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Vascular plant endemism in the Western Carpathians: spatial patterns, environmental correlates and taxon traits

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The Western Carpathians, as part of the Carpathian mountain range, are one of the most important centres of vascular plant endemism in Europe. We analysed the distribution patterns of 85 vascular plant taxa (excluding apomictic groups) that are endemic to this region (Western Carpathian endemics) or to the whole Carpathians (pan-Carpathian endemics) across 125 operational geographic units (OGUs) delimited in the area, and assessed their niche and altitudinal breadths, habitat preferences, and life-history traits. Spatial pattern of endemic richness was not random, but was geographically structured with the highest values recorded in the OGUs from the central part of the Western Carpathians. The pan-Carpathian endemics had, on average, larger distributional ranges in the Western Carpathians than the Western Carpathian endemics and showed slightly different distribution patterns, probably affected by historical migrations from the Eastern and Southern Carpathians. A significantly higher proportion of endemics occurred in open non-forest habitats (i.e. rocks/screes and grasslands, 74%) than in forests (18%). Almost 64% of endemic taxa occurred on calcareous bedrock, while only 12% and 21% were confined to siliceous or both types of bedrocks, respectively. We found a strong positive correlation between the distribution range of endemic taxa and altitudinal and niche breadths. There were no differences between diploids and polyploids in any of tested traits, niche and altitudinal breadths and range size. The best linear model explained almost 75% of endemic richness patterns, and included maximal altitude and its interactions with the proportion of calcareous areas and total area of OGUs as the best predictors. Our data suggest that both environmental conditions and historical migrations have shaped the current pattern of endemic richness in the Western Carpathians. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

KEYWORDS: altitudinal breadth – areas of endemism – biogeography – habitat preferences – niche breadth – polyploidy – range size – β diversity.

INTRODUCTION

It has been recognized that endemic plants, i.e. those restricted to certain region, are not evenly distributed in space (e.g. Kruckeberg and Rabinowitz, 1985; Kier *et al.*, 2009; Hobohm, 2014). While some areas are very poor in endemics, other regions – called ‘areas of endemism’ (AOE) – harbour high numbers of endemic taxa. There are several hypotheses that aim to explain the causal reasons of endemism patterns. Generally, the number of taxa endemic to a certain area increases with its size and geographic isolation (Anderson, 1994). Geographic isolation, which prevents genetic interchange between allopatric populations and thus promotes allopatric speciation, is undoubtedly among the most important factors that underlie the patterns of endemism. Accordingly, the high richness in endemic vascular plants was found on islands, but also in mountainous areas that represent island-like ecosystems (Médail & Verlaque,

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1997; Kier *et al.*, 2009). Furthermore, the areas with long-term climatic stability (Fjeldså, 1995), less affected by periodic fluctuations of warm and cold periods during Pleistocene and Holocene (Jansson, 2003), show globally higher levels of endemism than regions that are environmentally less stable. Besides historical events and geography, recent environmental conditions (e.g. edaphic and climatic factors, topography) and specific life-history traits (e.g. persistence, dispersal ability, ecological plasticity; Lavergne *et al.*, 2004) might strongly shape the current distribution of endemic plants (Bruchmann & Hobohm, 2014).

In Europe, except for the Mediterranean region (Greuter, 1991), the highest number of vascular plant endemic taxa can be found in the highest mountain ranges such as the Caucasus, the Alps, the Pyrenees, the mountains of the Balkan Peninsula and the Carpathians (Pawłowski, 1970; Hendrych, 1981; Major, 1988; Ozenda, 1995; Hobohm, 2008; Kier *et al.*, 2009; Aeschimann, Rasolofo & Theurillat, 2011a; Vanderplank *et al.*, 2014). The Carpathians, which are slightly larger in area but substantially lower in altitude than the Alps, are rich not only in vascular plant endemics (Pawłowski, 1970; Hendrych, 1981; Kier *et al.*, 2009), but also are considered as one of the major diversity hotspots for other groups of organisms (Kenyeres, Rácz & Varga, 2009; Schmitt, 2009; Bálint *et al.*, 2011; Kováč, Parimuchová & Miklisová, 2016). Importantly, the Carpathians were almost completely free of ice during the glacial periods of Pleistocene and served as an important refuge for many temperate plant (Willis, Rudner & Sümegi, 2000; Magri *et al.*, 2006; Gömöry *et al.*, 2010) and animal species (Schmitt, 2009; Schmitt & Varga, 2012).

The Carpathians do not form a homogeneous geomorphological entity. They can be divided into three major units, the Western, Eastern and Southern Carpathians, and two minor entities – the Apuseni Mts and Transylvanian Basin (Kondracki, 1989). Because of the lack of a clear geomorphological boundary between the Eastern and Southern Carpathians, these two major units are often merged into one – the South-Eastern Carpathians (e.g. Pawłowski, 1970; Ronikier, 2011). In contrast, the northern and westernmost part of the Carpathians – the Western Carpathians – is very well differentiated from the rest of chain not only from a geomorphological point of view (see below) but also by striking floristic (Wołoszczak, 1896; Pax, 1898; Jasiewicz, 1965; Malinovskiï, 1991; Zemanek, 1991), cytogeographic (Mráz & Szeląg, 2004) and phylogeographic (reviewed by Ronikier, 2011) patterns.

There were many attempts to evaluate vascular plant endemism in the Western Carpathians (for the most exhaustive historical overviews see Hendrych, 1981; Kliment, 1999; Tasenkevich, 2011). Most of these studies focused on listing and commenting on the endemic taxa and their status and were restricted to one country or vegetation belt (e.g. Kiss, 1939; Futák, 1981; Hendrych, 1981; Kliment, 1999; Piękoś-Mirkowa & Mirek, 2003, 2009; Kliment, Šibíková & Šibík, 2011) or even smaller geographic units (Piękoś-Mirkowa, Mirek & Miechówka, 1996). Following the seminal work of Pawłowski (1970), the most comprehensive overview of the distributional endemism pattern in the Western Carpathians as a whole, and the Carpathian arc as well, was provided by Tasenkevich (2011, 2014) who used floristic regions as basic OGUs and mapped the areas of endemism. She found two main centres of diversity of endemic taxa in the Western Carpathians, namely the Západné Tatry Mts and the Nízke Tatry Mts. Despite that effort and according to our best knowledge there is no publication that attempts to quantitatively analyse the pattern of endemism in the Western Carpathians, its putative causes and principal underlying environmental factors.

The primary aim of the present study is thus to quantitatively evaluate the pattern of endemism in the Western Carpathians and to statistically assess its putative determinants. Specifically, we address the following questions: (1) How are vascular plant endemic taxa distributed across 125 operational geomorphological units (OGUs) in the Western Carpathians, and which OGUs harbour the highest endemic richness? (2) Does the distribution pattern of the Western Carpathian endemics differ from the distribution of the pan-Carpathian endemics in the territory of the Western Carpathians? (3) Which environmental factors underlie the endemic richness pattern in the Western Carpathians? (4) What is the altitudinal distribution of endemics and their habitat and bedrock preferences? (5) What is the range size, and niche and altitudinal breadths of narrow endemic species (the Western Carpathian endemics) and those with larger distribution (the pan-Carpathian endemics)? (6) Is there any association between the ploidy level of endemic taxa and range size, niche breadth and altitudinal preferences?

MATERIAL AND METHODS

STUDY AREA

The Western Carpathians (Fig. 1), alongside the Southern and the Eastern Carpathians (thereafter the South-Eastern Carpathians), are major geomorphological units of the Carpathian mountain range (Kondracki, 1989). They extend over the territory of five central European countries (Slovakia, Poland, Hungary, the Czech Republic and Austria) and occupy 70 000 km^2 representing approximately one-third of the total surface of the Carpathians (Kondracki, 1989). In the south/south-west and north, the Western Carpathians are delineated by the Pannonian (Carpathian) Basin and the Wyżyny Polskie highlands, respectively. In the east, the Western Carpathians are separated from the Eastern Carpathians by the most important narrowing and lowering of the Carpathian chain with minimal altitude reaching about 500 m a.s.l. Because this zone is relatively wide, however, the exact boundary between both units is still debated (Kondracki, 1989). For the purposes of this paper, the separation line between the Western and Eastern Carpathians was set to the Lupkovské sedlo (Przełęcz Łupkowska) pass and the zone (here called ‘transitional zone’) eastward of the Kurovské sedlo (Przełęcz Tylicka) pass (683 m a.s.l.) was included in the Western Carpathians (Fig. 2).

