Tuexenia 40: 499–526. Göttingen 2020.
doi: 10.14471/2020.40.018, available online at www.zobodat.at

Broad-scale plant diversity patterns of Central European *Carex humilis* steppes

Großräumige Diversitätsmuster der mitteleuropäischen *Carex humilis*-Steppen

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Abstract

To understand recent biogeographic patterns of Central European rocky steppes, we inspected phytosociological data from rocky steppes dominated by *Carex humilis* along an elevation gradient (from 140 to 1,350 m) and in four biogeographic regions (NW Pannonian Basin, Western Carpathians, Transdanubian Mountains and Transylvanian Basin). Due to the physiognomic uniformity, *Carex humilis*-dominated communities are ideal objects to reveal broad-scale vegetation patterns, which are not obvious from local and regional studies. We investigated the roles of geographic distance and environmental (climatic, topographic and geological) variables in shaping variability of the studied vegetation. We further looked for differences in structure and floristic composition regarding (1) gamma diversity, beta diversity and species richness; (2) life form spectrum; (3) species distribution patterns; and (4) representation of archaeophytes and habitat specialists. The large compositional variation in both lower- and higher-elevation rocky steppes was better explained by geographic distance than by the environment. Among the environmental variables, geological bedrock type and climate variables were most important. Gamma and beta diversity were higher for stands at lower elevation than those at higher elevation, with a peak in the colline belt at elevations between 300 and 500 m. Species richness did not differ with elevation or biogeographic region. The hemicryptophytes dominated in life-form spectra along the whole elevation gradient with the highest proportions at middle elevations. Low elevation plots had higher proportion of therophytes and higher elevation plots had more chamaephytes and geophytes. Large-range species prevailed at low elevations and middle range species at high

Manuscript received 11 December 2019, accepted 06 July 2020
Co-ordinating Editor: Steffen Boch

elevations. Also the narrow-range species increased with elevation and among the regions were best represented in the W-Carpathians. Species with a European distribution prevailed in most plots and their proportion increased with elevation. The proportion of steppe species decreased with elevation and was highest in the Transylvanian plots. The W-Carpathian plots had the highest proportions of alpine species, which were present along the whole elevation gradient with a significantly increasing trend towards the high elevation. The archaeophytes were represented only at low and middle elevations with a decreasing trend, and had highest proportions in the Transylvanian plots. Mean niche breadth had unimodal distribution along the elevation gradient with the highest values at 600 m a.s.l. Proportions of both specialist and generalist species increased with elevation. Despite the mentioned differences, rocky steppes from various elevation belts and biogeographic regions shared a set of species with similar ecology and distribution. We conclude that a detailed analysis of biogeographic patterns based on phytosociological data can provide a valuable insight into the structure of a particular vegetation type.

Keywords: archaeophyte, biogeography, distribution range, diversity, elevation, environmental variable, life form, rocky steppe, spatial variable

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The large-scale variability of Central European rocky steppes has so far mostly been characterised using syntaxonomy (e.g. MUCINA & KOLBEK 1993, CHYTRÝ 2007, JANIŠOVÁ & DÚBRAVKOVÁ 2010, BORHIDI et al. 2012, COLDEA 2012, BAUER 2014). However, the diversity patterns and biogeographic relationships have not yet been studied within a larger geographic area. To understand recent biogeographic patterns and possibly also past developments of Central European rocky steppes, we focussed on a special type of rocky steppes dominated by *Carex humilis*. This species is a clonal sedge which often forms very distinct rings (so called 'fairy rings' or 'Hexenringe') in grassland communities and thanks to its compact growth form and extensive tussock longevity it strongly impacts vegetation structure of the whole community (WIKBERG & MUCINA 2002). The striking similarity in physiognomy of vegetation dominated by *C. humilis* along broad geographic (large distribution area) and environmental gradients (e.g. elevation, pH, geology) evokes multiple questions, such as: (1) To what extent are species composition and diversity of plant communities dominated by *C. humilis* uniform and how is community composition related to the position along geographic and environmental gradients? (2) Is the similarity in species composition more related to similarity in habitat conditions or the spatial attributes such as geographic distance? (3) How does the representation of different biogeographic elements depend on elevation and geographic location? (4) Do species co-occurring with *C. humilis* have some similar traits with respect to habitat requirements, life form or size of distribution area? (5) Can the current biogeographic and diversity patterns provide insights into the biogeographic history of the studied habitat?

Carex humilis is regarded as a species of cold Pleistocene steppes (KLEOPOV 1941, WALTER and BRECKLE 1985) and in Central Europe it usually occurs in steppe-like grasslands considered to be relic vegetation from the Late Glacial that 'escaped' Holocene woodland invasions (KUNEŠ et al. 2015, POKORNÝ et al. 2015). Apart from Europe it occurs in the Caucasus Mts, and very locally in moutain ranges of eastern Kazakhstan and southern Siberia (Kazakh Uplands in Karaganda, Altai and Sayan Mts) (Supplement E1). With several exceptions, it is almost absent from the area covered by the continental ice sheet during the Last Glacial Maximum and has only a scattered distribution in the Mediterranean region (MEUSEL et al. 1965, CHATER 1980). *Carex humilis* is often described as a thermophilous species in Central Europe, as it frequently occurs in the warmest locations of southern lowlands and hillsides (ELLENBERG & LEUSCHNER 2010). However, it is actually a drought-adapted and cold-tolerant species (SMETÁNKOVÁ 1959). It requires a fair amount of light and so it prefers open habitats but is also found at the forest edges and within open woodland (e.g. DELARZE et al. 2015). It can grow under very different climatic conditions and is tolerant to different types of bedrock (JAKOVLJEVIĆ et al. 2014).

Studying broad biogeographic patterns of a certain vegetation type may elucidate vegetation features or processes, which are not obvious in local or regional studies, e.g. patterns of diversity can be properly interpreted only within the broad context of regional and historical influences (WIENS & DONOGHUE 2004). Elevation gradients are ideal for investigating ecological and biogeographical hypotheses (KÖRNER 2000, GRYTNES 2003). At present it is for instance not clear if there is a common pattern of species richness along elevation gradient. So far, decreasing (GRYTNES 2003), increasing (UJHÁZYOVÁ et al. 2016), hump-shaped (BRUUN et al. 2006), but also inversely unimodal (HRIVNÁK et al. 2014) patterns have been indicated by different studies. One of the major disadvantages of diversity studies on large elevation gradients is the effect of vegetation zonation, which may intermingle with the effect of elevation (GRYTNES 2003). Also, variation in size of individuals may affect species richness related to a constant plot size. In this respect uniform physiognomy and vegetation structure of *C. humilis*-dominated steppes along a large elevation gradient may provide ideal conditions to avoid the mentioned constraints. In our study area, situated in the centre of its continuous distribution area, *C. humilis* dominates plant communities on a gradient of at least 1,200 meters. This allowed us to study diversity and distribution patterns of vascular plant species co-occurring with the dominant *C. humilis*.

In our study, we compared *C. humilis* steppes in four biogeographic regions with different natural history as well as intensity and duration of human influence. The Transylvanian Basin has been affected by Neolithic people since the Early Neolithic (6000–5500 BC), the Transdanubian Mountains and NW Pannonia with adjacent regions since the Middle Neolithic (5500–5000 BC), while the Western Carpathians were inhabited much later, and remained almost unaffected at higher elevations (POSCHLOD 2015). This allowed us to compare not only the representation of different life forms, ecological and biogeographic groups of species, but also alien species such as archaeophytes introduced to the region since the Neolithic up to AD 1500.

In the present study, we trace the distribution patterns of the species occurring in the *C. humilis* steppes. Due to different evolutionary histories, different dispersal mechanisms, different migration routes and migration rates, and due to the effects of climate, soil and biotic interactions, plant distribution ranges are very different (e.g. MEUSEL et al. 1965, COMES & KADEREIT 1998). Combining similar ranges into range types or biogeographic elements (e.g. QIAN et al. 2003) reduces the diversity of distributions to comprehensible units. We used this approach to identify how the different biogeographic elements of the *C. humilis* steppes are distributed along the elevation gradient and in the compared biogeographic regions.

Rocky steppes usually occur on sun-exposed slopes with shallow soils and are regularly exposed to summer drought, which may act as limiting factor keeping the vegetation open (JANIŠOVÁ & DÚBRAVKOVÁ 2010). Similarly extreme habitats are supposed to be occupied mainly by habitat specialists, consisting of competitively week but stress-tolerant species. Habitat specialists are species with narrow ecological niches while species with broad ecological niches are considered to be generalists. Ecological specialization can be measured independently of detailed ecological measurements (DEVICTOR et al. 2010), it can be quantified from species' co-occurrence patterns based upon the assumption that generalist species should co-occur with many different species across sites, whereas specialists should co-occur with relatively few species (FRIDLEY et al. 2007). This measure also implicitly incorporates each species' impact on each other as co-occurrence patterns are shaped by biotic interactions (DEVICTOR et al. 2010). In our study, we used co-occurrence-based niche breadth as a measure of specialisation and compare the representation of specialists and generalists along the elevation gradient and in the studied biogeographic regions.

Understanding the extent to which species distributions at different scales are determined by dispersal limitation and niche differentiation may be important for interpretation of observed biogeographical patterns. Recent studies integrating niche explanations (i.e. a process-called species sorting or environmental filtering) and spatial explanations (i.e. dispersal processes) have clearly demonstrated the importance of both processes in shaping the plant and animal metacommunity patterns (e.g. COTTENIE 2005, NG et al. 2009, HÁJEK et al. 2011). One possibility to quantify contribution of both of them is to model spatial effects using the analysis of principal coordinates of neighbour matrices (PCNM; BORCARD & LEGENDRE 2002). However, there are few studies comparing environmental and spatial effects in grasslands at a broad scale. In our study, we incorporated a broad range of environmental variables (climatic, topographic, geological) as additional explanatory variables and compared their effects with the effect of the spatial variables.

Broad-scale ecological studies based on detailed coenological data are important but still rare, as they are much dependent on large phytosociological databases as well as on the availability of high-quality ecological information. Recently developed vegetation plot databases and archives (e.g. CHYTRÝ et al. 2016) and availability of GIS-derived ecological variables make such studies possible. We used phytosociological data stored in vegetation plot databases, as they provide plot-based lists of vascular plants and are available for a large part of the *C. humilis* distribution range (Supplement E1).

Our study focuses on vegetation patterns of rocky steppes dominated by *C. humilis* across four elevation belts (planar, colline, submontane and montane) and four biogeographic regions (NW Pannonian Basin, Western Carpathians, Transdanubian Mountains and Transylvanian Basin). We investigated the roles of geographic distance and environmental (climatic, topographic and geological) variables in shaping variability of the studied vegetation. We also looked for differences in structure and floristic composition with regard to (1) gamma diversity, beta diversity and species richness; (2) life form spectrum; (3) species distribution patterns; and (4) representation of archaeophytes and habitat specialists.

2. Materials and methods

2.1 Study area

The Carpathians constitute, beside the Alps and the Pyrenees, one of the main mountain chains forming the European Alpine System uplifted during the Alpine-Himalayan orogeny. They form an arch extending in Central Europe over about 1,300 km, reaching a width of 100–350 km and covering a total surface of 209,000 km^2 (KONDRACKI 1989). Geologically, the Carpathians consist of prevailing flysch in the northern and eastern rim, crystalline and metamorphic rocks in the central zone, limestone belts manifested discontinuously across the chain and volcanic rocks covering some areas. Overall, acidic habitats are more widespread than calcareous ones (RONIKIER 2011). An important biogeographic position between the Balkan ranges in the south, the Alps and Sudetes in the west, and the Scandinavian range in the north is reflected in extraordinarily high diversity of plants of various origins (KLIMENT 1999, WEBSTER et al. 2002, RUFFINI et al. 2006, MRÁZ & RONIKIER 2016). The climate of the Carpathians is moderately cool and humid; the warmest locations in the Carpathian foothills have mean annual temperature above 10 °C, while on the Tatra summits (the highest peak of the Carpathians reaching 2,655 m) the mean annual temperature is only -2 °C. The annual precipitation ranges from 600 to 1,800 mm depending on elevation and location, peaking either in June (in the south) or in July (in the north). Snow cover lasts from less than three months in the foothills to more than seven months in the alpine belt.

The Pannonian (Carpathian) Basin is enclosed by the Carpathians in the north and east, the Alps in the west and the Dinarides in the south. Alluvial plains dominate the landscape with sparse isolated hills in the interior (the Transdanubian Mountains) and low mountain ranges along the edges. During the Quaternary, the alluvial plains were covered with sand and silt, and deposits of loess were formed under the influence of the cool continental periglacial climatic conditions (FÉSÜS et al. 1992). The Transdanubian Mountains are built mainly by the Mesozoic carbonaceous rocks, while older Palaeozoic rocks, Tertiary sedimentary rocks and basalts also occur locally (ÁDÁM et al. 1988). The mean annual temperature in the central part of the Pannonian Basin is around 11 °C, ranging from -1 °C in January to 22 °C in July. The annual precipitation ranges from 500 to 800 mm, with snow cover usually lasting less than three months (KAKAS 1960).

2.2 Data selection

We used a large phytosociological data set for initial data selection including 40,077 grassland relevés from the Carpathian Mountains, the Pannonian Basin, and small adjacent parts of the Polish Uplands, the Bohemian Massif, the Eastern Alps and the north-western Dinaric Mts. In order to restrict our data selection to *Carex humilis* rocky steppes, in the first step, relevés with *C. humilis* covering at least 20% were selected (1414 relevés, see Supplement E2 for details). In the next step, relevés with incomplete information on geographic coordinates, elevation, aspect and slope were excluded (927 relevés remained). Further, relevés with plot size outside the range of 4–40 m^2 and small groups of relevés scattered on the periphery of the study area were excluded, resulting in 809 relevés from six countries (Austria, Czech Republic, Hungary, Romania, Slovakia and Ukraine), recorded between the years 1936 and 2010, and distributed along an elevation gradient from 140 to 1350 m a.s.l. To avoid the effect of oversampling in certain regions, the dataset was geographically stratified, so that a maximum of three relevés were retained in each grid cell of 0.75’ of latitude × 1.25’ longitude (approximately 1.4 km × 1.4 km). The stratified dataset contained 540 relevés. The non-metric multidimensional scaling (NMDS) method was used to check if the refined data set of 540 plots covers the whole variability of *C. humilis*-dominated grasslands included in the original data set (see the ordination plot in Supplement E2D). For the purpose of most analyses, the final data set of 540 plots was grouped within four distinct biogeographic regions (Fig. 1) and four elevation belts corresponding to the vegetation zonation in the Carpathian-Pannonian region (ELLENBERG & LEUSCHNER 2010, UJHÁZYOVÁ et al. 2016): planar (140–300 m; 161 plots), colline (300–500 m; 200 plots), submontane (500–800 m; 98 plots), and montane (800–1350 m; 81 plots). For some analyses we merged the two lower and two upper belts and considered only two broader elevation zones, which we call lower-elevation (below 500 m; 361 plots) and higher-elevation (above 500 m; 179 plots) belts.

