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FLORISTIC AND PHYTOGEOGRAPHIC CHARACTERISATION OF AREAS OF ENDEMISM FROM THE ROMANIAN CARPATHIANS

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Summary of the PhD thesis

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Introduction

The current distribution of plant species is, among others, highly correlated with historical and ecological factors acting on their areal and determining a continuous dynamic at the scale of geological time. The observed result (the current distribution) is a source of information for disentangling the main processes which shaped the species areal: speciation, migration and extinction. Nowhere is this message more clearly expressed than in the case of endemic species, often rare elements and, by definition, confined to a single biogeographic unit. Nevertheless, interpreting the endemism patterns raises several problematic aspects. First of all, to be able to discriminate between different factors affecting the current distribution of endemic species, we have to understand the processes governing their formation: speciation events. These are sources of biological diversification, but also causes of intraspecific variability, aspects which influence the delimitation of discrete units in biogeographic and biodiversity analyses. Consequently, we cannot discuss on models of speciation, migration paths or refugial areas without a clear delimitation of identifiable and quantifiable units in nature: species. However, this subject raises an essential problematic in biology: what is a species? What do we understand through the notion of species, how do we encompass its elements and which are the means through which we can apply any set of rules and principles for their clear delimitation in nature? Conceptual variability increased exponentially together with the emergence of evolutionary biology, currently having no less than 26 species concepts, many of them only applicable to a limited group of organisms.

Endemic species (or subspecies), representing biogeographic elements having the highest degree of particularity, are often used as criteria in delimiting and individualizing biogeographic areas. By analyzing the patterns of endemism and indentifying the centers of endemism, we can make assessments on both their evolutionary role for the flora of the Carpathians and their conservation status. Also, the areas of endemism, fundamental units in biogeography, indicate exactly those geographic regions bearing information on the areal dynamics and evolutionary processes of speciation. Clearly establishing the extent of these units is the initial condition necessary for any other type of biogeographic inference. Through the means of quantitative biogeography methods, endemic species distribution can be used to classify different biogeographic regions.

Often, areas of concentration for endemic species have been considered centers of refugium and speciation. These hypotheses are being currently tested through the use of species distribution modelling and the involvement of paleoclimatic data obtained from different general climatic circulation models. A constant potential presence of species in certain areas indicates the stability of ecological conditions favorable for populations' resilience in time. Anyhow, these potential distribution models, projected in time, start from two important assumptions: ecological niche stability in time and species equilibrium with the environment. Accepting these assumptions as true, the results can reflect the stability (refugial) zones for species, as well as the spatial dynamics in the postglacial period.

The use of these approaches becomes useful in the context of identifying the general patterns of endemism as well as discriminating between historical or ecological factors influencing the species distribution.

Through this study, we aimed at:

(1) Critically evaluating the list of Carpathian plant endemics occurring in Romania;

(2) Analyzing the patterns of plant endemism in the Romanian Carpathians (South – Eastern Carpathians);

(3) Identifying the centers of endemism from the Romanian Carpathians (South – Eastern Carpathians);

(4) Identifying the areas of endemism from the South – Eastern Carpathians through the use of two datasets and two systems for recording the chorological data;

(5) Generating models of potential distribution for selected endemic taxa and projecting them in the past by using paleoclimatic data, aiming at analyzing the congruence between areas of endemism and areas of resilience (presumed refugial and speciation areas) and to identify the general patterns of endemism in space and postglacial time;

(6) Identifying the biotic elements, meaning those species with a preponderant common distribution and the biogeographic analysis of their distribution in the Romanian Carpathians.

1. The phenomenon of endemism

Endemics (gr. ενδεμοσ = which lives in a single place, indigenous) are taxonomical units of different ranks (subspecies, species, genus, family) " (...) *limited in their distribution to a determined teritory (province, region, district etc.). The endemic is in consequence a taxon with a resticted area to a certain natural region*" (Dihoru & Pârvu, 1987, p.10). Vischi *et al.* (2004) offer a more general definition of endemism: the phenomenon of endemism characterizes those taxa whose distribution is restricted to a certain area, more reduced than of other taxa of the same rank.

The endemic cormophytes confer floristic identity to occupied geographical units, capturing the natural phenomenon of speciation and habitat evolution in correlation with orogenetic processes as well as paleoclimatic events. Hence, the major importance of identifying endemo - conservative and endemo - generative centers corresponding to different geographical areas. These are the marks of historical and eco-climatic phenomena, drivers of speciation, phenotypic and genotypic diversification.

Also, the conceptual variability regarding the notion of species, influences a lot the interpretation of endemics from taxonomic as well as evolutionary point of view.

Endemics have been often considered biological entities with a rare distribution. Due to this cause, but also to evolutionary and biogeography importance, the endemics have been and still are utilized especially as a differentiation criteria for the identification of areas that require special protection. Areas of endemism have often been related to evolution and speciation centers for different groups of organisms, since the distribution of some taxa limited to these areas denotes isolation of the area, representing a geographical unit with a special evolution of biota. The congruence between areas of endemism and the network of protected areas has been often considered as a good optimization criteria for conservation strategies.

Regarding all these aspects, namely the fundamental scientific importance (as evolutionary units and biogeography elements, areas of endemism identification and the analysis of areal dynamics in the context of climate change) but also practical (the role of endemic species in establishing conservation strategies), we can consider the study of endemism patterns as being a fundamental theme both to evolutionary and historical biogeography (Morrone, 2009), as well as to conservation oriented biology.

2. Plant endemism in the Romanian Carpathians

2.1. Geography of the Carpathians

2.1.1. Major geomorphological units of the Carpathian Mountain Range and their place in the European Alpine System (EAS)

Carpathian Mountain Range is part of the EAS, representing a major orographic unit, well individualized by orogenetic, geomorphological and floristic characteristics. Extending over 1600 km, the Carpathians are the longest unit of the EAS (compared with the Alps – 1200 km, Dinaric Mountains – 800 km or the Balkans – 500 km, Mihăilescu, 1963).

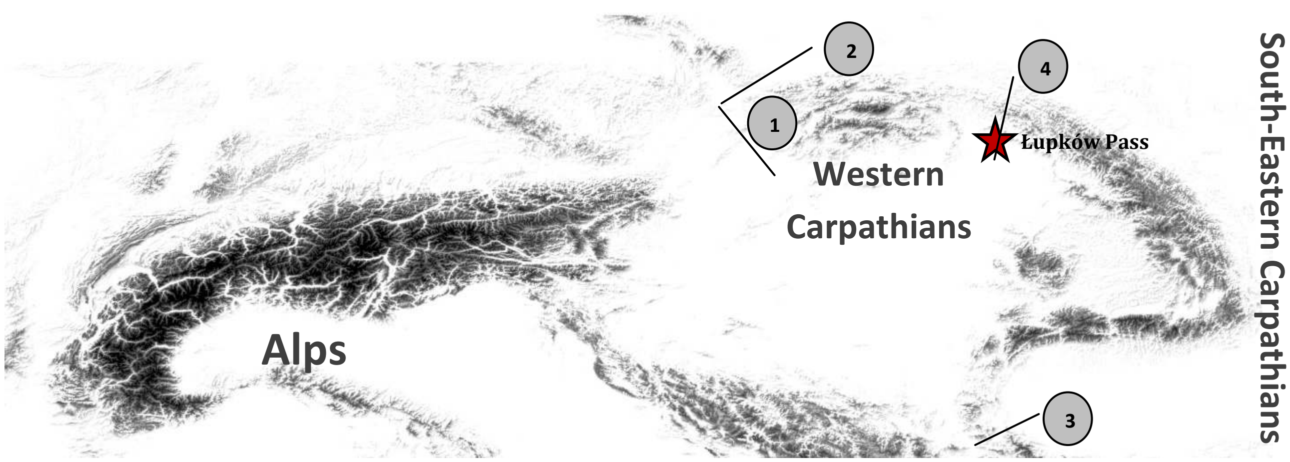

Fig. 1. Carpathians' place in North - Eastern **SAE** and their main units (for 1 →4, see the text)

The majority of geographers consider the Carpathians to be divided in two major, well individualised subunits,: Western (Northern) Carpathians and South – Eastern Carpathians. The latter is subdivided in Eastern Carpathians, Southern Carpathians and Apuseni Mountains (Mihăilescu, 1963; Pop, 2006).

The limits of the Carpathians are (Fig. 1):

(1) to the West, towards the Alps and Dinaric Mountains, they are separated by the Pannonic Plain, oriented NW – SE and crossed by the Danube;

(2) to the North, towards the Moravian Plateau and Bohemian Massif, the Carpathians are delimited by Morava Valley and Odra Valley;

(3) to the South, a frequent boundary is considered to be the Danube Gorge, although, as Mihăilescu (1963) pointed out, both morphology and geological structure entitle the positioning of this limit more to the South, along the Timoc – Nișava Corridor (near Stara Planina).

Pawłowski (1970) and other biogeographers, based on species distribution, place the boudary between the Western and South – Eastern Carpathians at *Łupków Pass*. We will adopt this delimitation, specifying that we also consider the Transdanubian unit to be part of the Carpathian Mountains.

2.1.2. South – Eastern Carpathians

The South – Eastern Carpathians, are divided into four major units:

(1) Eastern Carpathians, extending from Łupków Pass in the North to Prahova Valley in the South;

(2) the Southern Carpathians are delimited by Prahova Valley to the East and Timiș - Cerna – Bistra Corridor to the West;

(3) Banatului Carpathians, including here the Transdanubian unit, begin at Mureș and Timiș Valleys to the North and East, and extend to the Timoc Valley in the South;

(4) Apuseni Mountains, situated between Someș Valley to the North and Mureș Valley to the South.

As we mentioned before, one important caractheristic of the Carpathian Mountain Range is the degree of relief fragmentation. This is mainly caused by morphological, geological and hydrological factors, which led the geographers to the current delimitation of geographical units. Such a delimitation was also used in our analyses (Fig. 2). From a phytogeographic point of view, such fragnemtation of mountainous units has numerous effects on the distribution of species, generating habitat insularity and being possibly the prerequisite for the localized distribution of Carpathian endemics.

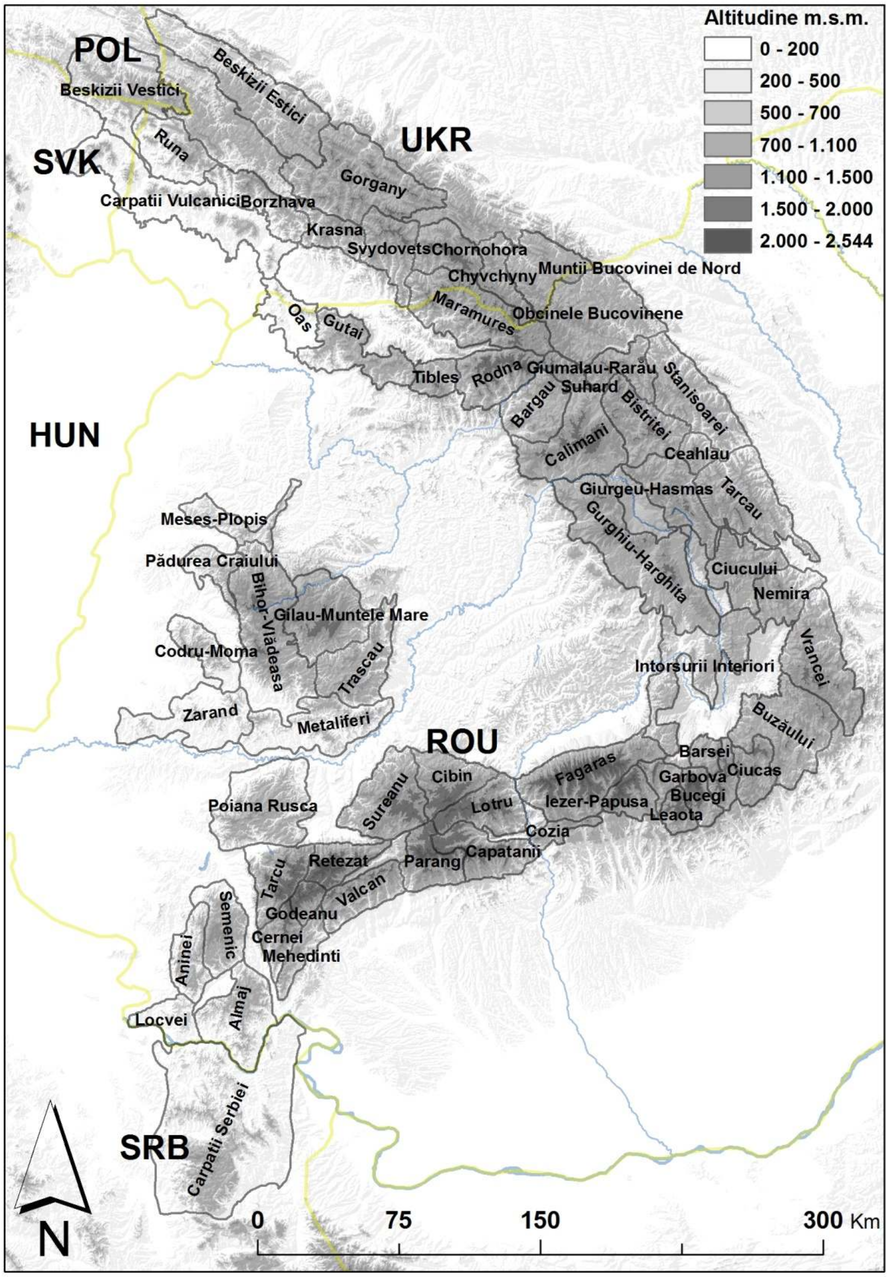

Fig. 2. Geographic units of the South – Eastern Carpathians

2.1. Opinions on the diversity of endemic taxa from Romania

"Il n'est pas possible d'indiquer le nombre exact d'espèces endémiques dans la flore des Alpes et des Carpates"

