Landscape classification of the Czech Republic based on the distribution of natural habitats

Klasifikace krajiny České republiky na základě rozšíření přírodních biotopů

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Divíšek J., Chytrý M., Grulich V. & Poláková L. (2014): Landscape classification of the Czech Republic based on the distribution of natural habitats. – Preslia 86: 209–231.

We propose the first statistical landscape classification of the Czech Republic based on the distribution of different types of natural habitats (mainly defined in terms of plant communities) that resulted from national habitat mapping. We used occurrences of natural habitats in 2370 grid cells of 5' longitude × 3' latitude covering the whole area of the country. To cluster grid cells with similar habitat composition, we used two methods. First, we applied spatially unconstrained hierarchical clustering to obtain landscape types with maximal internal homogeneity in the range of natural habitats they contain. Second, we added spatial constraints to the classification process in order to obtain spatially cohesive regions. In both cases, the cross-validation technique proposed seven clusters as the optimal result. We also determined the characteristic habitats for each landscape type and region and characterized them using ecologically relevant attributes of abiotic environment and land cover. Irrespective of the method used, our results showed that the separation of individual clusters is primarily determined by altitude and related climatic factors, and differences between the Bohemian Massif and Carpathians. We compared our results with existing expert-based phytogeographical, biogeographical and zoogeographical divisions of the Czech Republic and also with a recently published statistical landscape classification of the Czech Republic based on the abiotic environment. Our landscape classifications closely matched the phytogeographical divisions of the Czech Republic proposed by Skalický (1988) and Dostál (1957, 1966). They differed more when compared with the biogeographical division of the Czech Republic (Culek 1996). However, we do not suggest that any of these classifications is superior to the others, because each of them is based on different principles and data. Both expert-based and statistical classifications can produce multiple meaningful results depending on a priori weighting of input data, number of target units and classification methods used. The advantage of statistical classifications is that input data and classification process are clearly described and therefore their logic can be more easily understood. The classification based on natural habitats presented here is not intended to replace any of the previous classifications, but to provide useful insights into biogeographical patterns in this country in addition to the previous classifications.

K e y w o r d s: biogeographical division, biotopes, constrained clustering, Czech Republic, habitat types, landscape types, Natura 2000, phytogeographical division, regionalization, vegetation types

Introduction

Classification of landscape into internally homogeneous and well interpretable biogeographical and ecological units has been a traditional focus of researchers worldwide and across all spatial scales, because such units provide a useful framework for both ecological research and environmental management. The identification, description and assessment of types of landscapes or biogeographical regions constitute important baseline information for nature conservation planning and decision making. Such classifications may be based on various patterns observed in nature, including discontinuities in ecologically relevant attributes of the abiotic environment (Metzger et al. 2005, Chuman & Romportl 2010), taxonomic composition of species assemblages (Heikinheimo et al. 2007, Linder et al. 2012) or a combination and integration of both (Belbin 1993, Mackey et al. 2008). In the past, these classifications were based on expert knowledge, but recent advances in statistical methods coupled with much more data being available have stimulated the development of statistically derived classifications. The classification process can thus be formally described and is repeatable (MacDonald 2003).

In the Czech Republic, existing biogeographical classifications were all created based on expert knowledge. These include the maps of reconstructed and potential natural vegetation (Mikyška et al. 1968, Neuhäuslová et al. 1997), and phytogeographical (Dostál 1957, 1966, Skalický 1988), zoogeographical (Mařan 1958) and biogeographical divisions of the Czech Republic (Raušer 1971, Culek 1996, 2005). Expert-based classifications of the national territory were developed also for abiotic conditions, e.g. climate (Quitt 1971), or integrated different abiotic features (e.g. Demek et al. 1977). Such maps have become valuable tools for both scientists and nature managers, however, understanding the units they define is significantly limited by the fact that the decision criteria applied in the classification and mapping, their weighting and degree of consistency in their use are unknown. On the other hand, statistically derived landscape classifications are restricted to recently published landscape typology based on abiotic conditions, CORINE Land Cover data and the map of reconstructed vegetation (Chuman & Romportl 2010, Romportl et al. 2013).

Statistically derived classifications based on the distribution of vegetation types (plant community units) are of special importance, because they are directly linked to biodiversity. Vegetation is often used as a proxy for habitats of wild flora and fauna, which is a principle adopted in the nature conservation legislation of the European Union (European Commission 2013). There are currently several national or regional projects mapping habitats in Europe (Ichter et al. 2014), but few have been completed. An exceptional example of a synthesis of national habitat mapping in the form of landscape classification was recently published by Bölöni et al. (2011), based on the results of an extensive project in Hungary (Molnár et al. 2007).