2.3 Spatial and environmental variables

Of the topographic variables we used elevation and slope inclination. Of the climate variables we used mean annual temperature (°C), precipitation during the growing season (from April to September; mm), intra-annual extreme temperature range ($T_{max} - T_{min}$, °C) and potential direct solar radiation. Climate data were obtained from the E-OBS dataset (HAYLOCK et al. 2008) and the CRU TS dataset v. 1.2 (MITCHELL et al. 2004). We used the External Drift Kriging-based spatial interpolation (e.g. HUDSON & WACKERNAGEL 1994) to interpolate the climate data to the position of the study plots. The resolution of created climatic grids was 90 meters, derived from the resolution of the underlying digital

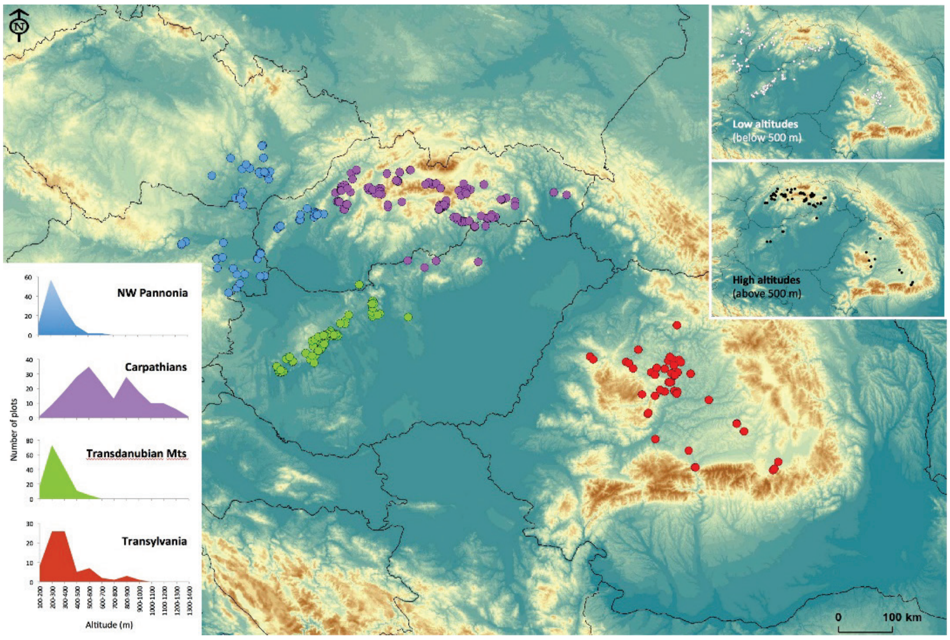

Fig. 1. Distribution of 540 plots dominated by *Carex humilis* in four biogeographic regions and along an elevation gradient.

Abb. 1. Verteilung der 540 Vegetationsaufnahmen von *Carex humilis*-Rasen in den vier biogeographischen Regionen und entlang des Seehöhengradienten.

elevation model (JARVIS et al. 2008). Potential direct solar radiation was calculated according to equation 3 in MCCUNE & KEON (2002) using the plot data on slope inclination, slope aspect and latitude. Based on data from http://portal.onegeology.org/OnegeologyGlobal/ and own experience we distinguished six geological bedrock types: (i) Palaeozoic shale, (ii) acidic crystalline rock, (iii) limestone and dolomite, (iv) sandstone and claystone, (v) intermediate and basic volcanic rock, and (vi) Quaternary sediments.

2.4 Statistical analyses

Principal coordinate analysis of neighbour matrices (PCNM; BORCARD & LEGENDRE 2002, DRAY et al. 2006) was used to derive spatial eigenvectors (LEGENDRE & LEGENDRE 2012). Initially, a matrix of Euclidean distances among all plots was computed based on longitude and latitude transformed into SJTSK Křovák projection and expressed in meters. A threshold distance was calculated to cover the nearest neighbour of the most isolated plot (i.e. the minimum distance to connect all plots together). Distances shorter than this threshold distance (36’042 m) were kept, while distances above this threshold were replaced by an arbitrary large distance value. The modified distance matrix was processed with principal coordinate analysis (PCoA). The plot scores on individual PCoA axes were then treated as independent spatial predictors (PCNM spatial eigenvectors according to LEGENDRE & LEGENDRE 2012). Canonical correspondence analysis (CCA; TER BRAAK 1986) was then used to partition the variation in species composition into fractions explained by environmental and spatial variables. In the matrix of species composition, species cover values were square-root-transformed and rare species were down-weighted. The best subsets of environmental variables and spatial predictors (PCNM eigenvectors) were selected by forward selection with a stopping rule based on the significance in Monte-Carlo permutation tests ($p < 0.05$). Spatial predictors contributing less than 1% of the total variation explained by all spatial predictors were not considered, even when statistically significant. Adjusted R^2 values were used to evaluate the proportion of variance explained by the environmental and the spatial variables, and the variance shared by both of them. CCA, Monte Carlo permutation tests and the variance partitioning were calculated in Canoco 5 (TER BRAAK & ŠMILAUER 2012).

Phi coefficient calculated in the program JUICE 7.0 (TICHÝ 2002) was used as a statistical measure of fidelity, i.e. the concentration of species occurrences in vegetation plots of four elevation belts and four biogeographic regions.

2.5 Calculation of diversity parameters

Gamma diversity of geographic regions and elevation belts was calculated by rarefying (GOTELLI & COLWELL 2001) all groups to the plot number in the least represented group using the program JUICE 7.0 (TICHÝ 2002) and considering the cumulative diversity of the selected plots. As a metric of species turnover, we used multiplicative beta diversity, $\beta = \gamma/\alpha$, where γ is the total number of species in the group and α is the mean species richness in the group (WHITTAKER 1972). It was calculated in JUICE 7.0 (TICHÝ 2002) from 100 random selections of 10 plots within each group of plots representing either the elevation belts or biogeographic regions, or elevation belts in the particular biogeographic region (in this analysis we selected only 5 random plots due to lower number of plots in groups). Gamma diversity was then the cumulative richness of the 10 (5) plots and alpha diversity was the mean richness of the 10 (5) plots. Alpha diversity was expressed as mean species richness per plot. To account for the effect of plot size which may be confounded with the effect of elevation, we used Generalized Linear Mixed Model with the plot size included in the model as a random effect. We used the R-library glmPQL for this analysis. Species richness of biogeographic regions was calculated for the plots sized between 15 and 25 m^2 to minimize the effect of the plot size.

2.6 Species distribution characteristics and life forms

We explored the representation of species with differently sized geographic ranges and belonging to various biogeographic elements. The size and type of the distribution range of particular species were evaluated based on the following databases and publications: BIOLFLOR (KLOTZ et al. 2002), EvaplantE (HOBOHM et al. 2014), KLIMENT et al. (2016), MEUSEL et al. (1965), Euro+Med PlantBase (2006–2018, ww2.bgbm.org/EuroPlusMed).

Regarding the size of the distribution range, we distinguished the following categories: i) *narrow-range species*: species with a distribution range smaller than or equal to the study area (approximately 500,000 km^2); ii) *medium-range species*: species with a distribution range between 500,000–5,000,000 km^2; and iii) *large-range species*: species with a distribution range larger than 5,000,000 km^2. Into the special category *endemics,* we included species with a distribution range below 100,000 km^2 (listed in Supplement E3). According to the location of the area of distribution, we distinguished the following biogeographic elements: i) species restricted to Europe (*E*); ii) species occurring in Europe, northern Africa and western Asia (*E+*); iii) species with circumboreal distribution (*CIR*); iv) species distributed W of E 40° (*WE*); v) Central European species distributed mainly between N 35° and N 60°, E 10° and E 40° (*CE*); vi) species distributed east of E 20° (*EE*); vii) boreal species distributed also north of N 60° and absent south of N 35° (*B*); viii) temperate species restricted to latitudes between N 35° and N 60° (*T*); ix) Mediterranean species distributed also south of N 35° and absent north of N 60° (*M*); x) species distributed prevailingly in the Eurasian steppe regions (*S*); xi) species distributed mainly in the continental biogeographic region (delimitation according to European Environmental Agency) (*C*); and xii) species distributed mainly in the alpine biogeographic region of Europe (delimitation according to European Environmental Agency) (*A*).

Archaeophytes (alien taxa introduced to the region from the beginning of Neolithic agriculture up to the year 1500) and neophytes (alien taxa introduced after the year 1500) were classified according to MEDVECKÁ et al. (2012), ANASTASIU & NEGREAN (2009), and Euro+Med PlantBase database (2006–2018, ww2.bgbm.org/EuroPlusMed) and are listed in Supplement E4. As the number and proportion of neophytes were very low in the studied vegetation, we did not further analyse them.

Plant life forms were defined according to Raunkiaér's classification (1934), based on the position of renewing buds in relation to the soil surface. We used the data included in the BIOLFLOR database (KLOTZ et al. 2002) and TUTIN et al. (2001). The proportion of life forms (hemicryptophyte, chamaephyte, therophyte, and geophyte) based on presence-absence data was calculated for each plot. Other life-forms were only occasionally present and were not analysed.

2.7 Size of ecological niches and representation of specialists vs. generalists

To assess the breadth of the species' realized ecological niche, we used co-occurring-species-based estimation of ß diversity (FRIDLEY et al. 2007, ZELENÝ 2009) within the relevé groups containing particular species. We used again multiplicative beta diversity with gamma diversity as the total species richness of plots containing a particular species and alpha diversity as the mean diversity of these plots. Calculations were based on a large species-by-plot matrix containing all grassland communities of the Carpathian Mountains and the Pannonian Basin. 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 included 40,077 plots and 2638 vascular plant taxa (vascular plants determined only to genera were excluded prior to the analyses). Beta diversity was calculated for 2091 vascular plant taxa with five or more occurrences in the data set. For each taxon, mean ß diversity was computed from 5 randomly selected plots containing this species. For each species we repeated this random selection 100 times. Calculation was made in the R environment using the script prepared by D. Zelený (https://raw.githubusercontent.com/zdeal-veindy/juice-r/master/generalists-specialists/generalists-specialists_v6.0.r). The 100 taxa with the lowest niche breadth were considered as specialists and the 100 taxa with the largest niche breadth were considered as generalists (Supplement E5). Mean niche breadth of all species and the proportions of specialists and generalists were calculated for each plot. These variables were then tested for differences between particular groups (biogeographic regions and elevation belts) by one-way ANOVA and post-hoc HSD test for unequal groups sizes (Statistica 7, StatSoft Inc., 2006).

2.8 Nomenclature of vascular plants

Taxonomic concepts used in different countries and by different authors were unified according to the Euro+Med PlantBase (2006–2018, ww2.bgbm.org/EuroPlusMed).

3. Results

3.1 Habitat conditions and vegetation characteristics of *Carex humilis*-dominated grasslands

Rocky steppes dominated by *Carex humilis* occurred at elevations between 140 and 1350 m on slopes with inclination from 3° to 70° and predominantly SE-S-SW aspect (Table 1). Most plots were located over calcareous bedrocks (69%), quaternary sediments (18%) and sandstones (9%), the remaining bedrock types were represented only by a few plots. The mean annual temperatures of the study plots ranged from 4.1°C to 10.8°C, extreme temperature ranges reached values from 47°C to 54°C, and precipitation during the growing season ranged from 310 to 705 mm. The studied vegetation was classified by original authors to the *Stipo pulcherrimae-Festucion pallentis* order of *Festuco-Brometea* class (at low elevations) or *Seslerietalia caeruleae* order of *Elyno-Seslerietea* class (at higher elevations, see Supplement E2 for details).

The biogeographic regions and elevation belts differed in the variability of topographic and climatic variables (Supplement E6). Plots in the colline belt varied most in topography (slope and radiation) and extreme temperature ranges, while the variation in precipitation during the growing season increased with elevation. Among the regions, the Transdanubian

Table 1. Environmental variables and their basic characteristics.

Tabelle 1. Die Umweltvariablen mit einigen allgemeinen Kennzahlen.

Environmental variable	Explanation	Mean	Minimum	Maximum
Elevation	Elevation (m a.s.l.)	469	140	1350
Slope	Slope inclination (°)	26	3	70
Precipitation	Precipitation total during the growing season from April to September (mm)	430	310	705
Temperature	Mean annual temperature (°C)	8.3	4.1	10.8
Extreme temperature range	Intra-annual extreme temperature range (T_{max} - T_{min}, °C)	49.7	46.9	53.7
Solar radiation	Potential direct solar radiation according to model 3 in MCCUNE & KEON (2002)	0.857	-0.054	1.006
Geological bedrock	Six possible values: Calcareous (limestone and dolomite, 370 plots), Sandstone/ Claystone (50 plots), Quaternary sediments (98 plots), Volcanic (intermediate and basic volcanic rocks, 10 plots), Shale (Palaeozoic shale, 4 plots), Crystalline (acidic crysta-lline rock, 8 plots)			

Mts had the highest variation in topographic variables and the lowest variation in climatic variables. The W-Carpathian plots varied most in mean temperature and precipitation during the growing season, while the Transylvanian ones varied most in extreme temperature ranges.

In the studied plots, the dominant *C. humilis* co-occurred with 749 vascular plant taxa. There were eight species co-occurring with *C. humilis* in more than 50% of the plots: *Anthericum ramosum*, *Asperula cynanchica*, *Euphorbia cyparissias*, *Helianthemum nummularium*, *Potentilla incana* agg., *Sanguisorba minor*, *Teucrium chamaedrys* and *T. montanum*. Apart from *Potentilla incana* agg. and *Sanguisorba minor* and together with *Festuca pallens* and *Anthyllis vulneraria* these taxa were also very frequent in all four elevation belts (percentage frequency > 30% in each elevation belt; Supplement E7). Twenty-four species were bound (i.e. *phi* > 0.2) mainly to the planar belt, 12 to the colline belt, 8 to the sub-montane belt, and a big group of species (59) occurred mainly in the montane belt. Five species (*Teucrium chamaedrys*, *T. montanum*, *Euphorbia cyparissias*, *Helianthemum nummularium*, and *Potentilla incana* agg.) occurred with a frequency higher than 30% in all of the four biogeographic regions while 37 species were restricted to a particular region (Supplement E8). Higher numbers of strongly region-specific species (*phi* > 0.4) were recorded in Transylvania (14) and the W-Carpathians (12), while these numbers were rather low in the Transdanubian Mts (5) and NW Pannonia (2).

3.2 Spatial versus environmental variables

The large-scale compositional variation of *C. humilis*-dominated vegetation was better explained by geographic distance than by the environmental variables based on current climate, topography and geology. This was true also for lower- and higher-elevation steppes if analysed separately. As indicated by the CCA, in the whole dataset geographic distance alone explained 44% of total explained variation while environmental predictors explained

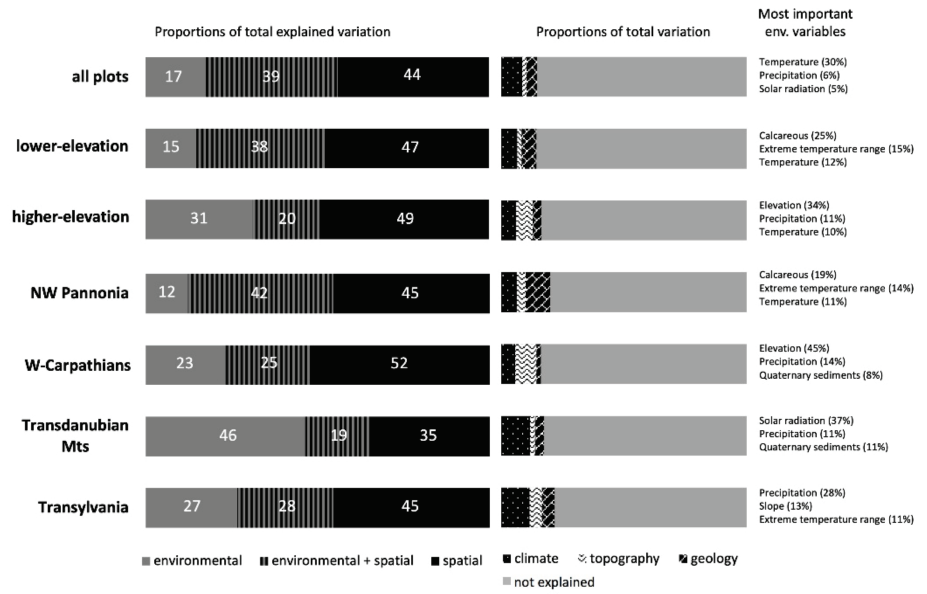

Fig. 2. Relative effects of environmental and spatial variables on species composition in *Carex humilis*-dominated vegetation in the whole data set (all plots) and in subsets distinguished according to elevation (lower and higher elevation) and biogeographic regions (NW Pannonia, W-Carpathians, Transdanubian Mts and Transylvania). Individual fractions (in %) of the total explained variation estimated by the CCA are shown in the left bar charts. Proportions of total variation accounted for by climatic, topographic and geological environmental variables are shown in the right bar charts, while environmental variables explaining the highest proportion of variation are listed right for each particular data (sub)set.

Abb. 2. Relativer Erklärungswert der standörtlichen und räumlichen Variablen im Gesamt-Datensatz sowie in zwei Höhenstufen und vier Regionen. Der prozentuelle Anteil an der gesamten erklärten Variation ist im linken Teil dargestellt. Rechts der von klimatischen, topographischen und geologischen Variablen erklärte Anteil der totalen Variation. Ganz rechts sind jeweils die drei Variablen mit dem höchsten Erklärungswert aufgelistet.

only 17%, and the remaining 39% were explained by both spatial and environmental predictors (Fig. 2, the test of the whole model as well as the tests of the variance explained by environmental and spatial predictors, respectively, were significant). Among the environmental predictors, mean annual temperature and geological bedrock were most important (Table 2).