Bogumil Pawłowski (1970, p.185)

Pawłowski (1970) observed a richness latitudinal gradient for endemic taxa, the number of endemics increasing from Northern to Southern Europe. He also emphasized the relationship between the number of endemics residing in a certain area and the age of that area's flora (an older flora was subject to an increased number of areal fragmentation and isolation processes, due especially to orogenic and climatic factors, intensifying speciation). In the same time, glacial periods determined profound modifications of distribution extent for old species, this finding refuge in unglaciated areas. This is the case for the Balkans and the Carpathians, mountain ranges which were less affected by glaciation and still hold numerous paleoendemics in their flora, species which did not have the capacity of extending a reconolizing their former areal.

Endemic species are tightly linked to the emergence and various transformation suffered by the Carpathians, lowland adjacent areas having an incomparable smaller amount of endemics in their flora. This is the reason why endemism in Romania's flora is so highly connected to the development of this phenomenon in the Carpathian Mountains. Both Pax (1898 - 1908) and Prodan (1939) considered the Romanian Carpathian's flora to be the richest in Europe. Insufficient knowledge on the chorology and a clearer species concept entitled them to make such remarks. The great explorers of Transylvanian flora (Heuffel, 1858; Schur, 1866; Simonkai, 1887) or even more recent authors described and typified as discrete units at the level of species or subspecies numerous morphological forms, granting them the quality of endemic. Many of these entities have later been reconsidered, being either sinonimized or invalidated due to their character's inconsistency (especially at critical genera such as *Hieracium*, *Centaurea*, *Alchemilla*, *Rubus* and so on). Some of these taxa were discovered in other areas, loosing their status of endemic. Nevertheless, these researchers of the Carpathian flora have the merit of detecting in high degree the morphological variability, many species still holding their name today.

Table 1. The number of endemics in the opinion of various authors

Author	Year published	Number of taxa	Area being considered
A. Borza	1931	283	Romania
I. Prodan	1939	280	Romania
T. Săvulescu	1940	340	Romania
A. Borza	1947-1949	148	Romania
A. Beldie	1967	97	Romanian Carpathians
I. Morariu & A. Beldie	1976	127	Romania
A. Beldie	1977, 1979	130	Romania
V. Sanda *et al.*	1983	169	Romania
H. Heltmann	1985	149	Romanian Carpathians
G. Dihoru & C. Pârvu	1987	80	Romania
G. Negrean & M. Oltean	1989	128	South – Eastern Carpathians

A more and more refined analysis of the taxonomical position (based on morphology, ecology, caryology, genetics *etc.*) and chorology of the endemic taxa led to a variety of interpretations but also to a reduced number of species included in this category. The number of Carpathian endemics may vary, depending on the author's decision on taking into account the microspecies and critical taxa of the polymorphic groups, on the personal opinion on various taxa's validity and chorology. The numbers shown in Table 1 are mainly referring to the whole Romanian Teritorry, but as we noted earlier, only a limited number of endemics is found elsewhere outside the Carpathian area, thus such a comparison can reflecting with good reason the discussed variability. Also, the numbers may vary due to the areal considered by every author. Thus, the studies of Borza (1931), Prodan (1939), Săvulescu (1940) and Borza (1947-1949) refer to the territorial extent or Romania prior to the second World War, while the following studies regard the current territory limits.

We conclude that there is not any universally accepted list of endemics (and for sure the controversy will continue from now on). In our analyses we aimed at synthesizing the available taxonomical and chorological information and reaching a more consensual opinion.

3. Analyzing the patterns of endemism from the Romanian Carpathians

ARTICLE 1: A CRITICAL EVALUATION OF CARPATHIAN ENDEMIC PLANT TAXA LIST FROM THE ROMANIAN CARPATHIANS

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Abstract: Although several studies on plant endemism have been carried out in the Romanian Carpathians, taxonomical inconsistencies still exist, along with insufficient distribution data availability. Our study aims at reducing these uncertainties by having a large coverage of available chorological data and searching consensus among different authors on taxonomic validity. For this reason, we produced a vast collection of chorological data, comprising literature sources, historical herbarium collections and field surveys covering the Romanian Carpathians. We subsequently surveyed the botanical literature from the neighboring areas (Serbia, Bosnia, Bulgaria) to have a better overview of the analyzed taxa's distribution. We considered 132 taxa as *'good endemics'* having mainly two types of distribution: *Pancarpathian* and *South – Eastern Carpathian*. All of these are occurring in the Romanian Carpathians, many of them being confined solely to our mountain range. Few of these taxa, namely *sub-endemic* taxa, are characterized by an ecological optimum which allows them to grow in lowland areas, having been cited from the neighboring regions of the Carpathians. We excluded the polymorphic genera *Hieracium*, *Alchemilla* and *Rubus* and numerous other taxa which were considered by various authors at certain times to possess the characteristics of endemics but without any consensus between different authors.

Keywords: endemic plants, Carpathians, taxonomical consensus, chorology, database

Materials and Methods

The database was compiled using a vast literature source published between 1866 and 2011, historical herbarium collections (Natural History Museum Herbarium Sibiu – SIB, Institute of Biology, Romanian Academy Herbarium - BUCA, Babes-Bolyai University Herbarium - CL, University of Belgrade Herbarium – BEOU and Hungarian Natural History Museum Herbarium - BP) and field surveys carried out between 2003 and 2010 by the authors.

The nomenclature was validated through the use of several works: Oprea (2005), Ciocârlan (2009), Dihoru *et* Negrean (2009) and Flora R.P.R.-R.S.R. vol. I-XIII, as well as two online databases: Flora Europaea (http://rbg-web2.rbge.org.uk/FE/fe.html), The Plant List Database (http://www.theplantlist.org/).

The available toponymic and topographic information was converted into geographic coordinates for every cited location. For a precise identification, we used digital elevation models, topographic, touristic and satellite maps. The estimated accuracy of the positions varied between 20 m and 5000 m. We generated a total of 9418 distinct spatial references for the 132 validated endemic taxa.

Results and Discussion

We considered 132 endemic taxa as valid from taxonomical and chorological point of view. From systematic perspective, the endemic flora of South-Eastern Carpathians is distributed in 30 families, of which *Asteraceae* is the richest (comprising 20 taxa), then *Poaceae* (17), *Brassicaceae* (15), *Caryophyllaceae* (15), *Campanulaceae* (7), *Ranunculaceae* (7), *Fabaceae* (5), *Apiaceae* (4), *Lamiaceae* (4) or *Primulaceae* (4) among them. There are 78 genera with endemic species or subspecies, with *Festuca* and *Centaurea* having both 8 endemic taxa, *Dianthus* (6), *Campanula* (5), *Draba* (4), *Thymus* (3), *Silene* (3), *Scabiosa* (3), *Primula* (3) and *Hesperis* (3) among the richest. Also, the group *Marginatus* from *Thymus* genus is endemic for the Carpathians, including *T. comosus*, *T. pulcherrimus* and *T. bihoriensis*. Two genera were previously considered endemic for the Romanian Carpathians (*Pietrosia* and *Polyschemone*) (Flora R.P.R.-R.S.R. vol. I-XIII), later being taxonomically reconsidered (Morariu & Beldie, 1976).

The two main types of shortfalls previously described (chorological and taxonomical), along with different interpretations of the Carpathian Southern limit has led to the previous exclusion of several taxa from the list of endemics. Taxa like *Campanula crassipes*, *Scabiosa columbaria* ssp. *banatica*, *Athamantha turbith* ssp. *hungarica* or *Dianthus giganteus* ssp. *banaticus* are distributed to the South of Danube Gorge, in the Serbian part of the Carpathians. For this reason they were considered Carpathian – Balkan elements by one or several authors, but without any cited occurences in the Balkan Mountains (Assyov & Petrova, 2006). Based on the inclusion of Transdanubian Mountains in the South – East Carpathian Mountain Range, we consider these taxa to be endemic for the South – Eastern Carpathians.

Gypsophila petraea was considered by some authors to be a Carpathian – Balkan element. Nevertheless, this species was solely cited by Hayek (1924) under the name *G. transsilvanica*, „Bu (Rhodope)"and later assumed to be a missidentification and excluded from the Balkan flora (Stojanov *et al.*, 1966 - 1967).

Galium kitaibelianum was cited from Velika Remeta and Krušedol lowland areas in Central Serbia (Obradović, 1966), these being the only localities outside the Carpathians.

Cerastium arvense ssp. *lerchenfeldianum* was cited from Serbia by Hayek (1924) "*In glandulosis [glareosis], rupestibus. Sb*", to be later considered a missidentification (Niketić, 2007).

Draba kotschyi was considered an Carpathian – Alpine element, but according to Pawłowski (1970), in the Alps, this species was mistaken for *D. norvegica* (Buttler, 1967).

Some critical taxa were also kept in our list, but these would require further chorological investigation to complete their known distribution: *Dactylorhiza cordigera* ssp. *siculorum* and *Dactylorhiza maculata* ssp. *schurii* were considered valid acording to the genus monography in Romania (Soó, 1967), while *Plantago atrata* Hoppe ssp. *carpatica* and *Salix kitaibeliana* were kept valid according to the IntraBioDiv project Consortium (Gugerli *et al.*, 2008).

Soldanella rugosa is a newly described endemic taxon, differentiated based on molecular data and geographic distribution (Zhang, 2001).

Several sub-endemic taxa, which have their optimum in the Carpathian Mountains, spread in their lowland vicinity: *Leucanthemum waldsteinii* (cited from Bosnia, Vranica Mountain) (Beck-Mannagetta *et al.*, 1950), *Crocus banaticus* (cited from Serbian, Šabac and Kladovo lower Mountains) (Ranđelović & Ranđelović, 1999), *Cardamine glanduligera* (cited from Hungary, Nagysom) (Javorka, 1935), or *Micromeria pulegium* (Tara Mountains in Serbia) (Diklić & Nikolić, 1986).

We excluded based on various reasons, several other taxa. These were considered either to have a critical taxonomy, or lacking sufficient distribution information. Among these species it is possible that in the future new studies would undoubtedly confirm their valid status either as good taxa or even as endemics.

We also excluded all taxa from *Hieracium*, *Alchemilla* and *Rubus* genera due to their critical nature, also a vast number of "presumed" *Aconitum* endemics and several other taxa among which some were often discussed in regards to their endemic status or taxonomic validity: *Androsace villosa* ssp. *arachnoidea*, *Sorbus umbellata* ssp. *banatica*, *Stipa crassiculmis* ssp. *heterotricha*, *Ranunculus flabellifolius*, *Pyrola carpatica*, *Poa laxa* ssp. *pruinosa*, *Pinus nigra* ssp. *banatica*, *Melampyrum herbichii* or *Hypericum richerii* ssp. *transsilvanicum*.