In the Czech Republic field mapping of natural habitats was carried out to provide baseline data for national implementation of the Natura 2000 network according to the Habitats Directive (92/43/EEC) of the European Union (Guth & Kučera 2005). It was done at a scale of 1:10 000 and the mapping legend was defined in the first edition of the Habitat Catalogue of the Czech Republic (Chytrý et al. 2001), which contains descriptions of all major habitat types occurring in this country and enables any site to be assigned to a particular habitat type. Individual habitats were mapped as patches, lines or point occurrences.

The baseline mapping was carried out in 2001–2004 and since 2006 regularly updated. The results of the baseline mapping with some updates were summarized by Härtel et al. (2009) and in the second edition of the Habitat Catalogue (Chytrý et al. 2010), but these previous syntheses focused on the distribution of individual habitats while summaries across multiple habitats were missing.

In this study, our aim is to produce a statistical classification of the Czech landscape based on the distribution of natural habitats resulting from the national habitat mapping, which would improve the understanding of the biogeographical patterns in this country. We applied two methods. First, we used spatially unconstrained clustering to obtain landscape types with maximal internal homogeneity in the range of natural habitats they contain. Although the definitions of the landscape types are typically more complex, including not only biotic but also abiotic features and human activities, in this study we define them only in terms of natural habitat types. This is justified by the fact that habitats strongly reflect the abiotic environment, biogeographical patterns and human activity. Landscape types defined in this way, however, are scattered in many patches, resulting in very complex mosaic-like maps, which may be of limited value for some purposes. Therefore, in parallel we used a second method, which involved adding spatial constraints to the classification process in order to obtain habitat-based regions that are spatially cohesive. In addition, we determined the characteristic habitats for individual landscape types and regions and characterized them based on ecologically relevant attributes of their abiotic environment and land cover. As a classification process may provide multiple meaningful results depending on input data and a priori classification criteria, we do not attempt to provide any definitive solution to the ecological or biogeographical classification of the Czech landscape. We rather use these two methods to provide different perspectives and show possible alternative solutions.

Methods

Habitat distribution data

We used habitat distribution maps published in the second edition of the Habitat Catalogue of the Czech Republic (Chytrý et al. 2010), which summarize the results of the baseline habitat mapping project realized in 2001–2004, with some newer updates and expert revisions. These maps contain occurrences of 127 natural and semi-natural habitat types (also termed ‘natural habitats’ or ‘habitats’ in this paper) in grid cells spanning 5' of longitude and 3' of latitude, which corresponds to ~5.6 × 6.0 km (33.3 km^2) on the 50th parallel. In our study, we adopted this spatial resolution because it is widely used for mapping of central-European flora. Although the Czech Republic is covered by 2552 grid cells in total, we considered only 2370 cells with more than 50% of their area within this country. The resulting data matrix thus contained occurrences of 127 habitat types in 2370 grid cells.

We created maps that showed the number of habitat types per grid cell (not shown). In two administrative regions, Karlovarský and Liberecký, these maps indicated that the mean number of habitat types per grid cell was remarkably higher than in other regions. This pattern did not correspond to real habitat diversity, but reflected a bias caused by the slightly different criteria used for mapping in these two regions: often rather untypical or fragmentary examples of particular habitats were mapped in these two regions but not in

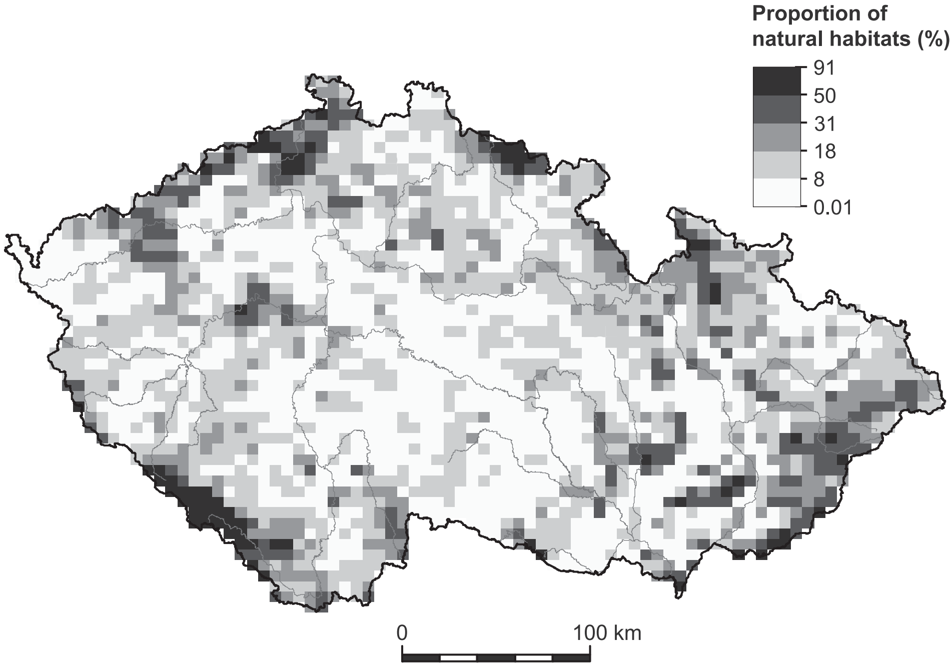

Fig. 1. – Percentages of the areas occupied by natural habitats in grid cells covering the Czech Republic. Percentage values were classified using natural breaks (Jenks) method. Note that in the Liberecký and Karlovarský regions only habitats of representativeness A and B were considered in order to reduce regional bias.

