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The alpine scrubs and dwarf heaths of the Balkan Peninsula - an exceptional center of floristic richness and endemism

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ABSTRACT:

Alpine scrubs (*Rosa pendulinae-Pinetea mugo*) and dwarf heaths (*Loiseleurio procumbentis-Vaccinietea*) are an exceptional assemblage of rich floristic units which contribute significantly to the overall diversity on the Balkan Peninsula. The main edificators of these types of habitats are mostly glacial relicts. Additionally, they are of the arctic, alpine, and boreal distribution types, which further emphasises their importance from the conservation point of view. We investigated their taxonomic richness, endemism, patterns of spatial distribution and diversification in the central Balkans as well as their coenotic composition using a comprehensive dataset (15,609 species occurrence data). The analyses were conducted at three hierarchical levels taking into account the ecological and geographic diversity of the alpine scrubs and dwarf heaths in the study area. The results obtained showed that in the alpine scrubs and dwarf heaths of the central Balkans 902 taxa (829 species and 73 subspecies) had been recorded, and that the proportion of endemics in these habitats is extremely high (ca. 22%). Our results further showed that in 180 randomly selected plots of medium size (≥ 10 and < 100 m²), the registered regional floristic richness for the unique sample size was 527 species, placing the alpine region of the Balkan Peninsula in second place among the richest alpine regions in the world. Moreover, significant regional differences in species composition were observed within the research area, with floristic richness and diversity increasing from north to south.

Keywords:

floristic diversity, endemics, relicts, hotspots, mountains, alpine region, environmental heterogeneity

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INTRODUCTION

It is well known that the Balkan Peninsula, as part of the Mediterranean basin, is one of the few extratropical biodiversity hotspots (BARTHLOTT *et al.* 2005) and that the main hotspots for species richness are confined to its mountainous areas (STEVANOVIĆ 1996). The heterogeneity of the environmental factors, geological-historical changes, and human influences on the Balkan Peninsula are the main reasons for the exceptional floristic and vegetation diversity of this area (HORVAT *et al.* 1974; ILIĆ *et al.* 2022).

Alpine scrubs and dwarf heaths represent specific vegetation types which occur mainly in the subalpine and alpine belts above the mountain-forest belt, at an altitude of (1200) 1600–2800 m a.s.l. This vegetation is primarily conditioned by a specific subalpine and alpine climate, characterised by heavy snow cover lasting for at least six months, which combined with the severe climate contributes significantly to the growth inhibition of tall woody vegetation.

In the European context, these types of vegetation have an arctic-alpine distribution, as they occur in the subarctic zone (north of the boreal region), in the Scan-

dinavian mountains and in Iceland, in addition to the southern high-mountain ranges (the Pyrenees, the Alps, the Carpathian Mountains, the Balkan Mountains, and the Caucasus) (BOHN *et al.* 2003). According to MUCINA *et al.* (2016), these include: a) Relic alpine silicicolous dwarf heath in the wind-exposed habitats of the nemoral mountain ranges of Europe (*Loiseleuria procumbentis*-*Vaccinium* Br.-Bl. in Br.-Bl. et Jenny 1926), b) Subalpine chionophobous silicicolous low juniper scrub of the nemoral mountain ranges of Europe (*Juniperion nanae* Br.-Bl. in Br.-Bl. et al. 1939), c) Supramontane and subalpine dwarf heath on the siliceous substrates of the Southern Carpathians and the Dinarides (*Bruckenthalia spiculifoliae* Horvat 1949), d) Subalpine silicicolous pine krummholz of the Alps, the Carpathians and the Balkans (*Pinion mugo* Pawłowski *et al.* 1928), and e) Subalpine calcicolous pine krummholz of the Balkan Peninsula (*Lonicero borbasianae*-*Pinion mugo* Čarni et Mucina 2015).

The main edificators of alpine scrubs and heaths are glacial relicts of arctic, alpine, and boreal origin, and rarely represent the remnants of ancient oro-Mediterranean flora (LAKUŠIĆ *et al.* 2005). Namely, the most important species characterising the alpine scrubs and dwarf heaths in the mountains of the central Balkan Peninsula are two conifer species (*Pinus mugo* Turr. and *Juniperus sibirica* Burgsdorf.) and a number of ericoid species [*Vaccinium myrtillus* L., *Vaccinium uliginosum* L., *Bruckenthalia spiculifolia* Rchb., *Empetrum nigrum* L., *Arctostaphylos uva-ursi* (L.) Spreng., and *Rhododendron ferrugineum* L.]. *Pinus mugo* occurs exclusively in the mountains, in sites limited to the Alps and Carpathians (FARJON & FILER 2013). It is distributed from the Pyrenees, to the Vosges Mountains, the Ore Mountains, the central Apennines (Abruzzia), the Balkan Mountains, Greece, and Albania (ALEXANDROV *et al.* 2019). *Juniperus sibirica* is distributed in the high mountains of southern Eurasia and western North America, and at low elevations in the cool maritime and arctic regions of Eurasia, Iceland, and southern Greenland (ECKENWALDER 2009). In mainland Europe, *J. sibirica* occurs in the Pyrenees, the Alps, the Carpathians, Corsica, the Balkan Mountains, and across N Turkey (FARJON & FILER 2013). The members of the Ericaceae family play an important role in the entire heath formation: *Vaccinium myrtillus* is a typical boreal-temperate Eurasian species, and *Vaccinium uliginosum* is a circumboreal species. *Bruckenthalia spiculifolia* occurs only in the Southern Carpathians and the Balkan Mountains (BOHN *et al.* 2003).

Although numerous floristic and phytocoenological data were collected during the 20th century, there are still no comprehensive studies which systematically address various aspects of the floristic diversity of the alpine scrubs and dwarf heaths of the Balkan Peninsula. Therefore, the main objectives of our work were to study: (1) the taxonomic and endemic richness, (2) the distri-

bution patterns, and (3) the coenotic and spatial diversification of alpine scrubs and dwarf heaths in the central part of the Balkan Peninsula.

MATERIALS AND METHODS

Study area, vegetation types, and data gathering principles. We analysed the subalpine and alpine scrub and heat vegetation of the central parts of the Balkan Peninsula, extending from the Snježnik Mountain in Croatia in the northwest to the Jakupica Mountain in northern North Macedonia in the south, and the central Stara Planina Mountains in the east (Fig. 1). We followed the definition of the phytogeographic boundaries of the Balkan Peninsula as given by REED *et al.* (2004).

The studied alpine scrubs and dwarf heaths are considered zonally developed alpine vegetation, since they naturally occur above the climatic tree line (KÖRNER 2003). In this sense, the alpine vegetation included in the present study corresponds to the mid-latitude alpine tundra as defined by QUINN (2008).

The concept of operational ecological units (JAX 2015) such as population, community, and ecosystem, are at the basis of ecological theory and research and have increasingly become the focus of conservation strategies. Concepts of these units still suffer from inconsistencies and confusions over terminology. The different concepts are treated here together as a common “conceptual cluster,” with similar ecological functions (roles is adapted to describe the different aspects of the species richness of the alpine scrubs and dwarf heaths in the central part of the Balkan Peninsula). The analyses were conducted at

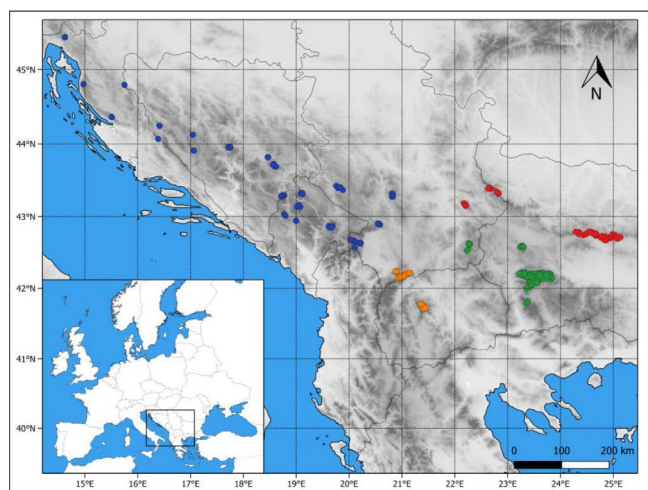


Fig. 1. The distribution of the alpine scrubs and dwarf heaths on the Balkan Peninsula – the position of the analysed plots. Red dots – the Balkan Mountains, blue dots – the Dinarides, green dots – the Rhodope Mountains, orange dots – the Scardo-Pindic Mountains.

Table 1. The operational ecological units and hierarchical levels of the scrubs and heaths on the central Balkan Peninsula for which the analyses were performed.