ARTICLE 2: PATTERNS OF PLANT ENDEMISM IN THE ROMANIAN CARPATHIANS (South – Eastern Carpathians)

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Contribuții Botanice (*in press*)

Abstract: The study of endemism, both a biogeographic and evolutionary phenomenon, can reveal valuable historical and ecological aspects of a region's flora. Nevertheless, due to taxonomical inconsistencies and distribution data availability, previous studies have shown differing results for the Romanian Carpathians. To reduce these shortfalls, we compiled a database using a vast coverage of existent literature and herbarium collections, complemented by field sampling. As a result, we considered 132 Pancarpathian and South – Eastern Carpathian endemic taxa as valid for the Romanian Carpathians. We present the general distribution of all discussed taxa, by covering the main literature from the other Carpathian countries. Then, in order to investigate the endemic plants richness distribution patterns in the study area, we used the framework of the morphological Carpathian units as natural, operational geographic units (OGU's). For spatial interpolation and visualization purposes, we then used an artificial, grid data registering system. Through the use of GIS and spatial analyses, we identified three main regions of endemism, five major and three minor centers of endemism. We also discuss the possible floristic barriers from the Romanian Carpathians and explore the relationship between endemic taxa richness and several important topographic variables (mean altitude, maximum altitude and altitudinal range). Finally, we highlight the biogeographic importance of the revealed centers of endemism.

Keywords: centers of endemism, species richness, weighted endemism, Carpathians, kriging, Geographic Information System (GIS), Operational Geographic Unit (OGU), Operational Geographic Set (OGS).

Results and Discussion

Of the 132 taxa taxonomical and chorological validated, 27 are Pan-Carpathian and 105 are limited in their range to the South-Eastern Carpathians. Pawłowski (1970) mentioned 25 endemics common to both Carpathian subunits and 100 South-Eastern Carpathian taxa. The total number of Carpathian endemics from Romania varied among different other authors, e.g. 97 (Beldie, 1967), 149 (Heltmann, 1985), 128 (Negrean *et* Oltean, 1989). Their distribution *per* country shows that

Ukraine has the largest number (60), excluding Romania (which hosts all the analyzed taxa). These endemic taxa are mostly concentrated in the high massifs North of the Maramureș Mountains (i.e. Chornohora, Svydovets, Chyvchyn), all exhibiting tight floristic connections. In the South-Western part of the South-Eastern Carpathians, the lower altitude Transdanubian unit from Serbia hosts several thermophilous endemic taxa common to Romanian Carpathians. These are mostly restricted to few lower mountains like Mehedinți (Cerna Valley) or Almăjului (especially the Danube Gorge area): *Primula auricula* ssp. *serratifolia, Tulipa hungarica*, *Dianthus giganteus* ssp. *banaticus*, *Campanula crassipes* or *Centaurea triniifolia*. The north range margins of several Balkan subendemic taxa are also known for this area – *Hypericum rumeliacum*, *Ferula heuffelii*, *Bupleurum apiculatum*, *Knautia macedonica*, as well as of many thermophilous nonendemic taxa. For these reasons, some biogeographers following Adamović (1909) consider that the Danube Gorge area actually belongs to the Western Moesian floristic dinstrict or Carpatho-Balcanic Serbia. Since the splitting of a compact unit such as the Iron Gate gorge is not the best solution, it should be clarified the transient nature of this area in the future. The general distribution of these taxa is shown *per* country in Table 2.

Endemism patterns describe an uneven distribution of endemic taxa richness throughout the Romanian Carpathians (Table 1). This can be observed by analyzing the richness levels of endemic taxa in the main natural OGU's. High mountains hosting alpine environments (e.g. Rodna, Bucegi, Făgăraș or Retezat) have a high degree of endemism. Limestone massifs like Piatra Craiului, Hăsmaș - Cheile Bicazului or Ceahlău have also a rich endemic flora, noticeable for its local restricted distribution. In contrast, lower mountains do not hold such a great level of endemism, except several limestone units (Mehedinți, Trascău).

Based on both natural and artificial OGS richness (Fig. 1) and weighted endemism (Fig. 2) analysis and on floristic affinities between different areas, we distinguished three main regions of high endemism, with five major centers and three minor ones. These, though, should not be confounded with the areas of endemism *sensu* Linder (2001), but interpreted rather as 'hotspots' of endemism with evolutionary and conservative implications. The major centers are characterized by both rich endemic flora and, occasionally, by the presence of local endemics, indicating their high conservative value.

Table 1: Endemic taxa richness for the main OGU's from the Romanian South – Eastern Carpathians

OGU	No. end.	OGU	No. end.	OGU	No. end.	OGU	No. end.
Rodna	73	Țarcu-Godeanu-Cernei	39	Vrancei	19	Oaș	7
Bucegi	72	Cindrel (Cibin)	35	Almăjului	18	Tarcău	7
Făgăraș	70	Stânișoarei	34	Metaliferi	18	Penteleu	6
Piatra Craiului	65	Nemira	31	Pădurea Craiului	17	Semenic	6
Retezat	63	Gilău - Muntele Mare	29	Gutâi	16	Codru-Moma	5
Hășmaș-Cheile Bicazului	62	Bihor-Vlădeasa	28	Harghita	16	Poiana Ruscă	5
Ceahlău	59	Iezer-Păpușa	28	Perșani	16	Meseș	6
Bârsei	57	Leaota	28	Șureanu	16	Bârgău	3
Parâng	55	Trascău	28	Latorița	15	Locvei	3
Ciucaș	51	Obcinele Bucovinene	26	Baiului	14	Buzăului	2
Căpățânii	50	Țibleș	26	Aninei	13	Ciucului	2
Rarău	50	Bistriței	24	Gurghiu	13	Culmea Codrului	2
Maramureș	47	Siriu	22	Suhard	12	Dognecea	2
Mehedinți	44	Cozia	20	Bodoc	10	Plopiș	2
Călimani	41	Lotrului	20	Zarand	8		

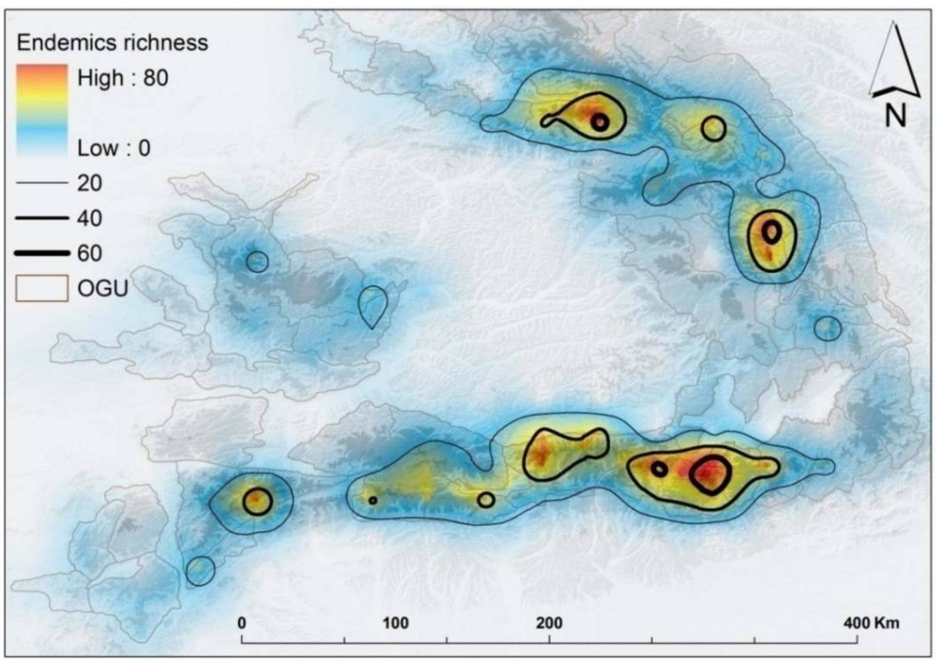

Fig. 1: Endemism patterns in the Romanian South – Eastern Carpathians obtained through krigging Interpolation technique

The three main regions of endemism are discriminated through differential endemic taxa and highlighted by their floristic richness:

(1) Central Eastern Carpathians (with Svydovets, Chornohora, Chyvchyn, Maramureș, Rodna, Țibleș, Călimani, Rarău, Ceahlău and Hășmaș - Cheile Bicazului Mountains);

(2) Southern Carpathians East of Olt river (with Ciucaș, Bârsei, Bucegi, Piatra Craiului, Iezer – Păpușa and Făgăraș Mountains);

(3) South-Western Carpathians spanning to the Danube Gorge (with Retezat, Țarcu – Godeanu – Cernei, Mehedinți – Oslea, Almăjului and Transdanubian Mountains).

When discussing patterns of endemism and areal dynamics of species, we are taking into account two important aspects:, Pleistocene refugia effect and biogeographic barriers which prevented further expansion of some endemics. In our studied territory, range limits of several taxa (provided in brackets) may highlight such floristic barriers, as well as indicate possible refugial areas (Fig. 2):

(a) the Curvature Carpathians, which are lower mountains that link the Eastern Carpathians with the Southern Carpathians (*Athamanta turbith* ssp. hungarica is limited to the West of this barrier, while *Dianthus henteri, Festuca bucegiensis, Poa rehmannii* and *Primula elatior* ssp. *leucophylla* are spread Eastwards);

(b) the Olt Valley, a transversal deep valley which sets the range limit for several endemic taxa (*D. kotschyi*, *Erigeron nanus*, *Gentiana cruciata* ssp. *phlogifolia, Heracleum carpaticum, Leontodon repens* and *Melampyrum saxosum* are distributed to the east of the barrier, while *Galium baillonii* and *Micromeria pulegium* are limited to the West);

(c) the Jiu – Strei corridor in the Western part of the South – Eastern Carpathians, delimiting Retezat Mountains from Parâng Mountains (*Cardaminopsis neglecta, Ranunculus carpaticus* and *Festuca bucegiensis* grow to the East of this limit, while *Primula auricula* ssp. *serratifolia* and *Dianthus giganteus* ssp. *banaticus* are stopping at the Western side of the barrier).

Based on our analyses, we identified the following major centers of endemism for the Romanian Carpathians:

(1) Rodna – Maramureș - Svydovets – Chornohora – Chyvchyn center of endemism has 7 differential taxa: *Armeria pocutica*, *Cochlearia borzaeana*, *Euphorbia carpatica*, *Festuca versicolor* ssp. *dominii*, *Lychnis nivalis*, *Saussurea porcii, Soldanella rugosa* and a total of 77 taxa (58%). The altitude reaches its maximum in Rodnei Mountains (Pietrosul Rodnei Peak: 2303 m a.s.l.), which also harbours 3 local endemics and the highest number of endemics from the South-Eastern Carpathians. These sugest a possible alpine refugia here;

(2) Hășmaș - Cheile Bicazului – Ceahlău – Rarău mountainous group form a center of endemism with high floristic diversity and 2 restricted endemics but without range congruency: *Astragalus roemeri*, *A. pseudopurpureus*, and several other rare endemics (*Asperula carpatica*, which grows also in Stânișoarei Mountains). These limestone massifs might be characterized by the

habitat insularity phenomenon, which has presumably acted on their floristic isolation. The total richness of this center of endemism is 77 taxa (58%);

