in caves above 2000 m a.s.l. was sporadic and consisted almost exclusively of males. This pattern seems fairly typical in the European context (e.g. Nardone et al. 2015), although not without exceptions. In the Tatra Mountains (Piksa 2008; Piksa and Brzuskowski 2026), capture sites near caves between 1,500 and 2,000 m a.s.l. yielded several species,

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including both males and females. However, at similar altitudes above sea level in the study by Dundarova and Popov (2024) in Bulgaria at capture site no. 3, "Cave 30", only six bat species were recorded, including a few females, with *P. auritus* as the most represented species. This can be considered an intermediate situation between the caves at 2,200 meters and Shpella e Haxhisë at 1,700 meters in our study.

The highest-altitude caves (e.g. Shpella e Valbonës, AVL-B-78, AVL-B-51; Fig. 1, Appendix 1) exhibited internal temperatures of approximately 2°C (e.g. 2.2°C in Sh. e Valbonës), which are likely too low to support regular summer bat occupancy. In contrast, a cave located several hundred meters lower (Shpella e Haxhisë, 1700 m a.s.l.) had a higher internal temperature (5.6°C) and supported greater bat abundance and species richness (Appendix 1, Table 1). The absence of bats emerging from high-altitude caves, combined with the lack of guano deposits and roosting individuals, further supports the conclusion that no one of these caves was used as summer roosts. These findings suggest temperature as a key limiting factor, likely overriding the availability of otherwise suitable rocky shelters. Confirmation of this hypothesis requires further detailed research.

In addition to the explanation proposed by Dundarova and Popov (2024), which identifies the site as both a swarming location and a migration point between summer and winter roosts, a further hypothesis is that the entrance of "Cave 30" site and the adjacent slope, in research conducted in Bulgaria, are exposed to the east–southeast. Consequently, receiving more direct solar radiation, they may be warmer and thus more suitable for bats. However, this hypothesis cannot be examined due to the lack of temperature measurements in the mentioned study. The Pirin mountain range is the highest in the south–north direction, while the mountain groups further south are lower. This may result in the area being more strongly influenced by a mild southern climate. This contrasts with the mountain group around the Valbona River Valley, where other high mountain massifs lie between it and the sea. The situation described by Dundarova and Popov (2024) may therefore be considered intermediate between the Albanian caves at 2,200 metres and Shpella e Haxhisë at 1,700 metres.

These general patterns are further illustrated by species-specific responses observed in the study area. Notably, the recording of *M. capaccinii* at both low- and medium-altitude water bodies indicates a broader ecological plasticity than previously recognised. This species is typically associated with lowland rivers and calm water bodies (Carmel & Safriel 1998; Russo & Jones 2003), yet our observations suggest that, in the absence of suitable riverine habitats, it may exploit small higher-altitude ponds. Similarly, the capture of a female *M.*

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alcathoe at 1700 m a.s.l. represents the highest known record for this species to date and suggests that it may exploit higher-altitude habitats. Previous records of this species in mountainous areas are largely restricted to forested zones at lower elevations (Sachanowicz et al. 2012; Bashta et al. 2011; Piksa et al. 2011; Piksa & Nowak 2013), with otherwise limited data from the Balkans (Niermann et al. 2007).

The presence of sexually active males *M. emarginatus* at relatively high altitude (1700 m a.s.l.) in consecutive years indicates that such sites may function as swarming areas near the upper altitudinal limit of the species. The absence of individuals inside caves during daytime, combined with the presence of mud-covered individuals, suggests that roosting likely occurs in rock crevices rather than in large caves in the area. Comparable studies indicate that this species becomes increasingly rare above 1000 m a.s.l. and only sporadically reaches higher elevations (Holzhaider & Zahn 2001; Piksa 2008; Toffoli et al. 2016). In this context, the studied cave represents one of the highest elevated swarming sites for this species.