The relief of the whole Carpathian chain is of Tertiary age, when these mountains were uplifted during the Alpine–Himalayan orogenic process (Kondracki, 1989). Most ranges of the Western Carpathians are of moderate altitude (ranging between 500 and 1300 m a.s.l.), only a few of them exceed 1500 m a.s.l. The highest point of the whole Carpathians, however, is located in this area (Gerlachovský štít Peak, 2655 m a.s.l., the Vysoké Tatry Mts, OGU59). The lowest parts are situated in the southern foothills in contact with the Pannonian Basin (around 100 m a.s.l.). A large part of the Western Carpathians reaching ~47% of the area is covered by deciduous (oak, hornbeam, beech), mixed (fir-beech) and conifer (spruce) forests. When excluding anthropogenic landscapes, only a small part (< 1%) of the Western Carpathian territory remains naturally treeless. Such open areas include alpine grasslands, rocky outcrops and cliffs, and the steppe formations on extremely steep and dry slopes. The geological structure of the Western Carpathians is very diversified, especially in the inner part of the

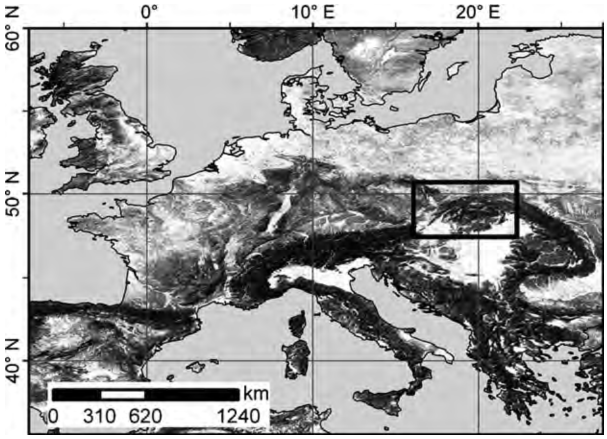

Figure 1. Geographical position of the Western Carpathians depicted schematically on the map of Europe.

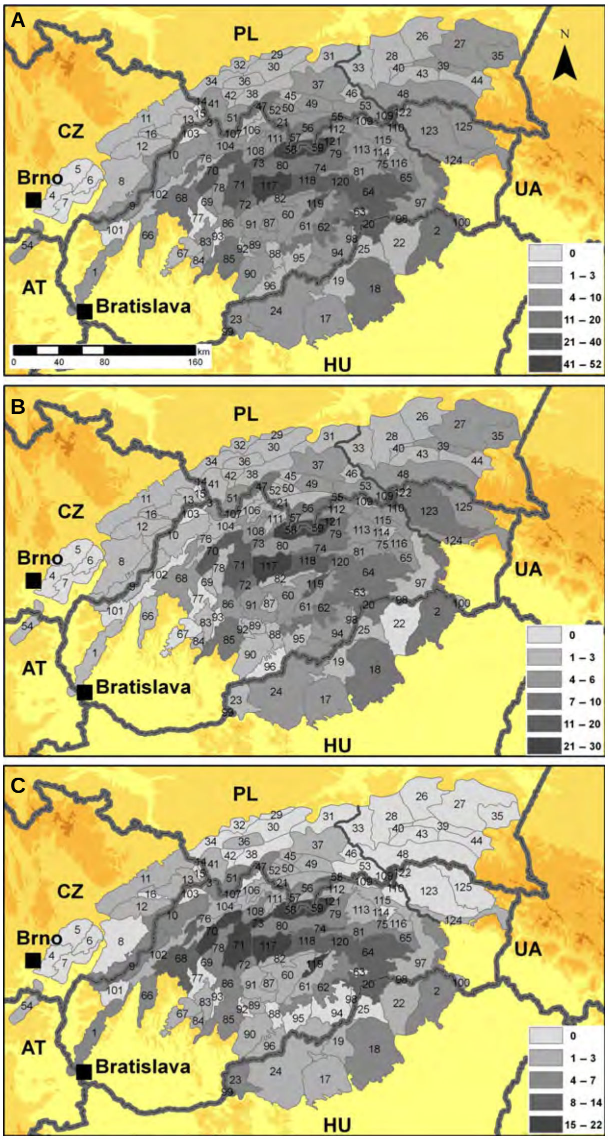

Figure 2. Patterns of vascular plant endemic richness in the geomorphological units (OGUs) of the Western Carpathians. A, Total endemism (pan-Carpathian and Western Carpathian endemics together). B, Pan-Carpathian endemism. C, Western Carpathian endemism. The OGUs are numbered according to Appendix S1. Increasing gray intensity of OGU indicates higher level of endemic richness (number of endemic taxa per OGU, see the Legends on the right bottom corners). Grey thicker line in northeast part of the Western Carpathians delineates the ‘transitional zone’ (see Study area section in Materials and Methods). Abbreviations: AT – Austria, CZ – the Czech Republic, HU – Hungary, PL – Poland, SK – Slovakia, UA – Ukraine.

arc where various kinds of bedrock (Mesozoic limestones and dolomites, Paleozoic granites and metamorphic rocks, Tertiary volcanic rocks) alternate at small distances. In contrast, the outer Western Carpathians are built almost solely from sedimentary rocks (flysch), a factor that is reflected in their rather uniform and monotonous relief (Grecula, 1997). During the Pleistocene cycles, the whole area of the Western Carpathians remained mostly unglaciated. The northernmost foothills of the Polish part, however, were reached by the continental Scandinavian ice sheet during its maximal extent in the Middle Pleistocene (the Weichselian glaciation), and the valleys in the highest ranges (usually above 1700 m a.s.l.) were covered by mountain valley glaciers (Lukniš, 1964). The mountain glaciers covered an area up to 300 km^2 during the last glacial maximum (the Würm glaciation; Gajdoš & Klaučo, 2010; Zasadni & Kłapyta, 2014) and they completely disappeared from the highest cirques around 8,500 years ago (Lindner *et al.*, 2003).

OPERATIONAL GEOMORPHOLOGICAL UNITS AND ENVIRONMENTAL VARIABLES

To show the chorological pattern of vascular plant endemism, we used the system of OGUs characterized by specific bedrock and tectonic characteristics (Czudek, 1972; Mazúr & Lukniš, 1980; Kondracki, 2002; http://www.carpates.org/cbis/orogs.html). These units thus represent ‘naturally’ delimited areas with relatively homogeneous environmental parameters and include mostly mountain ranges and inter-mountain basins. Because several OGUs in border regions were divided artificially into two different units by the state boundaries, these OGUs were merged together. In total, 125 OGUs were recognized, of which 16 were the cross-border units (Appendix S1, Fig. 2).

For each OGU we computed its size (in km^2); latitudinal and longitudinal coordinates (as centroid position of the polygon); minimal, maximal and mean altitude (in m a.s.l.); altitudinal range (in meters, computed as a difference between maximal and minimal altitude); and proportion of calcareous bedrock areas and proportion of forested area (European Commission, 1994; Miklós & Hrnčiarová, 2002; http://www.carpates.org/cbis/orogs.html). For each OGU we assessed also its endemic richness (an absolute number of endemic taxa) and weighted endemism index accounting for narrow endemic taxa (Crisp *et al.*, 2001). Because weighted endemism was tightly correlated with total number of endemic taxa per OGU (Spearman correlation test, $\rho = 0.94$, $P < 0.001$), only the latter parameter was included as a response variable in further statistical tests.

SELECTION OF TAXA

The list of endemic taxa principally follows Kliment’s (1999) survey of the endemic and subendemic taxa reported from the territory of Slovakia. Based on recent taxonomic/phylogenetic studies, our unpublished data and data kindly shared by specialists for particular taxonomic groups (see Acknowledgement), we performed further selection of taxa listed by Kliment (1999). Even after such a critical approach we are aware that our list may involve taxa that are not endemic and that some non-included taxa have been excluded erroneously. Nevertheless, we believe that such uncertainty concerns only a small number of taxa. In contrast with Kliment (1999), polyploid taxa of the large agamospermic groups as *Alchemilla*, *Hieracium s.s.*, the *Poa glauca* group, *Potentilla*, the *Ranunculus auricomus* group, *Rosa*, *Rubus*, *Sorbus* and *Taraxacum* were excluded from the present study, even though we are absolutely aware that apomixis is one of the most important speciation mechanism in vascular plants (Rieseberg & Willis, 2007). Two taxa, namely *Pilosella ullepitschii* and *Taraxacum pieninicum*, were retained in the list, as they are diploid, reproducing sexually, and detailed information on their distribution is available (Małecka, 1961; Šingliarová & Mráz, 2009; Šingliarová, Hodálová & Mráz, 2011). This situation is, however, not the case for diploid *Ranunculus carpaticola* Soó (the *R. auricomus* complex, Hörandl *et al.*, 2009) for which its detailed distribution is not known. Our major motivation for exclusion of apomictic polyploids was currently very unbalanced information on their taxonomy and distribution that may bias statistical analyses searching for putative surrogate indicators of endemic richness in the Western Carpathians.

