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Balkan endemic vascular plants of Montenegro – critical inventory with chorological and life-form analyses

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Abstract: Balkan endemic taxa are those whose distribution is restricted exclusively to the Balkan Peninsula. In the vascular flora of Montenegro there are 372 Balkan endemic taxa (at the species and subspecies levels), of which 39 taxa are distributed only in Montenegro. This paper presents an overview of the Balkan endemic taxa in Montenegro with their families, chorological groups, life-form categories and distribution by geographical subregion. The richest families in terms of Balkan endemic taxa are *Asteraceae* and *Caryophyllaceae*, while the richest genus is *Hieracium* (*Asteraceae*). The chorological structure of the flora shows that the largest numbers of Balkan endemic taxa are from the S European mountain and C European mountain chorological groups, while in the life-form spectrum of the flora hemicryptophytes and chamaephytes are the most numerous. The presence of Balkan endemic taxa in the six geographical subregions of Montenegro is also analysed. Floristic similarities among the geographical subregions are shown with a cluster analysis.

Key words: Balkan Peninsula, Montenegro, endemism, vascular plants, checklist, systematics, chorology, life form

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Introduction

The term "endemic" has many definitions and it is very differently understood due to a lack of uniform criteria for a more precise definition (Tomović 2007). One of these defines an endemic as "that which occurs nowhere except in the place in question" (Darlington 1957). According to Dihoru & Pârvu (1987), endemics are taxonomic units of different ranks, limited in their distribution to a determinate territory (province, region, district, etc.). The phenomenon of endemism characterizes those taxa whose distribution is restricted to a certain area and is more reduced than that of other taxa of the same rank (Vischi & al. 2004).

Balkan endemic taxa are those that are distributed only in the Balkan Peninsula (Turrill 1929; Strid & Tan 1997; Tomović & al. 2014). The Balkan Peninsula (or "the Balkans") is defined as the territory limited by the Danube and Sava rivers in the north, the Soča (or Isonzo) river in the northwest, the Black Sea in the east, the Aegean and Ionian seas in the south, and the Adriatic Sea

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in the west. Although an exhaustive list of the flora of all the Balkan countries has not yet been completed, it is estimated that the vascular flora of the Balkans today includes about 8000 species and subspecies (Stevanović 2005), while the number of endemic species and subspecies is estimated at between 2600 and 2700 (Stevanović & al. 2007).

The flora of Montenegro has been the subject of study for nearly 200 years, during which more than 3000 papers have been published by over 1000 authors (Pulević 2006). However, much credit for the exploration of the flora of Montenegro goes to the Czech botanist, Josef Rohlena, whose *Conspectus florae montenegrinae* (Rohlena 1942) remains to this day the most complete work on the flora of Montenegro. The *Conspectus* includes 2623 species and 194 subspecies of vascular plants, which makes a total of 2817 taxa. According to Stevanović & al. (1995), the vascular flora of Montenegro consists of 3136 species and subspecies and, when disputed taxa are also included, that number reaches 3336. Data that were not included in Rohlena's *Conspectus* for various reasons, as well as the findings of botanists after World War II, were integrated in the supplement to the *Conspectus* (Pulević 2005). Based on the data collected so far, it is estimated that the flora of Montenegro includes more than 3600 species and subspecies (Stešević & Caković 2013). The richness and diversity of this flora in a relatively small area of 13 812 km^2 can be explained by the position of Montenegro in the Balkans, the complex orography, diverse climatic elements, a heterogeneous land cover and the turbulent geological and biological history that the flora of the Balkan Peninsula has undergone (Stevanović & al. 1995).

Despite numerous floristic and taxonomic papers having been published, no detailed study of the Balkan endemic flora in Montenegro has been conducted so far. According to Blečić (1958), who was referring to Turrill (1929) and who also included later data, the flora of Montenegro includes 220 taxa (species and subspecies) endemic to he Balkan Peninsula and 20 taxa endemic to Montenegro. According to Stevanović & al. (1995), the flora of Montenegro includes 223 Balkan endemic taxa accounting for 11.7 % of the total flora of the country. In addition, papers on Balkan endemic taxa found in Montenegro for the first time have been published recently by the following authors: Stevanović & Lakušić (2006), Stešević & al. (2007), Stešević & Drescher (2010) and Caković & al. (2014); and papers on newly described endemic taxa, which have mostly resulted from the revision of certain genera, have been published by the following authors: Bräuchler & Cikovac (2007), Niketić & Stevanović (2007), Schönswetter & Schneeweiss (2009), Surina & al. (2009), Kučera & al. (2010), Mereďa & al. (2011), Lakušić & al. (2013), Šingliarová & al. (2013), Janković & al. (2016) and Tomović & al. (2016).