others. To remove this bias, we replaced habitat occurrences in these two regions obtained from the Habitat Catalogue of the Czech Republic by data extracted directly from the GIS database of the Agency for Nature Conservation and Landscape Protection of the Czech Republic (updated as of 5 May 2010). This database contains polygons of the (semi-)natural habitat types with assigned levels of representativeness (A–D). For our purpose, we selected only polygons with the two highest levels of representativeness (A and B) and assigned their occurrences to the grid cells in the Liberecký and Karlovarský regions. The updated data set, containing fewer habitat types per grid cell in these two regions, did not show any obvious bias when the number of habitat types per grid cell was plotted on the country map. It was therefore used in further analyses. It is important to note that natural habitats cover a relatively small area in most grid cells (Fig. 1), while the rest is covered by arable land, forestry plantations, built-up areas and similar habitats that were not considered as natural habitats in the national habitat mapping project and not used in the current analyses.

Environmental explanatory variables

To relate the patterns based on habitat types to ecologically relevant attributes of the environment, we established a set of environmental explanatory variables. For each grid cell, we calculated mean altitude, altitudinal range and terrain ruggedness on the basis of a digital elevation model of the Czech Republic (resolution 50 × 50 m). Terrain ruggedness was expressed as the mean value of the vector ruggedness measure for each grid cell (VRM; Sappington et al. 2007). It combines variation in slope and aspect into a single measure and provides better information about terrain heterogeneity than indices based on slope or altitude only. The mean VRM values ranged from 0 to 2.033 (higher VRM values represent a more rugged terrain).

We also computed percentage areas of seven geological formations in each grid cell: (1) Proterozoic and Palaeozoic rocks (except limestone and serpentine), (2) Cretaceous sediments (except calcareous), (3) Carpathian flysch sediments, (4) Tertiary volcanic rocks, (5) Upper Tertiary and Quaternary sediments, (6) Limestone and calcareous sediments and (7) Serpentines (see corresponding maps in Chytrý 2007, their Figs 3, 4). Geological data were extracted from the geological maps of the Czech Republic provided by the Czech Geological Survey. Limestone and calcareous sediments were extracted from the maps at a scale of 1:50 000 and all other geological formations from the maps at a scale of 1:500 000.

On the basis of climatic data extracted from the Climate Atlas of Czechia (Tolasz 2007), we calculated the mean annual temperature and annual precipitation for each grid cell and the range of these climatic variables within each grid cell.

Finally, we determined the percentage areas of arable fields, coniferous tree plantations and urbanized areas within each grid cell to explore if patterns based on habitat types are affected by land use and landscape management. These variables were extracted from CORINE 2000 Land Cover data (Bossard et al. 2000). To obtain the area of coniferous tree plantations in each grid cell, we calculated the areas occupied by CORINE 2000 Land Cover type 3.1.2 Coniferous forests that do not overlap with natural coniferous forests according to the habitat mapping. All calculations and data processing were done using ArcGIS 10 software (ESRI 2011).

Landscape classification based on cluster analysis

In order to classify the landscape of the Czech Republic based on the distribution of natural habitats, we used a matrix of 127 habitats × 2370 grid cells and calculated pairwise dissimilarities in habitat composition between grid cells using the beta-sim index (β_{sim}). The advantage of β_{sim} is its independence of the species richness gradients in the study area (Lennon et al. 2001, Koleff et al. 2003, Baselga et al. 2007). This index calculates the compositional dissimilarity between two grid cells:

$$\beta_{sim} = 1 - \frac{a}{\min(b, c) + a},$$

where a is the number of shared habitat types, b is the number of habitat types unique to the first grid cell and c is the number unique to the second grid cell. Values of β_{sim} vary between 0 for identical habitat composition of two grid cells to 1 for grid cells that do not share any habitat type. This index is implemented in the ‘betadiver’ function of ‘vegan’ package (Oksanen et al. 2013) and its application to our habitat data resulted in a matrix containing 5,616,900 dissimilarity values (2,807,265 unique pairwise comparisons). Subsequently, this matrix was subjected to two agglomerative hierarchical clustering procedures: (i) spatially unconstrained and (ii) spatially constrained clustering. In both cases, we used Ward’s minimum variance method (Ward 1963), which minimizes the sum of the within-group sums of squares. As this method works in Euclidean space, it cannot be directly applied to a dissimilarity matrix calculated using the β_{sim} index (Legendre & Legendre 2012). To make the dissimilarity matrix Euclidean, we used Cailliez (1983) correction method, which computes the smallest positive value (constant; in our case 184.653) and adds it to each dissimilarity value. This method is implemented in the 'ade4' package (Dray & Dufour 2007). In the case of spatially constrained clustering, we first determined the spatial connections between each pair of grid cells according to the rook scheme (Fortin & Dale 2005). Using this scheme, each grid cell is considered to be connected with four other grid cells in four cardinal directions (N, E, S, W). According to this criterion, we calculated the binary connectivity matrix containing the values of 1 for connected grid cells and 0 for unconnected grid cells. Both the habitat dissimilarity matrix and the connectivity matrix were then used in a spatially constrained hierarchical clustering procedure as implemented in the R package 'const.clust' (Legendre 2011). This method clusters only those grid cells that are spatially connected. Spatially constrained clustering produces spatially coherent clusters, which may be advantageous and more readily interpretable in some cases. On the other hand, such clusters are often internally more heterogeneous than those resulting from spatially unconstrained cluster analysis. To select an appropriate number of clusters we used a cross-validation procedure implemented in the 'const.clust' package (Legendre 2011). This method calculates the value of the cross-validation residual error for each partition between 2 and 20 clusters and then it suggests the partition with the lowest cross-validation residual error, which best represents the pattern of habitat composition across the Czech Republic. For this partition we calculated the characteristic habitats and range of environmental conditions.

Cluster characterization

For the partition with the optimal number of clusters selected on the basis of the cross-validation technique, we determined the characteristic habitat types for each cluster (landscape type or region) using the phi (Φ) coefficient of association, which was calculated after virtual equalization of cluster sizes to remove the undesirable effects of the unequal number of cells per cluster on the coefficient values (Tichý & Chytrý 2006).

We also analysed the relationships between the spatial pattern of the resulting clusters and selected environmental explanatory variables using classification trees (CART; Breiman et al. 1984). The classification tree assigns each grid cell to a particular cluster using a set of explanatory variables. This method hierarchically splits the response variable (i.e. the grid cell membership) into smaller groups according to explanatory variables (environmental predictors) that minimize the misclassification error. At each split, grid cells are divided into two groups based on a single explanatory variable. To select the optimal tree size (optimal number of branches, also called nodes or splits) we used the 10-fold cross-validation method. This calculates classification trees on smaller subsamples of the entire data set and provides the value of cross-validation errors for trees of each size. As an optimal tree, we selected the smallest tree that reached the threshold value of the minimal cross-validation error plus 1 SE. For each node of the tree, we identified not only the primary splitter variable but also surrogates, i.e. the variables that are able to allocate grid cells to clusters in a similar way to the primary splitter. To consider a variable as a surrogate, we required that it allocated more than 90% of grid cells to the same group as the primary splitter. Classification trees were computed using 'rpart' package (Therneau et al. 2013). All statistical analyses were performed in R software (R Core Team 2013).

Results

Unconstrained clustering

Spatially unconstrained clustering resulted in the clusters being scattered in space but representing relatively homogeneous landscape types with specific habitat compositions (Fig. 2). Cross-validation technique suggested seven clusters as the optimal number (Fig. 3). Mountain to submontane landscape types (cluster 1 and 2) dominated by mountain meadows, natural spruce forests and mires were separated at the highest dendrogram level (Fig. 3).