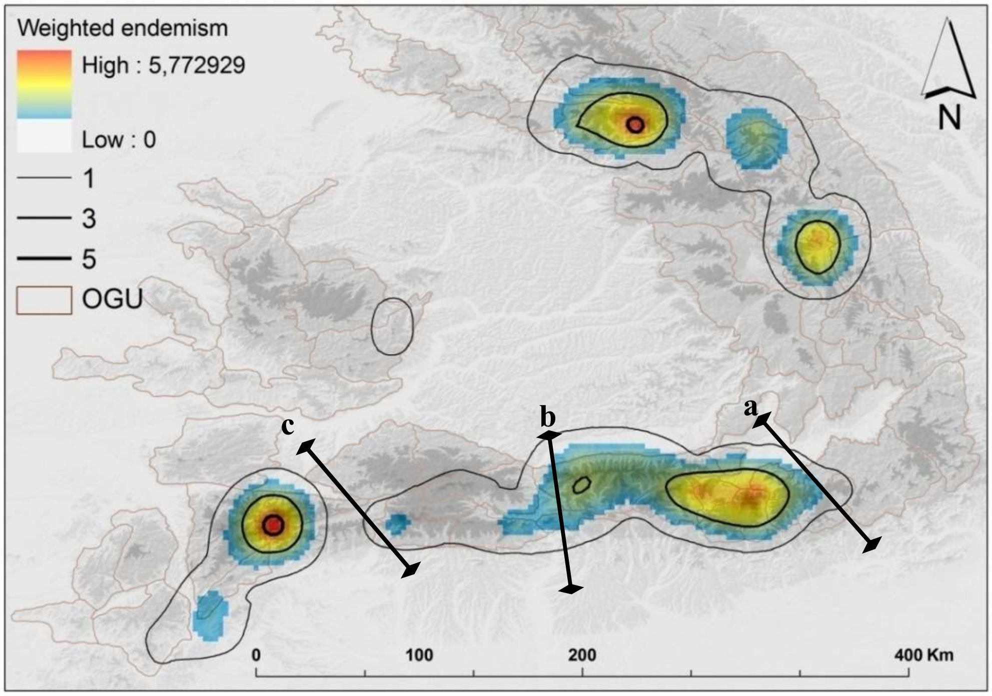

Fig. 2: Weighted endemism in the Romanian South – Eastern Carpathians obtained through Krigging Interpolation technique (a, b, c: floristic barriers; for explanation, see text above)

(3) Bucegi - Bârsei – Piatra Craiului – Ciucaș center of endemism possesses the highest diversity in the South-Eastern Carpathians, comprising 87 endemic taxa (66%). Moreover, it has several non-congruent local endemics: *Dianthus callizonus*, *Ornithogalum orthophyllum* ssp. *acuminatum, Primula wulfeniana* ssp. *baumgarteniana* and *Saxifraga mutata* ssp. *demissa*;

(4) Făgăraș Mountains have the most extensive compact alpine environment, together with Retezat Mountains. With a total of 70 endemic taxa, mostly alpine, it is the third most diverse unit in all the South-Eastern Carpathians. Remarkably, *Silene dinarica* is endemic solely to this massif (the species was cited also from Godeanu Mountains by Heuffel in 1858, but unconfirmed for the last 150 years);

(5) Retezat Mountains represent one of the most diverse units in South-Eastern Carpathians. It has a total of 5 local endemic taxa (*Anthemis kitaibelii*, *Barbarea lepuznica*, *Carduus kerneri* ssp. *lobulatiformis*, *Centaurea phrygya* ssp. *ratezatensis* and *Festuca pachyphylla*). Considering also the calcareous Southern part (Piule – Piatra Iorgovanului), it harbours 63 endemics.

We also identified three minor centers of endemism, characterized by local endemics, but having lower species richness compared to major centers:

(1) Cozia – Buila-Vânturarița center of endemism is formed by two limestone massifs separated by the Olt Valley. These two calcareous units have high floristic affinities, with taxa restricted to this area (*Rosa villosa* ssp. *coziae*). *Stipa crassiculmis* P. Smirnov ssp. *heterotricha* Dihoru *et* Roman, another endemic taxon, was cited as being restricted to Cozia Mountains. Despite that, we didn't consider it in our analyses, as it has a critical taxonomical status, being synonymized with subsp. *euroanatolica* by Ciocârlan in his last edition of Romanian Flora;

(2) Mehedinti – Almăjului – Transdanubian Carpathians center of endemism possesses several locally restricted taxa (*Minuartia hirsuta* ssp. *cataractarum*, *Prangos carinata*, *Stipa danubialis, Tulipa hungarica*) and several species that are extended in few mountains further north (*Campanula crassipes, Centaurea triniifolia, Dianthus giganteus* ssp*. banaticus, Primula auricula* ssp*. serratifolia* and *Sorbus borbasii*);

(3) Trascău – Scărița Belioara massifs constitute another minor center of endemism, characterized by lower altitude limestone cliffs and have two local endemics: *Sorbus dacica* and *Centaurea reichenbachii*;

At a coarser spatial resolution, Pawłowski (1970) identified four main centers of endemism in the South-Eastern Carpathians, with the main difference of considering the Southern Carpathians as a whole floristic unit. We stress that, due to endemic endemic floras affinities, the mountains located Eastwards of Olt Valley are more closely related to Eastern Carpathians. Similar findings have been presented by Negrean & Oltean (1989). Nevertheless, differences occurred as they separated Rarău Mountains and Cheile Bicazului from the Ceahlău and Hășmas Mountains, describing two different centers of endemism. Taxa such as *Asperula carpatica*, *Centaurea phrygia* ssp. *carpatica*, *Heracleum carpaticum*, *Hesperis moniliformis*, *Leontodon repens*, *Primula elatior* ssp. *leucophylla*, *Silene zawadzki*, *Thesium kernerianum* and *Trisetum macrotrichum*, ocurring in Rarău, Ceahlău and Hășmaș Mountains do not justify the existence of a floristic barrier between the abovementioned centers of endemism.

By analyzing the relationship between endemic taxa richness and different topographic variables (mean altitude, maximum altitude and altitudinal range *per* grid cell), we observed the strongest relationship to be between the maximum altitude and endemics richness (Fig. 3). It has been observed a general tendency of richness to increase with altitude, especially between lower mountain and alpine levels (up to ~ 2200 m a.s.l.). Endemics distribution throughout the Romanian Carpathians is tightly linked to the extent of the alpine belt, which is characterized by insularity. This is a known fact, as the alpine system acted through isolation mechanisms as both speciation environment and refugial area. Nevertheless, saturation is reached at a value of 50 and the curvature at about 40 for species richness, meaning that grid cells having similar maximum altitude vary largely in number of endemic taxa (50 – 80). This could be caused by several different factors, mainly the variation in climatic conditions, bedrock type and different historical backgrounds. To a lesser extent, the human impact on the habitat or a difference in sampling intensity might play a role.

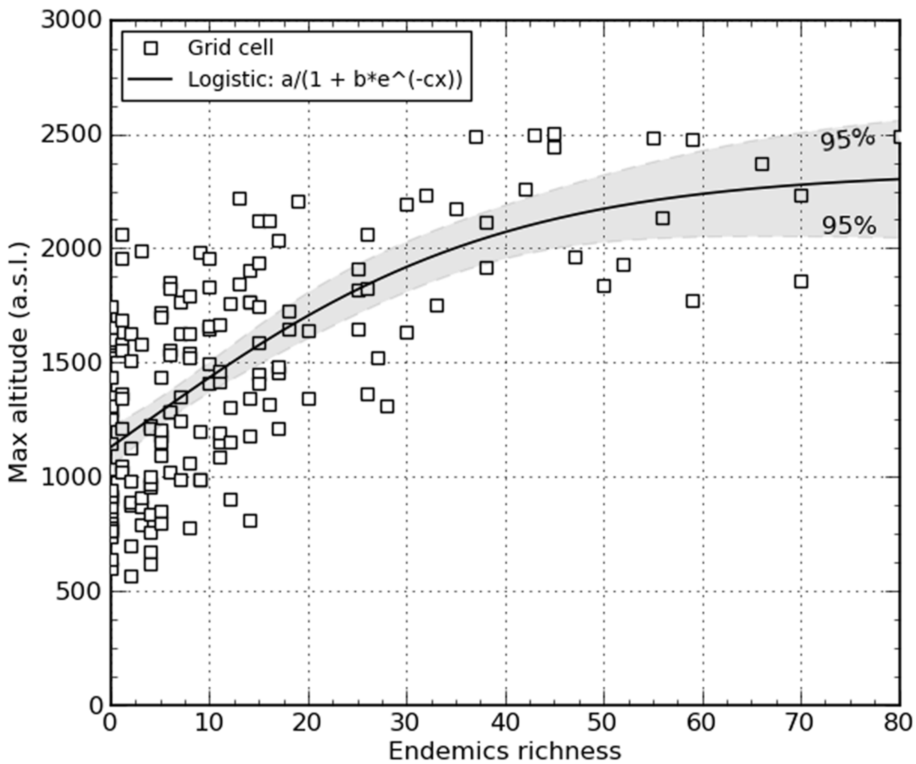

Fig. 3: The relationship between endemic taxa richness and maximum altitude *per* grid cell (AIC: 1900.95, Standard error: 352.09, *r*: 0.69)

Table 2: The complete list of Pan-Carpathian and South-Eastern Carpathian endemic taxa and their distribution *per* country along the Carpathian Mountain Range.

No.	Pan-Carpathian Taxa	Family	Carp. distribution					
			Ro	Ukr	Srb	Pol	Sk	Hu
1	*Centaurea phrygia* L ssp. *melanocalathia* (Borbás) Dostál	*Asteraceae*	+	+		+	+	
2	*Erigeron nanus* Schur	-,,-	+			+	+	
3	*Leontodon montanus* Lam. ssp. *pseudotaraxaci* (Schur) Finch & P.D.Sell	-,,-	+	+		+	+	
4	*Leucanthemum waldsteinii* (Sch.Bip.) Pouzar	-,,-	+	+		+	+	
5	*Symphytum cordatum* Waldst. & Kit. ex Willd.	*Boraginaceae*	+	+		+	+	
6	*Cardamine glanduligera* O.Schwarz	*Brassicaceae*	+	+		+	+	+
7	*Cardaminopsis neglecta* (Schult.) Hayek	-,,-	+	+		+	+	
8	*Erysimum witmanni* Zaw. ssp. *witmanni*	-,,-	+			+	+	
9	*Hesperis nivea* Baumg.	-,,-	+	+		+	+	
10	*Campanula carpatica* Jacq.	*Campanulaceae*	+	+			+	
11	*Campanula rotundifolia* L. ssp. *polymorpha* (Witašek) Tacik	-,,-	+	+		+	+	
12	*Campanula serrata* Hendrych	-,,-	+	+		+	+	
13	*Silene nutans* L. ssp. *dubia* (Herbich) Zapal.	*Caryophyllaceae*	+	+		+	+	

14	*Sempervivum montanum* L. ssp. *carpaticum* Wettst. ex Hayek	*Crassulaceae*	+	+		+	+	
15	*Oxytropis carpatica* R.Uechtr.	*Fabaceae*	+	+		+	+	
16	*Trifolium medium* L. ssp. *sarosiense* (Hazsl.) Simonk.	-,,-	+				+	+
17	*Luzula alpinopilosa* (Chaix) Breistr. ssp. *obscura* Frohner	*Juncaceae*	+	+		+	+	
18	*Thymus pulcherrimus* Schur	*Lamiaceae*	+	+		+	+	
19	*Dactylorhiza maculata* (L) Soo ssp. *schurii* (Klinge) Soó	*Orchidaceae*	+				+	
20	*Plantago atrata* Hoppe ssp. *carpatica* (Pilg.) Soó	*Plantaginaceae*	+	+		+	+	
21	*Festuca carpatica* F. G. Dietr.	*Poaceae*	+	+		+	+	
22	*Festuca rupicola* Heuffel. ssp. *saxatilis* (Schur) Rauschert	-,,-	+	+			+	
23	*Festuca versicolor* Tausch. ssp.*versicolor*	-,,-	+	+		+	+	
24	*Trisetum fuscum* Schultes	-,,-	+	+		+	+	
25	*Aconitum lycoctonum* L ssp. *moldavicum* (Hacq.) Jalas	*Ranunculaceae*	+	+		+	+	+
26	*Ranunculus carpaticus* Herbich	-,,-	+	+			+	
27	*Salix kitaibeliana* Willd.	*Salicaceae*	+	+		+	+	