In total, 85 endemic taxa at the level of species and subspecies were included in the list (nomenclature of taxa mostly follows Marhold *et al.*, 1998; Appendix S2, Fig. 3). Of these, 61 are endemic in the narrow sense and 24 are subendemic, whose ranges slightly exceed the territory of the Carpathians (in the case of widespread endemics not more than 5% of their localities and, in the case of very rare endemics, not more than 25% of their localities are outside of the Carpathians). In respect of the distribution within the Carpathians, we recognized two categories of endemics. The first category, the Western Carpathian endemics, includes taxa restricted to the Western Carpathians. The second category of endemics, here called the pan-Carpathian endemics, encompassed taxa that are distributed across the Carpathian arc, although not necessarily present in each of its main geomorphological units (see above). Thus, for the purpose of our study, when we attempt

Figure 3. Examples of endemic taxa of the Western Carpathians (A–D) and important habitats rich in endemic species (E, F). A. *Pulsatilla subslavica* Futák ex Goliášová – endemic to the Western Carpathians confined to the calcareous rocks and grasslands in lower and upper montane zones. B. *Daphne arbuscula* Čelak. – a narrow endemic to the Muránska planina Mts occurring on calcareous cliffs and rocks in the upper montane belt (see F). C, *Sempervivum carpathicum* subsp. *carpathicum* Wettst. ex Prodan – pan-Carpathian endemic species typical of siliceous bedrock in subalpine and alpine belts. D. *Cardamine glanduligera* O. Schwarz – pan-Carpathian sub-endemic species growing in beech and beech–fir forests. E. Calcareous rocks and alpine grasslands in the Belianske Tatry Mts (Slovakia). F. Calcareous cliffs in the forest belt in the Muránska planina Mts (Slovakia). Photograph credits: P. Turis.

to compare the Western Carpathian endemics with its narrow distribution with the Carpathian taxa with its larger distribution, we used the term 'pan-Carpathian' endemics less strictly than is usual in the literature (e.g. Kliment, 1999; Tasenkevich, 2011; Kliment, Turis & Janišová, 2016).

TAXON TRAITS, ECOLOGY AND DISTRIBUTION

For each taxon we searched for the following traits, and ecological and distributional parameters: (1) life forms according to Raunkiær (1934); (2) ploidy status (diploid vs. polyploid) and (3) ploidy level (both from Marhold *et al.*, 2007); (4) altitudinal maximum and minimum recorded (in m a.s.l.), (5) altitudinal mean value and coefficient of variation calculated from occurrence data from the Slovak Vegetation Database (Šibík, 2012; code EU-SK-001 in the Global Index of Vegetation-Plot Databases; Dengler *et al.*, 2011); (6) typical elevation zone (colline, lower montane, upper montane, sub-alpine, alpine; see Appendix S2); (7) bedrock preferences (calcareous, siliceous, intermediate, not attributed); (8) typical habitat type [grassland, woodland, sparsely vegetated habitat (rocks, cliffs, screes), not attributed; cf. EUNIS, 2008]; (9) presence/absence in plant communities classified at the level of phytosociological alliances and classes (based on the Slovak Vegetation Database, classification follows Jarolímek & Šibík, 2008); and (10) endemic status (pan-Carpathian and Western Carpathian (sub)endemics) (Appendix S2). Life forms, altitudinal maxima and minima, habitat, elevation and bedrock preferences were excerpted mostly from so-far published volumes of the multivolume compendium 'Flóra Slovenska' (Flora of Slovakia) and specialized papers focused to particular taxa. We used the number of OGUs as a proxy of the geographic range size of each taxon. Altitudinal breadth of endemics were expressed as: (1) altitudinal range (difference between minimal and maximal value ever recorded); (2) altitudinal occurrence variation expressed as a coefficient of variation from occurrence data (inferred from the Slovak Vegetation Database). To assess the width of the taxon's realized ecological niche, we used two parameters: (1) number of vegetation units (alliances) in which the taxon was recorded (classification according to the original author's assignment of the particular relevé was taken into consideration); (2) co-occurring-species-based estimation of β diversity within the relevé groups containing particular (sub)endemic taxa. Data for both parameters were derived from the Slovak Vegetation Database. For taxa with insufficient number of relevés from the Slovak part of the Western Carpathians, additional relevés from Hungarian and Polish parts were added. Multiple records of species in different layers within a relevé were combined, so that each species appeared in each relevé only once. The final matrix was based on 26 592 relevés (including 9684 relevés containing at least one endemic taxon) and 2168 vascular plant taxa (bryophytes and lichens were excluded prior to the analyses). To calculate β diversity indices, we used an algorithm proposed by Botta-Dukát (2012). This procedure, in contrast with others (e.g. Fridley *et al.*, 2007; Zelený, 2009), considers species pool matrix instead of the original species data and gives unbiased results also for saturated communities. Outliers detected using a distance-based algorithm (McCune & Mefford, 1999) were excluded. Beta diversity was calculated for taxa with seven or more occurrences in the data set. For each taxon, mean β diversity was computed from five randomly selected plots and this random selection was repeated 100 times. Calculation was made in R environment using the script prepared by D. Zelený (https://raw.githubusercontent.com/zdealveindy/juice-r/master/generalists-specialists/generalists-specialists_v6.0.r).

STATISTICAL ANALYSES

We used parametric, non-parametric and goodness-of-fit tests (specified in Results) to assess putative differences in traits, habitat and elevation zone preferences, and niche breadth of endemic taxa. To explain endemic richness patterns in the Western Carpathians expressed as a total number of endemics per OGU (square-root transformed to fit the normality of distribution of residuals) we first tested the significance of each of environmental/spatial predictors separately using linear models (maximum altitude, altitudinal range, mean altitude, proportion of calcareous bedrock areas and proportion of forest areas) and non-parametric correlation tests (area, latitude and longitude). Then, we built a multiple linear regression model with all environmental variables, but the altitudinal mean and altitudinal range (both strongly correlated with altitudinal maximum, $\rho = 0.87$ and 0.9, respectively, Spearman tests), and proportion of forested area (strongly correlated with altitudinal maximum, $\rho = 0.8$, Spearman test). We used the 'glmulti' function from the 'glmulti' library (Calgano & de Mazancourt, 2010) and information criteria (AIC, BIC) to select the best linear model. To visualize the relationships among the OGUs that had at least one endemic taxon, we performed different hierarchical cluster analyses (UPGMA, single linkage, complete linkage, ward method) using a binary distance approach within the hclust and pvclust libraries. The robustness of the obtained trees was tested using multiple scale bootstrap resampling procedure (10 000 replications). All computations and plotting were made using basic statistic packages in the R environment (R Core Team, 2013).

RESULTS

General evaluation of vascular plant endemism in the Western Carpathians

In total, 85 pan-Carpathian and Western Carpathian endemic and subendemic taxa were included in our study representing 2.8% of native vascular plant flora of the Western Carpathians (all plants but neophytes, calculation based on Tasenkevich, 1998). The total number of taxa in the Western Carpathian flora, however, encompasses also around 500 taxa belonging to the large apomictic groups (e.g. *Alchemilla*, *Hieracium*, *Sorbus*, *Taraxacum*), the endemic polyploid taxa of which have not been included in our list (see Materials and Methods). When omitting apomictic complexes, the endemic taxa would represent 3.4% of native vascular flora of the Western Carpathians. When considering only taxa endemic or subendemic to the Western Carpathians, then 1.8% of native Western Carpathian flora (apomictic complexes excluded) is endemic to that region.