In contrast, the few *Plecotus* individuals captured above 2000 m a.s.l. do not provide clear evidence of swarming behaviour, despite all being sexually active males. Their consistent movement into caves, rather than out of them, suggests that caves are not used as primary roosting sites, and that individuals likely occupy rock crevices, as proposed in some studies (Alberdi et al. 2015). Similarly, Rhinolophid bats were rarely recorded at high altitudes, confirming their general association with lower altitudes (Georgiakakis et al. 2010; Piksa et al. 2013; Toffoli 2019). While *R. hipposideros* was detected at a high-altitude lake, it was not recorded in caves at comparable elevation, whereas *R. ferrumequinum* remained restricted to lower elevation (Appendix 1), consistent with its known ecological preferences (Bologna & Vigna 1985; Spitzenberger 2001). The sighting of *R. hipposideros* specimens hanging beneath a small rock overhang in the valley floor (site 11), apparently not very suitable, may suggest a lack of adequate summer shelters for bats, such as large and warm caves (Presetnik & Knapič 2014). *R. ferrumequinum*, the biggest Rhinolophid bat in the Mediterranean, was found only inside the mine and in an artificial building (Appendix 1). Taken together, these species-specific patterns positively indicate that high-altitude environments are used primarily by bat males and non-breeding individuals, while females probably remain restricted to more thermally favourable habitats at lower elevation.

In addition to roosting ecology, similar altitudinal patterns were observed in flight activity. Acoustic recordings revealed clear differences between the lower and upper ponds (Tab. 2, Fig. 3). Despite the karstic environment providing potential rocky shelters, the upper

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pond supported only moderate bat activity and lower species richness, whereas the lower site exhibited significantly higher activity levels and was dominated by species associated with aquatic and forested habitats, such as *P. kuhlii*, *P. pygmaeus*, *H. savii*, and *M. daubentonii*. Four species from among those found at the lower pond, surrounded by trees, were not found at all at the pond at the top of the mountain pass (they were *C. nilssonii*, *P. nathusii*, and *B. barbastellus*). The most likely explanation is the absence of woody vegetation at higher elevations, which limits habitat suitability for many species, primarily preferring forested habitat, such as *B. barbastellus* (Russo et al. 2004; Zeale et al. 2012; Rachwald et al. 2021, or *P. nathusii* (Meschede & Heller 2000; Flaquer et al. 2009). In contrast, *T. teniotis*, a species associated with rocky environments (Arlettaz et al. 2000; Ciechanowski et al. 2005), was more frequently recorded at the upper site. Despite this, we observed a higher biodiversity index at the higher elevation, which resulted from a much more uniform species distribution. At the pond on the valley floor, we observed more species at very low densities, as well as a few dominant species that occurred in high numbers.

Our study expands current knowledge by documenting ten bat species previously unrecorded in this region and by providing new insights into the ecology of bats in high-mountain environments of southern Europe. The results suggest that, in the absence of suitable lowland habitats, bats may exploit higher elevations for foraging and swarming, even though these environments remain suboptimal. The strong sex bias observed across elevation not only confirms previous findings (Nardone et al. 2015) but also highlights the need for further research into how this pattern of vertical sex segregation varies along the Valbona River Valley altitudinal gradient and whether it becomes less pronounced at lower altitude (for example towards the village of Bajram Curri (360 m a.s.l.), outside the alpine zone).

Pioneering observations conducted in 2007 in the Valbona River Valley by one of the authors (AR) (Sachanowicz et al. 2015) revealed that this area is naturally valuable, difficult to access, sparsely inhabited by local people engaged in traditional pastoralism, and almost completely forgotten by tourism. Observations of this area after 17 years (as well as available published data) paint a drastically different picture, with the Valbona River Valley becoming a crowded tourist area during the summer season subject to intensive use and infrastructure development, possibly beyond the capacity of this biotope (Lushaj and Malsia 2008; Byberaj et al. 2014; Kortoci & Kortoci 2017). The pace of change can also be described as unprecedented. The expected effects of these changes on bat populations may include an increasing proportion of synanthropic species (such as *C. serotinus*) and negative impacts on species associated with forest habitats. Artificial light at night (ALAN), resulting from the

expansion of infrastructure and construction in the area, may substantially affect the local occurrence of bats by altering both their behaviour and the species composition of bat assemblages (Stone et al. 2015; Meola et al. 2026). Furthermore, increasing water demand, potentially resulting in declining groundwater levels and the loss of smaller water bodies, may reduce water availability for wildlife, including bats. The Valbona River constitutes the main water source for the entire valley and is also the principal source of groundwater recharge in the area (Diku et al. 2017).