No.	South-Eastern Carpathian Taxa	Family	Ro	Ucr	Srb	Pol	Sk	Hu
1	*Athamanta turbith* (L.) Brot. ssp. *hungarica* (Borbás) Tutin	*Apiaceae*	+		+			
2	*Heracleum carpaticum* Porcius	-,,-	+	+				
3	*Heracleum sphondylium* L. ssp. *transsilvanicum* (Schur) Brummitt	-,,-	+	+				
4	*Prangos carinata* Griseb. ex Degen	-,,-	+					
5	*Achillea oxyloba* (DC.) Sch.Bip. ssp. *schurii* (Sch.Bip.) Heimerl	*Asteraceae*	+	+				
6	*Andryala levitomentosa* P.D. Sell.	-,,-	+					
7	*Anthemis carpatica* Willd. ssp. *pyrethriformis* (Schur) Beldie	-,,-	+					
8	*Anthemis kitaibelii* Spreng.	-,,-	+					
9	*Carduus kerneri* Simk. ssp. *kerneri*	-,,-	+	+				
10	*Carduus kerneri* Simk. ssp. *lobulatiformis* (Csürös & Nyár.) Soó	-,,-	+					
11	*Centaurea phrygia* L. ssp. *carpatica* (Porcius) Dostál	-,,-	+	+				
12	*Centaurea phrygia* L. ssp. *rarauensis* (Prodan) Dostál	-,,-	+					
13	*Centaurea phrygia* L. ssp. *ratezatensis* (Prodan) Dostál	-,,-	+					
14	*Centaurea pinnatifida* Schur	-,,-	+					
15	*Centaurea reichenbachii* DC.	-,,-	+					
16	*Centaurea trichocephala* Bieb. ssp. *simonkaiana* (Hayek) Dostál	-,,-	+					
17	*Centaurea triniifolia* Heuffel	-,,-	+		+			
18	*Doronicum carpaticum* (Griseb. & Schenk) Nyman	-,,-	+	+				
19	*Leontodon repens* Schur	-,,-	+	+				
20	*Saussurea porcii* Degen.	-,,-	+	+				
21	*Eritrichium nanum* Schrader ssp. *jankae* (Simonk.) Jáv.	*Boraginaceae*	+					
22	*Pulmonaria filarszkyana* Jav.	-,,-	+	+				
23	*Barbarea lepuznica* Nyár.	*Brassicaceae*	+					
24	*Cochlearia borzaeana* (Coman & Nyár.) Pobed.	-,,-	+					
25	*Draba dorneri* Heuff.	-,,-	+					
26	*Draba haynaldii* Stur	-,,-	+					
27	*Draba kotschyi* Stur	-,,-	+					
28	*Draba simonkaiana* Jav.	-,,-	+					
29	*Erysimum witmanni* Zaw. ssp. *transsilvanicum* (Schur) P.W.Ball	-,,-	+	+				
30	*Hesperis moniliformis* Schur	-,,-	+					

31	*Hesperis oblongifolia* Schur	-,,-	+				
32	*Thlaspi dacicum* Heuff. ssp. *banaticum* (R.Uechtr.) Jáv.	-,,-	+				
33	*Thlaspi dacicum* Heuff. ssp. *dacicum*	-,,-	+	+			
34	*Campanula crassipes* Heuffel	*Campanulaceae*	+		+		
35	*Campanula rotundifolia* L ssp. *kladniana* (Schur) Witasek	-,,-	+	+		+	
36	*Phyteuma tetramerum* Schur	-,,-	+	+			
37	*Phyteuma vagneri* Kerner	-,,-	+	+			
38	*Cerastium arvense* L. ssp. *lerchenfeldianum* (Schur) Asch. & Graebn.	*Caryophyllaceae*	+				
39	*Cerastium transsilvanicum* Schur	-,,-	+				
40	*Dianthus callizonus* Schott & Kotschy	-,,-	+				
41	*Dianthus giganteus* d'Urv. ssp. *banaticus* (Heuff.) Tutin	-,,-	+		+		
42	*Dianthus glacialis* Haenke. ssp. *geldius* (Schott, Nyman & Kotschy) Tutin	-,,-	+				
43	*Dianthus henteri* Heuff. ex Griseb. & Schenk	-,,-	+				
44	*Dianthus spiculifolius* Schur. ssp. *spiculifolius*	-,,-	+	+			
45	*Dianthus tenuifolius* Schur	-,,-	+	+			
46	*Gypsophila petraea* (Baumg.) Rchb.	-,,-	+				
47	*Lychnis nivalis* Kit.	-,,-	+				
48	*Minuartia hirsuta* (M.Bieb.) Hand.-Mazz. ssp. *cataractarum* (Janka) Soó	-,,-	+				
49	*Minuartia verna* L. ssp. *oxypetala* (Woloszczak) G.Halliday	-,,-	+	+			
50	*Silene dinarica* Sprengel	-,,-	+				
51	*Silene zawadzkii* Herbich	-,,-	+	+			
52	*Scabiosa columbaria* L. ssp. *banatica* (Waldst. & Kit.) Diklić	*Dipsacaceae*	+		+		
53	*Scabiosa columbaria* L. ssp. *pseudobanatica* (Schur) Jáv. & Csapody	-,,-	+	+			+
54	*Scabiosa lucida* Vill. ssp. *barbata* Nyár.	-,,-	+	+			
55	*Euphorbia carpatica* Woloszczak	*Euphorbiaceae*	+	+			
56	*Astragalus pseudopurpureus* Gusul.	*Fabaceae*	+				
57	*Astragalus roemeri* Simonk.	-,,-	+				
58	*Genista tinctoria* L. ssp. *oligosperma* (Andrae) Borza	-,,-	+	+			
59	*Gentiana cruciata* L. ssp. *phlogifolia* (Schott & Kotschy) Tutin	*Gentianaceae*	+				
60	*Crocus banaticus* Gay	*Iridaceae*	+	+	+		
61	*Micromeria pulegium* (Rochel) Bentham	*Lamiaceae*	+		+		
62	*Thymus bihoriensis* Jalas	-,,-	+				
63	*Thymus comosus* Heuff. ex Griseb.	-,,-	+				
64	*Ornithogalum orthophyllum* Ten. ssp. *acuminatum* (Schur) Zahar.	*Liliaceae*	+				
65	*Tulipa hungarica* Borbas	-,,-	+		+		
66	*Linum uninerve* (Rochel) Jáv.	-,,-	+				
67	*Syringa josikaea* J.Jacq. ex Rchb.	*Oleaceae*	+	+			
68	*Dactylorhiza cordigera* (Fries) Soó ssp. *siculorum* (Soó) Soó	*Orchidaceae*	+				
69	*Papaver alpinum* L. ssp. *corona-sancti-stephani* (Zapal.) Borza	*Papaveraceae*	+				
70	*Armeria pocutica* Pawł.	*Plumbaginaceae*	+	+			
71	*Alopecurus pratensis* L. ssp. *laguriformis* (Schur) Tzvelev	*Poaceae*	+	+			

72	*Festuca bucegiensis* Mark. - Dan.	-„-	+					
73	*Festuca nitida* Kit. ssp. *flaccida* (Schur) Markgr.-Dann.	-„-	+					
74	*Festuca pachyphylla* Degen ex Nyár.	-„-	+					
75	*Festuca porcii* Hackel	-„-	+	+				
76	*Festuca versicolor* Tausch. ssp. *dominii* Krajina	-„-	+					
77	*Helictotrichon decorum* (Janka) Henrard	-„-	+					
78	*Koeleria macrantha* (Ledeb.) Schult. ssp. *transsilvanica* (Schur) A. Nyár.	-„-	+	+				
79	*Poa granitica* Braun-Blanq. ssp. *disparilis* (Nyár.) Nyár.	-„-	+	+				
80	*Poa rehmannii* (Asch. & Graebn.) Woloszczak	-„-	+	+				
81	*Sesleria heuflerana* Schur ssp. *heuflerana*	-„-	+	+				+
82	*Stipa danubialis* Dihoru & Roman	-„-	+					
83	*Trisetum macrotrichum* Hackel.	-„-	+					
84	*Primula auricula* L. ssp. *serratifolia* (Rochel) Jáv.	*Primulaceae*	+		+			
85	*Primula elatior* L. ssp. *leucophylla* (Pax) Hesl.-Harr.f. ex W.W.Sm. & H.R.Fletcher	-„-	+					
86	*Primula wulfeniana* Schott ssp.*baumgarteniana* (Degen & Moesz) Lüdi	-„-	+					
87	*Soldanella rugosa* L.B.Zhang	-„-	+					
88	*Aconitum tauricum* Wulf. ssp. *hunyadense* (Degen) Ciocârlan	*Ranunculaceae*	+					
89	*Aquilegia nigricans* Baumg ssp. *subscaposa* (Borbás) Soó	-„-	+					
90	*Aquilegia transsilvanica* Schur	-„-	+	+				
91	*Delphinium simonkaianum* Pawł.	-„-	+					
92	*Hepatica transsilvanica* Fuss	-„-	+					
93	*Rosa villosa* L. ssp. *coziae* (Nyár.) Ciocârlan	*Rosaceae*	+					
94	*Sorbus borbasii* Jav.	-„-	+					
95	*Sorbus dacica* Borbas	-„-	+					
96	*Asperula carpatica* Morariu	*Rubiaceae*	+					
97	*Galium baillonii* D.Brândza	-„-	+					
98	*Galium kitaibelianum* Schult. & Schult.f.	-„-	+					
99	*Thesium kernerianum* Simonk.	*Santalaceae*	+					
100	*Chrysosplenium alpinum* Schur	*Saxifragaceae*	+	+				
101	*Saxifraga mutata* L. ssp. *demissa* (Schott & Kotschy) D.A.Webb	-„-	+					
102	*Melampyrum saxosum* Baumg.	*Scrophulariaceae*	+	+				
103	*Pedicularis baumgarteni* Simonk.	-„-	+					
104	*Viola declinata* Waldst. & Kit.	*Violaceae*	+	+				
105	*Viola jooi* Janka	-„-	+	+				
	TOTAL	**30**	**132**	**60**	**9**	**23**	**27**	**5**

List of abbreviations and main sources for endemics distribution along the Carpathian range: Ro: Romania (Flora R.P.R.-R.S.R., 1952 – 1976; Beldie, 1977-1979; Morariu *et* Beldie, 1976; Negrean *et* Oltean, 1989; Ciocârlan, 2009; Dihoru *et* Negrean, 2009**); Ukr: Ukraine (**(Tasenkevich, 1998; Antosiak *et al.*, 2009; Diduha, 2009**); Srb: Serbia (**Josifović, 1970-1977, Sarić *et* Diklić 1986, Sarić 1992**); Pol: Poland (**(Mirek *et al.*, 2002; Piekos-Mirkowa *et* Mirek, 2003**); Sk: Slovakia (**Marhold *et* Hindák, 1998**); Hu: Hungary; Carp: Carpathian (**Pawłowski, 1970; Tutin *et al.* (eds.), 1964-1980; Witkowski *et al.*, 2003**).**

Plant patterns of endemism in the Romanian Carpathians. Can paleodistribution models offer more insights?

The current distribution of species is the result of numerous historical events and ongoing processes of vicariance, dispersal and extinction. In many cases the use of data on endemic species provides a strong insight into these processes, as observed biological entities are tightly linked to the history of occupied biogeographical units. Although there is no "magic bullet" approach to elucidating this history, several techniques can contribute to unveiling these phenomena. Starting from the assumption of niche stability over time, we used species distribution models (SDM's) and parsimony analysis of endemicity (PAE) to delineate geographic and ecological barriers. Through the use of paleoclimatic data and state of the art statistical techniques implemented in R software (BIOMOD), we aim at revealing geographical shifts and conservatism during postglacial times.

Materials and methods

Distribution data

Carpathian endemic plant taxa dataset consists of 70 Carpathian endemic taxa having ≥ 30 occurrences, totaling 8516 presences gathered from literature, historical herbarium collections and field surveys. The distribution data covered the Romanian and Serbian part of the South-Eastern Carpathians. The precision of every point was estimated and subsequently classified based on that estimation, in order to give a bigger weight to the more accurate presences.

IntraBioDiv dataset comprises 355 Alps and 112 Carpathian alpine endemic taxa for the entire range of the two mountainous ranges, recorded in a equal grid-cell system. The selection of the taxa was made based upon their ecological attributes, while their nomenclature was agreed upon by the specialists from the Carpathian region (Gugerli *et al.*, 2008).

Climatic data

In order to describe the climatic niche of the species, we selected 6 explanatory variables characterizing current and past climate: Topographic Index, Potential Global Radiation, Degree-days, Minimum temperature of the coldest month, Minimum Summer Temperature and Precipitation of the driest quarter. These variables were chosen based on their explanatory power by first conducting a PCA exploratory analysis. We then verified the independence of the predictors by choosing a 0.7 correlation coefficient threshold.

Data on current climate (averaged from 1950 to 2000) were obtained from the Climatic Research Unit (Mitchell *et al.* 2004). Simulations of past climate were obtained from a global ocean-atmosphere climate model with a temporal resolution of 1,000 year and a spatial resolution of 3.75° by 2.5° based on the Hadley Centre climate model (HadCM3) and described in Singarayer & Valdes (2010).