The aim of this study is to present quantitative data on the floristics (a critical inventory), chorology (chorological groups) and life forms of the Balkan endemic vascular flora of Montenegro. We also aim to determine the degree of floristic similarity between geographical subregions of the country.

Material and methods

Study area

Montenegro is located in the SW part of the Balkan Peninsula at the crossroads of two major geographical units: the Dinaric Alps and the Mediterranean Sea. The coastal belt of Montenegro belongs to the Mediterranean, with the Adriatic coastline extending for 316 km (Fuštić & Đuretić 2000). Directly above the sea a range of the coastal Dinaric Alps rises and stretches farther back as a deep karst plateau. This area of high mountains intersected by river canyons and gorges stretches over an area to the north and east that belongs to the Adriatic and Black Sea (Danube) river system. The mountainous part of Montenegro covers the majority of the country with an elevational range from 700 m to high-mountain peaks above 2500 m. The continental part of the country lies in the northeast. It is a hilly and mountainous area intersected by the valleys of numerous large and small rivers (Fuštić & Đuretić 2000).

In Montenegro three main climatic zones can be distinguished: (1) Mediterranean; (2) temperate continental; and (3) mountain (Horvat & al. 1974). The Mediterranean climate in the narrow sense is restricted to the coastal region of the Adriatic Sea, and along the slopes of the Dinaric Alps up to an elevation of 300–400 m. The modified Mediterranean climate or the submediterranean perhumid variant is present at elevations above 400 m and deeper inland in the gorges and canyons as well as in some valleys exposed to Mediterranean influences. The modified Mediterranean climate in Montenegro belongs to the perhumid variant due to high annual precipitation of between 1500 and 2200 mm. The temperate continental climate is characteristic in the NW, N and E parts of Montenegro. In the mountains in the area of temperate continental climate, two subtypes of mountain climate can be distinguished: (3a) the perhumid Mediterranean-submediterranean mountain climate with a precipitation of over 4500 mm, pronounced in the coastal Dinaric Alps of Montenegro; and (3b) a humid mountain climate of the alpine type, characteristic of the mountains of the NW, N and E of Montenegro (Stevanović & Stevanović 1995).

According to the *Conspectus of classes of European vegetation* (Mucina 1997), the following vegetation types and classes are present in Montenegro: (1) aquatic vegetation (*Lemnetea*, *Charetea fragilis*, *Potametea*, *Ruppietea maritimae*, *Zosteretea*); (2) vegetation of freshwater marshes and fens (*Isoëto-Littorelletea*, *Isoëto-Nanojuncetea*, *Montio-Cardaminetea*, *Phragmito-Magnocaricetea*, *Scheuchzerio-Caricetea fuscae*); (3) coastal vegetation (*Cakiletea maritimae*, *Crithmo-Stati-*

Fig. 1. Geographical subregions of Montenegro (modified after Stešević & Caković 2013). – C: central; E: eastern; M: Mediterranean; N: northern; SM: submediterranean; W: western.

cetea, *Thero-Salicornietea*, *Salicornietea fruticosae*, *Juncetea maritimi*, *Ammophiletea*); (4) chasmophytic vegetation (*Asplenietea trichomanis*, *Adianthetea capilli-veneris*, *Epipetrea lichenosa*, *Thlaspietea rotundifolii*); (5) arctic and alpine vegetation (*Loiseleurio-Vaccinietea*, *Salicetea herbaceae*, *Juncetea trifidi*, *Carici rupestris-Kobresietea bellardii*, *Elyno-Seslerietea*, *Mulgedio-Aconitetea*); (6) synanthropic vegetation (*Bidentetea tripartiti*, *Polygono arenastri-Poetea annuae*, *Stellarietea mediae*, *Artemisietea vulgaris*, *Galio-Urticetea*, *Epilobietea angustifolii*); (7) temperate heathlands and grasslands (*Calluno-Ulicetea*, *Koelerio-Corynephoretea*, *Molinio-Arrhenatheretea*, *Trifolio-Geranietea sanguinei*, *Festuco-Brometea*); (8) temperate and boreal woodlands and scrub (*Rhamno-Prunetea*, *Salicetea purpureae*, *Alnetea glutinosae*, *Populetea albae*, *Franguletea*, *Querco-Fagetea*, *Quercetea pubescentis*, *Quercetea roboris*, *Erico-Pinetea*, *Vaccinio-Piceetea*); (9) oromediterranean grasslands and scrub (*Daphno-Festucetea*); and (10) Mediterranean vegetation (*Thero-Brachypodietea ramosi*, *Helianthemetea guttati*, *Cisto cretici-Micromerietea julianae*; *Euphorbietea dendroidis*, *Nerio-Tamaricetea*, *Quercetea ilicis*).