Our findings are particularly relevant in the context of planned conservation measures, including the potential inclusion of the Valbona River Valley in the Natura 2000 network following Albania's accession to the European Union. Under current regulations, the designation of a Natura 2000 site requires prior research into the protected areas (habitats and animal species listed in Annex II of the EU Habitats Directive). Of the bat species we identified in the Valbona Valley, six are listed in the Annex II (*R. ferrumequinum*, *R. hippposideros*, *M. emarginatus*, *M. blythii*, *M. capaccinii*, *B. barbastellus*), and further research will likely expand this list, e.g. by the remaining three European Rhinolophid species, all already known form Albania (Sachanowicz & Ciechanowski 2018; Théou & Bego 2018).

Given the rapid environmental changes currently affecting the region, such as increasing tourism and human pressure, a better understanding of bat ecology across altitudinal gradients is essential for effective conservation planning. Overall, our study demonstrates that high-mountain environments, although suboptimal, play a previously underestimated role in the spatial ecology of bats in southern Europe. Our research also describes a certain state of the natural environment that can change quickly.

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation and data collection Andrea Pereswiet-Soltan, Alek Rachwald, Grzegorz Apoznański, Sylwia Pospuła, Marian Polok, Marcin Klisz and Jakub Jeleń. Analyses were performed by Grzegorz Apoznański, Alek Rachwald, Andrea Pereswiet-Soltan and Sylwia Pospuła. The first draft of the manuscript was written by Andrea Pereswiet-Soltan and Alek Rachwald, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request

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Bat species/group	mean n/h	
	Lower pond	Upper pond
P. pygmaeus	23.53	0.03
P. kuhlii	16.14	0.22
M. daubentonii	5.44	0.08
H. savii	4.33	0.67
P. nathusii	1.42	0
E. serotinus	0.5	0.39
P. pipistrellus	0.69	0.03
N. noctula	0.53	0.14
R. hipposideros	0.47	0.08
M. mystacinus/brandtii	0.03	0.03
M. capaccinii	0.11	0.19
N. leisleri/V.murinus	0.44	0.83
M. alcathoe	0.25	0.39
Plecotus spp.	0.17	0.14
T. teniotis	0.11	0.61
E. nilssonii	0.03	0
B. barbastellus	0.06	0
Mean value for whole activity	54.25	3.83

Table 2. Average bat activity (taken from numbers of 5 s activity units per 1 hour) near the lower pond (left) and near the upper pond (right). Mean n/h: mean number of activity units per one hour. Data from recordings in August 2021 and 2024, combined, total 36 hours of night recordings for each point.

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alt. (m)	Hsav	Malc	Mbly	Mcap	Mdau	Mema	Mnat	Nnoc	Ppyg	Paur	Pmac	Pspp.	Rhip	Vmur
739	7	2	2	-	1	-	-	1	2	-	-	-	-	2
776	4	-	-	-	-	-	-	-	-	-	-	-	-	-
1093	-	-	-	1	-	-	-	-	-	-	-	1	-	-
1700	2	1	-	-	-	15	2	-	-	1	2	-	7	-
2078	-	-	-	-	-	-	-	-	-	1	-	-	-	-
2108	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2180	-	-	-	-	-	-	-	-	-	2	1	7	-	-

Table 1. The abundance of different bat species captured in relation to altitude (alt.) above sea level (in m a.s.l.) of the certain capture sites. Hsav = *Hypsugo savii*, Malc = *Myotis alcathoe,* Mbly = M. *blythii*, Mcap – *M. capaccinii,* Mdau = *M. daubentonii*, Mema = *M. emarginatus*, Mnat = *M. nattereri*, Nnoc = *N. noctula*, Ppyg = *Pipistrellus pygmaeus*, Paur = *Plecotus auritus*, Pmac = *Plecotus macrobullaris*, Pspp. = *Plecotus* species (whole genus, without distinguishing species), Rhip = *Rhinolophus hipposideros*, Vmur = *Vespertilio murinus*. Detailed information regarding the individual capture sites is provided in Appendix 1.