Level	Operational ecological units	Codes	Estimated Area of Occupancy (in ha)
I	Krummholz scrub (<i>Pinetea mugo</i>)	Pinetea mugo	168,773
II	Krummholz scrub (<i>Pinion mugo</i>)	Pinion mugo	168,773
III	Krummholz scrub (<i>Pinion mugo</i>) in Dinarides	Pin_Mug_Din	
III	Krummholz scrub (<i>Pinion mugo</i>) in Scardo-Pindhic mountains	Pin_Mug_ScPind	
III	Krummholz scrub (<i>Pinion mugo</i>) in Rhodope mountains	Pin_Mug_Rhod	
III	Krummholz scrub (<i>Pinion mugo</i>) in Balkan mountains	Pin_Mug_Balk	
I	Dwarf heaths (<i>Vaccinietea</i>)	Vaccinietea	149,730
II	Low juniper scrub (<i>Juniperion sibiricae</i>)	<i>Juniperion sibiricae</i>	19,655
III	Low juniper scrub (<i>Juniperion sibiricae</i>) in Dinarides	Jun_sib_Din	
III	Low juniper scrub (<i>Juniperion sibiricae</i>) in Scardo-Pindhic mountains	Jun_sib_ScPind	
III	Low juniper scrub (<i>Juniperion sibiricae</i>) in Rhodope mountains	Jun_sib_Rhod	
III	Low juniper scrub (<i>Juniperion sibiricae</i>) in Balkan mountains	Jun_sib_Balk	
II	Bruckenthalia ericoid dwarf heath (<i>Bruckenthalion spiculifoliae</i>)	Bruckenthalion spiculifoliae	110,640
III	Bruckenthalia ericoid dwarf heath (<i>Bruckenthalion spiculifoliae</i>) in Dinarides	Bruck_spic_Din	
III	Bruckenthalia ericoid dwarf heath (<i>Bruckenthalion spiculifoliae</i>) in Scardo-Pindhic mountains	Bruck_spic_ScPind	
III	Bruckenthalia ericoid dwarf heath (<i>Bruckenthalion spiculifoliae</i>) in Rhodope mountains	Bruck_spic_Rhod	
III	Bruckenthalia ericoid dwarf heath (<i>Bruckenthalion spiculifoliae</i>) in Balkan mountains	Bruck_spic_Balk	
II	Bilberry dwarf heath (<i>Vaccinion myrtilli</i>)	Vaccinion myrtilli	5045
III	Bilberry dwarf heath (<i>Vaccinion myrtilli</i>) in Dinarides	Vacc_myrt_Din	
III	Bilberry dwarf heath (<i>Vaccinion myrtilli</i>) in Scardo-Pindhic mountains	Vacc_myrt_ScPind	
III	Bilberry dwarf heath (<i>Vaccinion myrtilli</i>) in Rhodope mountains	Vacc_myrt_Rhod	
III	Bilberry dwarf heath (<i>Vaccinion myrtilli</i>) in Balkan mountains	Vacc_myrt_Balk	
II	Bog bilberry dwarf heath (<i>Vaccinion uliginosi</i>)	Vaccinion uliginosi	5165
III	Bog bilberry dwarf heath (<i>Vaccinion uliginosi</i>) in Dinarides	Vacc_uli_Din	
III	Bog bilberry dwarf heath (<i>Vaccinion uliginosi</i>) in Scardo-Pindhic mountains	Vacc_uli_ScPind	
III	Bog bilberry dwarf heath (<i>Vaccinion uliginosi</i>) in Rhodope mountains	Vacc_uli_Rhod	
III	Bog bilberry dwarf heath (<i>Vaccinion uliginosi</i>) in Balkan mountains	Vacc_uli_Balk	

three hierarchical levels representing the ecological diversity and geographical specificity of the alpine scrubs and dwarf heaths in the study area.

At the first level, we distinguished two basic groups: A) subalpine communities of mountain pine (*Rosa pendulinae-Pinetea mugo* Theurillat in Theurillat et al. 1995), and B) subalpine and alpine dwarf scrub and dwarf heath communities (*Loiseleurio procumbentis-Vaccinietea* Eggler ex Schubert 1960), which according to BOHN et al. (2003) both belong to vegetation formation C, i.e. subarctic, boreal and nemoral-montane open woodlands as well as subalpine and oro-Mediterranean vegetation. In the text, we used the composite name krummholz scrub (*Pinetea mugo*) for the first group and dwarf heaths (*Vaccinietea*) for the second. Within these

two basic vegetation types, we singled out five units at the second level, corresponding to the scrubs and heaths dominated by the main species which make up the alpine scrubs and heaths on the Balkan Peninsula. Within the scrubs, we selected krummholz scrub (*Pinion mugo*) and the low juniper scrub (*Juniperion sibiricae*), while within the dwarf heaths, three units were selected with the main edificators being: *Bruckenthalia ericoid* dwarf heath (*Bruckenthalion spiculifoliae*), the bilberry dwarf heath (*Vaccinion myrtilli*), and the bog bilberry dwarf heath (*Vaccinion uliginosi*).

Finally, the third level defines the operational units which make up the geographic variants of alpine scrubs and dwarf heaths registered in the basic mountain systems of the Balkan Peninsula. According to STEVANOVIĆ

et al. (2009), the mountains are classified into four mountain systems [the Dinarides, the Scardo-Pindic Mountains, the Rhodope Mountains, and the Balkan (Stara planina) Mountains] and 16 mountain groups. The hierarchical levels, names, and codes of the operational units are listed in Table 1.

The names of the plant formations used in this manuscript are used as associative names, corresponding to the different scrub and dwarf vegetation types and have no formal syntaxonomic meaning.

The total estimated extent of the study area is 309,278 ha, while the estimated area occupied by Level I and Level II of the operational ecological units is shown in Table 1. The evaluation of these areas was calculated based on the Map of the Natural Vegetation of Europe, scale 1:2,500,000 (BOHN *et al.* 2003).

For the purposes of species occurrence data, we collected vegetation data from original phytocoenological tables in research articles, book chapters, and dissertations published between 1938 and 2008 (Table S1), with data from four publications exported from the Balkan Vegetation Database (VASSILEV *et al.* 2016, 2020).

In total, data from 650 plots with a total area of approximately 30 ha (309,278 m²) were included in the analyses. Although the area where the species data were collected is small (only 30 ha), especially compared to the extent of the entire region, it is at the same time very representative. In fact, the size of the plots included in the analyses corresponds to the area representing the floristic composition of scrub and heath stands, which is commonly used for phytosociological research on this type of vegetation. Moreover, the dataset from which the species data were taken is very well distributed over the studied area on the central Balkan Peninsula (Fig. 1).

In each plot, taxon occurrences across different layers were merged into one, and non-vascular plants were removed from the analyses. The final dataset included 15,609 species-occurrence data, and was the subject of further analyses.

For non-georeferenced, or inaccurately georeferenced plots, secondary georeferencing was performed in Ozi Explorer and Google Earth. Centers of floristic richness were shown on MGRS maps of 50 × 50 km, based on UTM projection (LAMPINEN 2001).

The taxon concepts and nomenclature largely followed the Checklist for Central Europe adopted for the EuroVegChecklist expert system in the JUICE program (TICHÝ 2002). For a smaller number of species, primarily restricted to the area of the Balkan Peninsula, the nomenclature generally followed the EURO + MED PLANT-BASE (2006+).

Statistical analyses. All the statistical analyses (univariate and multivariate) were performed on binary (presence-absence) matrices prepared for different levels of analyses.

The similarity and distance indices, as well as the diversity indices were calculated using the Past v. 2.17 software package (HAMMER *et al.* 2001). We used two indicators of diversity: species richness to describe the absolute species number in the designated area, and the LogS/LogA index of species density to describe the number of species (S) per surface unit (A).

The cluster analysis (pairwise with Jaccard distances) was performed using the Past v. 2.17 software package (HAMMER *et al.* 2001), while principal coordinate analysis using Jaccard distances was carried out using Canoco 5 (TER BRAAK & ŠMILAUER 2012).

RESULTS AND DISCUSSION

Species richness and diversity. The collected dataset of the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula contained information on 902 taxa (829 species and 73 subspecies), with 15,609 species-occurrence data. This registered number of taxa corresponds to ca. 14% of the estimated total number of vascular plant taxa on the Balkan Peninsula (ŠPANIEL & REŠETNIK 2022) and ca. 8% of the total European flora (MUTKE *et al.* 2010). Considering that approximately 5500 species have been recorded in the Alps, one of the major European mountain systems (MUTKE *et al.* 2010), the total of 902 taxa recorded in the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula alone represents a considerable species richness, which is in line with the previously reported relatively high floristic richness of the high-mountain flora of the central Balkans (JIMÉNEZ-ALFARO *et al.* 2021; ILIĆ *et al.* 2022).

Although from a global perspective, the mountains of the Balkan Peninsula are expected to be at intermediate species richness levels when compared with the other alpine regions in the world (TESTOLIN *et al.* 2021), our results show that the mountains studied have significantly higher species richness than estimated in the work of TESTOLIN *et al.* (2021). Namely, our results show that in 180 randomly selected plots of medium size (≥ 10 and < 100 m²), the registered floristic richness for a unique sample size is 527 species. This places the Balkan Peninsula mountains second among the richest alpine regions in the world, just behind the Colombian and Ecuadorian Andes (Neotropics), for which the estimated regional richness for a unique sample size is 543 species of 180 plots. In contrast, according to the estimated regional richness for a unique sample size of 180 plots presented in TESTOLIN *et al.* (2021), the richest alpine regions in the Western Palaearctic are the Central and Eastern Alps (Sest = 387 species) and the Western Carpathians (Sest = 252 species), while the poorest regions were Rila (Sest = 147 species) and the Northern Scandes (Sest = 98 species).

Interestingly, we found that the floristic richness in 180 randomly selected plots in the Dinaric Mountains to be 538 species, while in the Rila-Rhodope Mountains, it

is only 196 species, which is close to the estimated species richness for a comparable number of 180 plots for the Rila Mountain (Sest = 147). This is consistent with the data on regional species pools in alpine grasslands in the European mountains, which showed that the Dinarides region has the highest richness for all species with 742 recorded taxa, followed by the Western Alps with 651 taxa and the Scardo-Pindic regions with 631 taxa (JIMÉNEZ-ALFARO *et al.* 2021). Although there is a certain possibility of underrecording within some of the regions compared, our results also confirm the fact that the Dinaric Mountains represent one of the key centers of floristic diversity at the European level.