Selection of taxa

"Taxa" are here counted as species and subspecies. A species with no or one subspecies is counted as one taxon, while a species with two subspecies is counted as two taxa, and so on. A checklist of Balkan endemic vascular plant taxa in Montenegro was made based on data from studies on floristics, taxonomy, morphology, phytocoenology and karyology. The *Conspectus florae montenegrinae* (Rohlena 1942) and its supplement (Pulević 2005) and the catalogue of the vascular flora of Montenegro (Stešević & Caković 2013) were used as the basis for the inventory.

Taxonomy and nomenclature follow contemporary checklists and Floras (Tutin & al. 1964–1980, 1993; Jalas & Suominen 1972–1994; Greuter & al. 1984–1989; Jalas & al. 1996, 1999; Strid & Tan 1997; Kurtto & al. 2004, 2007; Greuter & Raab-Straube 2008), online databases (IOPI 1996–2007; Euro+Med 2006+; The Plant List 2013; IPNI 2013+) and in some cases older basic floras (Pančić 1875; Rohlena 1942).

Data analysis

To define the chorological groups, the methods of Meusel & al. (1965, 1978), Meusel & Jäger (1992) and Stevanović (1992) were used, modified and adapted to Montenegro as proposed by Tomović & al. (2014). The taxa were classified into the following chorological groups: central European mountain (CEM); southern European mountain (SEM); Mediterranean-submediterranean (MED-SUBMED); central European (CEUR); and Pontic (PONT).

The classification of taxa as particular life forms is based on the Raunkiaer (1934) system, supplemented by Mueller-Dombois & Ellenberg (1974) and modified by Stevanović (1992). The taxa were classified as phanerophytes (P), chamaephytes (Ch), hemicryptophytes (H), geophytes (G), and therophytes (T).

The geographical regionalization was conducted according to Marković (1970) and Stešević & Caković (2013) with some minor modifications (Fig. 1). Consequently, Montenegro is divided into two regions – maritime and mountain – and six subregions. Within the maritime region there are two subregions: Mediterranean (M) and submediterranean (SM); within the mountain region there are four subregions: central (C); eastern (E); northern (N); and western (W). The distribution of Balkan endemic taxa within each of these geographical subregions was established.

The clustering method based on Sørensen distances and the unweighted pair-group average hierarchical sorting strategy (unweighted pair-group method with the arithmetic mean) was used for identification of the hierarchical floristic similarities among the six geographical subregions. The cluster analysis was performed using the package Statistica 5.1 by StatSoft (http://www.statsoft.com/).

Results

The total number of vascular plant taxa that meet the criteria of Balkan endemics according to Turrill (1929) and Strid & Tan (1997) is 372 (Table 1, see Supplemen-

tary Material online), which is equivalent to 10.4 % of the total vascular flora of Montenegro. The Balkan endemic taxa in the study area have been classified into 46 families and 147 genera. Pteridophytes have no endemic representatives, while gymnosperms are represented by only one taxon (*Pinus peuce* Griseb.). Angiosperms make up 99.7 % of the Balkan endemic taxa. The Balkan endemic flora of Montenegro has no endemic families, but there is one unispecific Balkan endemic genus: *Petteria* C. Presl (*Fabaceae*). The families richest in Balkan endemic taxa (Fig. 2) are *Asteraceae* with 108 taxa, followed by *Caryophyllaceae* with 34 taxa, while the richest genus (Fig. 3) is *Hieracium* (*Asteraceae*) with 71 taxa.

The chorological spectrum (Fig. 4) shows that almost two-thirds of the Balkan endemic taxa are made up of orophytes, which belong to two chorological groups: the S European mountain group (145 taxa, 39.0 %) and the C European mountain group (100 taxa, 26.9 %). Thus, we can state that mountain and alpine endemism dominates the flora of Montenegro. A proportionally large number of taxa (81, 21.8 %) is represented by the Mediterranean-submediterranean chorological group, which is an indicator of the strong Mediterranean and submediterranean influences deep into the interior of the country. The C European chorological group is represented by 45 taxa (12.1 %), mostly represented by elements of C European deciduous forests. The Pontic group is represented by only one taxon: *Stipa joannis* subsp. *balcanica* Martinovský (*Poaceae*).