When only the subset of lower-elevation rocky steppes was analysed, the role of environmental and spatial variables was about the same as in the whole data set. For the higher-elevation rocky steppes, the variation explained by the environmental variables alone was higher (31% compared to 15%) while variation explained by a combination of environmental and spatial variables was lower (20% compared to 38%) compared to the lower-elevation plots (Fig. 2). For lower-elevation steppes, geological bedrock was most important, while for the higher-elevation ones, elevation and topographic variables contributed most to the explained variation. Biogeographic regions differed in relative effects of environmental and spatial variables as well as in environmental variables explaining the highest proportion of compositional variation (Fig. 2).

Table 2. Variation in species composition of *Carex humilis* steppes (the whole study area, 540 vegetation plots) explained by environmental variables selected by forward selection in CCA (sorted by the order of selection). Coefficient of determination R^2 (%) represents the conditional effect of the variable in addition to the effect of previously selected variables. Adjusted R^2 of selected environmental variables was 12.9%.

Tabelle 2. Von den Umweltvariablen in der kanonischen Korrespondenzanalyse erklärte Variation der Artenkombination (alle 540 Vegetationsaufnahmen). Das Bestimmtheitsmaß R^2 (%) gibt jeweils die in der schrittweisen Regression im Vergleich zu den vorangegangenen Variablen zusätzlich erklärte Variation an. Das adjustierte R^2 der ausgewählten Variablen betrug 12,9 %.

Name	R^2 (%)	pseudo-F	*p*
Temperature	5.5	31.2	< 0.001
Calcareous	2.6	15.3	< 0.001
Extreme temperature range	1.3	7.4	< 0.001
Solar radiation	1.0	6.2	< 0.001
Elevation	1.0	6.1	< 0.001
Precipitation	0.9	5.5	< 0.001
Sandstone/claystone	0.7	4.0	< 0.001
Slope	0.6	3.7	< 0.001
Shale	0.4	2.6	< 0.001
Crystalline	0.4	2.5	< 0.001
Volcanic	0.3	1.9	< 0.001

3.3 Differences in gamma and beta diversity

Transylvanian steppes had the largest gamma diversity, followed by the W-Carpathian and NW Pannonian ones. The gamma diversity in the Transdanubian Mts was smaller in comparison with other regions (Table 3). Lower-elevation rocky steppes had a larger gamma diversity than the higher-elevation ones. The colline rocky steppes had the largest and the montane ones had the smallest gamma diversity. The same pattern was found when elevation belts of individual biogeographic regions were compared (Supplement E9).

There were no differences in beta diversity among the biogeographic regions. Beta diversity was highest in colline plots, followed by planar and submontane plots, while montane plots had the lowest beta diversity (Table 3). The same pattern was found if elevation belts of individual biogeographic regions were compared. In Transylvania, planar and colline plots had similar beta diversity, but in the Transdanubian Mts and NW Pannonia, the colline plots had higher beta diversity than the planar plots. In the W-Carpathian plots, beta diversity was highest in colline and lowest in montane elevation belts (Fig. 3).

3.4 Differences in species richness

Local species richness varied from 14 to 67 (average 37) species of vascular plants per 25 m^2. Elevation (GLMM, $p = 0.600$) and biogeographic regions (ANOVA, $p = 0.692$; Table 3) had no effect on species richness.

3.5 Differences in life-form spectrum

The representation of species life forms changed along the elevation gradient (Fig. 4). A non-linear relationship was found for the proportion of therophytes (U-shaped and mainly decreasing) and hemicryptophytes (unimodal with peak at middle elevations between 500

Table 3. Comparison of diversity parameters in biogeographic regions and elevation belts: gamma diversity estimated by sample-based rarefaction corresponding to the number of plots in the smallest group (79 for the biogeographic region and 81 for the elevation belt), multiplicative beta diversity (calculated from 10 randomly selected plots of the group and repeated 100 times), and average species richness (average number of species per plot). Different letters in superscript indicate statistically significant differences between biogeographic regions or elevation belts tested by one-way ANOVA.

Tabelle 3. Vergleich der Diversitätsparameter in den biogeographischen Regionen und Höhenstufen: Gamma-Diversität (bezogen auf die Anzahl der Aufnahmen in der kleinsten Gruppe: 79 für Regionen und 81 für Höhenstufen); multiplikative Beta-Diversität (errechnet aus 10 zufällig ausgewählten Aufnahmen mit 100 Wiederholungen); durchschnittliche Artenzahl pro Aufnahme. Unterschiedliche Buchstaben zeigen signifikante Unterschiede innerhalb der Regionen bzw. Höhenstufen an.

	Estimated gamma diversity	Multiplicative beta diversity	Average species richness
Biogeographic region			
Transylvania	357	3.48^{a}	37.0^{a}
Transdanubian Mts	227	3.50^{a}	34.8^{a}
NW Pannonia	317	3.41^{a}	37.1^{a}
W-Carpathians	333	3.51^{a}	36.1^{a}
Elevation belt			
Planar (< 300 m)	314	3.78^{b}	37.8^{a}
Colline (300–500 m)	413	4.21^{c}	36.3^{a}
Submontane (500–800 m)	368	3.70^{b}	36.6^{a}
Montane (> 800 m)	261	2.66^{a}	35.2^{a}

and 800 m a.s.l.). A linear relationship with elevation was found for the proportion of chamaephytes (strongly increasing) and geophytes (slightly increasing).

The proportion of therophytes was highest in the Transdanubian Mts. and lowest in Transylvania and W-Carpathians. The Transylvanian plots had the highest proportion of hemicryptophytes, and the W-Carpathian ones had the highest proportion of chamaephytes and geophytes (Table 4).

3.6 Representation of species with different geographic ranges

The proportions of narrow- and medium-range species and number of endemics increased with elevation; they were highest in the W-Carpathians and lowest in NW Pannonia and Transylvania. The proportion of large-range species decreased with elevation and among the biogeographic regions had the highest values in Transylvania and NW Pannonia. The Transdanubian Mountains had intermediate values of all chorological categories (Table 4, Fig. 4–6).

Regarding the location of distribution ranges, species with European distribution prevailed in most plots and their proportion increased with elevation, reaching over 70% above 800 m a.s.l. Species occurring also outside Europe and circumboreal species decreased with elevation. The proportion of Central-European, East-European, boreal, and temperate species increased with elevation, while the proportion of Mediterranean species and species of Eurasian steppes decreased along the elevation gradient. Species distributed mainly in the continental biogeographic region showed a unimodal distribution with a peak between 400 and

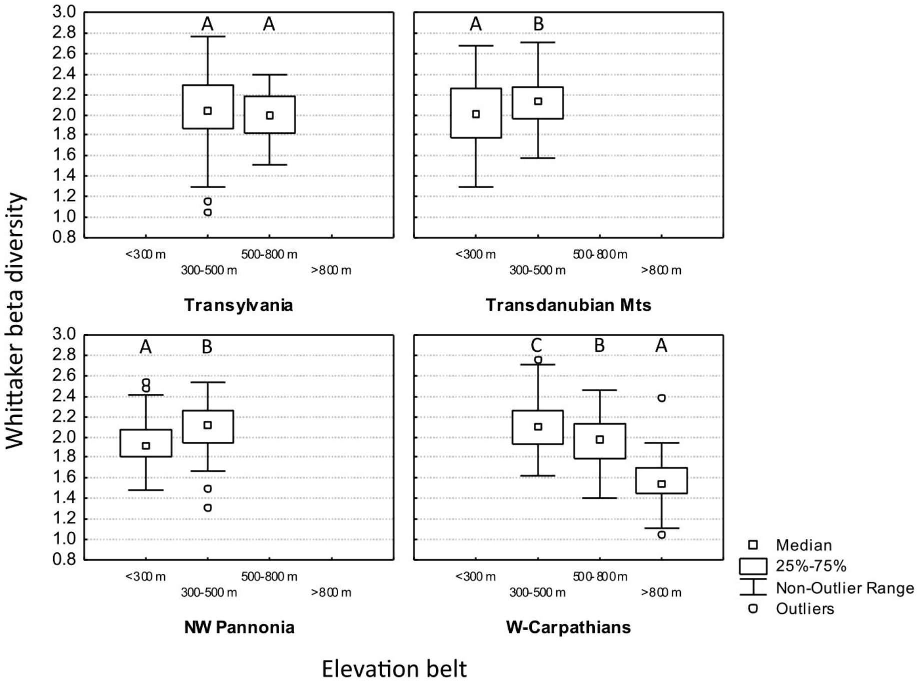

Fig. 3. Multiplicative beta diversity in different elevation belts of individual biogeographic regions. Beta diversity was calculated out of 5 randomly selected plots of the group using 100 random selections. Only groups with more than 10 plots were compared. Different letters above the boxes indicate statistically significant differences.

Abb. 3. Multiplikative Beta-Diversität in den verschiedenen Höhenstufen der vier Regionen. Die Beta-Diversität wurde aus 5 zufällig ausgewählten Aufnahmen mit 100 Wiederholungen errechnet. Nur Gruppen mit mehr als 10 Aufnahmen wurden verglichen. Unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Höhenstufen.

600 m a.s.l. On the other hand, species bound to the alpine biogeographic region of Europe had an inverse unimodal distribution with lowest values at about 300 m a.s.l. and steep increase mainly above 600 m a.s.l. (Fig. 4).

Comparison of the biogeographic regions shows that Transylvanian plots had the highest proportions of species occurring also outside Europe and circumboreal species, as well as species of Eurasian steppes (forming on average more than 20% of all species present). On the other hand, they contained the least West- and Central-European species and species bound to both the continental and alpine biogeographic regions of Europe. The W-Carpathian plots had the highest proportions of European, West- and Central-European, boreal, and temperate species, as well alpine species (forming on average 20% of all species present), and the lowest proportions of species occurring also outside Europe and circumboreal species, Mediterranean and steppic species. The Transdanubian Mts and NW Pannonia had usually intermediate values between the Transylvanian and W-Carpathian biogeographic regions (Table 4).

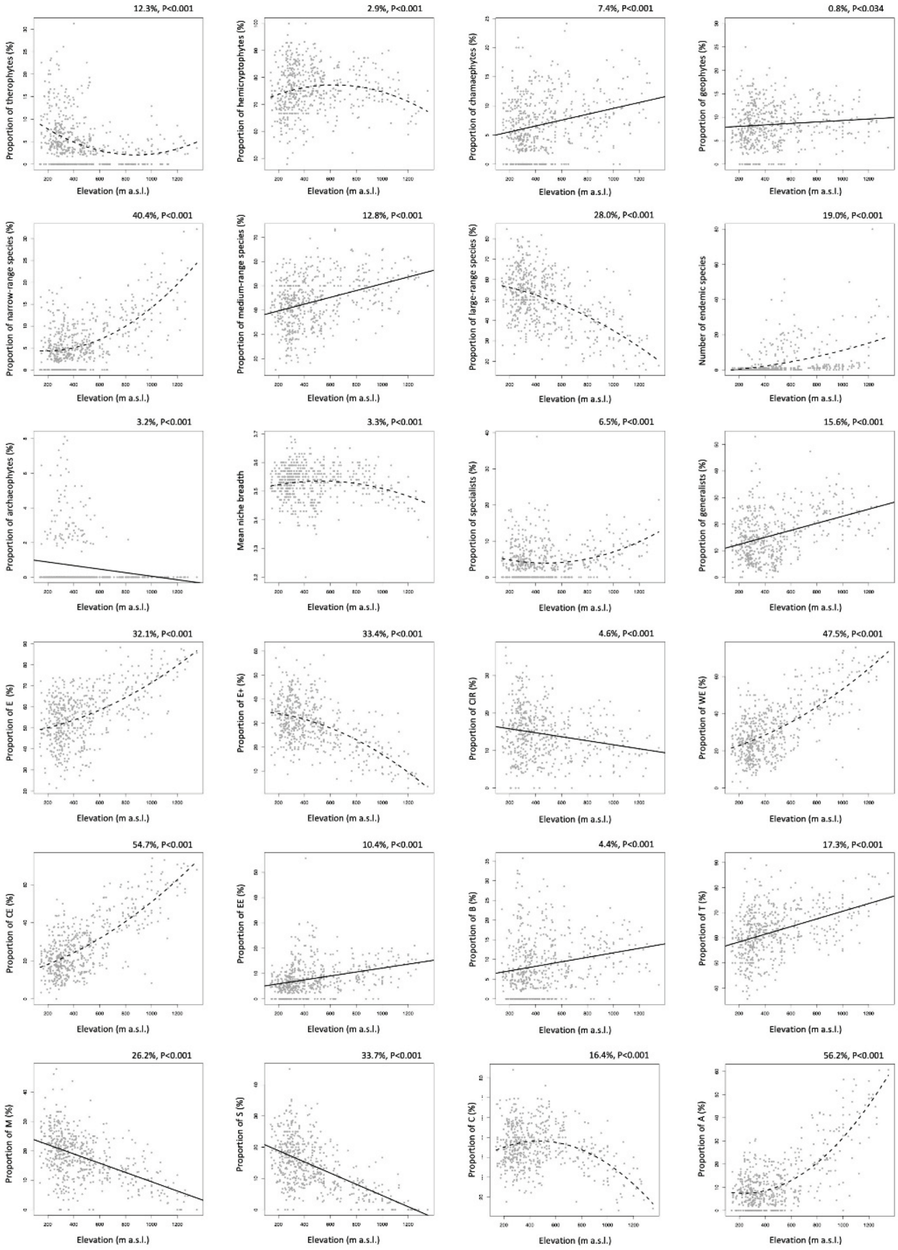

Fig. 4. Change in representation of life forms, ecological and biogeographic elements along the elevation gradient. Percentage variance explained by simple regression models for each dependent variable and elevation as a predictor is shown in the upper right corner of each graph. Solid lines are used for linear relationships. For abbreviation of the biogeographic categories see Table 4.

Abb. 4. Veränderungen im Anteil der Lebensformen, Spezialisten/Generalisten und biogeographischen Elemente entlang des Seehöhengradienten. Die durch die jeweilige Variable erklärte Varianz ist rechts oberhalb jedes Diagramms angegeben. Durchgezogene Linien zeigen einen linearen Zusammenhang an. Die Kürzel der biogeographischen Elemente sind in der erweiterten deutschen Zusammenfassung erklärt.

Table 4. Representation of diagnostic species, life forms, ecological and biogeographic elements in the four studied biogeographic regions. Mean values and standard deviations are shown. Different letters in superscript indicate differences between the groups tested by one-way ANOVA.

Abbreviations: E species restricted to Europe; E+ species occurring in Europe, northern Africa and western Asia; CIR species with circumboreal distribution; WE species distributed W of E 40°; CE Central European species distributed mainly between N 35° and N 60°, E 10° and E 40°; EE species distributed east of E 20°; B boreal species distributed also north of N 60° and missing south of N 35°; T temperate species restricted to latitudes between N 35° and N 60°; M Mediterranean species distributed also south of N 35° and absent north of N 60°; S species distributed prevailingly in the Eurasian steppe regions; C species distributed mainly in the continental biogeographic region; A species distributed mainly in the alpine biogeographic region.

Tabelle 4. Anzahl der diagnostischen Arten sowie prozentueller Anteil der Lebensformen, Spezialisten/Generalisten und biogeographischen Elemente in den Aufnahmen der vier Regionen (Mittelwert ± Standardabweichung). Unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Regionen an. Die Kürzel der biogeographischen Elemente sind in der erweiterten deutschen Zusammenfassung erklärt.