One of the explanations for such large differences between the estimated and observed floristic richness is certainly the fact that the researched area (the central part of the Balkan Peninsula) unites five mountain systems, of which the Dinaric Mountains are a natural continuation of the Alps, while the Balkan Mountains have a natural connection with the southern Carpathians. In this sense, the alpine flora of the mountains of the central part of the Balkan Peninsula represent a very heterogeneous group of plants of different origin and age, which is described in more detail in previous studies (e.g. STEVANOVIĆ *et al.* 2009; VUKOJIČIĆ *et al.* 2014).

The large differences are certainly due in part to different methodological approaches. While our values represent the absolute numbers observed in different sets of plots, the values reported by TESTOLIN *et al.* (2021) represent mathematically calculated estimates which should not be interpreted as representative of the total regional species pools, but rather as comparable estimates of regional floristic richness.

Within the investigated area, the plant species maxima [the number of species on a plot of 100 m² and 1000 m² – according to WILSON *et al.* (2012)] is found in the krummholz scrub (Pinion mugo) on Suva Planina Mountain (46 on 100 m²) and Vranica Mountain (64 on 1000 m²). Although this value of the plant species maxima is far below the 313 species per 1000 m² in Colombia, or the 233 taxa per 100 m² of the Costa Rican tropical rainforest (WILSON *et al.* 2012), and half that of the unmanaged (natural) relict forests of Serbian spruce on Tara Mountain (71 on 100 m²) and Zvijezda Mountain (125 on 1000 m²) (ILIĆ *et al.* 2022), it is in the range of plant species maxima values for the α -diversity of the coniferous forests of central and southeastern Europe, where the richest plots contain between 45 and 72 species (VEČEŔA *et al.* 2019).

The majority of the top hotspots for alpine scrubs and dwarf heaths in the Central Balkans are registered on limestone or other calcareous bedrock types, which is consistent with the results of the study of the alpha diversity of vascular plants in European forests (VEČEŔA *et al.* 2019; ILIĆ *et al.* 2022) or that on ecological indicator values, which indicate that the vast majority of

Central European vascular plant species prefer base-rich and calcareous soils, which is also true for forest flora (EWALD 2008; UJHÁZYOVÁ *et al.* 2016). The results of our study showed that floristic richness on non-carbonate substrates is almost half that of the richness on carbonate, with a greater number of species inhabiting ultramafic (species maximum 46 per 1000 m²) rather than silicate substrates (species maximum 27 per 1000 m²), just as in recent studies of the diversity of mountain conifer forests on the Balkan Peninsula (ILIĆ *et al.* 2022).

The analyses at the scrub and heath types level I (Level I) showed that the diversity indices differed only slightly. The species richness for the krummholz scrub (*Pinetea mugo*) is 654 compared to 635 in the dwarf heaths (*Vaccinieta*), and both the number and percentage of endemics are almost the same for both vegetation types, namely 145 endemics (22.83%) for the krummholz scrub (*Pinetea mugo*) and 148 endemics (22.63%) for the dwarf heaths (*Vaccinieta*) (Table 2).

Accounting for almost 23% of endemic taxa, the alpine scrubs and dwarf heaths on the Balkan Peninsula are among the mountain ranges with the highest proportion of endemics in the Mediterranean region, where the endemism rate ranges from 10.2% in the Pindos Mountains in Greece to 28.18% in the Baetic Mountains in Spain (PEÑAS *et al.* 2005). The estimated number of endemics in other high European mountain systems indicate that 7% of the flora is endemic in the Alps, 5% in the Pyrenees, 6% in the montane flora of Crimea (DAVIS & HEYWOOD 1994), and 12% in the Carpathians (FAVARGER 1972).

The total area of the plots from which the species data were taken is almost identical for both habitat types at the first level (168,773 m² vs. 140,505 m²), and the species density (logS/logA index) has almost identical values of 0.536 vs. 0.547. These species density values are similar to the values of species density of the montane coniferous forests of the central Balkans (ILIĆ *et al.* 2022), but lower than those of the total number of vascular plants for individual European countries with similar geographical locations to the Balkan Peninsula, such as Spain (0.723) or Italy (0.684), which are areas with the greatest species richness in Europe (STEVANOVIĆ *et al.* 1995).

The analyses at the scrub and heath types level II (Level II) showed that the krummholz scrub (*Pinion mugo*) has significantly more taxa than the other scrub and heath types, with 635 recorded taxa. The low juniper scrub (*Juniperion sibiricae*) with 408 taxa and the *Bruckenthalia* ericoid dwarf heath (*Bruckenthalion spiculifoliae*) with 328 taxa showed intermediate species richness, while the bilberry dwarf heath (*Vaccinion myrtilli*) with 194 taxa and the bog bilberry dwarf heath (*Vaccinion uliginosi*) with 265 taxa have significantly fewer taxa than the other scrub and heath types (Table 2).

Table 2. Relevé data and diversity parameters for all three levels of research. Abbreviations: **S**—number of taxa; **logS/logA**—species density index; **S End**—number of endemic taxa. **Pin mug Balk**—Pinion mugo in the Balkan Mountains; **Pin mug Din**—Pinion mugo in the Dinarides; **Pin mug Rhod**—Pinion mugo in the Rhodope Mountains; **Pin mug ScPind**—Pinion mugo in the Scardo-Pindic Mountains; **Bruck spi Balk**—Bruckenthalion spiculifoliae in the Balkan Mountains; **Bruck spi Din**—Bruckenthalion spiculifoliae in the Dinarides; **Bruck spi Rhod**—Bruckenthalion spiculifoliae in the Rhodope Mountains; **Bruck spi ScPind**—Bruckenthalion spiculifoliae in the Scardo-Pindic Mountains; **Jun sib Balk**—Juniperion sibiricae in the Balkan Mountains; **Jun sib Din**—Juniperion sibiricae in the Dinarides; **Jun sib Rhod**—Juniperion sibiricae in the Rhodope Mountains; **Jun sib ScPind**—Juniperion sibiricae in the Scardo-Pindic Mountains; **Vacc myr Balk**—Vaccinon myrtilli in the Balkan Mountains; **Vacc myr Din**—Vaccinon myrtilli in the Dinarides; **Vacc myr Rhod**—Vaccinon myrtilli in the Rhodope Mountains; **Vacc myr ScPind**—Vaccinon myrtilli in the Scardo-Pindic Mountains; **Vacc uli Balk**—Vaccinon uliginosi in the Balkan Mountains; **Vacc uli Din**—Vaccinon uliginosi in the Dinarides; **Vacc uli Rhod**—Vaccinon uliginosi in the Rhodope Mountains; **Vacc uli ScPind**—Vaccinon uliginosi in the Scardo-Pindic Mountains.

Level I	No. Relevés	Relevé area (m ²)	S	logS/logA	S End	% End
Pinetea mugo	270	168,773	635	0.536	145	22.83
Vaccinietea	380	140,505	654	0.547	148	22.63
Level II	No. Relevés	Relevé area (m ²)	S	logS/logA	S End	% End
Pinion mugo	270	168,773	635	0.536	145	22.83
Bruckenthalion spiculifoliae	119	110,640	328	0.499	71	21.65
Juniperion sibiricae	139	19,655	408	0.608	91	22.30
Vaccinon myrtilli	39	5,045	194	0.618	41	21.13
Vaccinon uliginosi	83	5,165	265	0.653	60	22.64
Level III	No. Relevés	Relevé area (m ²)	S	logS/logA	S End	% End
Pin mug Balk	6		83		10	12.05
Pin mug Din	141		450		81	18.00
Pin mug Rhod	108		229		52	22.71
Pin mug ScPind	15		179		38	21.23
Bruck spi Balk	37		98		20	20.41
Bruck spi Din	27		133		15	11.28
Bruck spi Rhod	32		96		21	21.88
Bruck spi ScPind	23		175		44	25.14
Jun sib Balk	27		187		34	18.18
Jun sib Din	34		207		35	16.91
Jun sib Rhod	75		148		42	28.38
Jun sib ScPind	3		45		12	26.67
Vacc myr Balk	8		48		12	25.00
Vacc myr Din	25		132		17	12.88
Vacc myr Rhod	3		61		17	27.87
Vacc myr ScPind	3		36		7	19.44
Vacc uli Balk	17		81		17	20.99
Vacc uli Din	10		96		24	25.00
Vacc uli Rhod	38		94		24	25.53
Vacc uli ScPind	18		73		17	23.29

Regarding the number of endemics, the krummholz scrub (Pinion mugo) stands out with 145 taxa, but in percentage terms the results are almost the same in all the subtypes, within the range from 21.13% for the bilberry dwarf heath (Vaccinon myrtilli - 0.618) and the bog bilberry dwarf heath (Vaccinon uliginosi - 0.653) for

the krummholz scrub (Pinion mugo). Somewhat different relations were found in terms of species density (logS/logA index), with the highest indexes for the bilberry dwarf heath (Vaccinon myrtilli - 0.618) and the bog bilberry dwarf heath (Vaccinon uliginosi - 0.653),



Fig. 2. The centers of floristic richness of the alpine scrubs and dwarf heaths on the Balkan Peninsula – the number of taxa recorded within 50 × 50 MGRS squares.

and the lowest for the krummholz scrub (*Pinion mugo* - 0.536) and the *Bruckenthalia* ericoid dwarf heath (*Bruckenthalion spiculifoliae* - 0.499) (Table 2).