Analysis of the life-form spectrum (Fig. 5) indicates hemicryptophytes are prevalent with 234 Balkan endemic taxa (62.9 %), followed by chamaephytes (88 taxa, 23.7 %), geophytes (22 taxa, 5.9 %), therophytes (19 taxa, 5.1 %) and phanerophytes (nine taxa, 2.4 %).

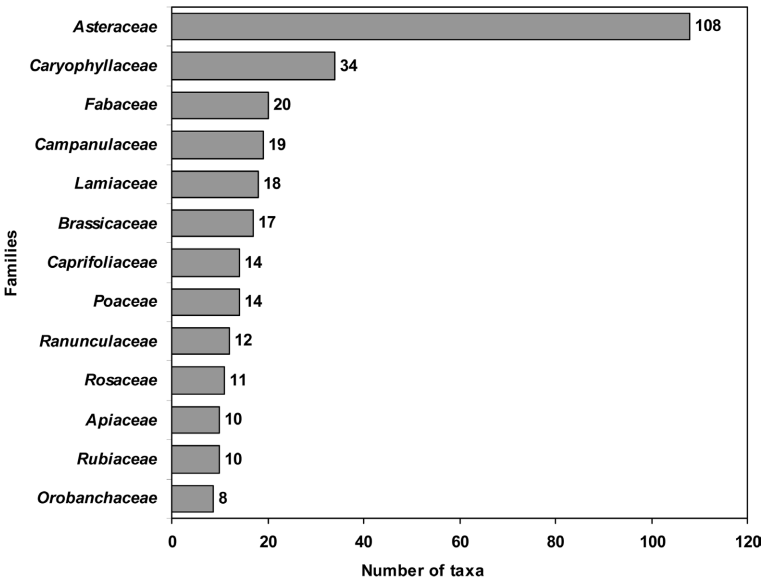

Fig. 2. Taxon richness at the family level in the Balkan endemic vascular flora of Montenegro.

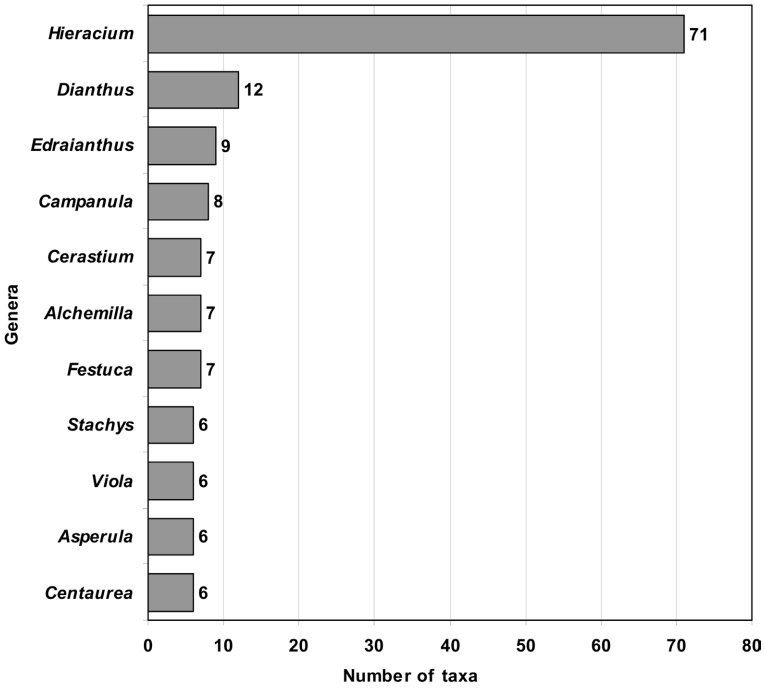

Fig. 3. Taxon richness at the genus level in the Balkan endemic vascular flora of Montenegro.

The largest number of Balkan endemic taxa is recorded in the eastern (224) and northern (205) geographical subregions (Fig. 6). A large number is also present in the submediterranean (162) and western (94) subregions. The central and Mediterranean subregions are characterized by a relatively small number of taxa (60 and 57, respectively).