Biogeographic region	Transylvania	Transdanubian Mts	NW Pannonia	Carpathians
Number of plots	79	148	112	201
Number of diagnostic species with *phi* > 0.2 (> 0.4)	63 (14)	21 (5)	29 (2)	44 (12)
Proportion of therophytes (%)	3.2 ± 2.8^{a}	8.0 ± 6.8^{c}	5.5 ± 4.9^{b}	3.2 ± 3.9^{a}
Proportion of hemicryptophytes (%)	81.8 ± 6.6^{c}	70.5 ± 8.7^{a}	77.7 ± 8.4^{b}	75.4 ± 6.5^{b}
Proportion of chamaephytes (%)	2.6 ± 2.8^{a}	6.7 ± 4.7^{b}	6.6 ± 5.1^{b}	8.9 ± 4.2^{c}
Proportion of geophytes (%)	9.0 ± 4.1^{ab}	8.4 ± 5.5^{ab}	7.2 ± 3.8^{a}	9.1 ± 3.8^{b}
Proportion of narrow-range species (%)	4.2 ± 4.1^{a}	6.5 ± 4.6^{b}	3.6 ± 3.9^{a}	9.2 ± 6.5^{c}
Proportion of medium-range species (%)	36.7 ± 9.1^{a}	44.1 ± 9.0^{b}	39.7 ± 9.7^{a}	47.7 ± 9.3^{c}
Proportion of large-range species (%)	59.1 ± 11.1^{c}	49.5 ± 11.1^{b}	56.8 ± 11.5^{c}	43.1 ± 13.1^{a}
Number of endemic species	0.1 ± 0.4^{a}	0.2 ± 0.4^{a}	1.0 ± 2.9^{a}	8.5 ± 11.9^{b}
Proportion of archaeophytes (%)	1.7 ± 2.2^{b}	0.3 ± 1.1^{a}	0.7 ± 1.5^{a}	0.3 ± 1.1^{a}
Mean niche breadth (%)	3.47 ± 0.1^{a}	3.54 ± 0.1^{b}	3.53 ± 0.1^{b}	3.53 ± 0.1^{b}
Proportion of specialists (%)	7.7 ± 6.2^{c}	5.6 ± 5.0^{b}	1.6 ± 2.3^{a}	4.5 ± 4.2^{b}
Proportion of generalists (%)	7.7 ± 5.4^{a}	18.1 ± 8.1^{c}	12.0 ± 6.7^{b}	19.9 ± 8.2^{c}
Proportion of *E* (%)	44.8 ± 11.9^{a}	54.7 ± 10.6^{b}	52.2 ± 9.8^{b}	64.0 ± 11.3^{c}
Proportion of *E+* (%)	36.7 ± 8.3^{c}	32.2 ± 9.7^{b}	31.9 ± 7.6^{b}	23.1 ± 9.0^{a}
Proportion of *CIR* (%)	18.5 ± 6.4^{c}	13.1 ± 6.8^{a}	15.8 ± 6.6^{b}	12.9 ± 5.3^{a}
Proportion of *WE* (%)	20.5 ± 9.9^{a}	28.8 ± 10.8^{b}	24.9 ± 9.5^{ab}	42.5 ± 14.8^{c}
Proportion of *CE* (%)	17.1 ± 8.9^{a}	23.4 ± 10.0^{b}	20.4 ± 8.3^{ab}	39.4 ± 15.1^{c}
Proportion of *EE* (%)	15.7 ± 8.7^{c}	5.3 ± 3.9^{a}	5.2 ± 3.4^{a}	8.6 ± 5.0^{b}
Proportion of *B* (%)	7.9 ± 5.9^{b}	3.9 ± 4.7^{a}	11.2 ± 8.3^{c}	11.1 ± 6.2^{c}
Proportion of *T* (%)	64.1 ± 9.4^{bc}	62.0 ± 9.1^{b}	57.5 ± 10.0^{a}	64.9 ± 8.6^{c}
Proportion of *M* (%)	19.6 ± 6.3^{b}	20.3 ± 9.1^{b}	20.0 ± 6.4^{b}	14.3 ± 7.3^{a}
Proportion of *S* (%)	20.5 ± 7.0^{c}	16.5 ± 7.7^{b}	16.3 ± 6.3^{b}	8.5 ± 5.8^{a}
Proportion of *C* (%)	38.8 ± 8.4^{a}	44.0 ± 9.3^{b}	51.6 ± 9.1^{c}	45.5 ± 12.6^{b}
Proportion of *A* (%)	3.7 ± 3.6^{a}	11.7 ± 6.9^{b}	6.1 ± 5.8^{a}	20.0 ± 14.7^{c}

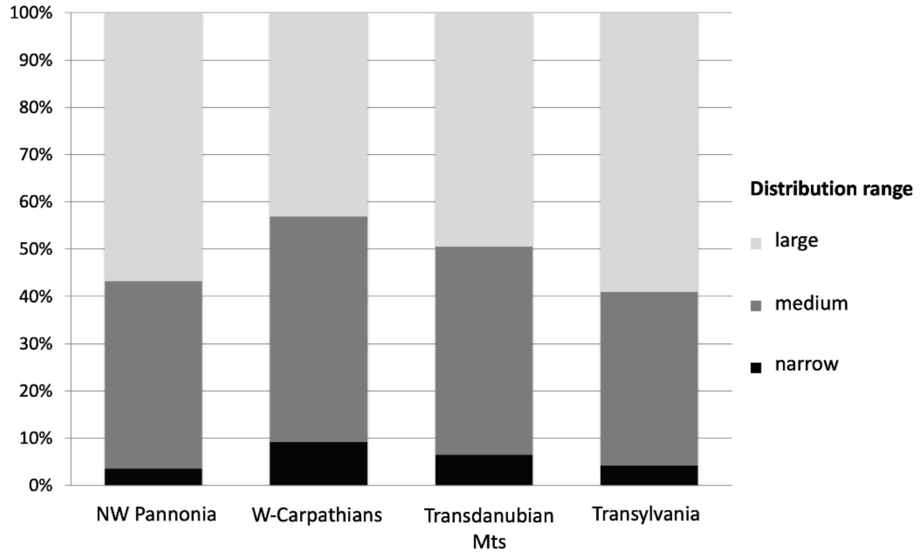

Fig. 5. Representation of taxa with narrow, medium and large geographic ranges in four biogeographic regions.

Abb. 5. Anteil der Taxa mit kleinem (schwarz), mittlerem (dunkelgrau) und großem (hellgrau) Gesamtareal in den vier untersuchten Regionen.

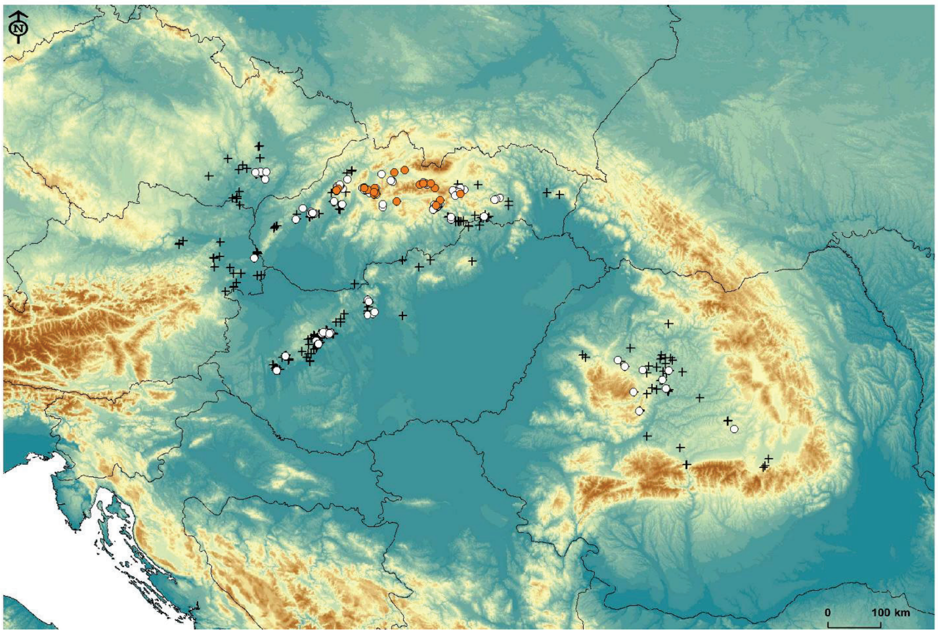

Fig. 6. Distribution of plots with 0 (+), 1–2 (white) and 3–6 (orange) endemic species with distribution area smaller than 100,000 km^2.

Abb. 6. Aufnahmen mit 0 (+), 1–2 (weiß) und 3–6 (orange) stenochoren Arten (= Arten mit einem Gesamtareal < 100.000 km^2).

3.7 Representation of archaeophytes

Archaeophytes were present in 16.7% of the studied plots. Among them, *Convolvulus arvensis*, *Melampyrum arvense* and *Reseda lutea* were most common. The proportion of archaeophytes decreased linearly with elevation, while plots above 820 m a.s.l. did not have any (Fig. 4). Transylvania had a significantly higher proportion of archaeophytes than the three remaining biogeographic regions (Table 4).

3.8 Niche breadth and representation of generalists and specialists

Mean niche breadth had a unimodal distribution along the elevation gradient with highest values at about 600 m a.s.l. The proportion of specialists showed an inversely unimodal trend with the highest values in the highest elevations. The proportion of generalists increased linearly with elevation (Fig. 4). The biogeographic regions had similar mean niche breadth except for Transylvania with significantly lower values. Transylvania had the highest proportion of specialists, while the W-Carpathians and Transdanubian Mts had the highest proportions of generalists (Table 4).

4. Discussion

4.1 Environmental impact on rocky steppes variation

According to the recent syntaxonomic synthesis of Europe (MUCINA et al. 2016), the subdivision of rocky steppes in Central and south-eastern Europe (the *Stipo pulcherrimae-Festucetalia pallentis* order) is based on a combination of geological (silicicolous and calcareous groups of alliances) and historical (de-alpine relic group of alliances) criteria. The subdivision of (sub-)alpine calcareous grasslands of the *Seslerietalia caeruleae* order, which also contain *Carex humilis*-dominated vegetation, is based mainly on geographic criteria (separate alliances for the Central and Eastern Alps, Western Carpathians, Southern Carpathians, Pyrenees, Cantabrian Mountains, or a combination of the Alps and the Carpathians). Although we studied only a narrow selection of this vegetation – stands with a strong dominance of *C. humilis* – all these factors were confirmed as important drivers of vascular plant composition. The type of geological bedrock had the strongest impact on the compositional variation in areas where the *C. humilis*-dominated rocky steppes occur on a large variety of geological substrates, such as in the NW Pannonia (CHYTRÝ 2007). Among the six distinguished bedrock types, calcareous bedrock had the strongest effect on the compositional variation, and it was the most important environmental variable at lower elevations as well as in the biogeographic region of NW Pannonia. By contrast, for species composition of higher-elevation rocky steppes and biogeographic regions with the largest elevation ranges (W-Carpathians and Transylvania), elevation-related climate variables were more important than geology.

4.2 Spatial versus environmental variables

Our study indicated a strong impact of spatial variables on the compositional variation of rocky steppes which exceeded the impact of environmental variables at low as well as high elevation and in all but one biogeographic regions. This finding suggests that dispersal limitation plays an important role in shaping the recent compositional pattern of the rocky steppe vegetation. It is not a surprise if we consider the fact that apart from larger continuous areas at higher elevations, *C. humilis*-dominated vegetation usually occurs in isolated patches within the forest zone or anthropogenic habitats. Another possible explanation of the high amount of variance explained by spatial variables is that some relevant environmental variables were not included in the analyses or that the environmental variables used included too much uncertainty, e.g., due to discrepancies between the coarse resolution of environmental variables and small plots size.

Along with geographic location also the impact of Quaternary history could be responsible for the compositional variation of the studied rocky steppes. Relic communities may be shaped by the climatic factors and biogeographic processes which prevailed in the past rather than by the recent environmental factors (WILLNER et al. 2009). As indicated by fossil pollen analyses (JANKOVSKÁ and POKORNÝ 2008, KUNEŠ et al. 2008), during the full glacial and late glacial period, the mountain valleys of the north-western Carpathians supported taiga or hemi-boreal forest along with some steppe and tundra formations. The post-glacial fate of Central European steppe grasslands has been debated by palaeoecologists and biogeographers for decades. The fundamental question on continuity of open habitats throughout the Holocene and especially during its critical period of maximum afforestation motivated the formulation of several theories (BORBÁS 1900, SOÓ 1929, GRADMANN 1933, WENDELBERGER 1954, ZÓLYOMI 1958). Many recent studies provide strong evidence for the continuous local occurrence of steppe grasslands in Central Europe throughout the Holocene and claim that the Neolithic farming started in a landscape that was already open and contained remnants of natural steppes (KUNEŠ et al. 2015, POKORNÝ et al. 2015, POSCHLOD 2015, FEURDEAN et al. 2015, 2018). According to relevant studies (WILLIS et al. 1998, SÜMEGI 1999), human impact had usually only local effects on spatial pattern of vegetation in the Neolithic facilitating mainly the patchiness of the vegetation in the Pannonian Basin, while anthropogenic homogenization as general impact has started just from the middle phase of the Bronze Age by more intensive agricultural land use.

4.3 Diversity patterns

One of the important motivations behind our study was a question whether the broad-scale diversity patterns can teach us about the broad-scale biogeographic processes. It is known that biological diversity differs between comparable habitats in regions that have different histories or geographic configurations (WIENS and DONOGHUE 2004, JIMÉNEZ-ALFARO et al. 2018). In our study, we found a larger gamma and higher beta diversity in lower-elevation steppes than in higher-elevation ones, with maxima in the colline belt at elevation between 300 and 500 m. This finding was also supported when individual biogeographic regions were analysed separately. There are several possible explanations for this pattern. (1) Species-pool size and heterogeneity of species composition reflect the heterogeneity in some topographic (slope and radiation) and climate variables (extreme temperature ranges) indicated for the colline elevation belt. (2) The colline rocky steppes have the longest historical continuity, providing sufficient time for development of the largest species pool. (3) The colline elevation belt represents some kind of ecotone where species typical of both planar and submontane rocky steppes occur together. (4) The colline rocky steppes have the longest continuity of human impact, and their species pool is enriched by species reflecting human activities, such as archaeophytes (the proportion of archaeophytes in the colline belt was significantly higher than in the other elevation belts).

There were no differences in beta diversity of the four biogeographic regions. However, except for Transylvania, the beta diversity within each of these regions was related to elevation, even though the elevation ranges and the heterogeneity of topographic and climate characteristics differed among the regions. Moreover, the differences in regional gamma and beta diversity did not simply reflect the heterogeneity of environmental conditions. We found the largest gamma diversity in Transylvania with only intermediate heterogeneity in topography and climate within our data set. The smallest gamma diversity was found in the Transdanubian Mts with very high heterogeneity in topographic variables such as slope and solar radiation (although rather low variability in climatic variables and rather uniform bedrock formed mainly by the Triassic dolomite; see also SOÓ 1941). These findings suggest that the heterogeneity of environmental conditions is not the only factor shaping the gamma and beta diversity of the studied vegetation. Historical factors, including the location of species migration routes, the proximity of glacial refuges, but also long-lasting impact of human activities such as transhumance, might play a crucial role in determining the diversity patterns of rocky steppe vegetation.

Species richness is generally thought to decrease monotonically with increasing elevation (GRYTNES 2003, ADAMS 2009) or to be unimodal with a mid-elevation peak (RAHBEK 1995, 2005; COLWELL & LEES 2000). However, we did not find differences in species richness neither along the elevation gradient nor among the biogeographic regions. The relatively small grain size used in our study may result in the patterns observed here having different causes than in studies having large grain sizes. Small plot sizes may emphasize the importance of local biological interactions or species richness may be controlled by current site conditions (rocky steppes occur in extreme dry habitats with a high probability of summer drought). Due to the limiting effects of local environment, species pool size may have low impact on species richness and so the effects of elevation and particular regions are not obvious. In some studies (GOTELLI & COLWELL 2001) elevation richness patterns may be a result of different number of individuals at different elevation. In our study, the vegetation structure of all plots is 'fixed' by the criterion of *C. humilis* dominance, thus the effect of elevation (being direct or indirect) may theoretically become more obvious. On the other hand, specific vegetation structure conditioned by a ring-forming morphology of the dominant *C. humilis*, biotic interactions and possibly also release of inhibiting allelopathic substances which could influence the distribution pattern of other species (WIKBERG & MUCINA 2002) may also (along with environmental filtering) be responsible for the lack of a well-defined elevation richness pattern.