These results are consistent with the size of the area they occupy and the heterogeneity of the environmental conditions inhabited by the different types of scrubs and heaths. Indeed, the floristically richest groups of the krummholz scrub (*Pinion mugo*) and the low juniper scrub (*Juniperion sibiricae*) occupy the largest areas on the studied mountains and at the same time inhabit the most ecologically heterogeneous habitats. In contrast, the bilberry dwarf heath (*Vaccinion myrtilli*) and the bog bilberry dwarf heath (*Vaccinion uliginosi*), which occupy small areas and uniform ecological habitat conditions, have the lowest number of recorded species.

The analyses at the scrub and heath types level III (Level III) At the regional level (Level III), all the groups show great variability in the values of all the diversity parameters, so no pattern could be observed. It is important to note that the greatest geographic variation is shown by the groups with the greatest floristic richness. For example, the floristic richness of the krummholz scrub (*Pinion mugo*) varied from 86 (the Balkan Mountains) to 450 (the Dinarides), and that of the low juniper scrub (*Juniperion sibiricae*) varied from 45 (the Scardo-Pindic Mountains) to 207 (the Dinarides). In contrast, the lowest geographic variation was recorded for the bog bilberry dwarf heath (*Vaccinion uliginosi*), where the lowest floristic richness of 73 taxa was registered in the Scardo-Pindic mountains and the highest of 96 taxa in the Dinarides (Table 2).

The endemic proportions, however, are completely different (Table 2). In contrast to the share of 21.13% to 22.83% of endemics from level I and level II, at level III the participation of endemics varies from 11.28% to 28.38%. Similar to the floristic richness, all the groups showed significant variation in terms of endemic proportions, and again no pattern could be observed. The greatest variation was recorded for the low juniper scrub (*Juniperion sibiricae*) at between 16.91% (the Dinarides) and 28.38% (the Rhodope Mountains) and the bilberry dwarf heath (*Vaccinion myrtilli*) at between 12.88% (the Dinarides) and 27.87% (the Rhodope Mountains), and the least for the bog bilberry dwarf heath (*Vaccinion uliginosi*) at between 20.99% (the Balkan Mountains) and 25.53% (the Rhodope Mountains).

Centers of floristic richness. The analysis of the centers of floristic richness within the alpine scrub and dwarf heath vegetation revealed three centers distributed in different parts of the Balkan Peninsula (Fig. 2). The first center is scattered from the western-central part of the Balkan Peninsula within the square YJ1 (235 taxa), followed by the square in the central part of the Balkan Peninsula CN1 (223 taxa). At the same time, the highest value is located in the eastern-central part of the Balkan Peninsula, within the square GM1 (250 taxa) (Fig. 2). The second center of diversity is located in the more central part of the Balkan Peninsula, in the squares: DN2 (177 taxa), EM2 (156 taxa), EN3 (154 taxa), DM3 (153 taxa), and DN2 (323 taxa). The lowest number of species were recorded in the squares on the western border (VK3 - 43 taxa), in

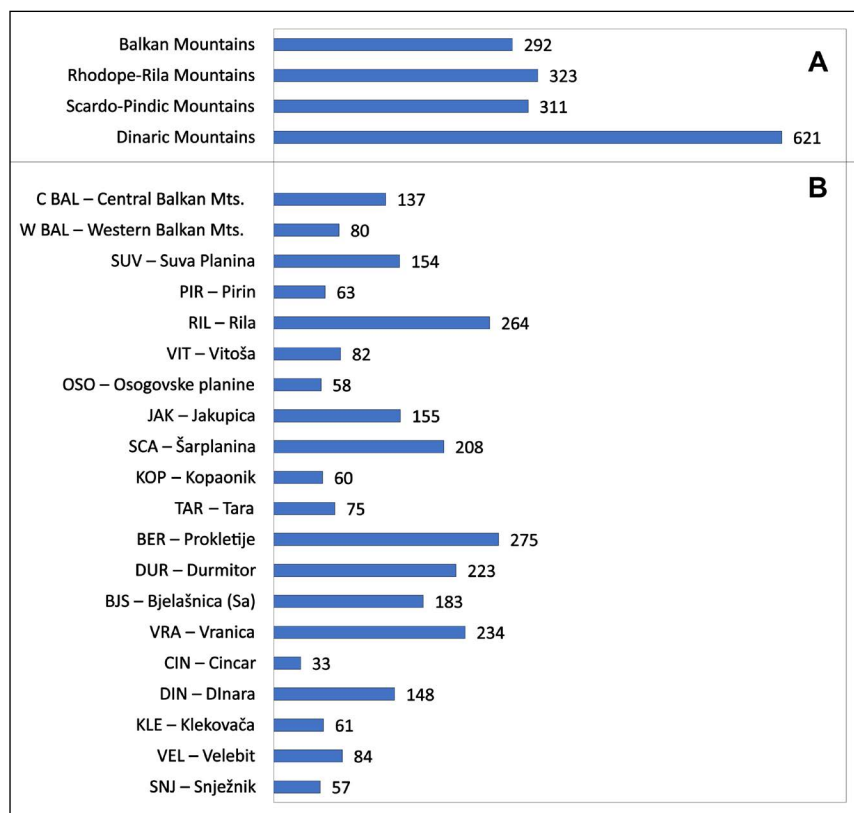


Fig. 3. The number of taxa by mountain systems (A) and mountain groups (B). Country codes: BGR – Bulgaria; BIH – Bosnia and Herzegovina; HRV – Croatia; MKD – North Macedonia; MNE – Montenegro; SRB – Serbia.

the central part in XJ3 (33 taxa) and CP4 (38 taxa), and on the northern border in FP2 (44 taxa). This finding is consistent with the previous findings of BOHN *et al.* (2003) that the formation is relatively uniformly developed in the northern mountains, whereas floristic differentiation increases from north to south, and is mostly pronounced in the central and southern Spanish, central Balkan and Greek mountains, as well as in the Caucasus.

Concerning the mountain systems (Fig. 3A), the largest number of taxa by far are recorded in the Dinaric Mountains (621 taxa) and the smallest in the Balkan Mountains (291 taxa) and the Scardo-Pindic Mountains (311 taxa). In terms of the individual mountain groups, the most species-rich groups are also within the Dinaric system in the Prokletije Mountains (275 taxa), and the Rhodope-Rila system in the Rila mountain range (264 taxa), followed by the mountain groups of Vranica (234 taxa) and Durmitor (223 taxa) in the Dinaric mountain system, and Šarplanina (208) in the Scardo-Pindic mountain system. The lowest number of taxa are recorded in the mountains of Cincar (33 taxa), western Osogovske planine (58 taxa), Kopaonik (60), Klekovača (61 taxa), and Pirin (63) (Fig. 3B). The country codes in Fig. 3 follow the ISO 3166 Standard Country Codes and refer to the mountain territories where the research was conducted, which belong to the present-day states.

Our results confirm previous findings on various aspects of the centers of floristic diversity on the Balkan

Peninsula. Namely, some comparative studies dealing with the distribution and diversity centers of the total flora (STEVANOVIĆ *et al.* 1995), Balkan endemics (STEVANOVIĆ *et al.* 2007; PETROVA & VLADIMIROV 2010; LUBARDA *et al.* 2014; TOMOVIĆ *et al.* 2014; VUKSANOVIĆ *et al.* 2016), Orophytic (STEVANOVIĆ 1996), Arctic-Alpine (STEVANOVIĆ *et al.* 2009), and Boreo-Montane plants (VUKOJIČIĆ *et al.* 2014), have shown that the highest mountains of the central part of the Balkan Peninsula, with altitudes above 2000 m (e.g., Prokletije, Durmitor, Šarplanina, Vranica, Rila) represent the primary centers of floristic diversity. Moreover, our results show certain discrepancies compared to previous findings. Namely, compared to the other highest mountains of the Balkans, which are recognised as centers of diversity, the Pirin, Vitoša, Kopaonik and Stara planina mountains have an unexpectedly low number of species recorded in the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula.

Coenotic and spatial diversification. The principal coordinate analysis (PCoA) showed that the main scrub and heath subtypes (level II) are well differentiated (Fig. 4A). The krummholz scrub (Pinion mugo) located in the positive parts of the first and second axes, and the bog bilberry dwarf heath (*Vaccinium uliginosum*) located in the positive part of the second axis and in the negative part of the first axis, showed the highest level of specificity.