Cluster analysis of the floristic similarities between the six geographical subregions of Montenegro based on the presence of Balkan endemic taxa (Fig. 7) permits the identification of two groups of subregions. The first group comprises the eastern and northern subregions and is well differentiated as a result of the largest number of Balkan endemic taxa occurring therein. The second group comprises the submediterranean and western subregions, between which the close phytogeographical connection is obvious, because both are geographically close to each other and both share a similar climate as well as ecological and floristic features. The central subregion shows some floristic, climatic, geological and ecological similarities with the four aforementioned subregions, whereas the Mediterranean subregion stands

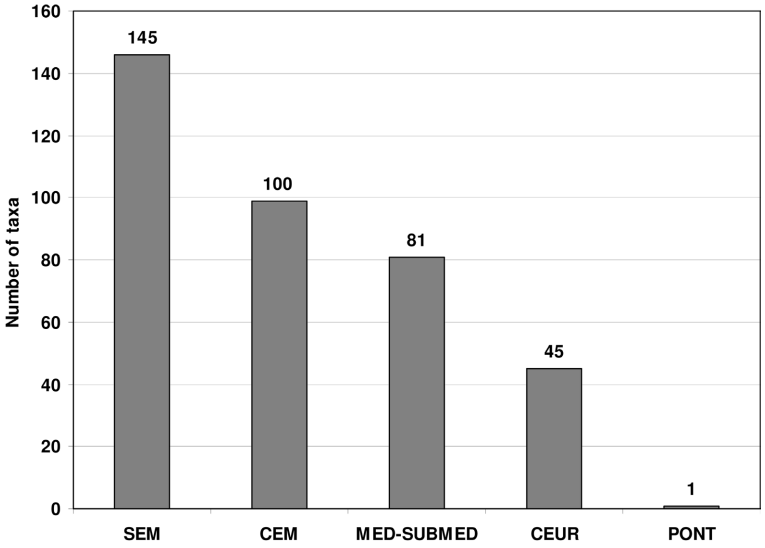

Fig. 4. Spectrum of chorological groups in the Balkan endemic vascular flora of Montenegro. – SEM: southern European mountain; CEM: central European mountain; MED-SUBMED: Mediterranean-submediterranean; CEUR: central European; PONT: Pontic.

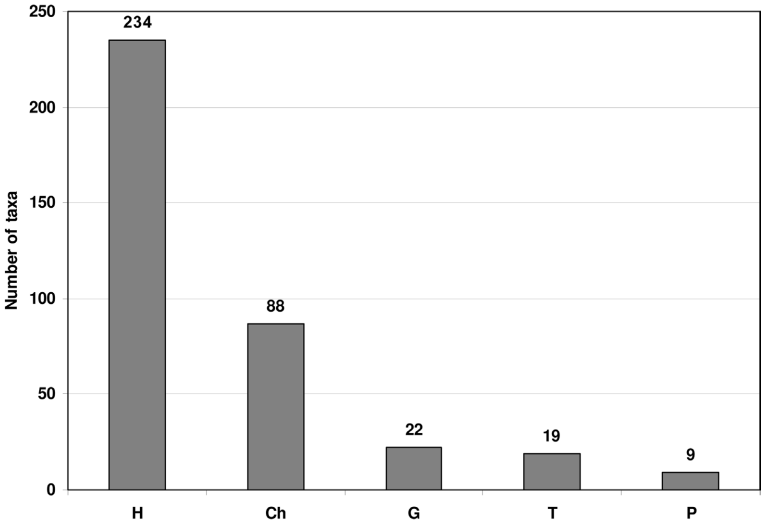

Fig. 5. Spectrum of life forms in the Balkan endemic vascular flora of Montenegro. – H: hemicryptophytes; Ch: chamaephytes; G: geophytes; T: therophytes; P: phanerophytes.

separately as a result of its poor Balkan endemic flora compared to that of the mountain subregions.

Discussion

The floristic analysis of Balkan endemic taxa singled out some families that represent an important contribution to the flora of the Mediterranean basin. *Asteraceae* are the largest family in the area stretching from N Europe to the Mediterranean, over which range the taxonomic diversity of the family increases from north to south (Stevanović & al. 1995). The families *Caryophyllaceae* and *Brassicaceae* have a large number of genera in the Mediterranean basin (Heywood & al. 2007), and the Mediterranean is also a centre of diversity for the families *Campanulaceae* (Kovačić 2004) and *Lamiaceae* (Heywood & al. 2007). *Campanulaceae*, with a large number of Balkan endemic taxa in Montenegro (19), occupies fourth place, which suggests strong influences from the Mediterranean climate, despite the high-mountain barriers (Stevanović & al. 1995). Also, the 10 to 12 families richest in Balkan endemic taxa more or less coincide with those in Greece (Georghiou & Delipetrou 2010), Bosnia and Herzegovina (Lubarda & al. 2014) and the regions of C Serbia and Kosovo (Tomović & al. 2014). The main differences between these four regions are noted in the number of Balkan endemic taxa that belong to, e.g., *Rubiaceae* (a higher ranking in Greece), *Poaceae* (lower ranking in Montenegro), *Lamiaceae* (higher ranking in Bosnia and Herzegovina) and *Campanulaceae* (lower ranking in C Serbia and Kosovo).