4.4 Life form patterns

As expected, life form spectrum changed along the elevation gradient, reflecting thus morpho-ecological adaptation of plants to changing climatic gradients (RAUNKIAÉR 1934). The regression model for therophytes, indicating a U-shaped response, was the strongest, explaining 12.3% of variation. Although therophytes rarely represented more than 15% of species in our plots, their contribution to the cover of the herb layer was significant, reaching up to 70% in some special cases. Especially winter annuals may perform very high interannual variability in abundance in dry grasslands although their relative proportions remain nearly constant (GEIßELBRECHT-TAFERNER et al. 1997). The high representation of therophytes at low elevation can be explained by a sufficient length of the growing season allowing the annuals to complete their life cycle before more competitive perennials occupy the space. Increasing representation of therophytes at high elevation (above 1000 m) may be caused by increased distrurbance due to higher slopes and harsher climate. But it can also be interpreted as an artefact of the model. According to RAUNKIAER (1910), therophytes become increasingly rare with increasing elevation and commonly do not represent more than 2% of the total alpine flora. However, in some arid regions therophytes increase in dominance and/or abundance along the elevation gradient (PAVÓN et al. 2000).

Hemicryptophytes was the best represented life form along the whole elevation gradient and in all biogeographic regions covering usually between 70 and 80% of species in the community. Similarly to other studies (KLIMEŠ 2003), percentage of geophytes was remarkably stable among the regions but also along the elevation gradient showing only a very slight increase towards high elevations. On the other hand, the percentage of chamaephytes increased more substantially, representing 5 to 20% of species in the highest plots, which is comparable to the alpine zone of some Asian mountain ranges (KLIMEŠ 2003, MAHDAVI et al. 2013).

4.5 Biogeographic patterns

In accordance with previous findings, higher-elevation rocky steppes contained more narrow-range species while lower-elevation ones had a higher proportion of large-range species. This could be related to geographic isolation of high-elevation sites, which supports the evolution of endemics (HOBOHM et al. 2014). Among the biogeographic regions, the W-Carpathians were richest in narrow-range species, as well as in species classified as endemics by our criteria. This is not surprising as the W-Carpathians include the sites with the highest elevation among all studied regions. The higher elevation range may provide increased habitat heterogeneity as well as increased chance to survive in refuges with suitable microclimatic conditions during climatically distinct periods (KLIMENT et al. 2016). Although the Transylvanian Basin is poor in endemic species (KLIMENT et al. 2016), which is evident also from our comparison, the studied plots from this biogeographic region contained more narrow-range species than the generally lower situated regions of NW Pannonia and Transdanubian Mts.

Despite differences in species composition, low-, medium- and high-elevation rocky steppes dominated by *C. humilis* share a set of species with similar ecology and distribution, which belong to the most frequent species along the whole elevation gradient and in all biogeographic regions studied. These are mainly light-demanding species with medium-size ranges and broad ecological niches, which are diagnostic for the whole class of *Festuco-Brometea* (Supplement E10). Most of them are tolerant to a broad range of temperatures, which is reflected in their distribution from lowlands to high mountains within slightly sub-oceanic or slightly sub-continental climate. All of them are drought-tolerant and strongly bound to calcareous soils low in nutrients (ELLENBERG et al. 1991, BORHIDI 1995). In the lower-elevation plots, these constantly occurring species are accompanied by more species bound to steppe biogeographic region of Europe and Asia and less species bound to the alpine biogeographic region of Europe in comparison to the higher-elevation plots.

4.6 Archaeophytes

It is known that the two groups of alien species in Central Europe, archaeophytes introduced from the beginning of Neolithic agriculture to AD 1500, and neophytes that arrived later, differ in their ecology, invasion dynamics and habitat affinities. For the archaeophytes, habitat type and elevation were confirmed as the two most important predictors of the local invasion level in the Czech Republic, however, for dry and alpine grasslands the proportion of archaeophytes was independent of elevation (CHYTRÝ et al. 2009). ESSL & DIRNBÖCK (2008) reported a decrease in archaeophyte diversity with increasing elevation in dry grasslands at the edge of the Northern Limestone Alps in Austria. According to our study, *C. humilis* steppes exhibited a decreasing invasion level of archaeophytes along the elevation gradient, with no archaeophytes occurring above 800 m a.s.l. This could be related to geographic isolation of high-elevation sites, which hinders spread of invaders from lower elevations (CHYTRÝ et al. 2009, MEDVECKÁ et al. 2012). Along with the dispersal limitation, filtering along elevation gradients may be another possible explanation of the absence of archaeophytes at higher elevations (SEIPEL et al. 2012). The high proportion of archaeophytes in Transylvanian *C. humilis* steppes may be related to the fact that Transylvanian Basin has been affected by Neolithic people for several centuries (in case of the Transdanubian Mountains and NW Pannonia) or even several millennia longer (in the case of the Western Carpathians) than the other biogeographic regions studied (POSCHLOD 2015).

4.7 Niche breadth patterns

The lower-elevation rocky steppes were composed mainly of species with intermediate niche breadth, while at higher elevations both extreme groups of specialists and generalists were better represented. The large proportion of specialists at higher elevations can be associated with environmental heterogeneity (REITALU et al. 2012) and with the proportion of narrow-range and endemic species being generally higher at high elevations, providing that the range size is correlated with habitat specialisation (ESSL et al. 2009, KLIMENT et al. 2016). However, co-occurrence-based calculations are usually influenced by both the range of habitats represented in the dataset and the area covered by the dataset (ZELENÝ 2009). Therefore, some species just marginally distributed in the dataset may be identified as "specialists" while they actually could be widely distributed outside of the area or environmental range covered by the dataset. This may be the reason why species geographically bound to Transylvania (on the margin of our study area) were evaluated as specialists, and thus the proportion of specialists in this biogeographic region was the highest.

Erweiterte Deutsche Zusammenfassung

Einleitung – Die großräumige Variabilität der ostmitteleuropäischen Felssteppen wurde bislang vor allem syntaxonomisch beschrieben. Untersuchungen zu Diversitätsmustern und biogeographischen Beziehungen sind dagegen rar. Mit der vorliegenden Arbeit füllen wir diese Wissenslücke für die von *Carex humilis* dominierten Trockenrasen der pannonischen und karpatischen Region. Diese Gesellschaftsgruppe eignet sich aufgrund ihrer physiognomischen Einförmigkeit besonders gut, um großräumige Unterschiede zu untersuchen, welche in regionalen und lokalen Studien kaum zum Vorschein kommen. Im Detail analysierten wir den Einfluss von geographischer Distanz und Standortsfaktoren (Klima, Topographie, geologischer Untergrund) auf die floristische Zusammensetzung der Gesellschaften und verglichen die durchschnittliche Artenzahl, Beta- und Gammadiversität, Lebensformen-Spektrum, biogeographische Elemente und Anteil der Archäophyten und Habitatspezialisten zwischen verschiedenen Teilregionen und Höhenstufen.

Methoden – Aus einem Datensatz von 40.077 Vegetationsaufnahmen verschiedenster Rasengesellschaften des pannonisch-karpatischen Raums wählten wir zunächst jene 1414 Aufnahmen aus, in welchen *Carex humilis* eine Deckung von zumindest 20 % erreichte. Aufnahmen mit unvollständigen Standortsdaten und Flächengrößen von < 4 und > 40 m^2 wurden nicht berücksichtigt und die verbliebenen einer geographischen Stratifikation unterzogen (maximal drei Vegetationsaufnahmen pro Raster einer Größe von ca. 1,4 km × 1,4 km). Der finale Datensatz umfasste 540 Aufnahmen, welche aus folgenden vier Teilgebieten stammten: (1) nordwestliches Pannonikum (Süd-Mähren, Ost-Österreich, westliche Slowakei), (2) Westkarpaten, (3) Ungarische Mittelgebirge und (4) Siebenbürgen (Abb. 1). Für die Auswertung wurden die Aufnahmen zusätzlich in vier Höhenstufen gruppiert. Mit speziellen statistischen Verfahren (PCNM = *Principal Coordinate Analysis of Neighbour Matrices*; CCA = *Canonical Correspondence Analysis*) wurde bestimmt, wie viel der floristischen Variation durch räumliche bzw. standörtliche Variablen erklärt werden kann. Weiterhin verglichen wir folgende Parameter in den verschiedenen Gebieten und Höhenstufen: durchschnittliche Artenzahl pro Aufnahme; Beta-Diversität; Gamma-Diversität; Anteil von Arten mit kleinem, mittlerem und großem Gesamtareal; Anteil der Archäophyten; Anteil der einzelnen Lebensformen; mittlere Nischenbreite der Arten und Anteil der Spezialisten und Generalisten; Anteil diverser biogeographischer Elemente. Die Breite der realisierten Nische einer Art wurde anhand der Beta-Diversität der Aufnahmen, in welchen die betreffende Art vorkommt, bestimmt. Die 100 Taxa mit der engsten Nische definierten wir als Spezialisten, die 100 Taxa mit der breitesten Nische als Generalisten. Folgende biogeographischen Elemente wurden unterschieden: europäische Endemiten (*E*); europäisch-nordafrikanisch-westasiatische Arten (*E+*); circumboreal verbreitete Arten (*CIR*); Arten mit westeuropäischem (*WE*), mitteleuropäischem (*CE*) und osteuropäischem (*EE*) Verbreitungsschwerpunkt; Arten mit borealem (*B*), temperatem (*T*) und mediterranem (*M*) Schwerpunkt; Arten der Steppenzone (*S*); sowie Arten, die hauptsächlich in der "kontinentalen" (*C*) und "alpinen Region" (*A*) im Sinne der Fauna-Flora-Habitat-Richtlinie vorkommen.

Ergebnisse – Die floristischen Unterschiede innerhalb der *Carex humilis*-Rasen wurden am besten durch die geographische Distanz erklärt. Von den untersuchten Standortsfaktoren waren der geologische Untergrund und Klimafaktoren am bedeutendsten (Abb. 2, Tab. 2). Gamma- und Beta-Diversität waren in tiefen Lagen am höchsten, mit einem Maximum in der kollinen Stufe zwischen 300 und 500 m ü. M. (Abb. 3, Tab. 3). Die Artenzahl pro Aufnahme zeigte keine signifikanten Unterschiede zwischen den Höhenstufen und Regionen. Von den Lebensformen dominierten die Hemikryptophyten über den gesamten Höhengradienten, am stärksten in mittleren Lagen. Aufnahmen aus tiefen Lagen hatten einen größeren Anteil an Theropyhten, jene der Hochlagen einen größeren Anteil an Chamaephyten und Geophyten (Abb. 4). Der Anteil der Arten mit kleinem Gesamtareal nahm mit der Seehöhe zu und war insgesamt in den Westkarpaten am höchsten (Tab. 4, Abb. 5–6). Ebenso verhielten sich Arten mit Hauptverbreitung in der "alpinen Region". Der Anteil der Steppenarten nahm dagegen mit der Seehöhe ab und erreichte in Siebenbürgen sein Maximum. Archäophyten fanden sich nur in tiefen und mittleren Lagen und waren ebenfalls in Siebenbürgen am stärksten vertreten. Die mittlere Nischenbreite der Arten zeigte eine unimodale Verteilung entlang des Höhengradienten, mit einem Maximum bei 600 m ü. M. (Abb. 4).

Diskussion – Das Übergewicht der räumlichen gegenüber den standörtlichen Variablen in der Erklärung der floristischen Variation kann als Hinweis gewertet werden, dass historische Prozesse, wie etwa ein beschränktes Ausbreitungsvermögen der Arten, für die Zusammensetzung der *Carex humilis*-Rasen eine wichtige Rolle spielen. Die Felssteppen der kollinen Stufe zeigten die höchste interne Variabilität (Beta-Diversität) und größte Gesamtartenzahl (Gamma-Diversität), und zwar auch innerhalb der vier Teilgebiete. Für diese Beobachtung sind verschiedene Erklärungen denkbar: i) Die topographische und klimatische Vielfalt ist in der kollinen Stufe am größten. ii) Die kollinen *C. humilis*-Rasen haben die längste historische Kontinuität und deshalb auch den größten Artenpool. iii) Die kolline Stufe stellt ein Ökoton dar, in welchem Arten der planaren und (sub)montanen Stufe zusammentreffen. iv) Die kollinen *C. humilis*-Rasen haben die längste Nutzungsgeschichte, wodurch ihr Artenpool durch Archäophyten und andere Bewirtschaftungszeiger angereichert wurde. Der hohe Anteil an Therophyten in tiefen Lagen kann durch die Länge der Vegetationsperiode erklärt werden, welche nur in dieser Höhenstufe lang genug ist, dass die Einjährigen ihren Lebenszyklus abschließen, bevor die Konkurrenz der Ausdauernden zu stark wird.

Acknowledgement

Along with the authors, Claudia Bita-Nicolae, Zoltán Botta-Dukát, Milan Chytrý, Andraž Čarni, Daniela Dúbravková, Annamaria Fenesi, Ružica Igić, Zygmunt Kącki, Roman Kish, Joanna Korzeniak, Mirjana Ćuk, Daniel Krstonošić, Tamás Rédei, Eszter Ruprecht and Zvjezdana Stančić contributed to the preparation of the underlying phytosociological dataset of grassland vegetation from the Carpathian Mountains and the Pannonian Basin, from which beta diversity was calculated for vascular plant taxa as a measure of their niche breadth. We thank Milan Chytrý and David Zelený for valuable comments on an earlier version of the manuscript. Financial support for MJ and IŠ was provided by Slovak Academy of Sciences, grant VEGA 2/0095/19.

Author contribution

MJ contributed the idea, preparation of the data set (together with IŠ, CH and TH), data analysis and paper writing. NB, JC, JD, WW provided the data and valuable comments on the data analyses. All authors read and commented on the manuscript.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Global distribution range of *Carex humilis*.

Anhang E1. Weltweite Verbreitung von *Carex humilis*.

Supplement E2. Phytosociological affiliation and floristic differentiation of the studied vegetation.

Anhang E2. Pflanzensoziologische Zugehörigkeit und floristische Differenzierung der untersuchten Vegetation.

Supplement E3. List of taxa considered as endemic with distribution area below 100,000 km^2.

Anhang E3. Liste der als endemisch geltenden Taxa mit einem Verbreitungsgebiet unter 100.000 km^2.

Supplement E4. List of archaeophytes and neophytes.

Anhang E4. Liste der Archaeophyten und Neophyten.

Supplement E5. List of specialists and generalists.

Anhang E5. Liste der Spezialisten und Generalisten.

Supplement E6. Habitat characteristics of the studied biogeographic regions and elevation belts.

Anhang E6. Habitatmerkmale der untersuchten biogeografischen Regionen und Höhengürtel.

Supplement E7. Percentage frequency synoptic table of *Carex humilis*-dominated rocky steppes in four elevation belts.

Anhang E7. Synoptische Tabelle der prozentualen Häufigkeit von von *Carex humilis* dominierten Felssteppen in vier Höhengürteln.

Supplement E8. Percentage frequency synoptic table of *Carex humilis*-dominated rocky steppes in four biogeographic regions.

Anhang E8. Synoptische Tabelle der prozentualen Häufigkeit der von *Carex humilis* dominierten Felssteppen in vier biogeografischen Regionen.

Supplement E9. Gamma diversity in different elevation belts of individual biogeographic regions.

Anhang E9. Gamma-Diversität in verschiedenen Höhengürteln einzelner biogeografischer Regionen.

Supplement E10. Ecological indicator values of *Carex humilis* and eight most frequently co-occurring species in the studied rocky steppes.

Anhang E10. Ökologische Zeigerwerte von *Carex humilis* und acht am häufigsten gemeinsam vorkommenden Arten in den untersuchten Felssteppen.