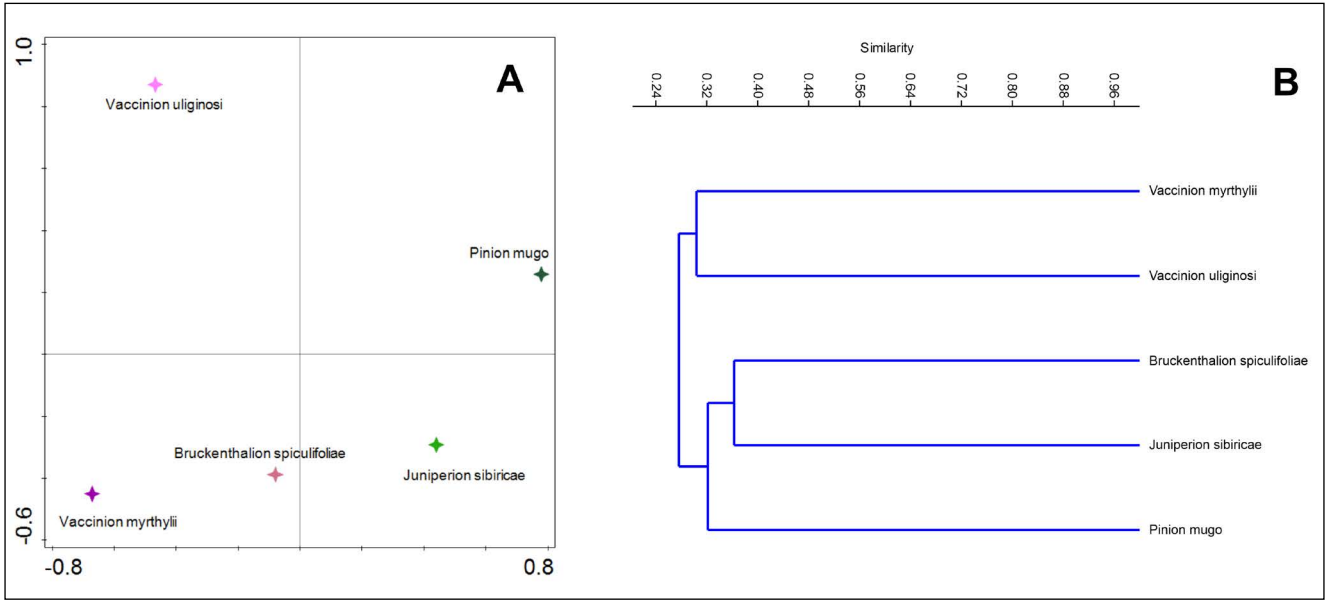


Fig. 4. (A) Principal coordinate analysis (PCoA) for the alpine scrub and dwarf heath subtypes at Level II; (B) Cluster analysis for the alpine scrub and dwarf heath subtypes at Level II.

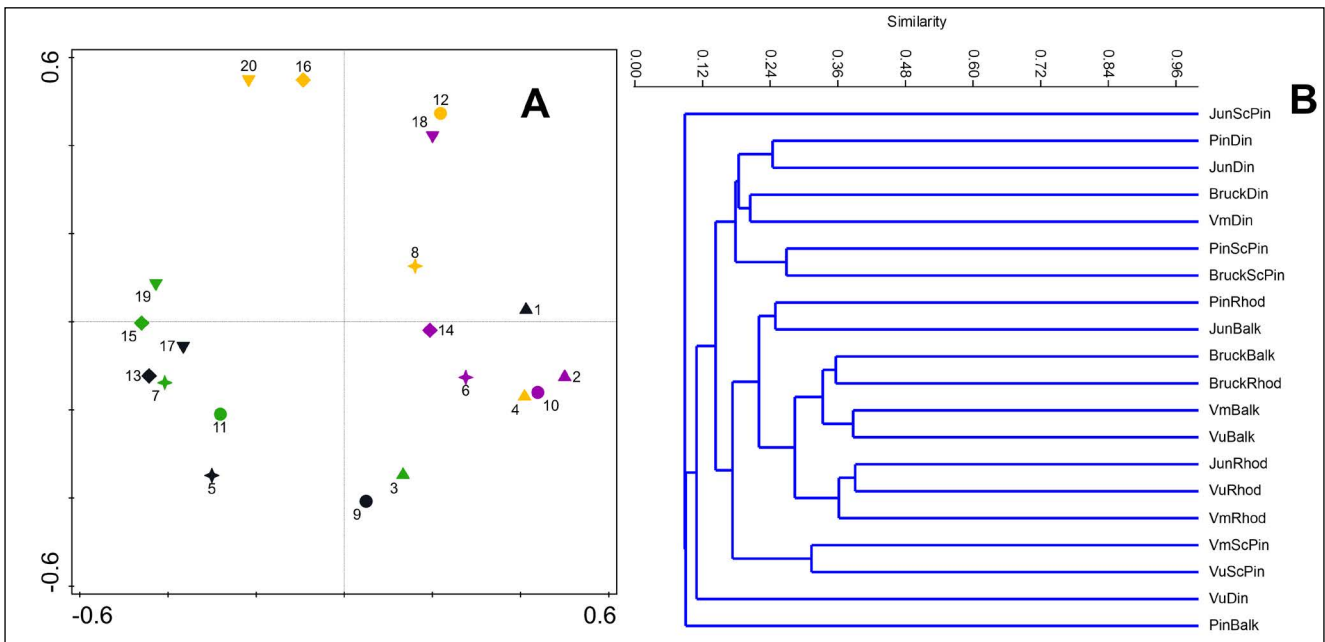


Fig. 5. (A) Principal coordinates analysis (PCoA) for the alpine scrub and dwarf heath sub-types at the regional level (Level III); (B) Cluster analysis for the scrub sub-types at the regional level (Level III). 1 - PinBalk, 2 - PinDin, 3 - PinRhod, 4 - PinScPin, 5 - BruckBalk, 6 - BruckDin, 7 - BruckRhod, 8 - BruckScPin, 9 - JunBalk, 10 - JunDin, 11 - JunRhod, 12 - JunScPin, 13 - VmBalk, 14 - VmDin, 15 - VmRhod, 16 - VmScPin, 17 - VuBalk, 18 - VuDin, 19 - VuRhod, 20 - VuScPin. The group abbreviations correspond to those provided in Table 2.

The low juniper scrub (*Juniperion sibiricae*) is separated along the first axis from the two remaining subtypes, occupying the quadrant bounded by the positive part of the first axis and the negative part of the second axis. The remaining two subtypes are located in different parts of

the quadrant bounded by the negative parts of the first and second axes (Fig. 4A).

Based on the similarity index, which exceeds 50% for all the pairs, the cluster analysis yielded the same relationships as the previous analysis. All the groups are

well-defined floristically, with the most similar pairs being the bilberry dwarf heath (*Vaccinion myrtilli*) and the bog bilberry dwarf heath (*Vaccinion uliginosi*), and the low juniper scrub (*Juniperion sibiricae*) and the *Bruckenthalia* ericoid dwarf heath (*Bruckenthalion spiculifoliae*), while the krummholz scrub (*Pinion mugo*) stands out in a separate clade (Fig. 4B).

The alpine scrubs and dwarf heaths operational units are characterised by unique lists of exclusive taxa - taxa occurring in only one group and not present in any of the other analysed groups (Appendix 1). This further confirms their floristic differentiation. The highest number of exclusive taxa were recorded in the krummholz scrub (*Pinion mugo* - 249 taxa), and the low juniper scrub (*Juniperion sibiricae* - 87 taxa). In the *Bruckenthalia* ericoid dwarf heath (*Bruckenthalion spiculifoliae*) 49 exclusive taxa were recorded, with 40 taxa in the bog bilberry dwarf heath (*Vaccinion uliginosi*), and in the bilberry dwarf heath (*Vaccinion myrtilli*) only 12 taxa were found.

The principal coordinate analysis (PCoA) for the alpine scrubs and dwarf heaths subtypes at the regional level (Level III) revealed two main geographic groups (Fig. 5A). The first group is located in the positive part of the first axis. It consists of most of the alpine scrubs and dwarf heaths of the Dinarides and the Scardo-Pindic Mountains, while the second group consists mainly of the subtypes of the Rhodope and Balkan mountain systems (Fig. 5A). This was confirmed by the cluster analyses (Fig. 5B).

Conservation value of the alpine scrubs and dwarf heaths of the central Balkan Peninsula. The main results of our research, showing that the alpine scrubs and dwarf heaths of the central Balkan Peninsula harbour a large proportion of the regional and global biodiversity, represent a unique biogeographical phenomenon, indicating that these habitats are also of exceptional importance for biodiversity conservation. This is confirmed by the fact that the Habitats Directive of the European Union as the main legal instrument in the field of nature conservation (COUNCIL OF EUROPE 1992), recognises the alpine scrubs and dwarf heaths of the central Balkan Peninsula as EU important habitat types 4060 Alpine and Boreal heaths and 4070 Bushes with *Pinus mugo* and *Rhododendron hirsutum* (*Mugo-Rhododendretum hirsuti*) requiring special measures to ensure the conservation of a wide range of rare, threatened or endemic animal and plant species. Among the species important for protection, the endemics, relicts and threatened species stand out.

In addition to the presence of 126 Balkan endemic and 80 subendemic species and subspecies (Appendix 2) in the alpine scrubs and dwarf heaths of the central Balkans, the results of our study also revealed the presence of 127 relict species (41 glacial, 81 boreal and 5 tertiary

relicts - Appendix 3), which further highlights the specific importance of the biodiversity of this part of the Balkan Peninsula.

Taking all this into account, it is evident that the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula represent significant centers of endemism. These habitats also served as a refugial area for many plants which shifted their ranges during the Pleistocene glaciation (TOMOVIĆ 2007; MAGRI 2008; STEVANOVIĆ *et al.* 2009; TZEDAKIS *et al.* 2013; TOMOVIĆ *et al.* 2014; VUKOJIČIĆ *et al.* 2014). The postglacial migrations from the refugia of the central Balkans were one of the key factors which shaped the present high species richness of various habitats in the Alps and Central Europe (JIMÉNEZ-ALFARO *et al.* 2016; UJHÁZOVÁ *et al.* 2016).

Finally, 5 taxa from the Habitats Directive of the European Union (*Aquilegia kitaibelii*, *Arabis scopoliana*, *Arnica montana*, *Gentiana lutea*, and *Tozzia carpathica*), 2 taxa from Resolution No. 6 of the Bern Convention (COUNCIL OF EUROPE 1998) (*Arabis scopoliana* and *Tozzia carpathica*) and 13 orchids listed in Appendix II of the CITES Convention (2022), including very rare species such as *Coeloglossum viride*, *Gymnadenia odoratissima*, *Nigritella nigra*, and *Pseudorchis albida*, were recorded in these habitat types. This provides further confirmation of the great conservation importance of the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula.