Species traits, habitat preferences, altitudinal and niche breadths

Eighty-five endemic taxa belonged to 55 genera and 25 APGIII (Angiosperm Phylogeny Group, 2009) families. The highest numbers of endemic taxa were found in the genera *Campanula*, *Dianthus* and *Soldanella*; and in families Asteraceae, Poaceae and Brassicaceae (Supporting Information, Figs S1 and S2). Hemicryptophytes were by far the most frequent among endemics (80%), while remaining life forms were substantially less common ($\chi^2 = 137.5$, d.f. = 3, $P < 0.001$, Fig. 4A). Polyploid taxa were slightly more frequent than diploid taxa (52% vs. 48%, Fig. 4B), but this difference was not significant ($\chi^2 = 0.195$, $P < 0.7$). Polyploids did not differ from diploids in any of tested traits (life forms, habitat preferences, distributional range, altitudinal and niche breadths; results not shown). Most endemics were confined to the upper and lower montane belts, followed by taxa with typically alpine and subalpine elevation zone preferences. Endemics of the colline belt were the least represented (Fig. 5A). There was no statistically significant difference, however, in the frequency of taxa confined to specific elevation zone ($\chi^2 = 7.294$, d.f. = 4, $P < 0.2$). Almost 64% of endemic taxa occurred solely on calcareous bedrock, while only 12% and 21% occurred on siliceous or both types of bedrocks, respectively ($\chi^2 = 72.6$, d.f. = 3, $P < 0.001$, Fig. 5B). The non-forest habitats (rocks/screes and grasslands, both having 37% of proportion, Fig. 5C) had significantly higher number of endemics compared with forest habitats (18% of proportion; $\chi^2 = 28.7$, d.f. = 1, $P < 0.001$). Woodland species showed a significantly larger distribution (as number of occupied OGUs) than typical grassland species, but not than the endemics confined to the rock habitats (Kruskal–Wallis multiple comparison test at $P < 0.05$, Fig. 6A). Endemics with no bedrock specialization ('intermediate') had significantly larger ranges than both calcareous and siliceous specialists, respectively (Kruskal–Wallis multiple comparison test at $P < 0.05$, Fig. 6B). Of 60 vegetation alliances, the highest occurrence of endemics (up to 45%) was recorded in vegetation communities typical of open rocky calcareous stands of montane to sub-alpine belts, with highest incidences in the *Astero alpini–Seslerion calcariae*, *Seslerion tatrae* and *Caricion firmae* alliances, all belonging to the *Elyno–Seslerietea* class. There was no significant difference between the diploid and polyploid taxa neither in their altitudinal and niche breadths, nor in their range sizes (expressed as number of OGUs, results not shown). The co-occurring-species-based β diversity character-

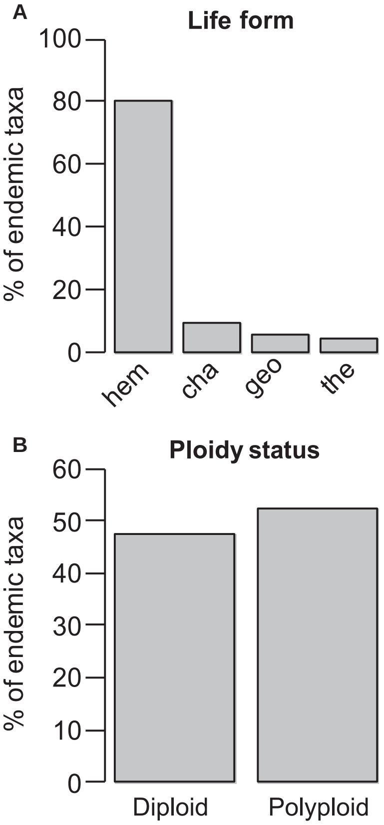

Figure 4. Proportions of life forms (A) ($\chi^2 = 137.5$, d.f. = 3, $P < 0.001$), and ploidy levels (B) ($\chi^2 = 0.195$, $P < 0.7$) in endemic vascular plants of the Western Carpathians. Abbreviations: hem – hemicryptophyte, cha – chamaephyte, geo – geophyte, the – therophyte.

izing the width of the taxon's realized niche was strongly correlated with the number of vegetation plots in which an endemic taxon was recorded, number of vegetation units (alliances), and altitudinal range (Spearman tests, $\rho = 0.757$, 0.825, 0.604; $P < 0.001$ for all) but not with altitudinal occurrence variation (Spearman test, $\rho = 0.369$, $P < 0.2$). There was a strong positive correlation between the distribution range of endemic taxa (expressed as number of OGUs) and breadth of their ecological niche based on β diversity values (Spearman test, $\rho = 0.436$, $P < 0.001$, Fig. 7). Larger distributional ranges were also positively correlated with an altitudinal range (Spearman test, $\rho = 0.571$, $P < 0.001$) and numbers of vegetation units in which endemics were recorded (Spearman test, $\rho = 0.595$, $P < 0.001$), but not with variation in altitudinal occurrence (Spearman test, $\rho = 0.109$, $P < 0.2$).

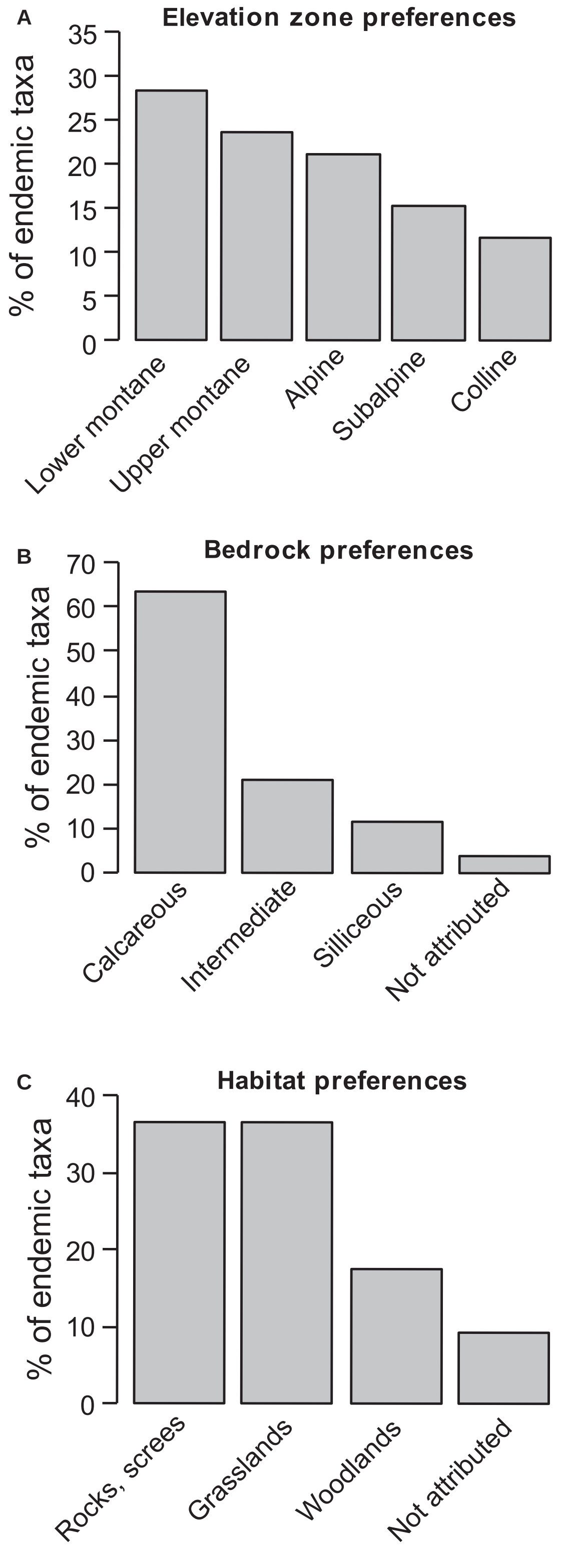

Figure 5. Proportions of typical elevation zones (A) ($\chi^2 = 6.9412$, d.f. = 4, $P < 0.2$), bedrock preferences (B) ($\chi^2 = 72.6$, d.f. = 3, $P < 0.001$), and habitat preferences (C) ($\chi^2 = 19$, d.f. = 3, $P < 0.001$) of endemic vascular plants of the Western Carpathians.

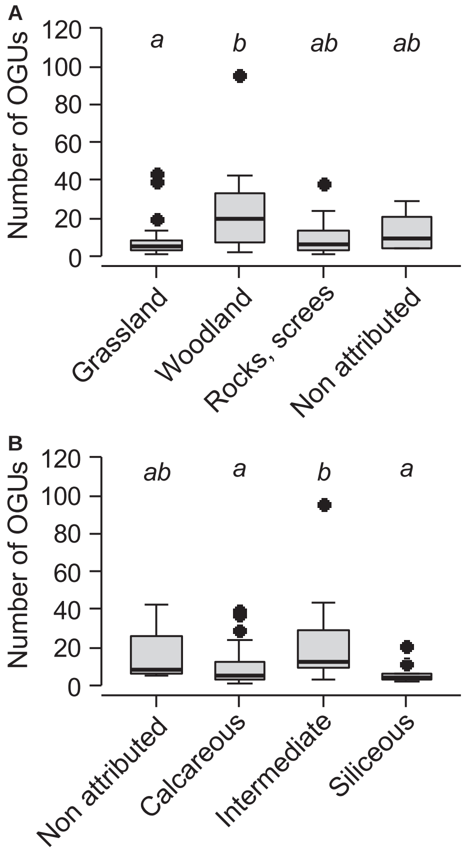

Figure 6. Variation in distribution ranges expressed as number of occupied OGUs in different classes of habitat (A) and (B) bedrock preferences of vascular plant endemics in the Western Carpathians. ^{a,b}Different letters above each boxplot mean statistically significant differences among the tested groups at the level $P < 0.05$ (Kruskal–Wallis multiple comparison test).