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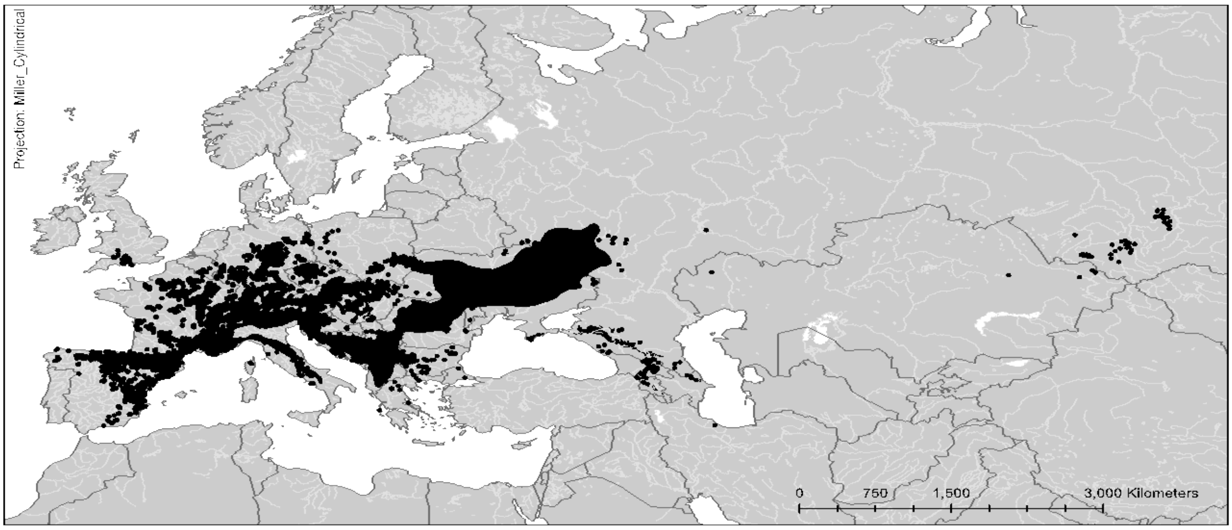
Janišová et al.: Broad-scale plant diversity patterns of Central European *Carex humilis* steppes

Supplement E1. Global distribution range of *Carex humilis*.
Provided by Erik Welk, Chorological Database Halle (CDH), German Centre for Integrative Biodiversity Research (iDiv), October 2017.

Anhang E1. Weltweite Verbreitung von *Carex humilis*.
Zur Verfügung gestellt von Erik Welk, Chorologische Datenbank Halle (CDH), Deutsches Zentrum für integrative Biodiversitätsforschung (iDiv), Oktober 2017.



Supplement E2. Phytosociological affiliation and floristic differentiation of the studied vegetation.

Anhang E2. Pflanzensoziologische Zugehörigkeit und floristische Differenzierung der untersuchten Vegetation.

A) Synopsis of phytosociological classes, orders and alliances of the studied rocky steppess dominated by *Carex humilis* (classification according to the original authors)

Elyno-Seslerietea BR.-BL. 1948
- *Seslerietalia caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926
  - *Astero alpini-Seslerion calcariae* Hadač ex Hadač et al. 1969

Festuco-Brometea Br.-Bl. et R. Tx. Ex Soó 1947
- *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968
  - *Alysso-Festucion pallentis* Moravec in Holub et al. 1967
  - *Asplenio septentrionalis-Festucion pallentis* Zólyomi 1936 corr. Soó 1971
  - *Bromion erecti* Koch 1926
  - *Bromo pannonici-Festucion pallentis* Zólyomi 1936 corr. 1966
  - *Chrysopogono grylli-Danthonion calycinae* Kojić 1959
  - *Diantho lumnitzeri-Seslerion* (Soó 1971) Chytrý et Mucina in Mucina et al. 1993
- *Brachypodietalia pinnati* Korneck 1974
  - *Cirsio-Brachypodion pinnati* Hadač et Klika ex Klika 1951
- *Festucetalia valesiacae* Soó 1947
  - *Festucion valesiacae* Klika 1931

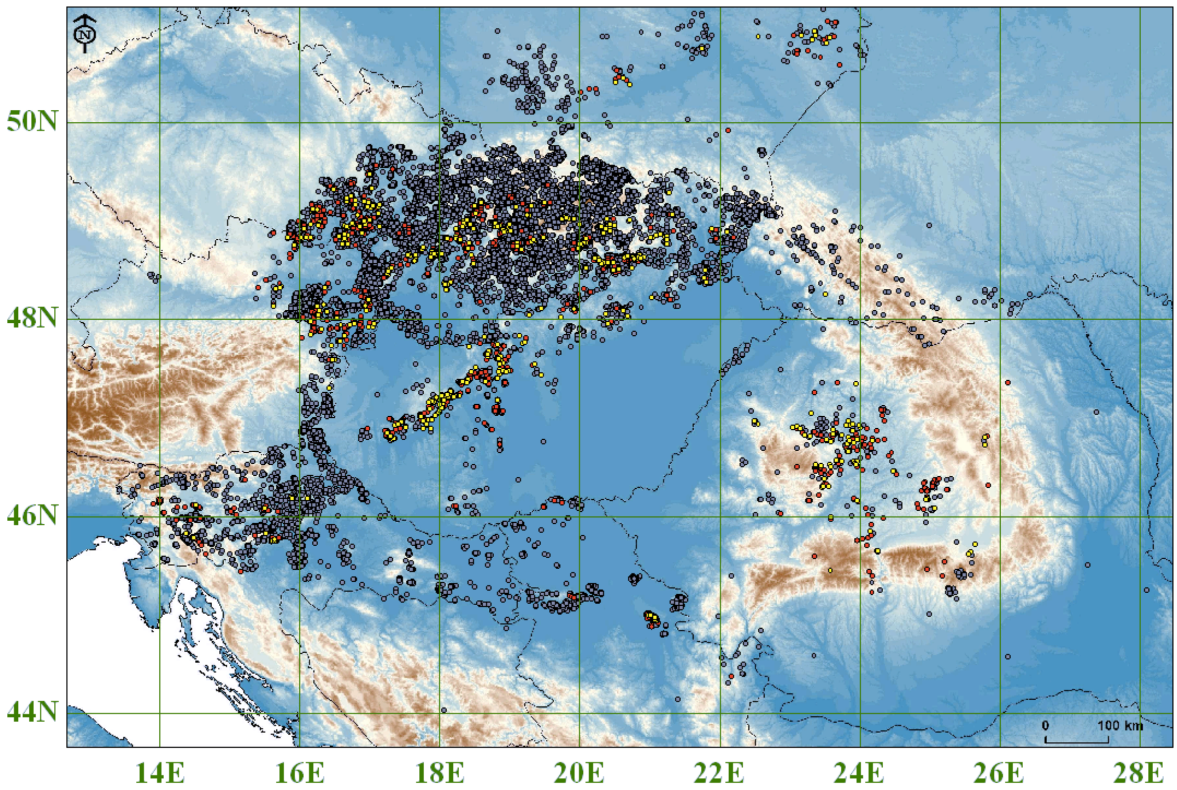
Trifolio-Geranietea sanguinei Th. Müller 1962
- *Antherico ramosi-Geranietalia sanguinei* Julve ex Dengler in Dengler et al. 2003
  - *Geranion sanguinei* R. Tx. in Th. Müller 1962

B) Differentiation of plots with *Carex humilis* covering at least 20% (first column), covering up to 20% (second column) and plots without *Carex humilis* (third column). In the synoptic table percentage frequency of the species is shown with a *phi* coefficient in superscript as a measure of fidelity (the values in the table are multiplied by 100). The table is not complete, only species with the highest fidelity to the three synoptic columns are shown with *phi* values above 10. The whole data set analysed here includes 40,077 grassland relevés from the Carpathian Mountains, Pannonian Basin and adjacent areas (see the figure below for the plot distribution).

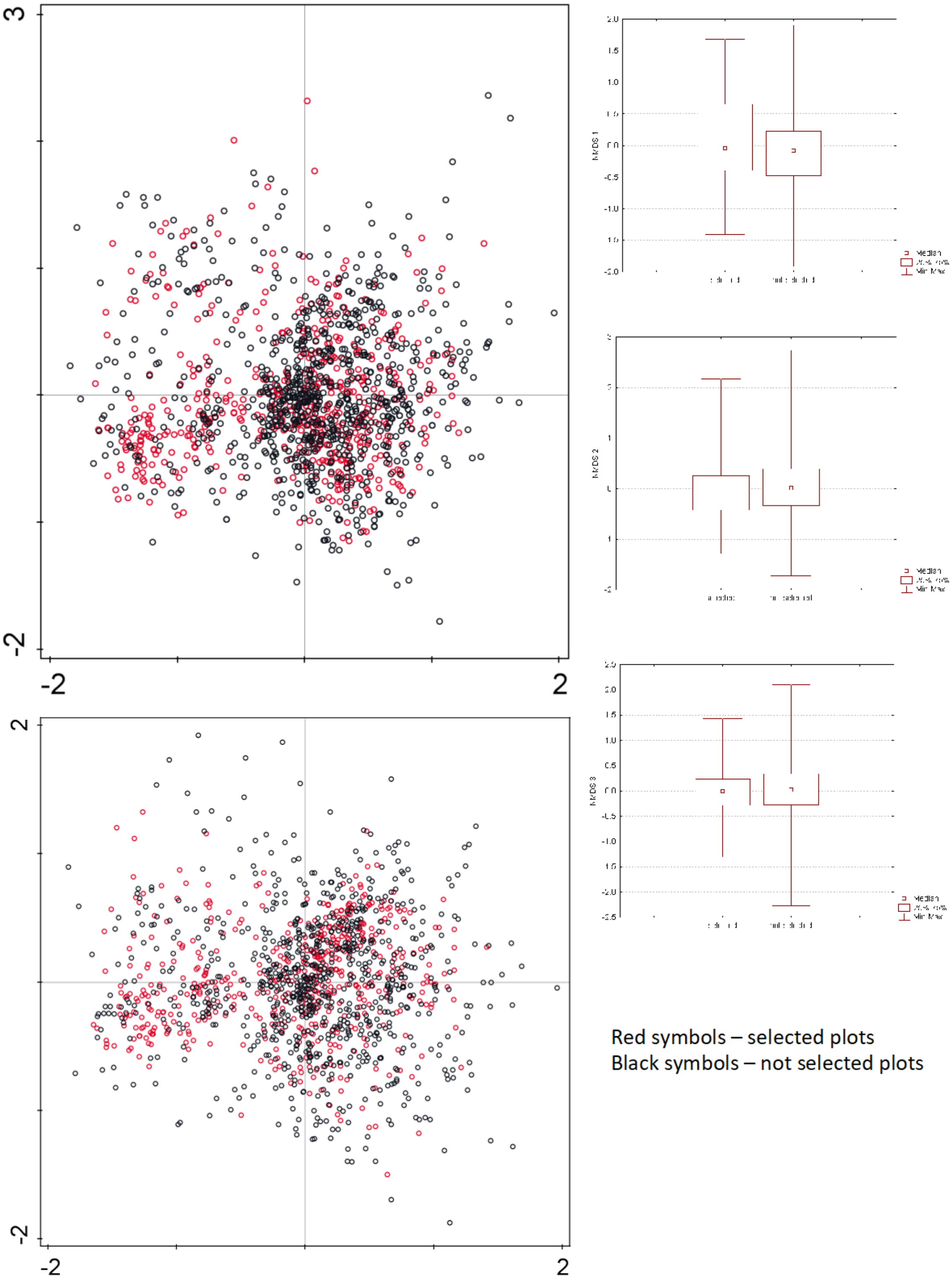
Groups according to *Carex humilis* (CH) cover	CH≥20%		CH<20%		CH=0%	
Number of plots	1414		3653		34999	
Carex humilis	100	**50.0**	100	50.0	.	---
Teucrium montanum	51	**31.9**	37	10.7	2	---
Anthericum ramosum	52	**31.1**	39	10.4	5	---
Teucrium chamaedrys	59	**26.3**	51	14.4	13	---
Helianthemum nummularium agg.	48	**25.2**	36	7.0	10	---
Potentilla incana agg.	59	**25.0**	55	19.4	11	---
Vincetoxicum hirundinaria	32	**24.6**	20	1.7	4	---
Asperula cynanchica	56	**24.0**	51	16.8	11	---
Sanguisorba minor	48	**22.7**	38	7.1	13	---
Euphorbia cyparissias	63	**22.5**	56	13.1	22	---
Inula ensifolia	35	**21.9**	29	11.1	3	---
Anthyllis vulneraria	38	**21.6**	27	2.6	10	---
Globularia bisnagarica	26	**21.0**	19	6.7	1	---
Genista pilosa	25	**20.9**	17	5.6	1	---
Linum tenuifolium	24	**20.7**	17	5.5	1	---
Pulsatilla halleri ssp. slavica	14	**20.4**	6	---	1	---
Stachys recta	27	8.5	32	**18.1**	6	---
Koeleria macrantha	26	7.7	31	**16.7**	7	---
Dorycnium pentaphyllum agg.	35	15.3	35	**16.4**	6	---
Centaurea stoebe	21	4.8	26	**15.5**	7	---
Phleum phleoides	9	---	17	**15.2**	4	---
Eryngium campestre	22	4.3	28	**14.2**	9	---
Festuca stricta ssp. sulcata	29	1.3	38	**14.1**	19	---
Pulsatilla vulgaris	12	6.2	15	**13.6**	1	---
Scabiosa ochroleuca	27	8.8	30	**13.3**	9	---

Festuca pallens s.lat.	35	19.4	31	**13.0**	4	---
Bothriochloa ischaemum	20	8.0	22	**12.9**	5	---
Thymus odoratissimus	12	2.2	17	**12.8**	4	---
Artemisia campestris	8	---	13	**12.6**	4	---
Galatella linosyris	15	8.2	17	**12.5**	2	---
Galium glaucum	20	10.4	21	**12.4**	4	---
Sedum album	8	1.1	13	**12.2**	3	---
Cytisus austriacus	2	---	6	**12.1**	1	---
Festuca valesiaca	17	5.2	20	**11.5**	6	---
Stipa capillata	18	9.7	18	**11.5**	3	---
Adonis vernalis	13	7.7	15	**11.5**	2	---
Medicago falcata	20	2.9	25	**11.3**	11	---
Centaurea scabiosa	27	8.1	29	**11.2**	11	---
Elytrigia intermedia	12	2.9	16	**11.2**	5	---
Astragalus onobrychis	6	---	10	**11.1**	2	---
Onobrychis viciifolia agg.	6	---	11	**11.1**	3	---
Thesium linophyllon	20	10.6	20	**11.0**	4	---
Astragalus austriacus	5	---	7	**10.9**	1	---
Thymus kosteleckyanus	10	3.3	13	**10.9**	3	---
Stipa pulcherrima	12	8.1	13	**10.8**	1	---
Brachypodium pinnatum agg.	19	---	25	**10.7**	13	---
Thymus praecox agg.	32	19.9	27	**10.7**	3	---
Allium flavum	17	9.9	18	**10.5**	3	---
Seseli osseum	27	15.1	25	**10.5**	5	---
Silene otites agg.	13	7.4	14	**10.3**	3	---
Scabiosa canescens	10	7.7	11	**10.0**	1	---

C) Distribution of plots with *Carex humilis* covering at least 20% (yellow symbols), covering up to 20% (red symbols) and plots without *Carex humilis* (grey symbols) in the large phytosociological data set (40,077 grassland relevés), which was the basis for the plot selection.



D) the NMDS ordination graphs of plots with more than 20% cover of *Carex humilis* based on an NMDS with three axes using the Bray-Curtis distance. Red symbols show plots included in the final selection of 540 relevés. Black symbols show the remaining 874 plots omitted from the analyses in the selection process (see Methods). The boxplots compare the scores of selected and omitted plots along the three NMDS ordination axes. The refined data set of 540 plots covers the whole variability of *Carex humilis*-dominated grasslands included in the original dataset (1414 plots).



Supplement E3. List of taxa considered as endemic with distribution area below 100,000 km^2. The region to which the particular taxon is endemic is shown in parentheses. Nomenclature follows Euro+Med PlantBase (http://www.emplantbase.org/home.html).

Anhang E3. Liste der als endemisch geltenden Taxa mit einem Verbreitungsgebiet unter 100.000 km^2. Die Region, in der das jeweilige Taxon endemisch ist, ist in Klammern angegeben. Nomenklatur nach Euro+Med PlantBase (http://www.emplantbase.org/home.html).

Astragalus peterfii (endemic to Transylvanian Basin)
Bromopsis pannonica subsp*. monoclada* (West-Carpathian endemic)
Cephalaria radiata (subendemic to the Transylvanian Basin)
Cyanus dominii (West-Carpathian endemic)
Daphne arbuscula (West-Carpathian endemic, Muránska planina Mts)
Dianthus praecox subsp. *praecox* (West-Carpathian endemic)
Dianthus praecox subsp. *lumnitzeri* (West-Carpathian endemic)
Festuca stricta subsp*. stricta* (endemic to Austria)
Festuca tatrae (West-Carpathian endemic)
Gentianella fatrae (West-Carpathian endemic)
Linum dolomiticum (endemic to Buda Mts)
Pulsatilla halleri subsp*. slavica* (West-Carpathian endemic)
Seseli leucospermum (endemic to the Transdanubian Mountains)

Supplement E4. List of archaeophytes and neophytes.