CONCLUSIONS

With 902 taxa recorded in the whole studied area and with 527 species recorded in 180 randomly selected plots of medium size, the alpine scrubs and dwarf heaths of the central part of the Balkan Peninsula represent a considerable species-rich area, placing the alpine regions of the Balkan Peninsula second among the most species-rich alpine regions in the world.

Compared to the estimated values of endemics in other massive European mountain systems, the alpine scrubs and dwarf heaths of the Balkan Peninsula have among the highest values within the mountain ranges in the Mediterranean region, with almost 23% of endemic taxa.

Habitat types which occupy large areas and have high environmental heterogeneity [the krummholz scrub (*Pinion mugo*) and low juniper scrub (*Juniperion sibiricae*)] have significantly higher diversity indicators compared to those habitats covering small areas and with uniform ecological habitat conditions [the bilberry dwarf heath (*Vaccinion myrtilli*) and bog bilberry dwarf heath (*Vaccinion uliginosi*)]. Most of the top hotspots for the alpine scrubs and dwarf heaths in the Central Balkans are registered on limestone or other calcareous bedrock types, which is consistent with the results of the study of the alpha diversity of vascular plants in Europe.

In terms of the mountain systems, the largest number of species by far is recorded in the Dinaric Mountains (621 taxa), while among the individual mountain groups, the most species-rich groups are also found within the Dinaric system in the mountains of the Prokletije (275 taxa).

As the habitats of many important species (endemics, relicts, and nationally and internationally protected species), the alpine scrubs and dwarf heaths of the central Balkan Peninsula are recognised as very important areas for biodiversity conservation.

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Appendix 1. List of the exclusive taxa for the operational units of the analysed alpine scrubs and dwarf heaths on the Balkan Peninsula.

Krummholz scrub (Pinion mugo)

Acer pseudoplatanus, *Achillea ageratifolia* subsp. *aizoon*, *Achillea clavennae*, *Aconitum lycoctonum*, *Aconitum lycoctonum* subsp. *neapolitanum*, *Aconitum lycoctonum* subsp. *vulparia*, *Actaea spicata*, *Agrostis vranicensis*, *Ajuga genevensis*, *Alchemilla glabra*, *Alchemilla reniformis*, *Allium schoenoprasum*, *Alopecurus riloensis*, *Alyssum alpestre*, *Amphoricarpos neumayeri*, *Androsace lactea*, *Androsace villosa*, *Anemone baldensis*, *Angelica sylvestris*, *Anthriscus sylvestris*, *Anthyllis aurea*, *Anthyllis kosaninii*, *Anthyllis vulneraria* subsp. *pulchella*, *Aquilegia bleicicii*, *Aquilegia kitaibelii*, *Arabis alpina* subsp. *alpina*, *Arabis nova*, *Arabis sudetica*, *Arenaria biflora*, *Armeria canescens*, *Armeria rumelica*, *Asplenium cuneifolium*, *Astrantia elatior*, *Asyneuma limonifolium*, *Asyneuma trichocalycinum*, *Barbarea balcana*, *Bellis perennis*, *Blechnum spicant*, *Bornmuellera dieckii*, *Bromus riparius*, *Calamagrostis epigejos*, *Calamagrostis villosa*, *Caltha palustris*, *Campanula trachelium*, *Cardamine bulbifera*, *Cardamine rivularis* auct., *Cardamine trifolia*, *Cardamine waldsteinii*, *Carduus crispus*, *Carex echinata*, *Carex humilis*, *Carex pallescens*, *Centaurea mollis*, *Centaurea phrygia*, *Cerastium arvense* subsp. *strictum*, *Cerastium grandiflorum*, *Cerinthe glabra*, *Cerinthe minor*, *Chaerophyllum hirsutum*, *Chenopodium bonus-henricus*, *Cirsium montanum*, *Cirsium waldsteinii*, *Clematis recta*, *Convallaria majalis*, *Corylus avellana*, *Cryptogramma crispa*, *Daphne alpina*, *Daphne cneorum*, *Daphne oleoides*, *Digitalis viridiflora*, *Doronicum austriacum*, *Doronicum orientale*, *Dorycnium germanicum*, *Draba scardica*, *Dryopteris carthusiana*, *Dryopteris dilatata*, *Dryopteris villarii*, *Edraianthus montenegrinus*, *Epilobium alpestre*, *Epilobium anagallidifolium*, *Epipactis helleborine*, *Eriophorum latifolium*, *Eriophorum vaginatum*, *Eryngium alpinum*, *Erysimum comatum*, *Euphorbia dulcis*, *Euphrasia pectinata*, *Galium aristatum*, *Galium odoratum*, *Galium pumilum*, *Galium schultesii*, *Gentiana lutea* subsp. *lutea*, *Geranium columbinum*, *Geranium pratense*, *Geranium sylvaticum* subsp. *caeruleatum*, *Geum molle*, *Glechoma hirsuta*, *Globularia meridionalis*, *Globularia vulgaris*, *Gymnadenia odoratissima*, *Gymnocarpium dryopteris*, *Gymnocarpium robertianum*, *Heracleum sphondylium*, *Heracleum sphondylium* subsp. *orsinii*, *Heracleum sphondylium* subsp. *sibiricum*, *Hesperis matronalis* agg., *Hieracium bifidum*, *Hieracium cymosum*, *Hieracium marmoreum*, *Hieracium oxyodon*, *Hieracium pseudopilosella*, *Hieracium vulgatum*, *Hippocrepis comosa*, *Hladnikia golaka*, *Hypericum umbellatum*, *Hypochaeris maculata*, *Hypochaeris maculata* subsp. *pelivanoviczii*, *Juncus alpinoarticulatus*, *Juncus monanthos*, *Juniperus sabina*, *Knautia fleischmanii*, *Lamium album*, *Lamium galeobdolon*, *Laser trilobum*, *La-*

serpitium latifolium, *Laserpitium siler*, *Lathyrus alpestris*, *Lathyrus laevigatus*, *Lathyrus niger*, *Leucanthemum rotundifolium*, *Leucanthemum vulgare* agg., *Lilium carnioolicum*, *Linum flavum*, *Lonicera alpigena* s. *formanekiana*, *Lonicera nigra*, *Lonicera xylosteum*, *Luzula alpino-pilosa*, *Luzula forsteri*, *Melampyrum pratense* subsp. *vulgatum*, *Melica uniflora*, *Mercurialis perennis*, *Milium effusum*, *Minuartia bosniaca*, *Minuartia verna*, *Muscari neglectum*, *Myrrhis odorata*, *Onobrychis alba* subsp. *calcareia*, *Onobrychis montana* subsp. *scardica*, *Orobanche caryophyllacea*, *Pancicia serbica*, *Paris quadrifolia*, *Paronychia kapela*, *Pedicularis heterodonta*, *Petasites albus*, *Peucedanum austriacum*, *Peucedanum carvifolia*, *Peucedanum cervaria*, *Physospermum verticillatum*, *Phyteuma spicatum* subsp. *coeruleum*, *Pinus nigra* subsp. *pallasiana*, *Plantago gentianoides*, *Plantago major*, *Plantago reniformis*, *Pleurospermum austriacum*, *Poa hybrida*, *Poa nemoralis*, *Polygala chamaebuxus*, *Polygala croatica*, *Polygonatum multiflorum*, *Potentilla australis*, *Potentilla clusiana*, *Potentilla micrantha*, *Potentilla speciosa*, *Prenanthes purpurea*, *Prunella vulgaris*, *Pulmonaria angustifolia*, *Pulmonaria rubra*, *Pulsatilla vulgaris*, *Pyrola chlorantha*, *Pyrola minor*, *Pyrola rotundifolia*, *Pyrola uniflora*, *Ranunculus lanuginosus*, *Ranunculus polyanthemus* agg., *Rhamnus fallax*, *Rhinanthus angustifolius*, *Ribes petraeum*, *Rosa canina*, *Rosa glauca*, *Rubus hirtus*, *Rumex scutatus*, *Sagina saginoides*, *Salix caprea*, *Salix lapponum*, *Sanicula europaea*, *Saxifraga adscendens*, *Saxifraga androsacea*, *Saxifraga glabella*, *Saxifraga pedemontana* subsp. *cymosa*, *Saxifraga sempervivum*, *Saxifraga stellaris*, *Scilla bifolia*, *Scrophularia nodosa*, *Scrophularia scopolii*, *Scutellaria alpina*, *Sedum album*, *Senecio cacaliaster*, *Senecio erraticus*, *Senecio nemorensis* agg., *Senecio papposus* subsp. *wagneri*, *Senecio thapsoides* subsp. *visianianus*, *Seseli libanotis*, *Sesleria albicans* subsp. *angustifolia*, *Sesleria robusta*, *Silene acaulis*, *Silene alpestris*, *Silene alpina*, *Silene bupleuroides*, *Silene ciliata*, *Silene multicaulis*, *Silene saxifraga*, *Silene vallesia* subsp. *graminea*, *Soldanella dimonieii*, *Sorbus aucuparia* subsp. *aucuparia*, *Sorbus aucuparia* subsp. *glabrata*, *Sorbus austriaca*, *Spiraea chamaedryfolia*, *Stachys recta*, *Stellaria alsine*, *Stellaria glochidisperma*, *Stellaria nemorum*, *Stipa pennata*, *Streptopus amplexifolius*, *Swertia perennis*, *Taraxacum palustre*, *Thalictrum minus*, *Thymus boissieri*, *Tozzia alpina*, *Trifolium noricum*, *Tussilago farfara*, *Valeriana pancicii*, *Verbascum nigrum* subsp. *abietinum*, *Veronica aphylla*, *Veronica orsiniana*, *Veronica serpyllifolia*, *Viburnum lantana*, *Vicia incana*, *Viola reichenbachiana*