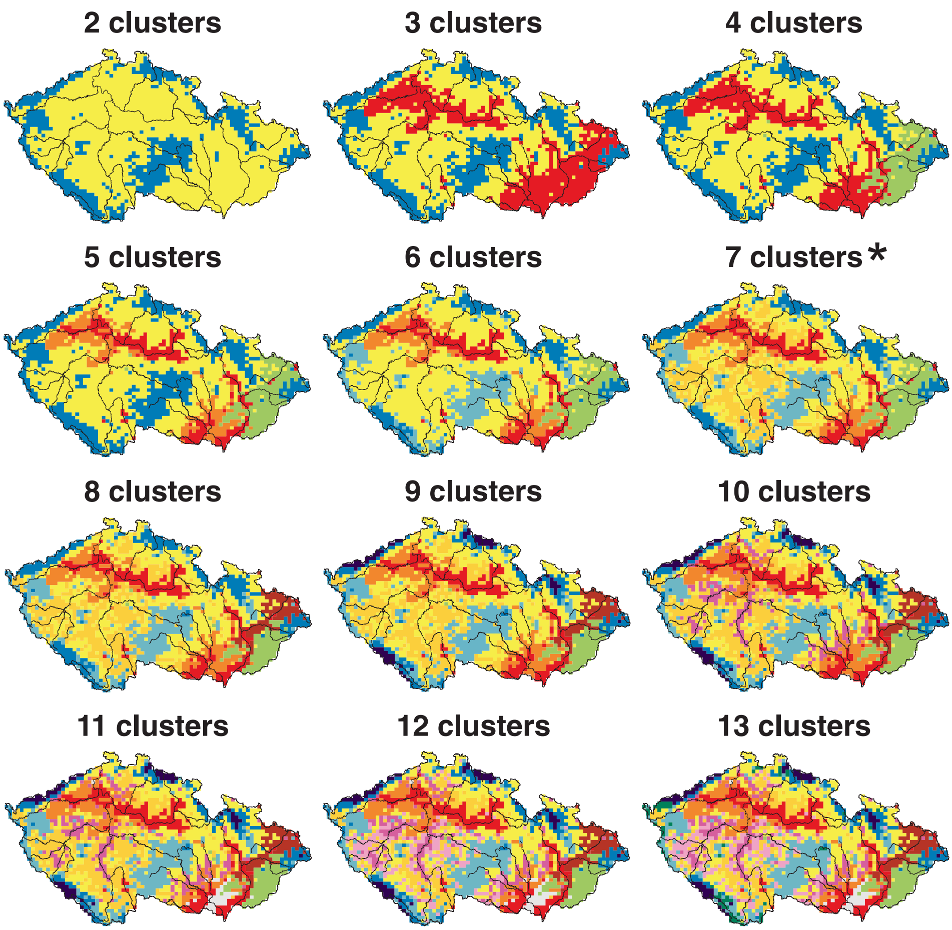

Fig. 2. – Clustering sequence of spatially unconstrained clustering of the natural habitats of the Czech Republic using the β_{sim} dissimilarity measure and Ward's minimum variance method. Asterisk denotes the optimal number of clusters according to the cross-validation procedure.

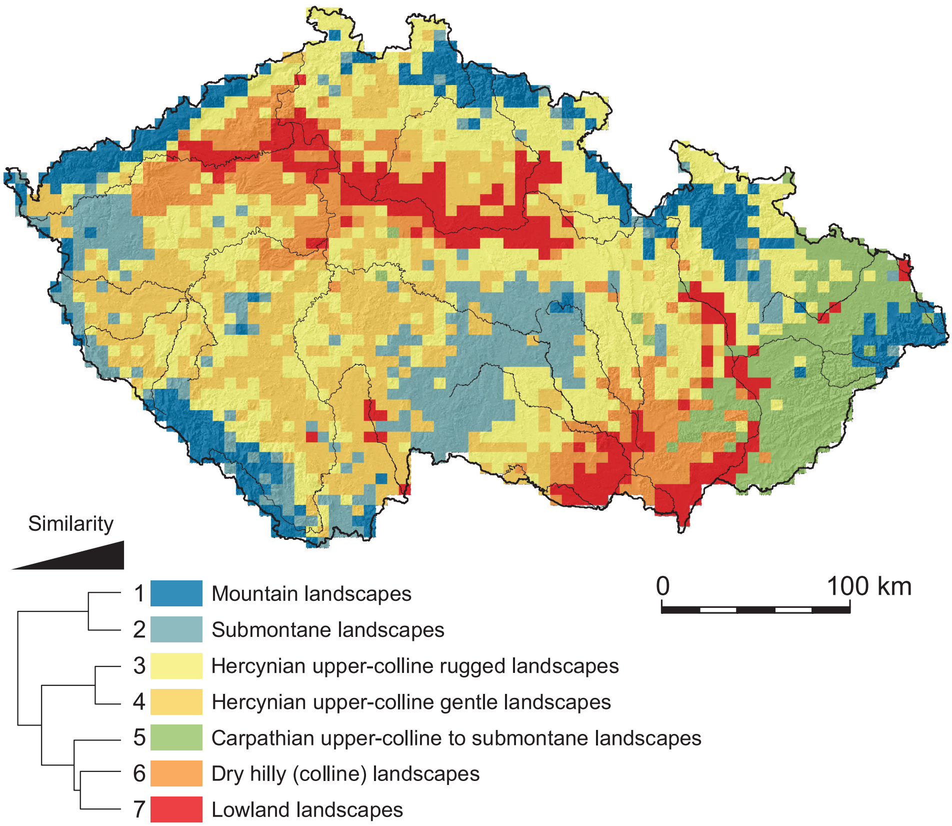

Fig. 3. – Landscape classification of the Czech Republic based on spatially unconstrained clustering with the optimal number of seven clusters according to the cross-validation procedure.