Species distribution modelling

We used the R software (2.12.0) and BIOMOD (Thuiller *et al.*, 2009) platform developed under it to generate ensemble forecasts of species distribution for our 70 Carpathian endemics. Such an approach is desired for several reasons: the robustness of the statistical techniques implemented in R software and the reduction of model variability (and thus uncertainty) by averaging an entire array of modelling approaches. Because our data comprises mostly literature and herbarium data, too few "true" absences were assumed to be correct, so we opted for generating pseudo-absences ("sre" strategy), with the *Models* function.

The advantage of such a strategy is that we can keep the prevalence to 0,5, not risking to over-fit the resulting models. We selected 5 iterations for averaging the final results with each pseudo-absence set of data. For generating the ensemble forecasts we used three different techniques (GLM, GAM and GBM) and TSS criteria to convert the probabilities into binary format. The resulting composite richness maps are based on all the species distribution models. For validating our models we used a cross-validation technique, by splitting our data in 80%-20% sub-sets for evaluation, respectively validation procedures. In the end we had 70 sp. x 5 PA iterations x 2 CV x 3 modelling techniques, totaling 2100 individual models. Such an intense computational procedure, being known that R requires a lot of RAM memory, was carried out on a 64 bit Linux cluster provided by WSL institute (HERA), with 48 GB of RAM memory.

Parsimony analysis of endemicity

We used maximum parsimony algorithm implemented in the TNT software to search for the most parsimonious tree topologies and applying the strict consensus criterion on the final tree. The clades sustained by at least two synapomorphic taxa and having a minimum bootstrap score of 50 (100 iterations) were considered as candidates for areas of endemism s*enso* Morrone (1994).

In the case of PAE, we used the IBD dataset comprised of alpine-subalpine taxa registered in a regular grid system of 40' x 24 ' resolution.

Results and discussions

Potential habitat distribution models

The results shown here reveal a general trend of upwards migration in the altitudinal gradient during the Holocene towards the current conditions (fig. 4 - 5). This, in fact, is in accordance with the current known pattern of endemism, expressed stronger in the alpine flora of the Carpathians. Following the current tendency of global climate warming, the trend in the potential distribution of endemic taxa would lead to a decrease in areal occupancy through both competition and physiological limitation phenomena. Considering the lower degree of glaciation that occured in the Carpathians, with extended alpine areas, could explain the high potential richness observed in the projection from 11.000 BP.

Another observed situation is the stability of both global endemic richness and individual resilience of taxa, confined to several areas. Depicted in yellow, the middle of the richness spectrum represented in the map shows the stability of alpine areas such as Bucegi, Făgăraş or Rodna Mountains (Fig. 6). This would reflect a lack of change in species richness, typical for alpine refugia, but would not indicate if there was a high turnover rate or not. Also, it can be observed that areas in Eastern Carpathians, such as Maramureşului or Rodnei Mountains, have a high level of species richness gain considering the difference between 11.000 BP and present. This would reflect possible peripheral glacial refugia (Holderegger & Thiel-Egenter, 2009) for endemic plant species inhabiting these mountainous areas. This, in fact, is in accordance with several other studies describing this resilience phenomenon during the glacial ages in the Carpathians (Ronikier *et al.*, 2008).

Through the stability analysis of every taxon which was carried out in BIOMOD (Fig. 7), we can better reflect those areas where conditions would allow a high number of species to persist during postglacial climatic shifts. Although non-climatic variables (like bedrock type or level of ice during the LGM) weren't included in the models, we can assert that such alpine refugia were harboring many different endemic taxa. In high mountainous areas including Rodna Mountains, Făgăraş Mountains, Retezat Mountains or Bucegi Mountains, characterized by extensive alpine environments and also a higher degree of glaciated areas, the high richness of endemic plants at 11.000 BP and at the same time, their resilience depicted in fig. 7, could indicate the existence of several nunatak glacial refugias, especially for stenobiont strictly adapted species. However, considering the lower amplitude of glaciation effects in the Carpathians, we would assume such high mountain microrefugias were of a lower inflence on the distribution of endemic taxa compared to peripheral or even lowland glacial refugias in this mountain range.

We can conclude that such an analysis confirms that the phenomenon of endemism has a high frequency in the alpine flora, constituting also an environment for the resilience on numerous endemic taxa. However, through such a process of altitudinal migration, we can only encompass a fraction of the ecological gradient a species withstands, this affecting the results of our models.

Areas of endemism

Through parsimony analysis of endemism, we identified tree areas of endemism in the South – Eastern Carpathians. These are located in the Northern part of the Eastern Carpathians (Rodna and Maramureşului Mountains), Mid-Eastern Carpathians (Ceahlău, Rarău and Hăghimaş Mountains) and Eastern part of Southern Carpathians (Bucegi and Piatra Craiului Mountains) (Fig. 3). The areas we identified in our analyses as areas of endemism are overlapping with the zones where a high resilience of endemic taxa during Postglacial times. This could mean that, despite the assumptions behind PAE analysis, these areas hold an historical value for the current distribution of the Carpathian endemic taxa. These areas follow the habitat insularity, expressed either through geological or alpine climatic conditions.

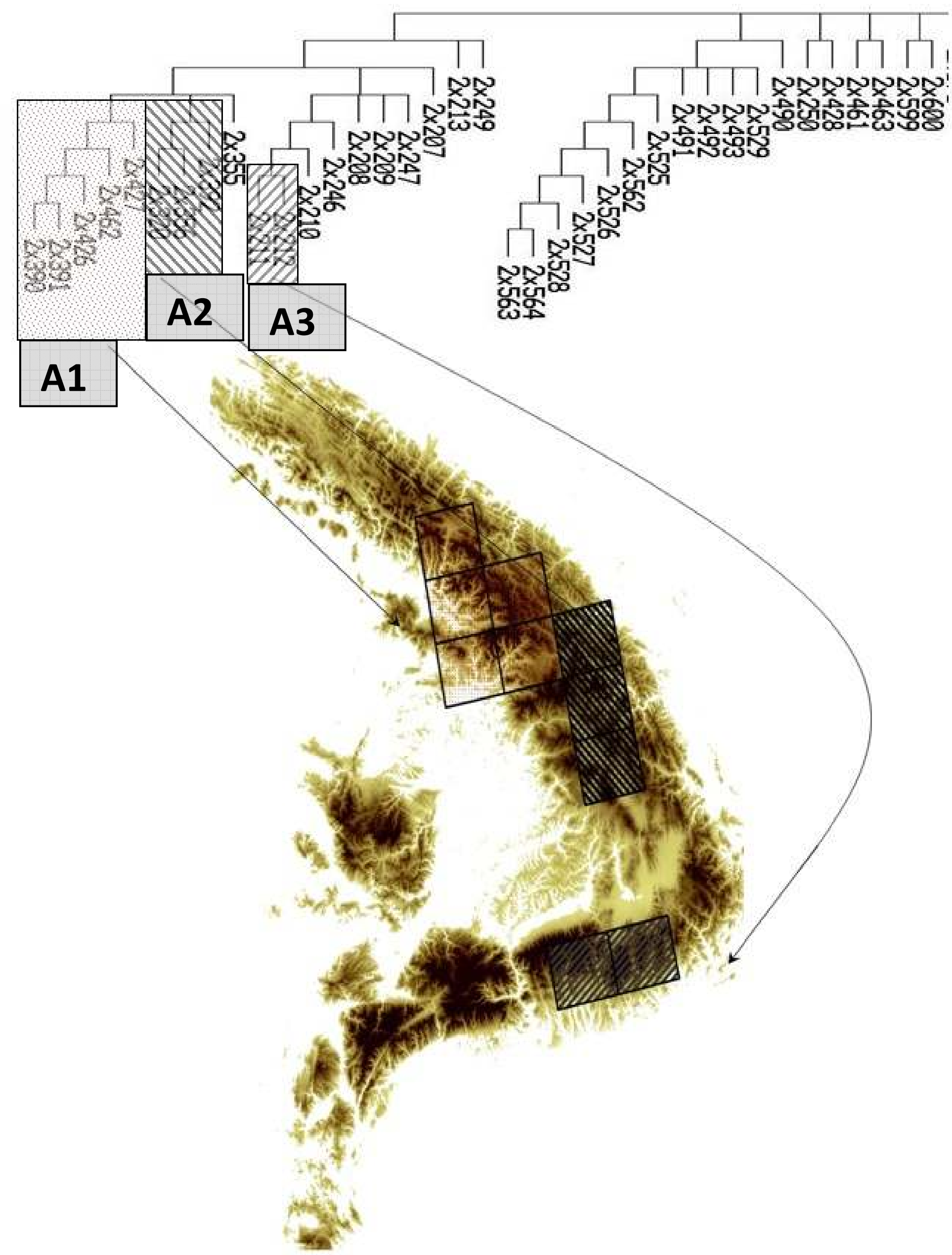

Fig 3 Areas of plant endemism in the Romanian Carpathians delineated through PAE of the IBD alpine species dataset: A1 (Rodnei and Maramureş - Chornohora Mountains); A2 (Hăşmaş, Ceahlău and Rarău Mountains); A3 (Ciucaş, Bucegi and Piatra Craiului Mountains)

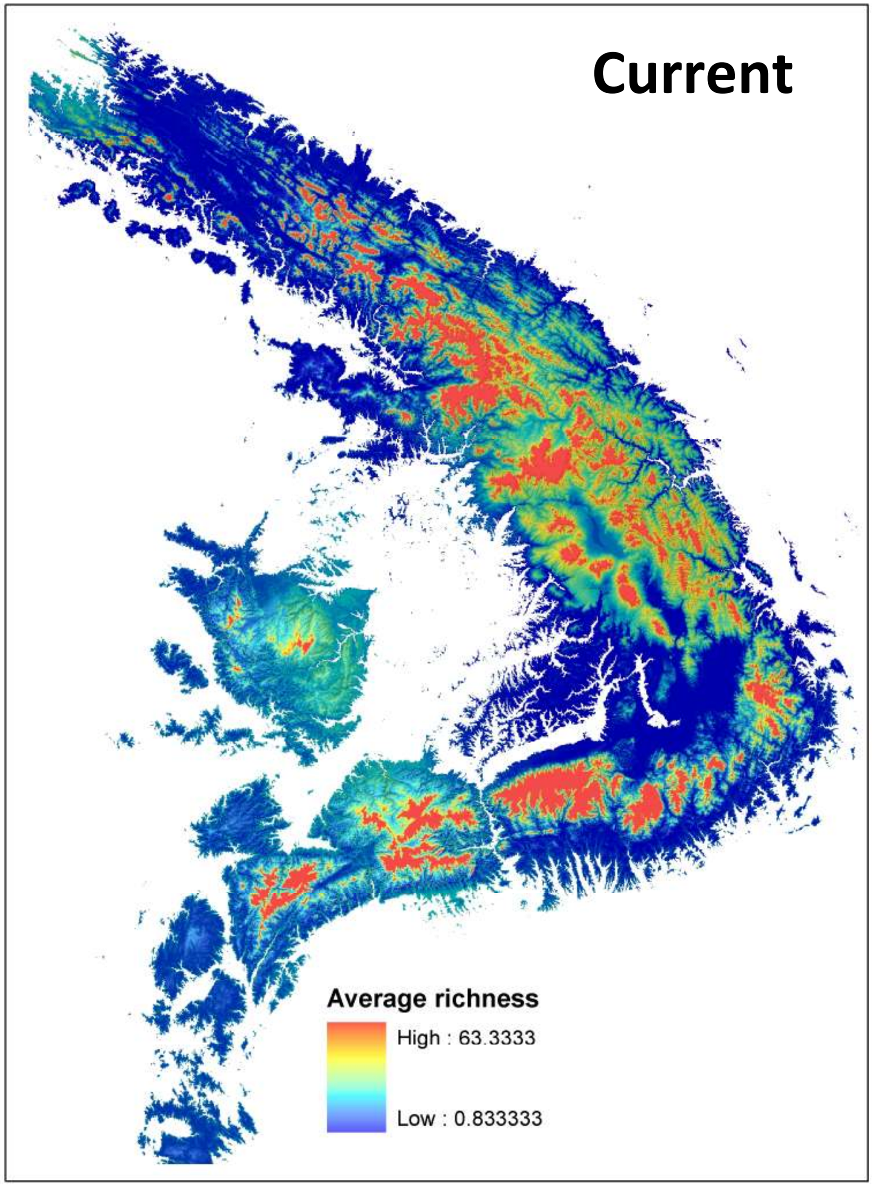

Fig. 4 Current potential species richness distribution of Carpathian endemic plant taxa