Anhang E4. Liste der Archaeophyten und Neophyten.

Archaeophytes:
Apera spica-venti
Buglossoides arvensis
Camelina microcarpa (subsp. *sylvestris* is considered to be an archaeophyte in Slovakia, MEDVECKÁ et al. 2012)
Cardaria draba
Carduus acanthoides
Caucalis platycarpos
Chenopodium album
Cichorium intybus
Consolida regalis
Convolvulus arvensis
Descurainia sophia
Digitaria ischaemum
Fallopia convolvulus
Fumaria vaillantii
Isatis tinctoria
Lactuca serriola
Lepidium campestre
Melampyrum arvense
Melilotus officinalis
Myosotis arvensis
Reseda lutea
Verbena officinalis
Veronica arvensis
Vicia hirsuta
Vicia sativa
Vicia tetrasperma
Vicia villosa
Viola arvensis

Neophytes:
Crepis nicaeensis (according to EuroMed Plant Base its native origin in Romania is doubtful)
Sempervivum tectorum (neophyte in Romania, ANASTASIU & NEGREAN 2009)

Neophytes were not further analysed as they only occurred in 5 relevés from Transylvania at elevations between 296 and 780 m.

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Supplement E5. List of specialists (species with a narrow ecological niche) and generalists (species with a broad ecological niche). Niche breadth (multiplicative beta diversity) based on co-occurrence analysis (FRIDLEY et al. 2007, ZELENÝ 2009) is shown for 100 specialists and generalists.

Anhang E5. Liste der Spezialisten (Arten mit enger ökologischer Nische) und Generalisten (Arten mit breiter ökologischer Nische). Die Nischenbreite (multiplikative Beta-Diversität) basierend auf der Co-Occurrence-Analyse (FRIDLEY et al. 2007, ZELENÝ 2009) wird für 100 Spezialisten und Generalisten gezeigt.

Specialists		**Generalists**	
Astragalus peterfii	2.01434	*Cotoneaster melanocarpus*	3.72889
Koeleria splendens	2.07384	*Corylus avellana*	3.72891
Nepeta ucranica	2.17192	*Gagea pusilla*	3.73284
Pilosella hoppeana	2.31873	*Sesleria heuflerana*	3.73310
Linum dolomiticum	2.36234	*Potentilla argentea*	3.73697
Asperula neilreichii	2.37898	*Sesleria caerulea*	3.73839
Gypsophila collina	2.41842	*Helianthemum nummularium agg.*	3.73943
Onosma tornensis	2.50228	*Rumex acetosella s.lat.*	3.73955
Peucedanum ruthenicum	2.53442	*Asplenium ruta-muraria*	3.73969
Cyanus dominii	2.56855	*Papaver dubium*	3.73973
Daphne arbuscula	2.65257	*Acer platanoides*	3.74198
Ornithogalum comosum	2.65944	*Filago germanica*	3.74258
Hieracium glaucinum	2.66483	*Scabiosa columbaria*	3.74327
Androsace villosa	2.67919	*Solidago virgaurea*	3.74491
Crepis nicaeensis	2.68751	*Polygonatum odoratum*	3.74511
Crepis alpestris	2.75131	*Odontites vulgaris*	3.74711
Stipa lessingiana	2.76412	*Euonymus verrucosus*	3.74744
Festuca stricta ssp. stricta	2.76611	*Tilia platyphyllos*	3.74861
Prunus domestica	2.76683	*Origanum vulgare*	3.74903
Seseli leucospermum	2.78450	*Crupina vulgaris*	3.75032
Pilosella pavichii	2.79627	*Holosteum umbellatum*	3.75092
Psephellus trinervius	2.82080	*Centaurea atropurpurea*	3.75422
Allium moschatum	2.84284	*Erophila verna*	3.75502
Cephalaria uralensis	2.84966	*Cardaria draba*	3.75569
Linum nervosum	2.85446	*Consolida regalis*	3.75609
Viola canina	2.86385	*Saxifraga paniculata*	3.75645
Polygala chamaebuxus	2.86811	*Cerastium semidecandrum*	3.75760
Crepis biennis	2.87605	*Galium pumilum agg.*	3.75817
Carum carvi	2.87729	*Potentilla recta*	3.75992
Prunus tenella	2.87731	*Hieracium umbellatum*	3.76259
Allium paniculatum	2.88588	*Valeriana officinalis agg.*	3.76853
Jurinea transylvanica	2.89526	*Fagus sylvatica*	3.76978
Astragalus danicus	2.89614	*Poa bulbosa*	3.77041
Astragalus exscapus	2.89756	*Euonymus europaeus*	3.77205
Paronychia cephalotes	2.91100	*Arabis turrita*	3.77395
Trisetum flavescens	2.92119	*Euphorbia seguieriana*	3.77576
Jurinea ledebourii	2.92248	*Tilia cordata*	3.77658
Aethionema saxatile	2.92851	*Myosotis stricta*	3.78268
Lathyrus latifolius	2.92981	*Hepatica nobilis*	3.78275
Polygala vulgaris	2.93850	*Festuca ovina s.lat.*	3.78386
Ajuga laxmannii	2.94015	*Arabidopsis thaliana*	3.78719
Echinops ritro	2.94290	*Phyteuma orbiculare*	3.78747
Gentianella fatrae	2.95498	*Asplenium trichomanes*	3.78951
Cirsium acaulon	2.95504	*Seseli libanotis*	3.78992
Klasea radiata	2.95796	*Cerastium brachypetalum*	3.79096
Salvia nutans	2.95890	*Sorbus aucuparia*	3.79147
Ranunculus bulbosus	2.96380	*Bupleurum longifolium*	3.79153
Onosma visianii	2.96944	*Polypodium vulgare*	3.79205
Astragalus vesicarius	2.97007	*Polygala amara agg.*	3.79519
Allium fuscum	2.97290	*Geranium columbinum*	3.79629
Carex montana	2.98704	*Chondrilla juncea*	3.79653
Carex firma	2.99710	*Senecio ovatus*	3.80341

Veronica officinalis	2.99873
Ononis pusilla	3.00040
Cytisus procumbens	3.01592
Trifolium dubium	3.01630
Neotinea tridentata	3.01631
Hornungia petraea	3.01698
Astragalus dasyanthus	3.02002
Platanthera chlorantha	3.02832
Tragopogon pratensis	3.02990
Ophrys insectifera	3.03130
Euphrasia rostkoviana agg.	3.04316
Ferulago sylvatica	3.04918
Dianthus plumarius	3.05371
Salvia transylvanica	3.06059
Festuca tatrae	3.06223
Trifolium rubens	3.06436
Jacobaea erratica	3.06438
Amelanchier ovalis	3.06584
Bupleurum pachnospermum	3.07017
Rhinanthus minor	3.07409
Carduus hamulosus	3.07507
Trifolium medium	3.07821
Trifolium ochroleucon	3.07987
Minuartia laricifolia	3.08448
Cirsium pannonicum	3.08545
Senecio umbrosus	3.08618
Alchemilla spec.div.	3.08951
Helictochloa praeusta	3.09871
Polygala comosa	3.10098
Sorbus dacica	3.10188
Viola riviniana	3.10252
Luzula campestris agg.	3.10867
Campanula serrata	3.11169
Colutea arborescens	3.11224
Draba lasiocarpa	3.11341
Colchicum autumnale	3.11390
Prospero autumnale	3.11483
Brassica elongata	3.11925
Selinum silaifolium	3.12621
Ajuga reptans	3.12885
Hieracium bupleuroides	3.13078
Cyanus pinnatifidus	3.13133
Primula veris	3.13273
Gentiana clusii	3.13533
Erysimum wittmannii	3.13658
Campanula carpatica	3.14123
Taraxacum serotinum	3.14235
Clematis recta	3.14502
Larix decidua	3.80696
Pilosella cymosa	3.80766
Descurainia sophia	3.81039
Verbena officinalis	3.81276
Silene bupleuroides	3.81290
Festuca valesiaca ssp. parviflora	3.81512
Poa compressa	3.81647
Carduus crispus	3.82442
Brachypodium sylvaticum	3.82563
Vincetoxicum hirundinaria	3.82615
Euphorbia amygdaloides	3.83236
Arenaria serpyllifolia agg.	3.83782
Digitalis grandiflora	3.84214
Cynoglossum officinale	3.84256
Poa stiriaca	3.84508
Rubus caesius	3.84577
Fraxinus excelsior	3.84923
Melica nutans	3.84973
Calamagrostis epigejos	3.85042
Pinus sylvestris	3.85416
Verbascum phlomoides	3.85654
Euphorbia cyparissias	3.85681
Verbascum nigrum	3.86363
Silene italica	3.86441
Thalictrum aquilegiifolium	3.87295
Silene latifolia	3.88067
Abies alba	3.88286
Melampyrum sylvaticum	3.88309
Viola arvensis	3.88591
Hylotelephium maximum agg.	3.89394
Epipactis helleborine	3.90559
Biscutella laevigata	3.91704
Campanula rotundifolia	3.91716
Buglossoides arvensis	3.92612
Hieracium murorum	3.93509
Allium schoenoprasum	3.96192
Minuartia verna agg.	3.98782
Convolvulus cantabrica	3.98887
Fallopia convolvulus	4.00280
Galium sylvaticum	4.00511
Geranium robertianum	4.00850
Lactuca serriola	4.01954
Arabidopsis arenosa	4.04352
Chenopodium album agg.	4.05506
Apera spica-venti	4.05917
Aconitum lycoctonum	4.12132
Fumaria vaillantii	4.19580
Poa nemoralis	4.21312

Supplement E6. Habitat characteristics of the studied biogeographic regions and elevation belts.

Anhang E6. Habitatmerkmale der untersuchten biogeografischen Regionen und Höhengürtel.

	Biogeographic region				**Elevation belt (m)**			
	Transylvania	**Trans-danubian Mts**	**NW Pannonia**	**Carpathians**	**planar <300**	**colline 300-500**	**sub-montane 500-800**	**montane >800**
Number of plots	*79*	*148*	*112*	*201*	*161*	*200*	*98*	*81*
Slope	29.1±15.5	22.0±15.7	20.1±11.0	29.7±11.7	20.0±12.7	26.1±15.4	26.5±10.9	33.8±11.3
Solar radiation	0.90±0.10	0.78±0.23	0.88±0.09	0.88±0.12	0.85±0.15	0.83±0.19	0.88±0.13	0.90±0.11
Temperature	8.5±0.8	10.0±0.3	8.9±0.7	6.7±1.2	9.7±0.7	8.9±0.8	7.3±0.8	5.5±0.8
Precipitation	428±39	356±19	365±28	519±79	354±23	402±47	486±55	580±67
Extreme temperature range	51.0±1.6	47.7±0.4	49.4±1.2	50.8±0.8	48.7±1.3	49.8±1.9	50.7±1.2	50.1±1.0

Supplement E7. Percentage frequency synoptic table of *Carex humilis*-dominated rocky steppes in four elevation belts. Species with a frequency > 30% that are not associated with any region are shown in the top part and the rest of the species are ordered by decreasing fidelity within the elevation belts (** - phi coefficient above 0.4, * - phi coefficient above 0.2). Only species with a frequency ≥ 10% in at least one column are shown.

Anhang E7. Synoptische Tabelle der prozentualen Häufigkeit von *Carex humilis* dominierten Felssteppen in vier Höhengürteln. Arten mit einer Häufigkeit> 30%, die keiner Region zugeordnet sind, werden im oberen Teil angezeigt, und der Rest der Arten wird nach abnehmender Treue innerhalb der Höhengürtel geordnet (** - *phi*-Koeffizient über 0,4, * - *phi*-Koeffizient über 0,2). Es werden nur Arten mit einer Häufigkeit von ≥ 10% in mindestens einer Spalte angezeigt.

Elevation belt	**lowland**	**colline**	**submontane**	**montane**
Meters a.s.l.	**<300m**	**300-500m**	**500-800m**	**>800m**
Number of plots	161	200	98	81
Carex humilis	100	100	100	100
Frequently co-occurring species				
Anthericum ramosum	42	42	70	85 *
Helianthemum nummularium	41	49	69	74
Euphorbia cyparissias	58	71	76	86
Teucrium montanum	47	52	67	56
Teucrium chamaedrys	55	70	74	56
Asperula cynanchica	53	53	61	42
Festuca pallens s.lat.	39	30	39	54
Anthyllis vulneraria	30	33	47	43
Species associated with particular altitudinal belt				
Seseli hippomarathrum	26 **	2	1	.
Euphorbia seguieriana	34 *	12	1	.
Fumana procumbens	41 *	14	11	.
Helictochloa pratensis	15 *	2	.	.
Chrysopogon gryllus	16 *	3	.	.
Carex liparocarpos	13 *	1	.	.
Sanguisorba minor	74 *	46	54	20
Petrorhagia saxifraga	12 *	1	.	.
Cerastium pumilum agg.	26 *	10	7	.
Muscari neglectum	17 *	6	1	.
Stipa pennata agg.	39 *	30	11	.
Eryngium campestre	36 *	28	8	.
Hornungia petraea	21 *	12	1	.
Poa bulbosa	14 *	2	2	.
Scorzonera austriaca	32 *	16	15	.
Dorycnium pentaphyllum agg.	47 *	40	26	1
Linum tenuifolium	39 *	24	24	.
Astragalus onobrychis	12 *	4	1	.
Galium verum	24 *	15	7	1
Globularia bisnagarica	43 *	26	36	.
*Ranunculus polyanthemos *serpens*	11 *	2	2	.
Thymus praecox agg.	50 *	40	34	9
Minuartia rubra	11 *	2	3	.
Salvia austriaca	.	13 *	2	.
Stachys recta	14	42 *	24	9
Dictamnus albus	2	13 *	1	.
Salvia nutans	.	12 *	4	.
Vinca herbacea	2	10 *	.	.
Galatella linosyris	12	20 *	4	.
Iris pumila	7	14 *	1	.
Adonis vernalis	11	20 *	6	.
Galium glaucum	12	28 *	8	12
Convolvulus arvensis	3	11 *	2	.
Veronica orchidea	1	10 *	4	.
Potentilla heptaphylla	4	10	41 *	14
Genista pilosa	11	18	46 *	27
Salvia verticillata	2	10	22 *	4
Scabiosa ochroleuca	25	23	41 *	4

Hippocrepis comosa	4	9	38 *	36
Inula ensifolia	24	40	58 *	41
Pulsatilla halleri subsp. *slavica*	.	3	31	83 **
Minuartia laricifolia	.	1	6	54 **
Sesleria caerulea	2	8	45	85 **
Thesium alpinum	.	2	7	53 **
Allium ericetorum	1	2	13	59 **
Carduus defloratus	.	.	5	47 **
Primula auricula	.	.	2	42 **
Thymus pulcherrimus	.	.	3	41 **
Galium pumilum agg.	3	4	16	54 **
Erysimum wittmannii	.	.	14	47 **
Kernera saxatilis	.	.	6	38 **
Jovibarba globifera	6	11	35	68 **
Phyteuma orbiculare	3	7	14	51 **
Scabiosa lucida	.	.	1	28 **
Polygonatum odoratum	11	16	22	60 **
Hieracium bupleuroides	.	.	7	32 **
Asplenium ruta-muraria	1	6	11	40 **
Laserpitium latifolium	.	1	9	33 **
Aster alpinus	.	.	.	22 **
Helianthemum rupifragum	.	.	2	23 *
Festuca tatrae	.	.	.	20 *
Buphthalmum salicifolium	.	2	1	22 *
Coronilla vaginalis	2	2	2	26 *
Euphrasia salisburgensis	.	1	1	21 *
Campanula cochleariifolia	.	.	.	16 *
Cyanus triumfettii	4	8	17	41 *
Ranunculus breyninus	.	.	.	15 *
Saxifraga paniculata	.	.	2	17 *
Globularia cordifolia	1	2	6	23 *
Asperula tinctoria	4	8	22	41 *
Leontodon incanus	9	14	42	56 *
Trisetum alpestre	.	.	.	12 *
Gentiana clusii	.	.	1	14 *
Leucanthemum vulgare agg.	4	8	18	36 *
Vicia cracca	.	2	2	16 *
Hieracium bifidum	.	2	3	17 *
Arabidopsis arenosa	1	3	9	23 *
Carlina acaulis	6	5	11	30 *
Sedum album	7	7	7	28 *
Koeleria pyramidata	1	.	.	11 *
Knautia kitaibelii	7	2	10	27 *
Gentianella fatrae	.	.	.	10 *
Convallaria majalis	.	.	4	15 *
Campanula carpatica	.	.	2	12 *
Seseli libanotis	.	2	3	15 *
Campanula rapunculoides	1	1	6	17 *
Achillea distans agg.	.	.	2	11 *
Epipactis atrorubens	.	2	13	22 *
Dianthus praecox	2	2	5	17 *
Thalictrum minus	8	18	16	37 *
Securigera varia	6	12	18	33 *
Dianthus carthusianorum	4	11	29	36 *
Linum catharticum	12	6	21	33 *
Calamagrostis varia	1	.	12	19 *
Polygala amara agg.	2	8	17	26 *
Seseli osseum	17	26	40	51 *
Potentilla incana agg.	69 *	68 *	43	15
Vincetoxicum hirundinaria	17	28	66 *	60 *
Clinopodium alpinum	.	5	34 *	36 *

Supplement E8. Percentage frequency synoptic table of *Carex humilis*-dominated rocky steppes in four biogeographic regions. Species with a frequency > 30% that are not associated with any region are shown in the top part and the rest of the species are ordered by decreasing fidelity within the regions (** - phi coefficient above 0.4, * - phi coefficient above 0.2). Only species with a frequency ≥ 10% in at least one biogeographical region are shown. Abbreviations of the biogeographical regions in the column headings: Transylv - Transylvania, Transdan - Transdanubian Mts, NW-Pann - NW Pannonia, Carpath - Carpathians.