Cluster 1 (Mountain landscapes) was characterized primarily by montane *Trisetum* meadows (habitat code T1.2) and natural spruce forests (L9.1, L9.2). Cluster 2 (Submontane landscapes) was characterized by acidic moss-rich fens (R2.2) and transitional mires (R2.3), however these habitats were also suggested as characteristic of cluster 1. The following dendrogram branching separated mid-altitude Hercynian landscapes (cluster 3 and 4) from lowland and Carpathian landscapes (clusters 5, 6 and 7). Cluster 3 (Hercynian upper-colline rugged landscapes) was characterized by Hercynian oak-hornbeam forests (L3.1) and cluster 4 (Hercynian upper-colline gentle landscapes) by acidophilous oak forests (L7.1, L7.2). The next dendrogram node separated cluster 5 (Carpathian upper-colline to submontane landscapes) characterized by Carpathian and Polonian oak-hornbeam forests (L3.3, L3.2) from lowland landscapes (cluster 6 and 7). Cluster 6 (Dry hilly (colline) landscapes) was characterized primarily by narrow-leaved dry grasslands (T3.3) and low xeric scrub (K4), and cluster 7 (Lowland landscapes) by deciduous forests along lowland rivers (L2.3, L2.4). Characteristic habitat types for each cluster, identified using the equalized phi coefficient of association, are summarized in Table 1.

Table 1. – Characteristic natural habitats of the seven clusters resulting from the spatially unconstrained clustering, based on the phi coefficient of association (× 1000), which increases with increase in the concentration of a habitat occurrence in a particular cluster. Habitats with Φ > 250 are considered as characteristic. They are indicated by shading and ranked by a decreasing value of Φ. Only positive Φ values are shown. Habitat codes are those used in the Habitat Catalogue of the Czech Republic.

Cluster		1	2	3	4	5	6	7
No. of grid cells		252	305	691	472	200	233	227
No. of characteristic habitats (including shared habitats)		21	4	1	3	4	12	8
No. of characteristic habitats (not including shared habitats)		17	0	1	3	4	12	8
Mountain landscapes (cluster 1)								
T1.2	Montane *Trisetum* meadows	655	–	–	–	–	–	–
L9.1	Montane *Calamagrostis* spruce forests	629	–	–	–	–	–	–
L2.1	Montane grey alder galleries	514	–	–	–	–	–	–
R3.1	Open raised bogs	465	–	–	–	–	–	–
R1.2	Meadow springs without tufa formation	434	104	–	–	–	–	–
L9.3	Montane *Athyrium* spruce forests	432	–	–	–	–	–	–
M5	*Petasites* fringes of montane brooks	427	–	10	–	137	–	–
R3.2	Raised bogs with *Pinus mugo*	403	–	–	–	–	–	–
L5.2	Montane sycamore-beech forests	394	–	–	–	–	–	–
T8.2	Secondary submontane and montane heaths	380	172	–	–	–	–	–
R3.3	Bog hollows	373	–	–	–	–	–	–
R3.4	Degraded raised bogs	324	–	–	–	–	–	–
A4.2	Subalpine tall-forb vegetation	315	–	–	–	15	–	–
R1.4	Forest springs without tufa formation	313	182	28	–	136	–	–
A4.3	Subalpine tall-fern vegetation	270	–	–	–	–	–	–
T2.2	Montane *Nardus* grasslands with alpine species	262	–	–	–	–	–	–
L10.1	Birch mire forests	261	123	–	23	–	–	–
Mountain and Submontane landscapes (cluster 1 and 2)								
R2.2	Acidic moss-rich fens	333	421	–	–	–	–	–
R2.3	Transitional mires	388	417	–	–	–	–	–
T2.3	Submontane and montane *Nardus* grasslands	371	407	–	–	–	–	–
L9.2	Bog spruce forests	569	346	–	–	–	–	–
Hercynian upper-colline rugged landscapes (cluster 3)								
L3.1	Hercynian oak-hornbeam forests	–	–	298	152	–	113	33
Hercynian upper-colline gentle landscapes (cluster 4)								
L7.2	Wet acidophilous oak forests	–	–	25	300	–	–	18
L7.1	Dry acidophilous oak forests	–	–	183	277	–	13	–
T1.4	Alluvial Alopecurus meadows	–	–	43	275	–	–	63
Carpathian upper-colline to submontane landscapes (cluster 5)								
L3.3	Carpathian oak-hornbeam forests	–	–	–	–	739	74	–
L3.2	Polonian oak-hornbeam forests	22	–	17	–	470	–	–
R1.3	Forest springs with tufa formation	–	–	–	–	394	74	–
R1.1	Meadow springs with tufa formation	–	–	–	–	330	–	–
Dry hilly (colline) landscapes (cluster 6)								
T3.3	Narrow-leaved dry grasslands	–	–	–	–	–	658	202
K4	Low xeric scrub	–	–	–	–	–	472	–
T4.1	Dry herbaceous fringes	–	–	–	–	–	437	32
L6.1	Peri-Alpidic basiphilous thermophilous oak forests	–	–	–	–	–	427	64
T3.4	Broad-leaved dry grasslands	–	–	59	–	173	422	161
L6.4	Central European basiphilous thermophilous oak forests	–	–	–	5	28	324	44
T3.1	Rock-outcrop vegetation with *Festuca pallens*	–	–	49	–	–	317	–
L6.5	Acidophilous thermophilous oak forests	–	–	125	–	–	314	–
T6.2	Basiphil. vegetation of spring therophytes and succulents	–	–	26	–	–	297	–
T3.2	*Sesleria* grasslands	–	–	–	–	–	282	15
L3.4	Pannonian oak-hornbeam forests	–	–	–	–	73	264	230
T8.1	Dry lowland and colline heaths	–	–	12	–	–	258	72