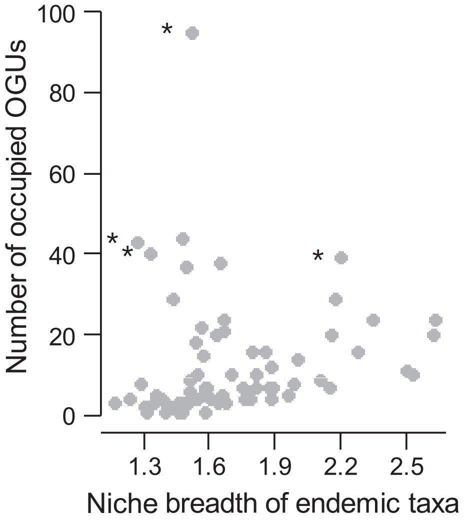

Figure 7. Relationship between breadth of ecological niche based on the co-occurrence data (β diversity) and distributional range of vascular plant endemics in the Western Carpathians ($\rho = 0.436$, $P < 0.001$). Asterisks depict woodland taxa (*Aconitum moldavicum*, *Cardamine glanduligera*, *Scilla kladnii* and *Symphytum cordatum*) with a very large distribution (# of occupied OGUs).

COMPARISON BETWEEN THE WESTERN CARPATHIAN ENDEMICS AND PAN-CARPATHIAN ENDEMICS

When searching for differences in traits, habitat preferences, distributional ranges and breadth of ecological niches between the Western Carpathian endemics with overall narrower distribution and the pan-Carpathian endemics showing overall larger distribution, we did not find statistically significant results for most comparisons (results not shown). Significant correlations, however, were displayed regarding frequency of taxa that were typical of a particular elevation zone, mean altitude and variation in altitudinal distribution.

In the first case, there was a higher proportion of taxa confined to the lower and upper mountain belts among the Western Carpathian endemics, while taxa confined to the sub-alpine and alpine belts prevailed among the pan-Carpathian endemics ($\chi^2 = 15.9$, d.f. = 4, $P < 0.01$, Fig. 8A). In the second comparison, the pan-Carpathian endemics had on average a higher mean value of altitudinal occurrences than the Western Carpathian taxa (*t*-test, $t = 2.06$, d.f. = 73.1, $P < 0.05$), this finding is in line with the results of the previous test. Finally, the Western Carpathian endemics varied more (mean of coefficient of variation = 22.8%) in their altitudinal distribution than the pan-Carpathian endemics (mean of coefficient of variation = 17.4%; *t*-test, $t = -1.95$, $P < 0.06$). Furthermore, the pan-Carpathian endemics had on average larger distribution ranges in the Western Carpathians than the Western Carpathian endemics (mean number of OGUs per taxon = 14 and 9, respectively, Wilcoxon test, $W = 1103$, $P < 0.1$, Fig. 8B). From an evolutionary point of view, it is worth noting that there were more polyploids than diploids among the Western Carpathian endemics (58% vs. 42%, Fig. 8C) than among the pan-Carpathian endemics (46% vs. 54%), although this difference was not significant ($\chi^2 = 0.7464$, d.f. = 1, $P < 0.4$). Moreover, the Western Carpathian endemics included more high ploidy

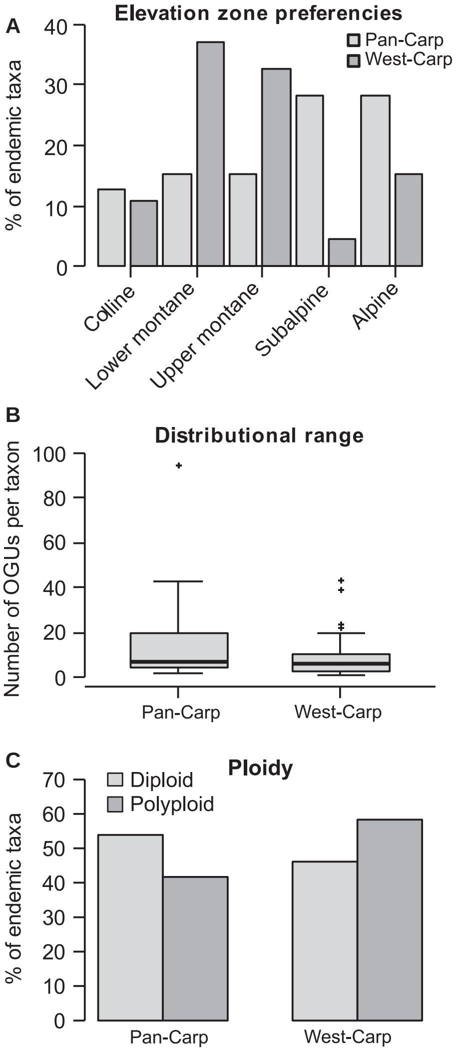

Figure 8. Comparison of Western Carpathian endemics with pan-Carpathian endemic taxa occurring in the Western Carpathians for elevation zones preferences (A) ($\chi^2 = 15.8$, d.f. = 4, $P < 0.01$), variation of distribution range (expressed as the number of OGUs occupied per taxon) (B) ($W = 1103$, $P < 0.1$, Figure 8B), and ploidy level proportion (C) ($\chi^2 = 0.7464$, d.f. = 1, $P < 0.5$).

taxa (i.e. those above the tetraploid level) than pan-Carpathian endemics, but again this difference was not significant ($\chi^2 = 0.52$, d.f. = 1, $P < 0.5$).

SPATIAL PATTERNS OF ENDEMIC RICHNESS AND THEIR ASSOCIATIONS WITH ENVIRONMENTAL VARIABLES

From 85 endemic taxa, 83 were recorded in Slovakia, 53 in Poland, 20 in Hungary, seven in the Czech Republic and two in Austria. Endemic richness per OGU showed a clear leptokurtic pattern, with many OGUs possessing few endemics, and few OGUs had high levels of endemism (Supporting Information, Fig. S3). The highest number of endemic taxa was recorded in the Západné Tatry/Tatry Zachodnie (OGU58) (61% of all surveyed endemics occurred here), followed by the Ďumbierske Nízke Tatry (OGU117) and Belianske Tatry (OGU121; Fig. 2A). These OGUs together with the Vysoké Tatry/Tatry Wysokie (OGU59) also exhibited the highest concentration of the endemics with a very narrow distribution (weighted endemism values in Appendix S1, and Supporting Information, Fig. S4). A similar pattern in endemic richness was observed for the pan-Carpathian endemics (in descending order: Západné Tatry/Tatry Zachodnie, Belianske Tatry, Ďumbierske Nízke Tatry), and for the Western Carpathian endemics [Západné Tatry/Tatry Zachodnie, and Ďumbierske Nízke Tatry, Malá Fatra (OGU70) and Vel'ká Fatra (OGU71), the three latter had the same number of endemic taxa] (Fig. 2B, C), respectively. The comparison of the geographical distribution patterns between the two groups of endemics, the pan-Carpathian and the Western Carpathian endemics, showed that the latter is completely absent from most of OGUs in the north-eastern part of the Western Carpathians, while at least some pan-Carpathian endemics are present there (Fig. 2B, C).

Different cluster analyses searching for similarities in the distribution patterns of endemic taxa among OGUs consistently showed three main clusters (A, B, C; see Fig. 10), but with no statistical support for each of them. The three major clusters roughly corresponded to the three geographic regions of the Western Carpathians. Cluster A included the OGUs situated on the north and north-east margin of the Western Carpathians (flysch zone in Poland and NE Slovakia), which showed generally the lowest endemic richness. In these OGUs only small numbers of the pan-Carpathian and almost no Western Carpathian endemics were recorded (Fig. 2B, C). Cluster B encompassed the OGUs situated mainly in the central part of the Western Carpathians with varying levels of endemic richness, but showing a higher proportion of the Western Carpathian endemics. Within this major cluster, seven OGUs with the highest endemic richness were clustered together (Fig. 10, cluster marked by '*') with a relatively high statistical support (AU = 88, where AU is the approximately unbiased P-value ranging from 0 to 100). Finally, cluster C consisted of OGUs situated on the eastern and southern margin of the Western Carpathians and showed in general higher endemic richness and more Western Carpathian endemics than the OGUs from cluster A.

ENDEMIC RICHNESS AND ITS ASSOCIATIONS WITH ENVIRONMENTAL VARIABLES

When tested separately, most of the environmental/geographical variables were rigorously associated with total endemic richness (Table 1). Specifically, endemic richness significantly increased with increasing altitude of OGU (all three variables), proportion of calcareous and forested areas, total area and eastern longitude, but significantly decreased with northern latitude. When considering multiple environmental variables and their interactions, the best linear model explained almost 75% of endemic richness in the Western Carpathians, with maximum altitude and its interactions with a proportion of calcareous areas and total area of OGUs as the best predictors (Table 2). In other words, endemic richness was highest in those OGUs that showed the highest altitude (Fig. 9A), and at the same time had a higher proportion of calcareous areas (Fig. 9B), and were larger. Model prediction slightly increased ($r = 79\%$) when the geographic position of OGU expressed as an interaction between longitude and latitude was added to the best model (Table 2).