Anhang E8. Synoptische Tabelle der prozentualen Häufigkeit der von *Carex humilis* dominierten Felssteppen in vier biogeografischen Regionen. Arten mit einer Häufigkeit > 30%, die keiner Region zugeordnet sind, werden im oberen Teil angezeigt, und der Rest der Arten nach abnehmender Treue innerhalb der Regionen geordnet (** - *phi*-Koeffizient über 0,4, * - *phi*-Koeffizient über 0,2). Es werden nur Arten mit einer Häufigkeit von ≥ 10% in mindestens einer Spalte angezeigt. Abkürzungen der biogeografischen Regionen in den Spaltenüberschriften: Transylv - Siebenbürgen, Transdan - Transdanubische Mts, NW-Pann - NW Pannonien, Carpath – Karpaten.

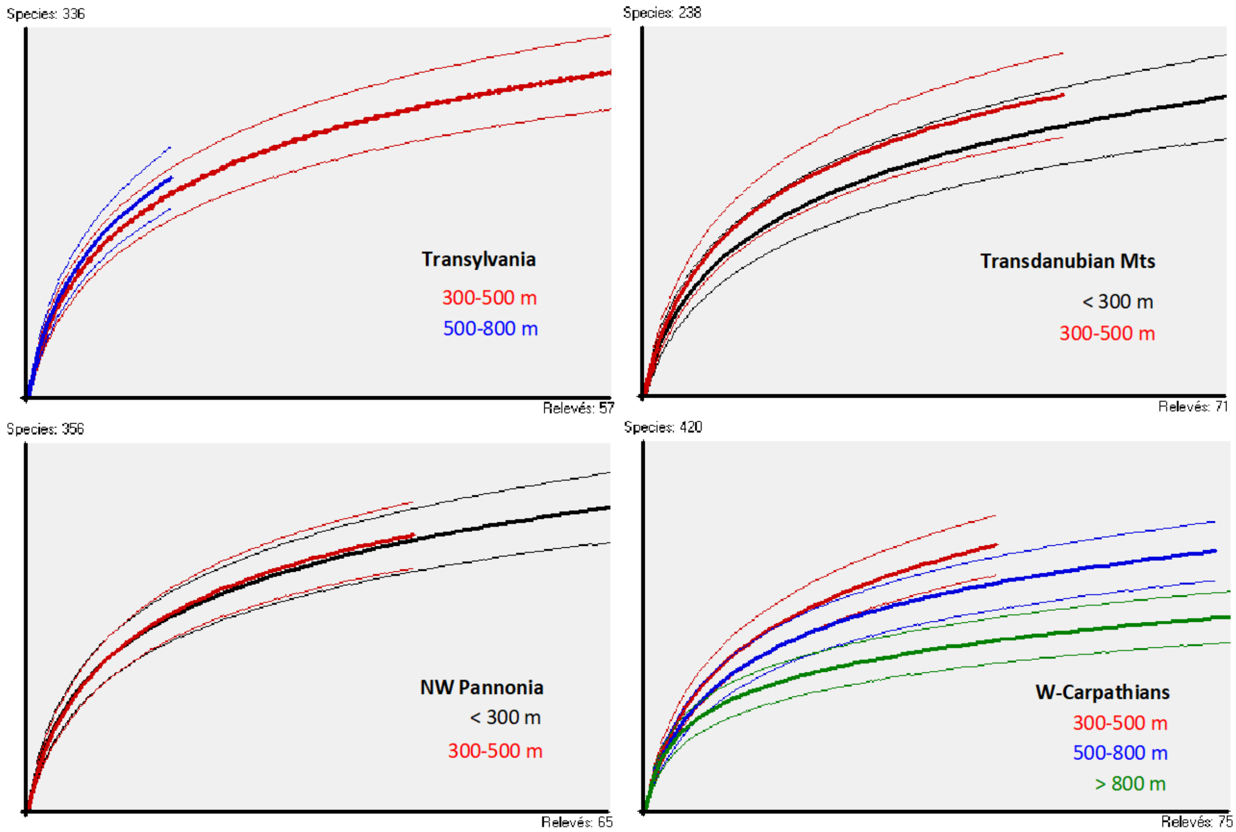
Biogeographical region	**Transylv**	**Transdan**	**NW-Pann**	**Carpath**
Number of plots	79	148	112	201
Carex humilis	100	100	100	100
Frequently co-occurring species				
Teucrium chamaedrys	84 *	40	70	72
Helianthemum nummularium	30	41	59	71 *
Euphorbia cyparissias	67	54	76	81
Teucrium montanum	56	53	43	60
Potentilla incana agg.	71	66	76	31
Species associated with particular biogeographical region				
Leontodon crispus	38 **	.	.	.
Salvia nutans	37 **	.	.	.
Salvia austriaca	35 **	.	.	.
Astragalus monspessulanum	34 **	.	.	.
Convolvulus arvensis	32 **	.	3	1
Cytisus albus	27 **	.	.	1
Fragaria viridis	49 **	5	12	9
Veronica orchidea	28 **	.	.	2
Stachys recta	67 **	18	23	16
Cephalaria uralensis	24 **	.	.	.
Pulsatilla montana	23 **	.	.	.
Seseli pallasii	20 **	.	.	.
Stipa lessingiana	20 **	.	.	.
Thymus comosus	20 **	.	.	.
Thymus kosteleckyanus	35 *	2	10	4
Carduus hamulosus	19 *	.	.	.
Klasea radiata	19 *	.	.	.
Dictamnus albus	27 *	5	2	.
Onobrychis viciifolia	27 *	.	7	.
Filipendula vulgaris	39 *	11	10	2
Jurinea transylvanica	18 *	.	.	.
Prunus tenella	18 *	.	.	.
Falcaria vulgaris	24 *	1	4	.
Salvia nemorosa	23 *	.	4	1
Crambe tataria	16 *	.	.	.
Ajuga laxmannii	16 *	.	.	.
Elytrigia intermedia	38 *	1	21	2
Adonis vernalis	38 *	7	16	2
Stipa pulcherrima	41 *	9	7	14
Leopoldia tenuiflora	15 *	.	.	1
Bothriochloa ischaemum	52 *	16	22	16
Nonea pulla	16 *	.	2	.
Pontechium maculatum	14 *	.	.	.
Peucedanum ruthenicum	14 *	.	.	.
Galium glaucum	43 *	7	15	16
Vinca herbacea	19 *	3	.	1
Agrimonia eupatoria	18 *	.	3	1
Salvia transylvanica	13 *	.	.	.
Allium paniculatum	13 *	.	.	.
Verbascum phoeniceum	18 *	2	2	1

Iris pumila	25 *	1	9	3
Salvia verticillata	25 *	.	2	13
Medicago falcata	43 *	1	32	13
Viola ambigua	14 *	1	2	.
Leopoldia comosa	14 *	.	3	.
Scorzonera hispanica	18 *	1	5	1
Cleistogenes serotina	16 *	1	.	4
Asparagus officinalis	10 *	.	.	.
Phleum montanum	10 *	.	.	.
Cephalaria radiata	10 *	.	.	.
Tragopogon dubius	13 *	1	1	1
Stipa capillata	39 *	19	21	5
Lembotropis nigricans	16 *	1	4	3
Polygala major	20 *	1	9	4
Koeleria macrantha	58 *	31	49	19
Plantago media	37 *	1	29	17
Veronica prostrata	15 *	.	10	.
Echium vulgare	24 *	1	13	10
Plantago argentea	15 *	11	.	.
Medicago lupulina	13 *	.	4	4
Stipa pennata agg.	4	61 **	28	3
Muscari neglectum	.	26 **	2	.
Hornungia petraea	.	33 **	8	.
Thymus praecox agg.	.	69 **	39	27
Euphorbia seguieriana	14	41 **	8	.
Cerastium pumilum agg.	.	32 *	13	2
Fumana procumbens	.	43 *	29	4
Hippocrepis emerus	.	16 *	.	.
Seseli leucospermum	.	16 *	.	.
Dianthus plumarius	.	16 *	.	1
Chrysopogon gryllus	.	18 *	3	1
Scorzonera austriaca	10	41 *	18	5
Globularia bisnagarica	.	51 *	38	19
Aethionema saxatile	.	13 *	.	.
Carex liparocarpos	.	14 *	.	1
Sanguisorba minor	14	76 *	66	41
Minuartia verna agg.	1	13 *	1	.
Allium moschatum	.	9 *	.	.
Dianthus pontederae	.	18 *	7	1
Helianthemum canum	14	34 *	11	11
Poa bulbosa	.	14 *	5	1
Helictochloa pratensis	.	.	25 **	.
Astragalus onobrychis	1	1	25 **	.
Pimpinella saxifraga agg.	16	6	53 *	26
Bupleurum falcatum	16	6	50 *	26
Pulsatilla vulgaris	.	4	27 *	7
Bromopsis erecta	8	1	25 *	1
Cytisus ratisbonensis	1	.	15 *	.
Festuca stricta subsp. *sulcata*	37	3	52 *	16
Scabiosa canescens	.	5	21 *	1
Minuartia rubra	.	1	16 *	2
Thymus odoratissimus	15	4	28 *	1
Centaurea scabiosa	22	6	47 *	31
Pilosella officinarum	9	6	31 *	12
*Ranunculus polyanthemos *serpens*	.	3	15 *	1
Alyssum montanum	3	16	32 *	11
Pulsatilla pratensis	.	1	10 *	.
Dorycnium pentaphyllum agg.	49	30	59 *	15
Seseli hippomarathrum	.	16	21 *	.
Carex caryophyllea	5	.	21 *	9
Sedum sexangulare	1	3	17 *	5
Brachypodium pinnatum	20	3	34 *	17
Salvia pratensis	19	16	43 *	27
Lotus corniculatus	10	7	32 *	22
Scabiosa ochroleuca	20	9	40 *	27
Centaurea stoebe	29	9	38 *	15
Dactylis glomerata	6	.	12 *	1
Galium verum	16	16	29 *	3

Petrorhagia saxifraga	.	6	12 *	.
Pulsatilla halleri subsp. *slavica*	.	.	2	50 **
Sesleria caerulea	.	.	13	59 **
Hippocrepis comosa	.	3	2	42 **
Jovibarba globifera	.	4	12	50 **
Allium ericetorum	.	.	.	32 **
Clinopodium alpinum	3	.	1	34 **
Erysimum wittmannii	.	.	.	26 **
Minuartia laricifolia	.	.	1	25 **
Thesium alpinum	.	.	2	25 **
Carduus defloratus	.	.	.	22 **
Asplenium ruta-muraria	1	1	1	25 **
Leontodon incanus	.	11	18	46 **
Galium pumilum agg.	.	5	4	30 *
Vincetoxicum hirundinaria	14	25	22	62 *
Primula auricula	.	.	.	18 *
Kernera saxatilis	.	.	1	18 *
Hieracium bupleuroides	.	.	.	17 *
Thymus pulcherrimus	.	.	1	18 *
Potentilla heptaphylla	4	5	5	31 *
Laserpitium latifolium	1	.	.	18 *
Seseli osseum	9	7	32	52 *
Epipactis atrorubens	.	1	.	17 *
Phyteuma orbiculare	.	10	2	28 *
Polygonatum odoratum	3	22	5	40 *
Asperula tinctoria	5	7	4	30 *
Anthericum ramosum	24	43	47	77 *
Genista pilosa	.	10	23	40 *
Calamagrostis varia	.	1	.	14 *
Scabiosa lucida	.	.	.	12 *
Lactuca perennis	.	.	.	11 *
Helianthemum rupifragum	.	.	.	11 *
Polygala amara agg.	.	9	1	21 *
Campanula rapunculoides	.	.	1	11 *
Leucanthemum vulgare agg.	8	8	2	24 *
Dianthus carthusianorum	18	.	11	29 *
Bromopsis pannonica	.	15	.	21 *
Knautia kitaibelii	.	.	11	18 *
Globularia cordifolia	.	.	4	12 *
Arabidopsis arenosa	.	5	1	13 *
Cyanus triumfettii	9	5	8	24 *
Origanum vulgare	3	.	3	12 *
Coronilla vaginalis	.	5	.	11 *
Linum catharticum	10	1	16	26 *
Achillea millefolium agg.	41 *	4	41 *	13

Supplement E9. Gamma diversity in different elevation belts of individual biogeographic regions. Only groups with more than 10 plots were compared. The x-axis shows number of plots and the y-axis number of species. The thin lines show confidence intervals.

Anhang E9. Gamma-Diversität in verschiedenen Höhengürteln einzelner biogeografischer Regionen. Es wurden nur Gruppen mit mehr als 10 Plots verglichen. Die x-Achse zeigt die Anzahl der Parzellen und die Anzahl der Arten auf der y-Achse. Die dünnen Linien geben Konfidenzintervalle an.



Supplement E10. Ecological indicator values of *Carex humilis* and eight most frequently co-occurring species in the studied rocky steppes. Two main sources for indicator values (both ranged from 1 to 9) were used: E – ELLENBERG et al. (1991), B – BORHIDI (1995).

Anhang E10. Ökologische Zeigerwerte von *Carex humilis* und acht am häufigsten gemeinsam vorkommenden Arten in den untersuchten Felssteppen. Zwei Hauptquellen für Zeigerwerte (beide reichen von 1 bis 9) wurden verwendet: E – ELLENBERG et al. (1991), B – BORHIDI (1995).

	Reference	**Light**	**Temperature**	**Continentality**	**Moisture**	**Soil reaction**	**Nutrients**
Carex humilis	**E**	**7**	**5**	**5**	**3**	**8**	**3**
	B	**7**	**6**	**5**	**3**	**9**	**3**
Anthericum ramosum	**E**	7	5	4	4	7	4
	B	7	6	4	3	7	4
Asperula cynanchica	**E**	7	7	5	3	8	3
	B	8	7	5	3	8	3
Euphorbia cyparissias	**E**	8	x	4	3	x	3
	B	8	5	4	3	7	3
Helianthemum ovatum	**E**	8	5	4	2	9	1
	B	7	5	4	3	9	2
Potentilla arenaria	**E**	7	6	6	1	8	1
	B	9	7	6	1	8	1
Sanguisorba minor	**E**	7	6	5	3	8	2
	B	7	6	5	3	8	2
Teucrium chamaedrys	**E**	7	6	4	2	8	1
	B	7	6	4	3	8	2
Teucrium montanum	**E**	8	7	4	1	9	2
	B	9	8	4	1	9	1

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