Low juniper scrub (Juniperion sibiricae)

Achillea millefolium subsp. *pannonica*, *Achillea stricta*, *Alchemilla alpina*, *Allium melanantherum*, *Alyssum bosniacum*, *Alyssum trichostachyum*, *Arenaria serpyllifolia*, *Arrhenatherum elatius*, *Asperula cynanchica*, *Asperula purpurea*, *Bupleurum ranunculoides*, *Campanula persici-*

folia, *Carduus hamulosus*, *Carduus kernerii* subsp. *scardicus*, *Centaurea kotschyana*, *Centaurea stenolepis*, *Cerastium tomentosum*, *Ceterach officinarum*, *Chaerophyllum aureum*, *Chamaecytisus hirsutus*, *Cirsium acaule*, *Cirsium eriophorum*, *Coronilla varia*, *Crataegus monogyna*, *Crepis alpestris*, *Crocus biflorus*, *Cytisus ciliatus*, *Cytisus nigricans*, *Cytisus rhodopeus*, *Dactylorhiza cordigera*, *Daphne blagayana*, *Dianthus barbatus* subsp. *compactus*, *Dianthus capitatus*, *Dianthus giganteus* subsp. *croaticus*, *Dianthus integer*, *Digitalis grandiflora*, *Erigeron acer*, *Eryngium amethystinum*, *Erysimum carniolicum*, *Euphorbia myrsinites*, *Euphrasia salisburgensis*, *Festuca glauca*, *Festuca valesiaca* agg., *Genista pilosa*, *Gentiana cruciata*, *Gentianella ciliata*, *Gentianella lutescens*, *Geranium robertianum*, *Geum urbanum*, *Helianthemum canum*, *Hippocrepis glauca*, *Huetia cynapioides*, *Inula conyza*, *Koeleria cristata*, *Koeleria macrantha*, *Linum extraaxillare*, *Lychnis atropurpurea*, *Minuartia setacea*, *Myosotis scorpioides*, *Nepeta nuda*, *Onobrychis montana*, *Onosma stellulata*, *Pedicularis oederi*, *Poa compressa*, *Poa pratensis*, *Polygala comosa*, *Potentilla argentea*, *Potentilla heptaphylla*, *Potentilla montenegrina*, *Potentilla recta*, *Potentilla tommasiniana*, *Rhinanthus rumelicus*, *Rosa tomentosa*, *Rubus ulmifolius*, *Scabiosa columbaria* subsp. *portae*, *Sedum hispanicum*, *Senecio jacobaea*, *Spiraea cana*, *Stachys alpina*, *Teucrium chamaedrys*, *Teucrium montanum*, *Thlaspi goesingense*, *Veratrum nigrum*, *Veronica austriaca* subsp. *jacquinii*, *Veronica teucrium*, *Vincetoxicum hirundinaria*, *Viola saxatilis*

Bruckenthalia ericoid dwarf heath (Bruckenthalion spiculifoliae)

Achillea distans subsp. *tanacetifolia*, *Agrimonia eupatoria*, *Alchemilla heterophylla*, *Anemone ranunculoides*, *Aquilegia aurea*, *Asyneuma pichleri*, *Calamintha grandiflora*, *Campanula foliosa*, *Carlina vulgaris*, *Centaurea velenovskyi*, *Cerastium fontanum* subsp. *vulgare*, *Chamaecytisus austriacus*, *Chamaecytisus polytrichus*, *Chamaecytisus pygmaeus*, *Chamaecytisus tommasinii*, *Cirsium arvense*, *Crepis geracioides*, *Dactylorhiza maculata*, *Dactylorhiza sambucina*, *Dianthus cruentus*, *Dianthus superbus*, *Euphrasia montana*, *Fraxinus excelsior*, *Gentianella germanica*, *Geranium lucidum*, *Hypericum barbatum*, *Inula britannica*, *Linaria vulgaris*, *Luzula pindica*, *Lychnis viscaria*, *Orchis tridentata*, *Pedicularis comosa*, *Plantago media*, *Plantago subulata*, *Poa angustifolia*, *Poa perconcinna*, *Polygonum bistorta*, *Primula acaulis*, *Senecio pancicii*, *Silene vulgaris* subsp. *antelopum*, *Silene waldsteinii*, *Sonchus asper*, *Stachys germanica*, *Succisa pratensis*, *Thesium bavarum*, *Thymus pulegioides* subsp. *montanus*, *Trifolium montanum*, *Veronica serpyllifo* subsp. *serpyllifo*, *Viola canina*

Bilberry dwarf heath (Vaccinion myrtilli)

Calluna vulgaris, *Carex brizoides*, *Hypericum ceras-toides*, *Linaria grandiflora*, *Melampyrum hoermannianum*, *Minuartia verna* subsp. *collina*, *Muscari botryoides*, *Phleum hirsutum*, *Poa annua*, *Polystichum aculeatum*, *Pulsatilla alpina*, *Trifolium campestre*

Bog bilberry dwarf heath (Vaccinion uliginosi)

Acer platanoides, *Adenostyles glabra*, *Androsace hedrae-antha*, *Aquilegia nigricans*, *Armeria alpina*, *Asphodelus albus*, *Bartsia alpina*, *Cardamine resedifolia*, *Carex alba*, *Cerastium lanatum* auct., *Cerastium semidecandrum*, *Chamaecytisus albus*, *Cota triumfettii*, *Cotoneaster ne-brodensis*, *Cystopteris montana*, *Edraianthus niveus*, *Helianthemum nummularium* subsp. *glabrum*, *Hieraci-um glaucum*, *Hieracium piloselloides*, *Jasione montana*, *Lathyrus vernus*, *Leontodon montanus*, *Linum austriacum*, *Lotus corniculatus* subsp. *corniculatus*, *Maianthemum bifolium*, *Minuartia recurva*, *Polygonum viviparum*, *Potentilla doerfleri*, *Ranunculus bulbosus*, *Salix hastata*, *Saxifraga bryoides*, *Saxifraga caesia*, *Saxifraga juniperifolia*, *Scleranthus perennis*, *Sedum alpestre*, *Sedum grisebachii*, *Soldanella pusilla*, *Taraxacum alpinum* agg., *Thlaspi ochroleucum*, *Tofieldia calyculata*

Appendix 2. The endemic taxa registered in the operational units of the analysed alpine scrubs and dwarf heaths on the Balkan Peninsula.

Balkan endemic taxa

Acer heldreichii subsp. *visianii*, *Achillea abrotanoides*, *Achillea ageratifolia* subsp. *aizoon*, *Aconitum burnatii* subsp. *pentheri*, *Agrostis vranicensis*, *Alchemilla vel-bitica*, *Allium melanantherum*, *Alopecurus riloensis*, *Alyssum bosniacum*, *Alyssum scardicum*, *Amphoricarpus neumayeri*, *Androsace hedraeantha*, *Anthyllis aurea*, *Aquilegia aurea*, *Aquilegia bleicicii*, *Arabis scopoliana*, *Armeria rumelica*, *Asperula longiflora*, *Athamantha haynaldii*, *Barbarea balcana*, *Bornmuellera dieckii*, *Campanula orbelica*, *Campanula spatulata*, *Asyneuma pichleri*, *Cardamine bulbifera*, *Carduus kernerii* subsp. *scardicus*, *Carex bulgarica*, *Carum graecum*, *Centaurea kotschyana*, *Centaurea velenovskyi*, *Centaurea stoebe* subsp. *serbica*, *Cerastium decalvans*, *Cerastium grandiflorum*, *Cerastium moesiaticum*, *Chamaecytisus tommasinii*, *Cirsium appendiculatum*, *Colchicum macedonicum*, *Crepis geracioides*, *Crocus veluchensis*, *Chamaecytisus tommasinii*, *Dianthus giganteus* subsp. *croaticus*, *Dianthus integer*, *Dianthus microlepis*, *Dianthus tristis*, *Dianthus scardicus*, *Digitalis viridiflora*, *Draba scardica*, *Edraianthus graminifolius*, *Edraianthus montenegrinus*, *Edraianthus niveus*, *Festuca adamovicii*, *Festuca balcanica*, *Festuca riloensis*, *Festuca panciana*, *Festuca bosniaca*, *Festuca valida*, *Gentianella bulgarica*, *Geum bulgaricum*, *Silene pusilla*, *Heracleum sphondylium* subsp. *verticillatum*, *Hieracium marmoreum*, *Hieracium pannosum*, *Hieracium sparsum*, *Hypochaeris illyrica*, *Hypochaeris maculata* subsp. *pelivanovicii*, *Jasione bulgarica*, *Knautia dinarica*, *Knautia midzorensis*, *Knautia sarajevensis*, *Lilium albanicum*, *Lilium bosniacum*, *Lilium carniolicum*, *Lilium jankae*, *Linaria dalmatica*, *Lonicera alpigena* subsp. *formanekiana*, *Lonicera caerulea*, *Melampyrum hoermannianum*, *Melampyrum doerfleri*, *Minuartia bosniaca*, *Myosotis suaveolens*, *Onobrychis montana* subsp. *scardica*, *Onosma stellulata*, *Pancicia serbica*, *Pedicularis brachyodonta* subsp. *grisebachii*, *Pedicularis heterodonta*, *Pedicularis orthantha*, *Peucedanum oligophyllum*, *Phyteuma pseudorbiculare*, *Pinguicula balcanica*, *Pinus peuce*, *Plantago reniformis*, *Polygala croatica*, *Potentilla australis*, *Potentilla doerfleri*, *Potentilla haynaldiana*, *Potentilla montenegrina*, *Primula deorum*, *Bornmuellera dieckii*, *Senecio abrotanifolius* subsp. *Carpathicus*, *Senecio pancicii*, *Senecio thapsoides* subsp. *visianianus*, *Senecio papposus* subsp. *wagneri*, *Sesleria albicans* subsp. *angustifolia*, *Sesleria comosa*, *Sesleria interrupta*, *Sesleria korabensis*, *Sesleria latifolia*, *Sesleria robusta*, *Sesleria filifolia*, *Silene pusilla*, *Silene roemerii*, *Silene sendtneri*, *Silene waldsteinii*, *Soldanella dimonieii*, *Spiraea cana*, *Thlaspi ochroleucum*, *Thymus praecox* subsp. *zygiformis*, *Thymus jankae*, *Trifolium medium* subsp. *balcanicum*, *Valeriana pancicii*, *Verbascum*

nicolai, *Veronica rhodopaea*, *Viola elegantula*, *Viola latise-pala*, *Viola macedonica*, *Viola saxatilis*.