In the chorological spectrum of the Balkan endemic flora of Montenegro, S European mountain and C European mountain taxa are predominant, and these together account for just about two-thirds of the Balkan endemic flora. The explanation for such a pronounced predominance of orophytic elements lies in the mountain and high-mountain areas of Montenegro being centres of florogenesis and of refugees from the orophytic flora of C and S Europe (Stevanović 1996a; Tomović & al. 2014). The Pleistocene periods of glaciation, and especially interglaciation, enabled a more or less unrestricted migration of species and the exchange of indigenous elements between the high-mountain flora of the Dinaric Alps and the Balkan mountains, and the Alps and the Carpathians (Kramp & al. 2008; Schmitt & Haubrich 2008; Huck & al. 2009; Stachurska-Swakon & al. 2013; Surina & al. 2014). Parallel to these processes, speciation occurred (in the indigenous Tertiary oromediterranean and newly coming Alpine/Carpathian floras) due to the separation between the mountains creating genetically isolated populations (Stevanović & Lakušić 1996; Stefanović & al. 2008; Surina & al. 2009; Kučera & al. 2010; Mereďa & al. 2011; Lakušić & al. 2013; Janković & al. 2016).

A high percentage of Balkan endemic taxa belong to the Mediterranean-submediterranean chorological group as a result of the presence of a large number of xerophytic and thermophytic habitats in the Mediterranean, submediterranean, central and western subregions of Montenegro. As thermophytic ecological elements, the Balkan endemic members of this chorological group are also

present in the mountain massifs of the eastern and northern subregions of Montenegro, usually in the lowest mountain belt on the S slopes of mountains, and also in river canyons under the influence of the Mediterranean climate. Furthermore, the more intense impact of anthropogenic factors has caused the spread of secondary vegetation types (xerophytic grass and shrub communities) at the expense of the primary forest and shrub vegetation. This has allowed the endemic taxa belonging to the Mediterranean-submediterranean chorological group to penetrate deeper into the continental part of Montenegro, as identified by Turrill (1929), and has thus caused an increase in the number of Balkan endemic taxa in this area. This phenomenon was also demonstrated by Zlatković & al. (2011) for some Mediterranean taxa that had extended their occurrence deep into the C part of the Balkan Peninsula (Serbia) from the N part of the Republic of Macedonia.

The Balkan endemic taxa that inhabit broad-leaved forests and mesophytic meadows in the W and C parts of the Balkan Peninsula belong to the C European chorological group (Tomović & al. 2014). They are less important contributors to the chorological spectrum of Balkan endemic flora in Montenegro.

The life-form spectrum of floras reflects the basic features of habitats as well as the continuum of changes in time and is the result of adaptation during the evolution of species (Stevanović & Janković 2001). Most holarctic plants or plants of the temperate zone, and of the Balkan Peninsula, belong to the life-form category of hemicryptophytes. In addition, hemicryptophytes and chamaephytes inhabit hill and mountain areas, and over 80 % of the territory of Montenegro is represented by hills and mountains. The high percentage of chamaephytes (as many as 23.4 %) inhabiting high-mountain and cold habitats, river canyons and gorges attests to the abundance of these habitats. Endemic chamaephyte dwarf shrubs are also present in the submediterranean subregion of Montenegro, where they usually inhabit thermophytic limestone rocks and rocky ground. Perennials that develop in such habitats are usually resistant to drought and are characterized by slow growth (Larson & al. 2000).

The geophytes in the life-form spectrum of the Balkan endemic flora of Montenegro inhabit thermophytic and xerophytic habitats (Mediterranean and temperate woodlands and scrub, as well as rocky ground) of the submediterranean and western subregions, but are mostly present in the high-mountain areas of the eastern and northern subregions (on rocky ground, screes, high-mountain grasslands and wet meadows).