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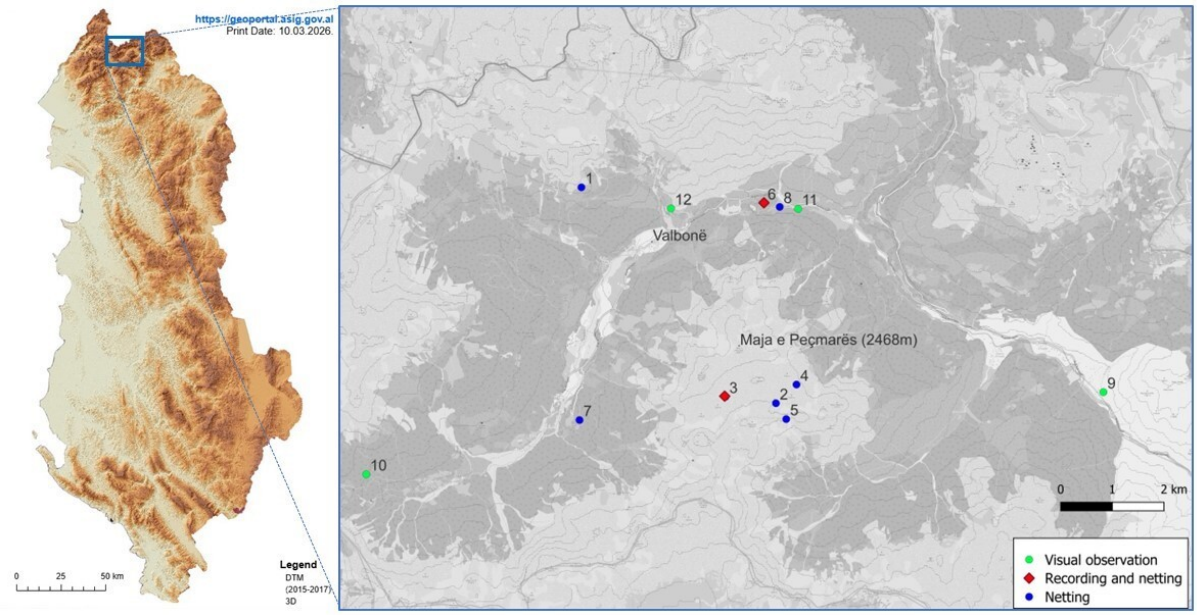


Figure 1. The study area is located in northern Albania (left panel). Study points are marked in color (right panel). Numbering descriptions are in Appendix 1.

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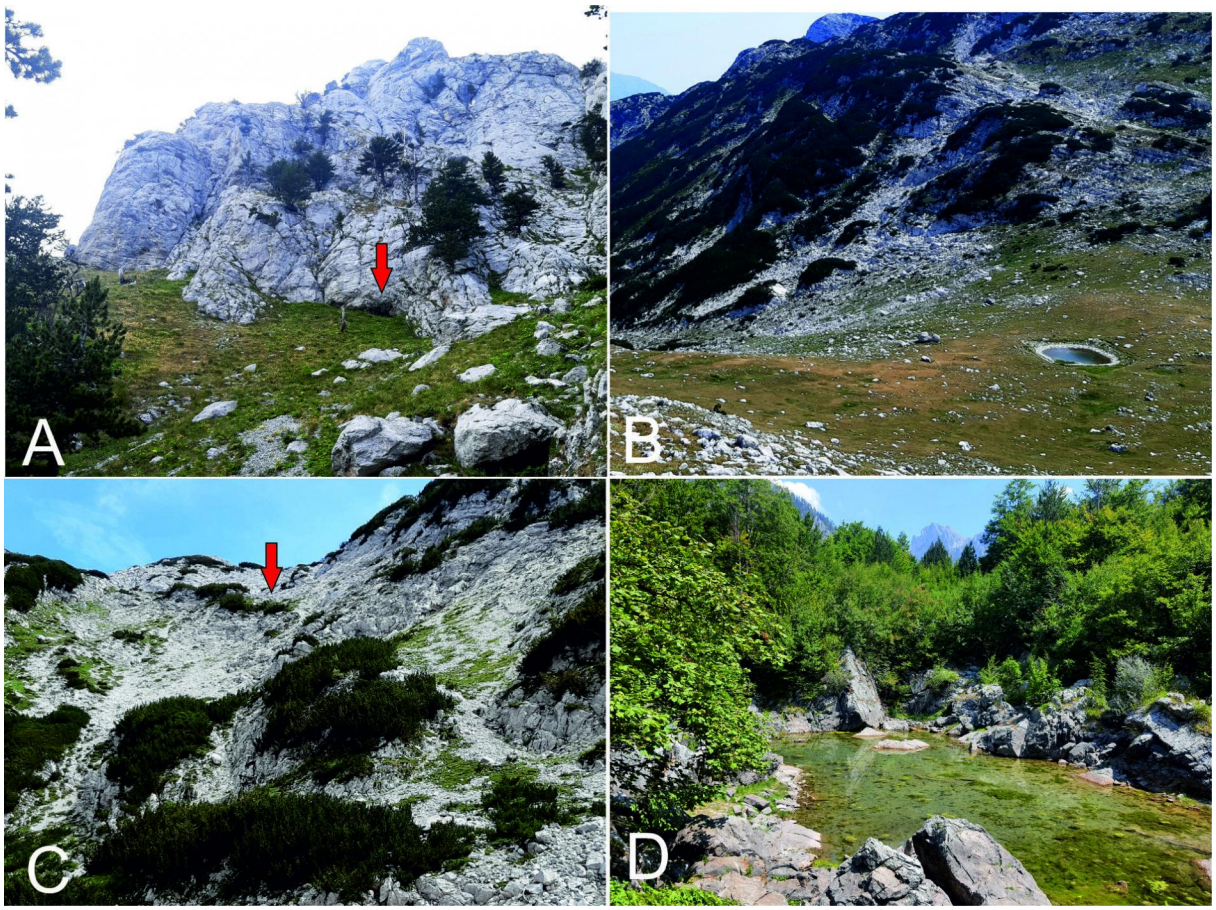