Table 1. Results of linear regression models (lm) and correlation tests (corrS, Spearman two-sided correlation test) that examine the relationship between endemic richness pattern and environmental and spatial variables across 125 OGUs in the Western Carpathians. Endemic richness expressed as the total number of endemic taxa (square-root transformed) per OGU was used as a response variable. All predictors were tested separately

OGUs variable	Test	r^2 or ρ	P-value
Maximal altitude	lm	0.56	< 0.001
Altitudinal range	lm	0.48	< 0.001
Mean altitude	lm	0.46	< 0.001
Latitude	corrS	−0.208	0.02
Longitude	corrS	0.244	0.006
Proportion of calcareous areas	lm	0.39	< 0.001
Proportion of forested areas	lm	0.25	< 0.001
Area size	corrS	0.19	0.03

Table 2. Results of two linear regression models which include the best environmental and geographic predictors of vascular plant endemic richness across 125 operational geomorphological units (OGU) in the Western Carpathians

Variable and interaction terms	Slope	SD	*P*-value
Model without spatial position of OGUs			
Intercept	3.01×10^{-1}	1.8×10^{-1}	0.09
Altitudinal maximum	1.34×10^{-3}	2.1×10^{-4}	< 0.001
Altitudinal maximum × calcareous area	2.02×10^{-5}	2.51×10^{-6}	< 0.001
Altitudinal maximum × area	6.85×10^{-7}	1.52×10^{-7}	< 0.001
Model with spatial position of OGUs			
Intercept	-4.68	-9.67×10^{-1}	< 0.001
Altitudinal maximum	1.35×10^{-3}	1.91×10^{-4}	< 0.001
Altitudinal maximum × calcareous area	2.07×10^{-5}	2.04×10^{-6}	< 0.001
Latitude × longitude	5.16×10^{-3}	9.89×10^{-4}	< 0.001
Altitudinal maximum × area	6.35×10^{-7}	1.38×10^{-7}	< 0.001

DISCUSSION

VASCULAR PLANT ENDEMISM IN THE WESTERN CARPATHIANS AND ITS COMPARISON WITH THE SOUTH-EASTERN CARPATHIANS

The absolute number of taxa endemic to the Western Carpathians is lower than the number of taxa endemic to the South-Eastern Carpathians (46 vs. 105, Hurdu *et al.*, 2012a), and the proportion of narrow endemics in the Western Carpathian flora (excluding apomicts) is 1.8%, i.e. almost two-fold lower than in the South-Eastern Carpathians (3.5%). Lower endemic richness in the Western Carpathians when compared with the South-Eastern Carpathians, even when accounting for different taxonomic concepts and criteria of selection of endemic taxa adopted by different authors (e.g. Pawłowski, 1970; Kliment, 1999; Tasenkevich, 2011; Hurdu *et al.*, 2012b), might be explained in principle by two interplaying factors.

The first important factor is the large difference in the area. The South-Eastern Carpathians cover twice as large a surface (two-thirds of the area of the Carpathians) than the Western Carpathians (see Materials and Methods). It is not surprising, therefore, that endemic richness in the former region is higher, as there is a generally accepted positive correlation between endemic richness and area size (e.g. Anderson, 1994).

The second major aspect likely influencing the differences in endemic richness is related to the different geographical position of the two ranges including their latitudinal extent (Fig. 1), and accordingly, to their climatic conditions at present (Spinoni *et al.*, 2015) and in the past (e.g. Urdea, 2004). This factor might have strongly influenced the endemic richness pattern in several ways. Pawłowski (1970) suggested that the impact of Pleistocene glaciation was greater in the Western than in the South-Eastern Carpathians, because of the northern position of the Western Carpathians and their closer proximity to the continental (Scandinavian) ice sheet during the course of repeated glacial periods (Marks, 2005). Consequently, the climate in the Western Carpathians was harsher with a *c.* 200 m lower snow line during the last glacial maximum than in the Southern Carpathians (Urdea, 2004). This difference might have shaped the distributional patterns of plant taxa, especially the thermophilous ones, and resulted in floristic impoverishment of the Western Carpathians. A further important factor is geographic interconnection between the South-Eastern Carpathians and the Balkan mountains (Fig. 1), which is known as one of the most prominent European biodiversity hotspots (Griffiths, Kryštufek & Reed, 2004). Indeed, the flora of the South-Eastern Carpathians has been influenced and enriched by interchange with the species-rich mountains of the Balkan Peninsula (e.g. Szeląg, 2006; Puşcaş *et al.*, 2008; Šingliarová *et al.*, 2011; Stachurska-Swakoń, Cieślak & Ronikier, 2013) more than more distant and isolated Western Carpathians flora. These factors together with an obvious latitudinal gradient in vascular plant diversity in Europe driven mostly by water–energy dynamics (cf. Kreft & Jetz, 2007) might contribute to the higher genetic pool available for speciation/survival in the South-Eastern Carpathians than in the Western Carpathians.

SPECIES TRAITS, POLYPLOIDY, HABITAT PREFERENCES, ALTITUDINAL BREADTHS AND NICHE BREADTHS

The highest number of endemic taxa was recorded in the largest families occurring in the Western Carpathians, i.e., in Asteraceae, Poaceae and Brassicaceae (cf. Tasenkevich, 1998), while at the generic level the endemics belong mostly to small- or medium-sized families (Campanulaceae, Primulaceae,

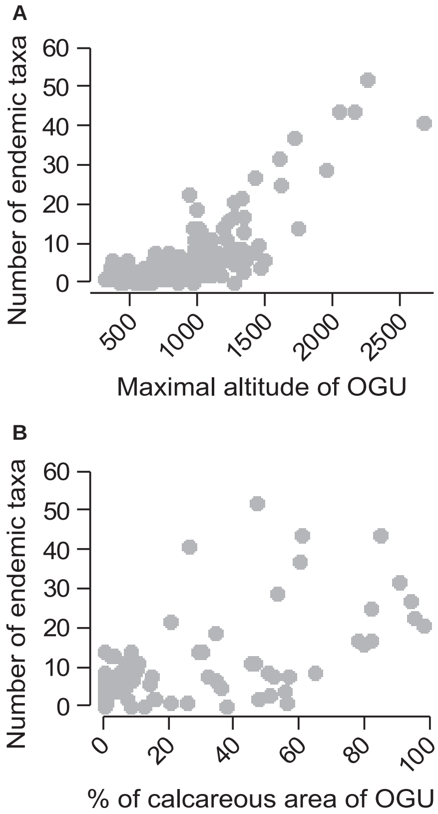

Figure 9. Relationship between endemic richness expressed as the number of endemic taxa per OGU in the Western Carpathians and maximal altitude of OGU (A) ($r^2 = 0.56$, $P < 0.001$), and proportion of calcareous areas of OGU (B) ($r^2 = 0.39$, $P < 0.001$).

Poaceae, Papaveraceae). Similar patterns were found in the Alps (Essl *et al.*, 2009; Aeschimann *et al.*, 2011a) and the South-Eastern Carpathians (Hurdu *et al.*, 2012b). The same trend holds for the overrepresentation of the hemicryptophytes among endemics (80%), as this life form is the most frequent in the central European mountains (cf. Aeschimann, Rasolofo & Theurillat, 2012a).

We found no differences between diploids and polyploids in any of tested traits, altitudinal and niche breadths, and distribution ranges. Furthermore, the proportion of both ploidy types among endemics was rather equal, although slightly in favour, for polyploids (52%). This trend was however more obvious when we compared the Western Carpathian endemics with the pan-Carpathian endemics. Based on the logical assumption that polyploid state is derived, while diploid is ancestral (Favarger & Contandriopoulos, 1961), the preponderance of polyploidy among the Western Carpathian endemics (58%) might indicate that most Western Carpathian endemics are younger (neoendemics) when compared with the pan-Carpathian endemics, in which the diploids prevailed (56%). In this respect, it would be interesting to perform a similar karyological comparison for the South-Eastern Carpathian endemics. It is important to note, however, that the overall proportion of polyploids among endemics in the Western Carpathians would dramatically change, reaching almost 79%, if the apomictic endemics were be included in the analyses.