Cluster		1	2	3	4	5	6	7
Lowland landscapes (cluster 7)								
L2.3	Hardwood forests of lowland rivers	–	–	–	–	193	–	753
L2.4	Willow-poplar forests of lowland rivers	–	–	–	–	223	52	729
M7	Herbaceous fringes of lowland rivers	–	–	–	–	–	34	411
L7.4	Acidophilous oak forests on sand	–	–	–	–	–	–	395
T5.3	*Festuca* sand grasslands	–	–	–	–	–	89	387
T1.7	Continental inundated meadows	–	–	–	–	–	16	308
T5.2	Open sand grasslands with *Corynephorus canescens*	–	–	–	–	–	62	287
M1.2	Halophilous reed and sedge beds	–	–	–	–	–	182	283

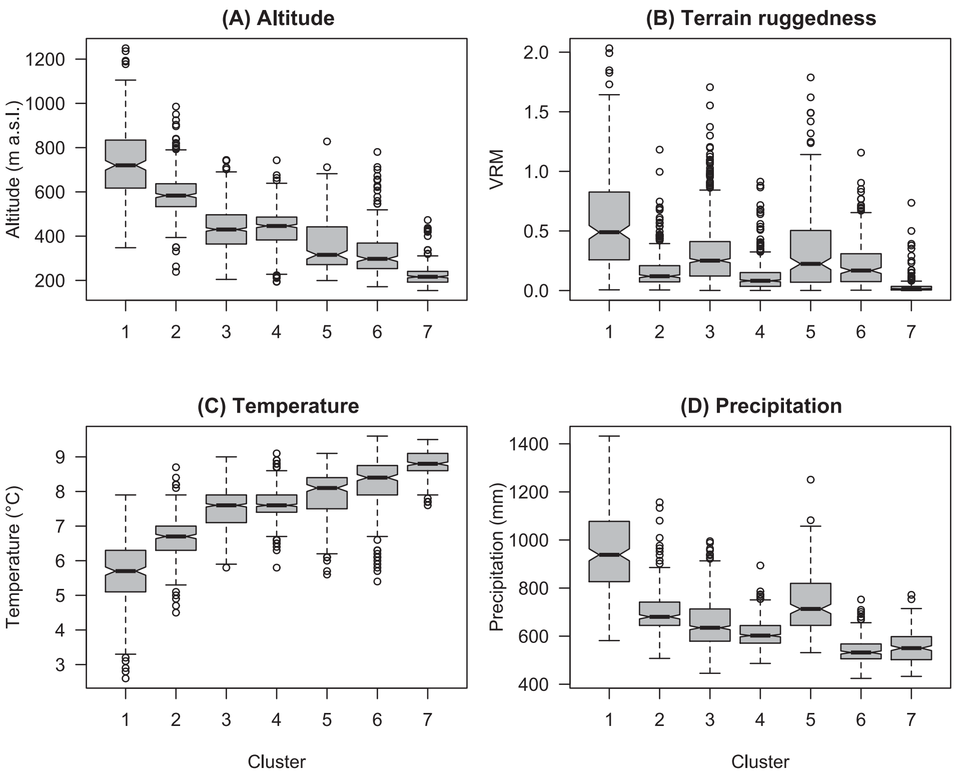

Fig. 4. – Environmental variables for seven clusters (landscape types) resulting from the spatially unconstrained clustering procedure. 1 – Mountain landscapes; 2 – Submontane landscapes; 3 – Hercynian upper-colline rugged landscapes; 4 – Hercynian upper-colline gentle landscapes; 5 – Carpathian upper-colline to submontane landscapes; 6 – Dry hilly (colline) landscapes; 7 – Lowland landscapes. Box-plots were constructed using mean values of the given environmental variables within grid cells. Thick horizontal lines indicate the median. The bottom and top of each box indicates the 25th and 75th percentiles, respectively. Non-overlapping box notches indicate significantly different medians. The vertical dashed lines (whiskers) represent either the maximum value or 1.5 × interquartile range depending on which is closer to the mean. Values outside the range of whiskers are defined as outliers and plotted individually. When there are no outliers, the whiskers show the maximum and minimum values. Terrain ruggedness is expressed as mean value of the Vector Ruggedness Measure (VRM; see Methods). The higher the VRM value the greater the terrain ruggedness.