Figure 2. Bet mist-netting sites. Shpella e Haxhisë entrance (A), upper pond at mountain pass, (distant shot, B), Shpella e Valbonës entrance (C), lower pond (Liqeni i Xhemës, D). All photos: A. Pereswiet-Soltan.

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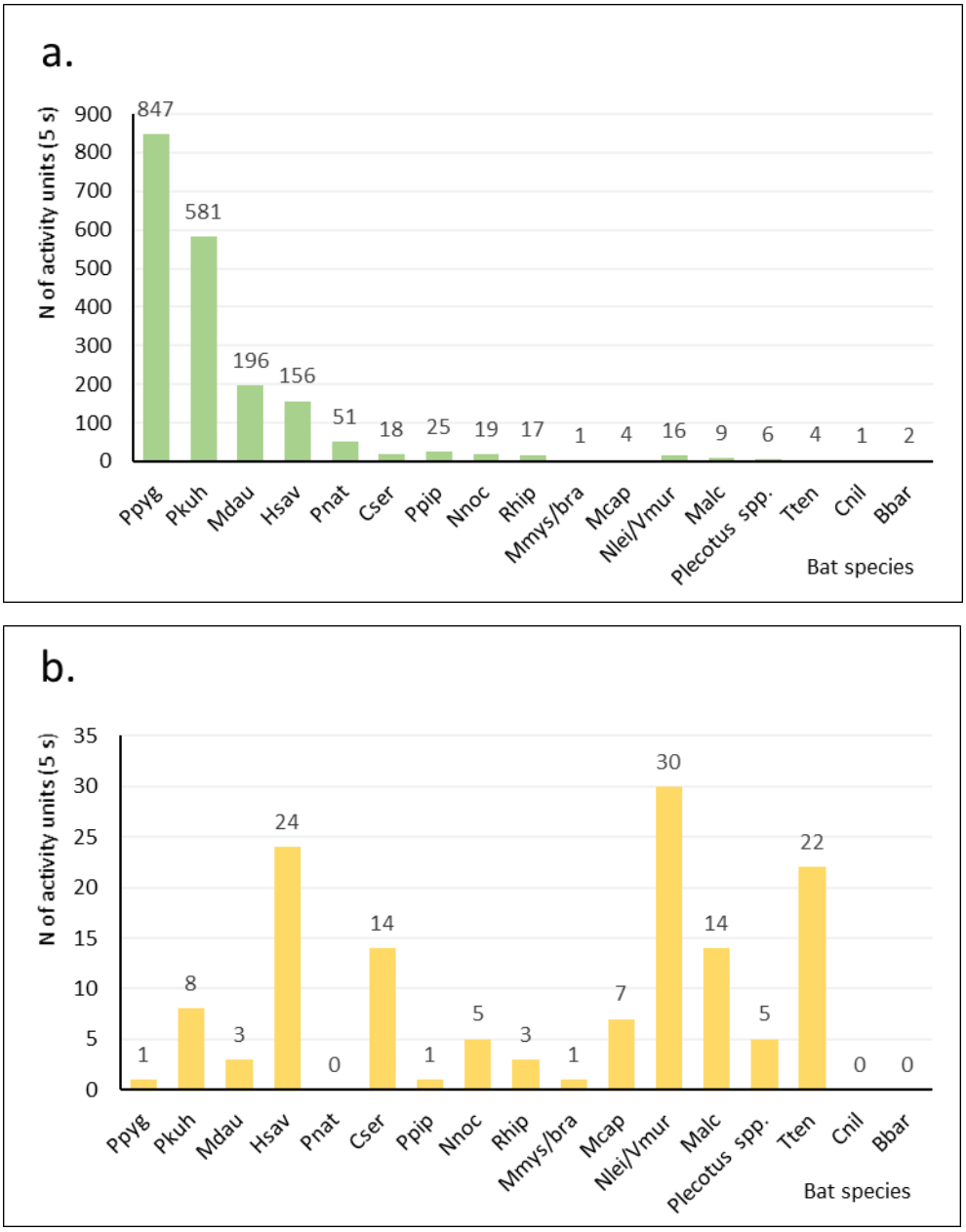