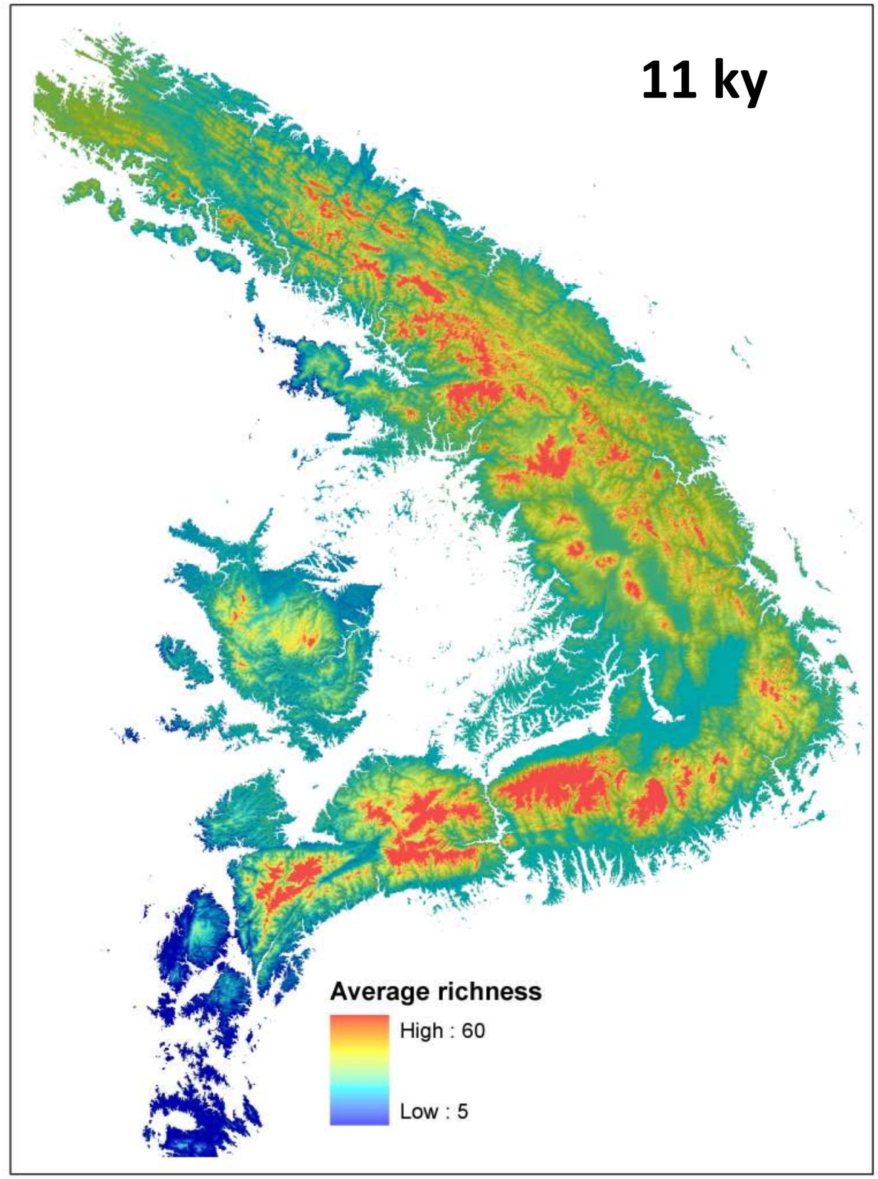

Fig. 5 Past (11.000 BP) potential species richness distribution of Carpathian endemic plant taxa

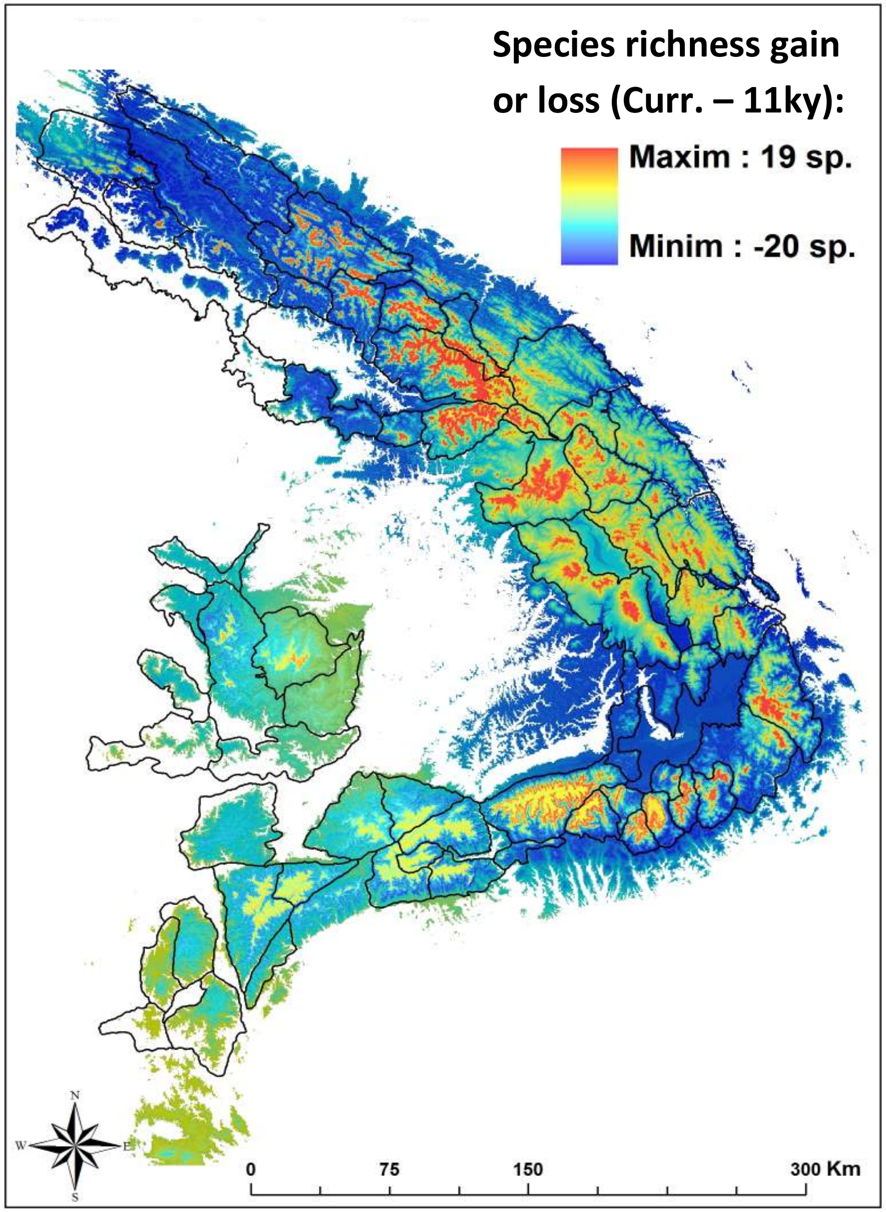

Fig. 6 Variation of endemic taxa richness between 11.000 BP and present

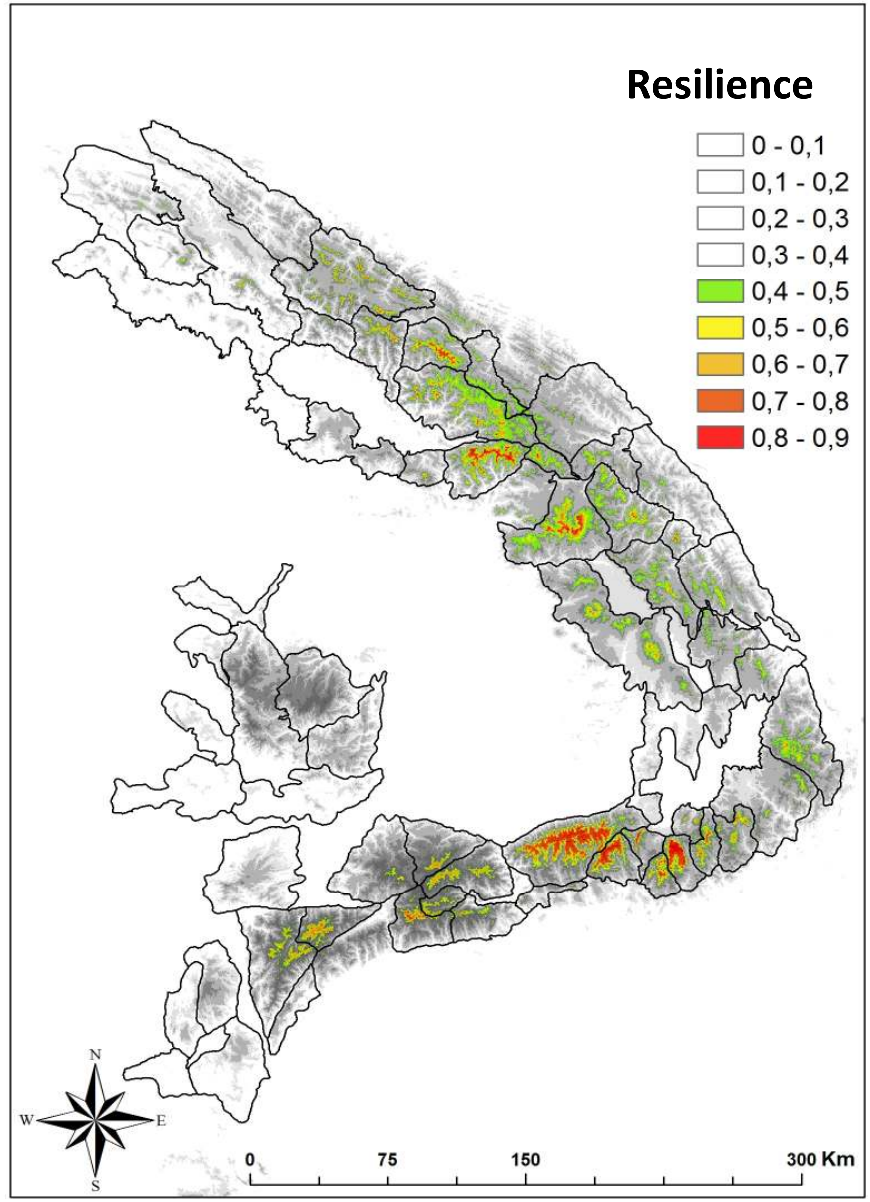

Fig. 7 Endemic taxa stability between 11.000 BP and present

4. Biogeographical analysis of the Romanian Carpathians

4.1. Parsimony analysis of endemicity (PAE)

Parsimony analysis of endemicity allows a clearer delimitation of areas of endemism, fundamental units in biogeography (Nelson & Platnick, 1981; Kitching, 1998).

Following the principle of maximum parsimony, which states that the best solution is the one implying the least evolutionary cost (and in the case of distribution analysis, the least amount of speciation, dispersion or extinction events), we used the algorithms implemented in TNT software (Tree analysis using New Technology, Goloboff *et al.*, 2008) with the aim of identifying the areas of endemism from the Romanian Carpathians. We used the following algorithms implemented in the software: TBS (Tree Bissection and reconnection), sectorial searches and parsimony ratchet. We used the area X species matrix, including only the endemic taxa limited to the South – Eastern Carpathians and excluding also the uninformative OGUs (areas which didn't host any endemic species). We used in the end 105 South – Eastern Carpathian endemics (two endemics were excluded due to incomplete knowledge on their distribution, to remove possible sources of bias from the analyses) and 61 OGUs (including a fictive area 0x0x, without any presences, to root the tree). We found 503 equally parsimonious trees with a minimum score of 453, based on which we obtained the strict consensus tree (Ci = 0,17; Ri = 0,44, Score = 592) in Winclada software (Nixon, 2002).