Our data indicate the predominance of the endemics (52%), which are typically confined to lower and upper montane elevations (500–1500 m a.s.l.), while those typically confined to the alpine and sub-alpine belts (1500–2650 m a.s.l.) are less frequent (37%) (Fig. 5). This pattern might be at first glance surprising given the fact that our data clearly showed that the highest endemic richness is confined to the highest mountain ranges. The highly elevated OGUs, however, always encompass the upper montane belt and sometimes, at least partly, also the lower montane belt (Appendix S1). Highly elevated OGUs thus show greater altitudinal variation suitable for a larger assembly of endemics with different altitudinal preferences than lower elevated OGUs. In the Alps the endemic richness pattern culminates at higher altitudes (Essl *et al.*, 2009; Aeschimann, Rasolofo & Theurillat, 2011b); this is not the case for the Western Carpathians. This discrepancy might be due to the different approach applied for the calculation of endemic richness. In our study we used a rather rough scale of typical altitudinal preferences of endemic taxa (see Material and Methods), while Essl *et al.* (2009) applied a more detailed distribution survey across a finely defined altitudinal gradient, and Aeschimann *et al.* (2011b) expressed endemic richness as a proportion of endemics of total numbers of species for a given belt. The last method, when applied to our data set would probably increase the proportion of endemic taxa in sub-alpine and alpine zones as the total species pool of these belts is considerably lower than that in the montane belt (cf. Aeschimann *et al.*, 2011b). Unfortunately, there are no available data on detailed altitudinal distribution of all native vascular plants in the Western Carpathians to confirm this assumption.

The statistically significant trend for the higher proportion of taxa confined to the lower and upper mountain belts was mostly driven by the Western Carpathian endemics, while the pan-Carpathian endemics prevailed among the alpine and sub-alpine taxa (Fig. 8). This finding goes against an intuitive assumption that the pan-Carpathian endemics with a larger distribution should prevail at lower altitudes due to the absence of strong migration barriers between the Western and South-Eastern Carpathians.

The Western Carpathian endemics with a narrower distribution should occur mainly at higher altitudes due to the more pronounced geographical isolation of alpine and sub-alpine belts between the Western and South-Eastern Carpathians. One plausible explanation could be the difference in average altitude between both chains, being much lower in the former and which might drive the preference of local endemics. Furthermore, given the fact that the endemic taxa analysed in this study represent a taxonomically heterogeneous group with a different evolutionary history and finally with different functional traits, there is probably no unifying, straightforward explanation for such a pattern and the putative causalities might be taxon dependent. We suppose that at least some portion of the Western Carpathians endemics could evolve relatively recently (see the discussion on different proportion of diploids and polyploids), and simply they had no time to spread further. In addition to young evolutionary history, effective spread of young endemics could be hampered, also due to the absence of suitable habitats. In fact, an absolute majority of the Western Carpathian endemics, which are typically distributed at lower altitudes (more than 80%), is strictly confined to the calcareous rocks – the habitat that is completely missing in the north-eastern part of the western and north-western part of the Eastern Carpathians. Habitat availability might thus explain the absence of the Western Carpathian endemics in that part of the Carpathians (Fig. 2, and below). In other taxa, as a narrow endemic *Daphne arbuscula*, low seed production might prevent the colonization of new suitable habitats even in geographically close regions (Erdelská & Turis, 1995; Erdelská, 1999).

Similar to other case studies focused on endemism in mountain systems (e.g. Médail & Verlaque, 1997; Casazza, Barberis & Minuto, 2005; Essl *et al.*, 2009; Aeschimann, Rasolofo & Theurillat, 2012b) we found that most of the endemics were confined to non-forest habitats, like rocks, screes or dry or alpine grasslands. Among these, rocky habitats offer stable environmental conditions through time and show at the same time high microtopological (aspect, inclination, substrate) and corresponding ecological (light, temperature, water, wind) heterogeneity at very short distances (centimetres/metres) (e.g. Scherrer & Körner, 2011). Thus, in the case of climatic instability, the plants can simply move vertically or horizontally (exposition) to find more suitable conditions. This environmental buffering on a microscale might explain that why the majority of plants endemic to Europe are confined to rocky/screes habitats (Hobohm, 2008) and this pattern is obvious also in the Western Carpathians with almost 37% of endemics occurring on rocks/screes. In contrast, despite their much larger area (see Material and Methods), forest habitats harboured only a small number of endemic taxa. This finding is likely due to repeated Pleistocene glaciations, which destroyed most of the forest flora in Central Europe (Vanderplank *et al.*, 2014) and to more homogeneous forest habitats with stronger interspecific competition.

The predominance of calcicolous taxa in the endemic flora of the Western Carpathians (64% of endemics) is striking when compared with the rather restricted surface of calcareous bedrocks in that area (13.1%). This pattern is, however, consistent with that found not only in different parts of the Alps (Médail & Verlaque, 1997; Casazza *et al.*, 2005; Essl *et al.*, 2009; Aeschimann *et al.*, 2012b) but also in Sicily (Bonanno, 2013). In these regions, the proportion of endemics favouring basic bedrocks reaches fairly similar values (59–65%), and it is in line with generally higher species richness on calcareous bedrocks in temperate zones of Europe (Ewald, 2003). As an explanation, it has been proposed that the larger species pool of calcicolous taxa (and accordingly higher proportion of calcicolous endemics) in Central Europe when compared with the silicicolous taxa is likely due to a strong environmental drift during long cold periods of Pleistocene when a disproportional reduction of mature soils happened in favour of young loess sediments rich in calcium (Pärtel, 2002; Ewald, 2003). As a result, the contemporary flora has been selectively impoverished in silicicolous taxa (Ewald, 2003).

Both, altitudinal and realized niche breadths appear to be important factors involved in the distribution success of endemic plants in the Western Carpathians. The wider the breadth, the larger is the taxon's range. The positive niche breadth–range size association seems to be a general pattern in plants (Slatyer, Hirst & Sexton, 2013), and was confirmed also by other studies focused on endemic species (e.g. Essl *et al.*, 2009; Trigas *et al.*, 2012; Bonanno, 2013; Totté, Delgado & Meerts, 2015). The same position holds for the positive relationship between altitudinal breadth and range size proved in ours and other studies (e.g. Essl *et al.*, 2009; Totté *et al.*, 2015).

SPATIAL PATTERNS OF ENDEMIC RICHNESS AND THEIR ASSOCIATIONS WITH ENVIRONMENTAL VARIABLES

Our data showed that pattern of vascular plant endemism is not random but is geographically structured (Figs 2, 10). The highest number of endemics is concentrated in the OGUs situated in the central part of the Western Carpathians. Conversely, the

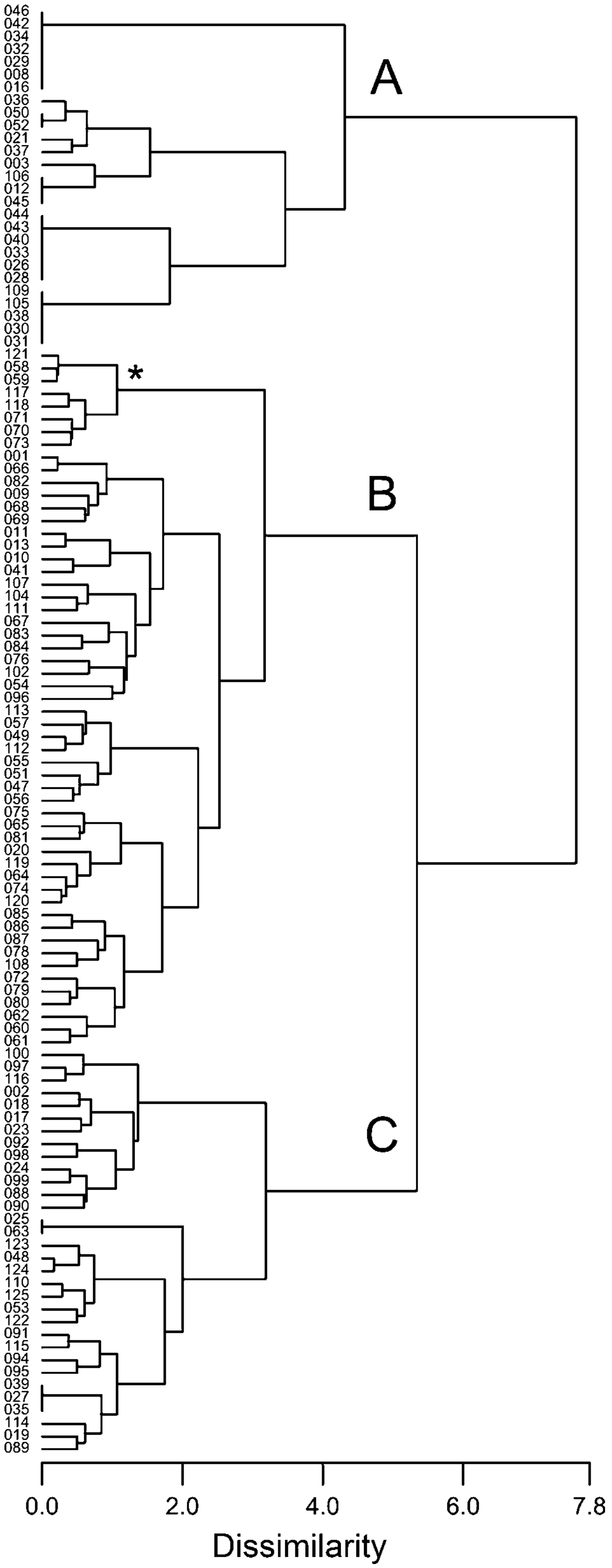

Figure 10. Cluster analysis of OGUs (Ward method) based on the distribution of vascular plant endemism in the Western Carpathians (OGUs with no endemics were excluded prior to the analysis). The OGUs are numbered according to Appendix S1 (see also Fig. 2). The letters denote three main clusters and asterisk ('*') depicts the sub-cluster encompassing the OGUs with the highest endemic richness in the Western Carpathians (see text for more details).