Figure 3. Total recorded activity of bats near lower (**a.**) and upper (**b.**) ponds. One activity unit = 5s. Ppyg = *P. pygmaeus*, Pkuh = *P. kuhlii*, Mdau = *M. daubentonii*, Hsav = *H. savii*, Pnat = *P. nathusii*, Cser = *C. serotinus*, Ppip = *P. pipistrellus*, , Nnoc = *N. noctula*, Rhip = *R. hipposideros*, Mmys/Mbra = *M. mystacinus/M. brandtii*, Mcap – *M. capaccinii*, Nlei/Vmur = *N. leisleri/V. murinus*, Malc = *M. alcathoe*, Plecotus spp. = *Plecotus* species (whole genus, without distinguishing species), Tten = *T. teniotis*, Cnil = *C. nilssonii*, Bbar = *B. barbastellus*.

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Tables

Table 1 - Download source file (15.22 kB)
Table 2. Average bat activity (taken from numbers of 5 s activity units per 1 hour) near the lower pond (left) and near the upper pond (right). Mean n/h: mean number of activity units per one hour. Data from recordings in August 2021 and 2024, combined, total 36 hours of night recordings for each point.

Table 2 - Download source file (15.51 kB)
Table 1. The abundance of different bat species captured in relation to altitude (alt.) above sea level
(in m a.s.l.) of the certain capture sites. Hsav = Hypsugo savii, Malc = Myotis alcathoe, Mbly = M. blythii, Mcap – M. capaccinii, Mdau = M. daubentonii, Mema = M. emarginatus, Mnat = M. nattereri, Nnoc = N. noctula, Ppyg = Pipistrellus pygmaeus, Paur = Plecotus auritus, Pmac = Plecotus macrobullaris, Pspp. = Plecotus species (whole genus, without distinguishing species), Rhip = Rhinolophus hipposideros, Vmur = Vespertilio murinus. Detailed information regarding the individual capture sites is provided in Appendix 1.

Figures

Figure 1 - Download source file (171.06 kB)
Figure 1. The study area is located in northern Albania (left panel). Study points are marked in color (right panel). Numbering descriptions are in Appendix 1.

Figure 2 - Download source file (4.88 MB)
Figure 2. Bet mist-netting sites. Shpella e Haxhisë entrance (A), upper pond at mountain pass, (distant shot, B), Shpella e Valbonës entrance (C), lower pond (Liqeni i Xhemës, D). All photos: A. Pereswiet-Soltan.

Figure 3 - Download source file (198.01 kB)
Figure 3. Total recorded activity of bats near lower (a.) and upper (b.) ponds. One activity unit = 5s. Ppyg = P. pygmaeus, Pkuh = P. kuhlii, Mdau = M. daubentonii, Hsav = H. savii, Pnat = P. nathusii, Cser = C. serotinus, Ppip = P. pipistrellus, , Nnoc = N. noctula, Rhip = R. hipposideros, Mmys/Mbra = M. mystacinus/M. brandtii, Mcap – M. capaccinii, Nlei/Vmur = N. leisleri/V. murinus, Malc = M. alcathoe, Plecotus spp. = Plecotus species (whole genus, without distinguishing species), Tten = T. teniotis, Cnil = C. nilssonii, Bbar = B. barbastellus.

Supplementary Online Material

Download source file (34.09 kB)
Appendix 1. Bats that were caught, as well as observed and visually identified during research in 2021-2025. Ad: adult, s-ad: sub-adult, C: catch, O: visual observation, m: male, f: female. The letter-numerical names of the caves are in accordance with the accepted cave nomenclature (https://grottocenter.org/ui/entrances).