Balkan sub-endemic taxa

Achillea lingulata, *Achillea clusiana*, *Alchemilla heterophylla*, *Anemone baldensis*, *Aquilegia kitaibelii*, *Armeria canescens*, *Asyneuma limonifolium*, *Asyneuma trichocalycinum*, *Campanula abietina*, *Campanula foliosa*, *Campanula sparsa*, *Cardamine waldsteinii*, *Carduus hamulosus*, *Carex kitaibeliana*, *Centaurea napulifera*, *Cerastium banaticum*, *Chamaecytisus absinthioides*, *Chamaecytisus austriacus*, *Chamaecytisus pygmaeus*, *Cirsium waldsteinii*, *Crepis dinarica*, *Crepis viscidula*, *Daphne blagayana*, *Dianthus barbatus* subsp. *compactus*, *Dianthus cruentus*, *Draba lasiocarpa*, *Erysimum comatum*, *Huetia cynapioides*, *Gentianella crispata*, *Gentianella crispata*, *Geranium sylvaticum* subsp. *caeruleatum*, *Geum coccineum*, *Geum molle*, *Heracleum sphondylium* subsp. *orsinii*, *Homogyne discolor*, *Homogyne sylvestris*, *Hypericum umbellatum*, *Jasione laevis* subsp. *orbiculata*, *Jovibarba heuffelii*, *Leontodon croceus* subsp. *milaensis*, *Linum capitatum*, *Moehringia pendula*, *Rhamnus fallax*, *Pedicularis friderici-augusti*, *Pedicularis petiolaris*, *Plantago gentianoides*, *Poa media*, *Potentilla aurea* subsp. *chrysocraspeda*, *Potentilla clusiana*, *Pulmonaria rubra*, *Ranunculus breyninus*, *Rhamnus fallax*, *Rhinanthus rumelicus*, *Rhododendron hirsutum*, *Rhododendron myrtifolium*, *Salix waldsteiniana*, *Salix silesiaca*, *Saxifraga glabella*, *Saxifraga pedemontana* subsp. *cymosa*, *Saxifraga juniperifolia*, *Saxifraga sempervivum*, *Scabiosa columbaria* subsp. *portae*, *Scabiosa silenifolia*, *Sedum grisebachii*, *Jovibarba heuffelii*, *Sempervivum marmoreum*, *Jovibarba heuffelii*, *Seseli rigidum*, *Sesleria coerulans*, *Silene alpestris*, *Silene vulgaris* subsp. *bosniaca*, *Silene ciliata*, *Thlaspi kovatsii*, *Thlaspi goesingense*, *Tozzia alpina*, *Trifolium noricum*, *Verbascum longifolium* subsp. *pannosum*, *Viola dacica*, *Viola calcarata* subsp. *zoysii*, *Wulfenia carinthiaca*.

Appendix 3. The relict taxa registered in the operational units of the analysed alpine scrubs and dwarf heaths on the Balkan Peninsula.

Glacial relicts

Alchemilla alpina, *Alchemilla glabra*, *Arabis alpina*, *Arctostaphylos alpinus*, *Aster alpinus*, *Bartsia alpina*, *Carex atrata*, *Cerastium alpinum* s.str., *Cryptogramma crispa*, *Cystopteris montana*, *Dryas octopetala*, *Empetrum hermaphroditum*, *Empetrum nigrum*, *Epilobium anagallidifolium*, *Gnaphalium supinum*, *Hieracium bifidum*, *Juncus trifidus*, *Luzula spicata*, *Luzula spicata* subsp. *Italica*, *Luzula sudetica*, *Minuartia verna*, *Minuartia verna* subsp. *collina*, *Nigritella nigra*, *Pedicularis oederi*, *Pedicularis verticillata*, *Persicaria alpina*, *Persicaria vivipara*, *Phleum alpinum*, *Poa alpina*, *Potentilla crantzii*, *Pseudorchis albida*, *Sagina saginoides*, *Salix hastata*, *Salix herbacea*, *Salix lapponum*, *Saxifraga adscendens*, *Saxifraga aizoides*, *Saxifraga paniculata*, *Saxifraga stellaris*, *Silene acaulis*, *Viola biflora*.

Boreal relicts

Adoxa moschatellina, *Ajuga pyramidalis*, *Alchemilla glaucescens*, *Allium schoenoprasum*, *Alnus incana*, *Antennaria dioica*, *Arctostaphylos uva-ursi*, *Asplenium ruta-muraria*, *Asplenium viride*, *Athyrium filix-femina*, *Avenella flexuosa*, *Betula pubescens*, *Blechnum spicant*, *Botrychium lunaria*, *Caltha palustris*, *Cardamine pratensis*, *Carex echinata*, *Carex flava*, *Carex ornithopoda*, *Cerastium arvense*, *Chamaenerion angustifolium*, *Cicerbita alpina*, *Coeloglossum viride*, *Corallorrhiza trifida*, *Dianthus superbus*, *Dryopteris carthusiana*, *Dryopteris dilatata*, *Dryopteris expansa*, *Epilobium palustre*, *Epipogium aphyllum*, *Equisetum hyemale*, *Equisetum sylvaticum*, *Eriophorum latifolium*, *Eriophorum vaginatum*, *Filipendula ulmaria*, *Galium boreale*, *Geum rivale*, *Goodyera repens*, *Gymnocarpium dryopteris*, *Gymnocarpium robertianum*, *Hieracium umbellatum*, *Juncus alpinoarticulatus*, *Juniperus communis* subsp. *alpina*, *Listera cordata*, *Maianthemum bifolium*, *Milium effusum*, *Molinia caerulea*, *Moneses uniflora*, *Orthilia secunda*, *Parnassia palustris*, *Persicaria bistorta*, *Phegopteris connectilis*, *Picea abies*, *Pinus sylvestris*, *Polygonum bistorta*, *Polystichum aculeatum*, *Polystichum lonchitis*, *Polytrichum commune*, *Polytrichum formosum*, *Populus tremula*, *Pyrola chlorantha*, *Pyrola media*, *Pyrola minor*, *Pyrola rotundifolia*, *Pyrola uniflora*, *Ribes alpinum*, *Rubus idaeus*, *Rubus saxatilis*, *Salix pentandra*, *Sanguisorba officinalis*, *Sorbus aucuparia* subsp. *glabrata*, *Sorbus lanuginosa*, *Stellaria alsine*, *Stellaria palustris*, *Thelypteris limbosperma*, *Thelypteris palustris*, *Trollius europaeus*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Viola rupestris*.

Tertiary relicts

Asarum europaeum, *Daphne alpina*, *Daphne blagayana*, *Daphne cneorum*, *Daphne oleoides*.

REZIME

Botanica
SERBICA

Alpski žbunjaci i patuljaste vrištine centralnog dela Balkanskog poluostrva – jedinstveni centar florističkog bogatstva i endemizma

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Alpski žbunjaci (*Rosa pendulinae-Pinetea mugo*) i patuljaste vrištine (*Loiseleurio procumbentis-Vaccinietea*) predstavljaju jedinstvenu florističku celinu koja značajno doprinosi ukupnom diverzitetu na Balkanskom poluostrvu. Glavni edifikatori ovih tipova staništa su uglavnom glacijalni relikti arktičkog, alpskog i borealnog porekla, što dodatno naglašava njihov značaj za očuvanje biodiverziteta. Imajući ovo na umu, istražili smo njihovo taksonomsko bogatstvo i raznovrsnost, karakteristike endemizma, obrasce prostorne distribucije, cenotičku i prostornu diverzifikaciju i horološke spektre i spektre životnih formi koristeći sveobuhvatan skup od 15.609 podataka o nalazima vrsta. Analize su sprovedene na tri hijerarhijska nivoa koji predstavljaju ekološku i geografsku raznovrsnost ovih tipova staništa. Rezultati istraživanja su pokazali da je u alpijskim žbunjacima i patuljastim vrištinama centralnog Balkana registrovano čak 902 taksona, i to 829 vrsta i 73 podvrste, kao i da je udeo endemita od ca. 22% u ovim staništima izuzetno visok. Dodatno, uočene su značajne regionalne razlike u sastavu vrsta na istraživanom području, pri čemu se florističko bogatstvo i diverzitet povećava od severa ka jugu.

Ključne reči: florističko bogatstvo, endemiti, životne forme, areal tipovi, alpski žbunjaci i patuljaste vrištine, Balkansko poluostrvo