The therophytes in the life-form spectrum predominantly inhabit the Mediterranean and submediterranean areas of Montenegro. Annual plants mainly inhabit low-productivity habitats, such as dry meadows and rocky ground, where they are exposed to droughts of greater or lesser intensity during the summer, as well as habitats that are frequently exposed to anthropogenic and natural distortions (Noble & Slatyer 1980). The number of therophytes present in the high-mountain regions of Montenegro is proportionally lower, while their presence can be explained by Mediterranean influences that penetrate deep into the interior of the country through

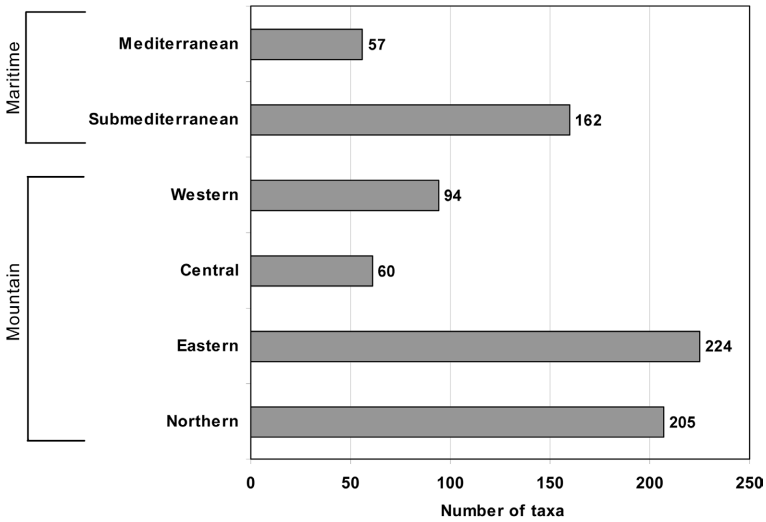

Fig. 6. Distribution of Balkan endemic vascular plant taxa in the two geographical regions and six geographical subregions of Montenegro.

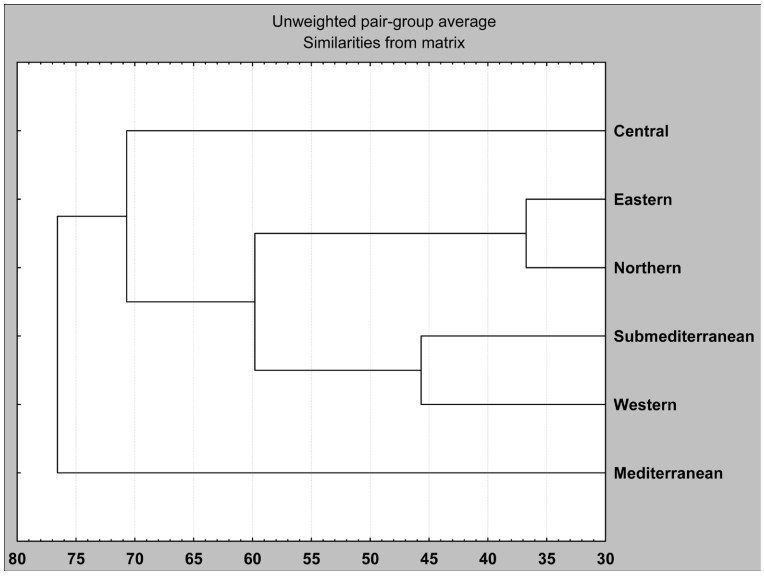

Fig. 7. Cluster analysis of floristic similarities among the six geographical subregions of Montenegro based on the occurrence of Balkan endemic vascular plant taxa. Using the Sørensen similarity coefficient.

river canyons and gorges. Phanerophytes are represented in the Balkan endemic flora of Montenegro by only nine taxa.

In Montenegro, Stevanović & al. (1995) recorded the presence of 223 Balkan endemic taxa (i.e. species and subspecies). In the Balkans, Greece is far ahead in first place with 1226 single-country endemic taxa (Georghiou & Delipetrou 2010). In other Balkan countries, the number of endemic taxa, whether single-country endemic or Balkan endemic, is much lower. In the flora of Bulgaria, 172 taxa are single-country endemics (Velchev & Kozhuharov 2006) and 270 are Balkan endemics (Petrova & Vladimirov 2010). Matevski & al. (2003) recorded 115 single-country endemic species (i.e. excluding subspecies) in the Republic of Macedonia. In the regions of C Serbia and Kosovo there are 492 Balkan endemic taxa (Tomović & al. 2014), in Croatia there are 376 Balkan endemic taxa (Nikolić & Milašinović 2012), and in Bosnia and Herzegovina Lubarda & al. (2014) recorded 298 Balkan endemic taxa. Ruci (1997) recorded 26 single-country endemic taxa and c. 150 Balkan endemic taxa in Albania, but, according to Tomović & al. (2014, quoting Turrill 1958), the actual numbers are much higher (50 and 320, respectively).