Based on this analysis, we identified three areas of endemism (Fig. 8), following the criteria stated by Linder (2001) and Morrone (1994). These areas, hosting at least two synapomorphic taxa, are:

(1) A36: **Mehedinti Mountains**, with the following differential endemic taxa: *Minuartia hirsuta* ssp. *cataractarum*, *Prangos carinata*, *Stipa danubialis*;

(2) A47: **Retezat Mountains**, with the following differential endemic taxa: *Festuca pachyphylla*, *Carduus kerneri* ssp. *lobulatiformis*, *Centaurea phrygya* ssp. *ratezatensis*, *Barbarea lepuznica*, *Anthemis kitaibelii*);

(3) A48: **Rodna Mountains**, with the following differential endemic taxa: *Festuca versicolor* ssp. *dominii*, *Lychnis nivalis, Soldanella rugosa*);

These areas are characterized by at least two local endemic taxa, which would imply a common history under the discussed assumptions, indicating the isolation of these areas. Of the three areas of endemism, Rodna Mountains and Retezat Mountains are characterized by the existence of extensive alpine environments. Moreover, Rodna mountains are isolated from the other mountain units surrounding it, being the only area from the Eastern Carpathians with an alpine level. This could have contributed possibly to favorable conditions for speciation to occur and newly formed taxa to emerge. Both Retezat and Rodnei Mountains have an preponderantly acid bedrock. However, in our analyses, we included the southern limestone unit of Retezat Mountains (Piule – Piatra Iorgovanului), which hosts two of the five endemics confined to this unit (*Festuca pachyphylla*, *Carduus kerneri* ssp. *lobulatiformis*). Limestone bedrock is known to have contributed to the appearance of habitat insularity through its patchy distribution, and subsequently to isolation conditions for the flora. The third area of endemism is tightly linked to the Balkanic and sub-Mediterranean influences, hosting many termophilous species. By it's lower altitude and termophilous conditions offered, we can assume that Mehedinti area of endemism not only contributed to the differentiation of endemic taxa but also represented a refuge for most of the termophilous taxa that could not advance northwards during Quaternary glaciations.

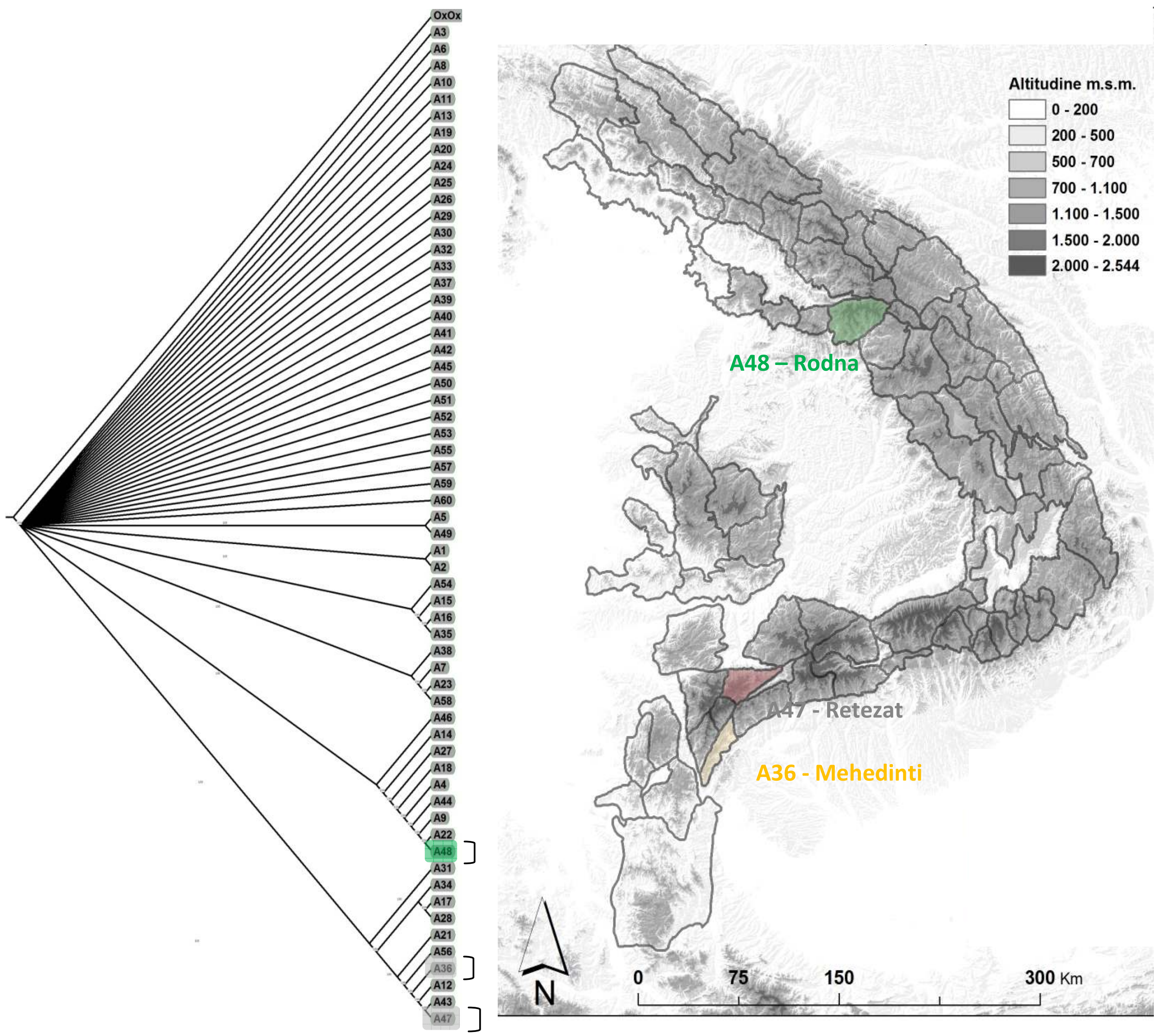

Fig. 8 Areas of endemism from the South – Eastern Carpathians: A36 (**Mehedinţi Mountains)**; A47 (**Retezat Mountains)**; A48 (**Rodna Mountains**);

4.2. Hierarchical clustering

This type of analyses leads to the identification of hierarchical clusters based on the floristic similarity (or distance) of the analyzed OGUs. This approach is recommended especially in biogeographical inferences, since the analyzed geographical units are grouped in a hierarchical manner, the results possibly bringing information on the processes that stood behind the current distribution of species. Of the utilized methods, we used Ward's algorithm and Euclidean distance to construct the cladograms.

Ward's method implies an analysis of variance between pairs of identified clusters, using an algorithm which aims at minimizing the sum of squares between two clusters through ANOVA. The classification of clusters is then realized based on the minimum cost principle Although this approach is ideal for optimizing the hierarchical arrangement of clusters (for this reason being often utilized in biogeographical regionalization), it has the tendency of over - splitting some groups.

We generated the species cladogram with the purpose of identifying biotic elements, namely those groups of species with similar distribution (but not necessary completely congruent, like in the case of PAE). The analysis was carried out in PAST statistical software, starting from the presence / absence matrix. Following the identification of clusters of species with relatively congruent distribution, we generated variation surfaces representing the percentage of the biotic element being analyzed in each OGU. Interpolations were made using IDW (Inverse Distance Weighting) technique, which allows a more detailed analysis of spatial variations. We used the centroids of each OGU for registering the presence / absence data of every taxon, prior to the spatial interpolation.

A similar approach was used by Nimis & Bolognini (1993) in their phytogeographical study of beech forests from Europe (Ward's method and Euclidean distance), with the difference that the authors used an area index for every geographical unit.

As a result of hierarchical clustering the endemic taxa from the South – Eastern Carpathians, we were able to identify 9 major groups of taxa and three minor ones (biotic elements *sensu* Hausdorf & Hennig, 2003), differentiating several floristic regions characterized by their endemic flora. We used the following terminology to offer a hierarchical meaning for the regions occupied by the biotic elements: area, group and district. This hierarchy does not necessarily imply total inclusion of the subordinate units, especially that the meaning of these areas is interpreted through biotic elements:

- Apuseni Mountains District
- South – Western Carpathian District
- Ţarcu – Mehedinţi – Almăjului Mountains Group
- Mehedinţi Mountains Area
- Retezat Moutains Area
- South – Eastern Mountains Group
- South – Eastern limestone massifs Group
- Eastern alpine mountains Group
- North – Eastern Carpathian District
- Moldavian limestone massifs Group
- Rodna – Maramureș Mountains Group

Conclusions

Based on our results and following our proposed aims at the beginning of this study, we can conclude that:

(1) Until now, a high variety of interpretation of endemism patterns from the Romanian Carpathians could be observed, this being mainly generated by two sources: the differing opinions

of authors on the taxonomical position of certain taxa and the varying degree of knowledge on their distribution. Aiming at reducing some of these uncertainties, we followed to obtain a general consensus list of endemic taxa between different authors, regarding the status of endemic attributed to plant species from the Romanian Carpathians. We agreed upon the validity of 132 Carpathian endemic taxa that exist in Romania, of which 105 are confined to the South – Eastern unit of the Carpathian Range, the rest of 27 being distributed also in the Western Carpathians. With the risk of omitting possible valid endemics, we excluded several critical taxa. Further studies will definitely improve and clarify the 'pool' of Carpathian endemics, both by exploring cryptic species divergences at a molecular level and by a better sampling coverage. We also did not consider the genera *Hieracium*, *Rubus* and *Alchemilla* because of the difficulties implied in their identification and their probable incomplete chorology, although these presumably possess a high number of endemics.

(2) Endemic plant species are spread in the South – Eastern Carpathians in tight connection with the insular – type distribution of alpine habitats (the case of Rodna, Bucegi, Făgăraș, Parâng or Retezat Mountains) or basophilous habitats present in the limestone massifs (Rarău, Ceahlău, Hășmaș-Cheile Bicazului, Piatra Craiului, Cozia – Buila Vânturarița and Mehedinți Mountains). Many spatially restricted endemic taxa are also confined to mountainous areas which are characterized by an extensive alpine environment or limestone bedrock. The relationship between richness and maximum altitude *per* grid cell was best fitted by a logistic function with saturation at a value of 50 taxa and a curvature at about 40. Endemics richness varies along the alpine belt, factors like bedrock type, human influence or sampling intensity being possibly behind this phenomenon.

(3) By analysing the endemism patterns through spatial interpolation using species richness and weighted endemism as measures, we identified five major and three minor centers of endemism. These are characterized by high values of endemism and weighted endemism, indicating the local character of the flora. Our findings are largely congruent with the analyses made by Pawłowski (1970) and Negrean *et* Oltean (1989), suggesting that the differences in richness could be the result of different taxonomical interpretations and available knowledge on distribution. The majority of these centers of endemism are already included in the legally protected areas. Nevertheless, they are still highly susceptible to human influences like illegal logging, domestic animal grazing or irresponsible tourism. Areas like the Maramureșului, Făgăraș or Bucegi Mountains are known to be more prone to such disturbances, thus requiring more strict measures.

(4) The areas of endemism were identified using two systems for registering the chorological data. Using an artificial grid type system, we identified three areas of endemism, characterized by the co-occurence of at least two endemic taxa confined to each area: Rodna – Maramureș Mountains, Ceahlău – Rarău – Hășmaș Mountains and Făgăraș - Bucegi – Piatra Craiului – Ciucaș Mountains. These analyses were carried out using solely the subalpine – alpine endemic taxa from the Romanian Carpathians and could not offer a good resolution for the interpretation of results. For this reason we used a natural system based on geomorphologic units, a more accurate account for the species distribution and we included all the endemic taxa from the Carpathians occurring in Romania. As a result, we identified three areas of endemism: Rodna

Mountains, Retezat Mountains and Mehedinți Mountains (including here the lowland area from the Danube's Iron Gates). These areas have both an evolutionary importance, by holding isolated ecosystems that contributed to speciation events, and a conservative value, with a refugial role for paleo-endemics.

(5) Through the usage of the potential distribution modelling approach and paleoclimatic information, we received information regarding the dynamics of species richness in time and on the stability areas, assumed to be potential refugial areas. Following the observed pattern of endemism, in the context of Postglacial climate warming, we can conclude that the majority of endemic taxa migrated in altitude, many of them currently being confined to the alpine belt of the Carpathians. In the same time, many alpine environments acted as areas of ecological stability, especially for taxa that were adapted to such climatic conditions. These stability areas are mostly congruent with the areas of endemism, partly confirming the important role they played in the evolution of local flora.

(6) Through the usage of several quantitative methods applied in biogeography, and especially Ward's algorithm for hierarchical clustering, we identified 12 biotic elements (*sensu* Hausdorf & Hennig), which were used to delimit three floristic districts and six floristic groups. These are mainly confined to basophilous or alpine environments.

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