endemics-poor OGUs are situated in the north, north-western and western margin of the Western Carpathians, and sometimes also in the inner parts, especially if they represent densely populated intermountain basins. The general pattern of endemic richness is very similar to those published by Pawłowski (1970) and Hendrych (1981), both however at a very coarse/schematic scale, and that of Tasenkevich (2011, 2014) who used phytogeographically defined OGUs. By using a finer, geomorphological division, our study provided with a more detailed view on endemic richness pattern in the Western Carpathians.

The strong geographical structure of the endemic richness pattern in this area is undoubtedly due to strong spatial autocorrelation with altitudinal maxima and proportion of calcareous areas of OGUs, which are highest in the central part of the Western Carpathians. Specifically, the highest endemic richness was found in those OGUs that reach at least 2000 m of altitude and at the same time show a relatively high proportion of limestone bedrock (around 30% and more of the OGU's area). The lower proportion of calcareous rocks in the Vysoké Tatry/Tatry Wysokie (OGU59, see Appendix S1) might thus explain why the highest mountain range in the Western Carpathians and in the entire Carpathian chain does not harbour the highest number of endemic taxa, but it is ranked behind the Západné Tatry/Tatry Zachodnie, Ďumbierske Nízke Tatry and Belianske Tatry which are from 400–600 m altitude lower.

The higher endemic richness found in higher elevated OGUs with a preponderant proportion of calcareous bedrock can be ascribed to greater environmental heterogeneity manifested in a greater range of altitudinal zonation (usually beginning from lower mountain belt), aspect, inclination and nutrient resources. All these attributes may dramatically vary even on a very small scale. Such levels of microhabitat diversity and topographically associated microclimate variation might not only offer a wide range of niches but also buffer the impact of climate changes during climatic fluctuations and might provide a chance for survival for spatially restricted species (Jansson, 2003; Stewart *et al.*, 2010; Scherrer & Körner, 2011).

Although we found significantly more endemics confined to open (i.e. non-forest) habitats than to forest habitats, the overall endemic richness was positively correlated with the proportion of forested areas per OGU. This seeming paradox is because the OGUs with a higher proportion of forest habitats are those OGUs that also have a higher proportion of relictual habitats (rocks, cliffs) to which the endemics are mostly confined.

SPATIAL ENDEMIC RICHNESS PATTERNS DIFFER AMONG WESTERN AND PAN-CARPATHIAN ENDEMICS

Interestingly, the distribution of pan-Carpathian endemics differs slightly from that of the Western Carpathian endemics in the north-easternmost margin of the Western Carpathians (Figs 3B, C, 10), which is considered to constitute a transitional zone between the Western and Eastern Carpathians (see Materials and Methods). The complete absence of the Western Carpathian endemics in that part of the Carpathians might be likely caused by the lack of suitable habitats as this part has low altitudes and is characterized by a uniform bedrock (Tertiary sedimentary flysch), which provides it with a rather flat relief without important formations of open rocky habitats. On the contrary, several pan-Carpathian endemics confined to the deciduous forests (*Cardamine glanduligera*, *Scilla kladnii* or *Symphytum cordatum*) occur there. The distribution patterns of these and other pan-Carpathian species, like *Campanula carpatica* or *Aconitum moldavicum* in the eastern and central parts of the Western Carpathians, might support the hypothesis on their origin in the South-Eastern Carpathians with subsequent migration to the Western Carpathians (Hendrych & Hendrychová, 1979). We suggest, therefore, that both environmental conditions and historic migrations shaped the current distributional patterns of vascular plant endemics in the Western Carpathians.

CONCLUDING REMARKS AND PERSPECTIVES

Our study provides the first detailed and synthetic insight on the endemic richness pattern of vascular plants and its associations with biological traits and environmental variables in the territory of the Western Carpathians as a whole, regardless of political boundaries. During the collection of taxonomic and chorological data and statistical analyses several issues have emerged that could outline further research on vascular plant endemism in the Western Carpathians and the Carpathians as well:

1. Although the taxonomic status of many Carpathian endemic taxa is indisputable, there is a large number of taxa which may be considered to be 'critical', i.e. with unclear taxonomy/distribution. Any effort, therefore, aimed at solving the taxonomy/systematics of such taxa including agamospermic groups within their distributional ranges is of a high interest, especially when an evidence is based on the combination of thorough morphological analysis with other methods (molecular, karyological). Hence, several recent studies have refused (e.g. Kolarčik, Zozomová-Lihová & Mártonfi, 2010; Španiel *et al.*, 2011), questioned (Olšavská *et al.*, 2015) or confirmed (Olšavská *et al.*, 2011; Kučera *et al.*, 2013; Šingliarová *et al.*, 2011) endemic status previously suggested for several taxa. In some cases, even new taxa, endemic to the Carpathians were distinguished (e.g. Letz & Marhold, 1998; Hodálová, 1999). Solid taxonomy should be, moreover, accompanied by critical and thorough revision of distribution (e.g. based on herbarium specimens) to provide biogeographically relevant data.
2. It has been proposed that several Western and pan-Carpathian endemic taxa are paleoendemics, i.e. of Tertiary age (e.g. Pax, 1898; Soó, 1933; Pawłowski, 1970; Futák, 1981; Hendrych, 1981; Kliment, 1999). These assumptions are based on striking morphological differences when compared with morphologically similar relatives. However, because morphological evolution might be very rapid and might include homoplasies, solid phylogenetic inference is necessary to reveal true evolutionary relationships and history. Surprisingly, there are no published studies with dated phylogenies that were aimed at testing the hypothesis on the Tertiary origin of Carpathian endemic plants, except Lendvay *et al.* (2016). This study based on the internal transcribed spacer marker has challenged the assumption on paleoendemic status of *Syringa josikaea* (Oleaceae), and rather suggested a more recent Pleistocene divergence event. With the advent of next generation sequencing tools, there is a hope that in the near future we gather more accurate and robust data on the evolutionary history of the Carpathian flora.
3. In our study, we used the geomorphological units as mapping operational units, which however vary several fold in their size. By applying more even reference systems (e.g. grid-based approach according to the central European grid mapping scheme, Niklfeld, 1971), estimation of distributional patterns of endemic taxa will be more precise and unbiased in respect of the area size. Such data might unravel some hidden aspects, although the general pattern as proposed in our study will probably remain unchanged (cf. Tribsch & Schönswetter, 2003; Tribsch, 2004; Essl *et al.*, 2009).

4. Several studies dealing with different aspects of endemism have recently been published in several Carpathian countries separately (e.g. Kliment, 1999; Piękoś-Mirkowa & Mirek, 2009; Tasenkevich, 2011; Hurdu *et al.*, 2012a,b). Therefore, if would be highly interesting to apply the same analytical approach as in the present paper on the data set concerning the Carpathians as a whole.

ACKNOWLEDGEMENT

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. List of operational geomorphological units of the Western Carpathians (OGUs) and their characteristics.

Appendix S2. List of endemic taxa of the Western Carpathians, their traits and habitat preferences.

Appendix S3. List of endemic taxa of the Western Carpathians and their distribution across the operational geomorphological units (OGUs) of the Western Carpathians.

Figure S1. Number of endemic taxa (species and subspecies) per AGPIII family in the Western Carpathians.

Figure S2. Number of endemic taxa (species and subspecies) per genus in the Western Carpathians.

Figure S3. Frequency of OGUs according to endemic richness (number of endemic taxa).

Figure S4. Patterns of weighted endemism scores (the higher values means a higher frequency of rare-range-restricted taxa) in the geomorphological units (OGUs) of the Western Carpathians.