The fact that most of the territory of Montenegro consists of hills and mountains, except for the narrow coastal belt, which belongs to the Mediterranean, is reflected by its Balkan endemic vascular flora. The distribution of Balkan endemic taxa by subregions shows that the high-mountain type of endemism is dominant in the flora, and there is also edaphic (limestone) endemism, and a combination of high-mountain and edaphic endemism is consistent with previous studies (Lakušić 1985; Stevanović & al. 1995; Tribsch & Schönswetter 2003; Georghiou & Delipetrou 2010; Tomović 2014; Jeanmonod & al. 2015). Almost the entire mountain part of Montenegro, starting from the coastal Dinaric Alps, which belong to the submediterranean and western subregions, to the mountains of the eastern and northern subregions, including the canyons and gorges between the massifs, can be characterized as a unique centre of diversity of taxa endemic both to the Balkan Peninsula and to Montenegro (Stevanović & al. 1995). In the eastern subregion, the Prokletije mountain range stands out on account of its extraordinary richness in endemic taxa. This range of mountains is located at the intersection of the Dinaric Alps and Scardo-Pindic mountains and is characterized by the different orientations of the mountain branches, their massiveness, high average elevation and a complex relief. The mosaic of geological substrata (limestone and silicate), exposure to different climates, and diversity of habitats in this range have enabled the survival and development of a number of high-mountain endemic taxa that have differentiated during a long process of speciation (Stevanović & al. 1995). The endemic flora of the Montenegro part of the Prokletije mountains represents a link between the ancient orophytic flora of the Alps and the Carpathians with the oromediterranean tertiary flora. The current composition of the flora of the Prokletije massif largely bears the features of these dynamic processes of florogenesis (Bulić & al. 2010). The mountain Bjelasica also belongs to the eastern subregion, and this silicate "island" of limestone is also an important centre of silicate endemic flora. The combination of high-mountain and edaphic endemism occurs exclusively in the eastern subregion, which is also the richest in Balkan endemic taxa in the flora of Montenegro. In the northern subregion, the mountain of Durmitor dominates with its rich flora and its endemic taxa, together with the canyons of the Piva and Tara rivers. Despite its uniform limestone geological composition, Durmitor is one of the most important developmental and also refuge centres of endemic alpine flora in the whole Balkan Peninsula (Stevanović & Lakušić 1996). Also, the canyons of the Piva and Tara rivers represented an important refuge area of nemoral and chasmophytic tertiary flora during the Pleistocene glaciations in the Dinaric Alps. In the submediterranean subregion, the centres of endemism are the limestone coastal mountains of Lovćen and Rumija, and in the western subregion they are the coastal mountain of Orjen and its branches surrounded by an extreme karst area. In the central subregion, the alpine type of endemism also prevails, in the Morača Mountains along the upper course of the River Morača and its tributaries.

The main generators of endemism in the high mountains of the eastern and northern subregions and in the coastal Dinaric Alps are a combination of edaphic, climatic (the presence of mountain, temperate continental and modified Mediterranean climates in the mountain belt and canyons) and habitat conditions, which have also been noticed in the Balkan endemic flora of C Serbia and Kosovo (Tomović & al. 2014). The differentiation of endemic taxa occurred mostly during the glaciation and interglaciation of the indigenous tertiary oromediterranean and alpine floras (Stevanović 1996b). The areas of endemism located outside the high-mountain ranges include limestone river canyons (the Cijevna river and the middle course of the Morača river) and some karst areas in the submediterranean subregion. A relatively small number of Balkan endemic taxa in the narrow coastal area of Montenegro (the Mediterranean subregion) can be explained by the absence of a large number of islands and the dominance of Adriatic taxa in lowland habitats. Lowland habitats rarely form refuges suitable for endemics (at least in temperate latitudes) because of their much harsher and less stable ecoclimatic conditions, which is not the case in the mountains (Tribsch & Schönswetter 2003; Tribsch 2004; Jeanmonod & al. 2015). Also, it should be noted that lowland areas in the Mediterranean subregion have been intensely transformed by human activity (urbanization, cultivation and infrastructure).

Cluster analysis clearly demonstrates that the floristically most similar subregions of Montenegro are (1) the two richest in Balkan endemic taxa: the eastern and

northern subregions; and (2) the two closest geographically and climatically: the submediterranean and western subregions.

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