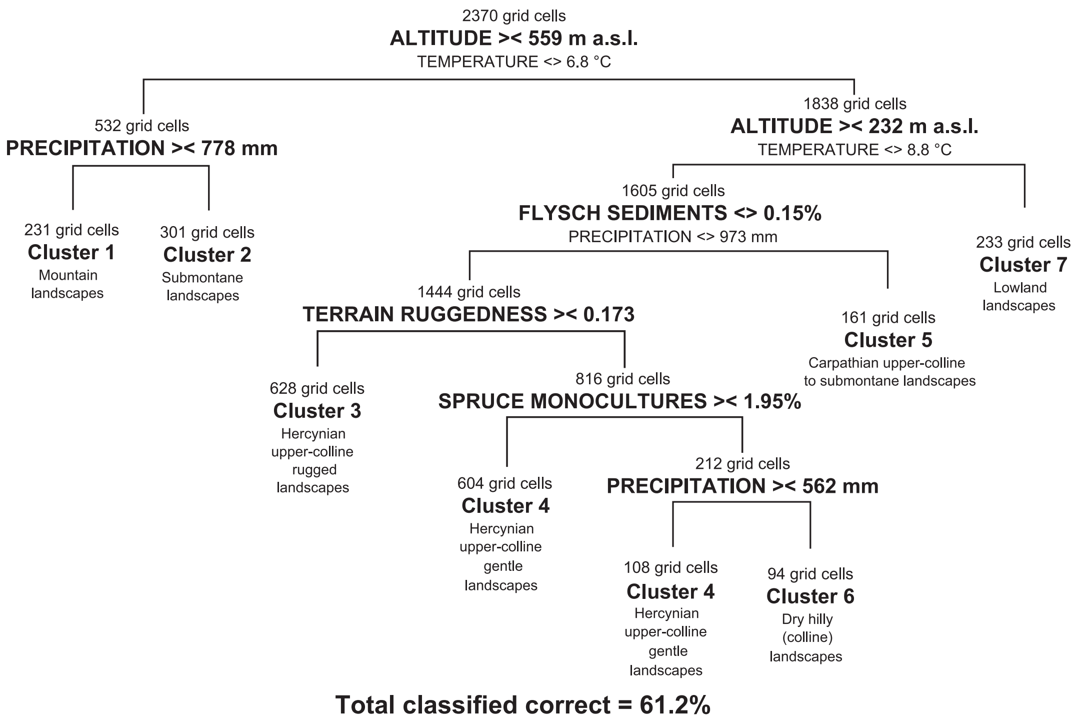

Fig. 5. – Classification tree describing the separation of the seven clusters (landscape types) resulting from spatially unconstrained clustering in terms of abiotic factors and land-cover types. Each node contains information on the number of assigned grid cells. The primary splitter variable and its split value at each node are given in bold. Surrogates, defined as variables that allocate more than 90% of the grid cells to the same group as the primary splitter, are given in smaller letters below the primary splitter.

Table 2. – Percentage areas of the main geological formations in clusters (landscape types) resulting from spatially unconstrained clustering. 1 – Mountain landscapes; 2 – Submontane landscapes; 3 – Hercynian upper-colline rugged landscapes; 4 – Hercynian upper-colline gentle landscapes; 5 – Carpathian upper-colline to submontane landscapes; 6 – Dry hilly (colline) landscapes; 7 – Lowland landscapes.

Geological formations	Cluster						
	1	2	3	4	5	6	7
Proterozoic and Palaeozoic rocks	79.3	91.9	65.9	67.9	7.3	28.3	5.8
Cretaceous sediments	3.7	2.7	14.3	13.7	0.6	15.8	17.3
Upper Tertiary and Quaternary sediments	4.3	4.3	15.5	17.6	37.9	35.0	69.7
Carpathian flysch sediments	11.1	0.3	0.3	–	53.1	7.2	0.8
Tertiary volcanic rocks	0.4	0.5	1.9	0.2	0.6	9.3	0.5
Limestone and calcareous sediments	1.1	0.2	2.0	0.5	0.5	4.1	5.9
Serpentines	0.1	0.1	0.1	0.1	–	0.3	–

The above-mentioned landscape types differ in various attributes of their abiotic environment (Fig. 4) and also in the proportional areas occupied by different geological formations (Table 2). Classification trees revealed that landscape types derived from unconstrained clustering are primarily separated by altitude and related climatic conditions (Fig. 5).

The first node in the tree was split by a mean altitude of 559 m, followed by annual precipitation, in the group of mountain grid cells. Geology and terrain ruggedness were important differentiating variables in the group of lowland to submontane landscape types, however they split at lower nodes in the tree. The optimal tree for spatially unconstrained clusters had eight terminal nodes and correctly classified 61.2% of the grid cells.

Spatially constrained clustering

The spatially constrained clustering yielded contiguous regions (Fig. 6). The cross-validation technique proposed a partition with seven clusters as optimal (Fig. 7). Due to the spatial constraints added to the clustering procedure, the resulting dendrogram showed a reversal at the highest level. The first partition thus separated a group containing clusters 1 and 2

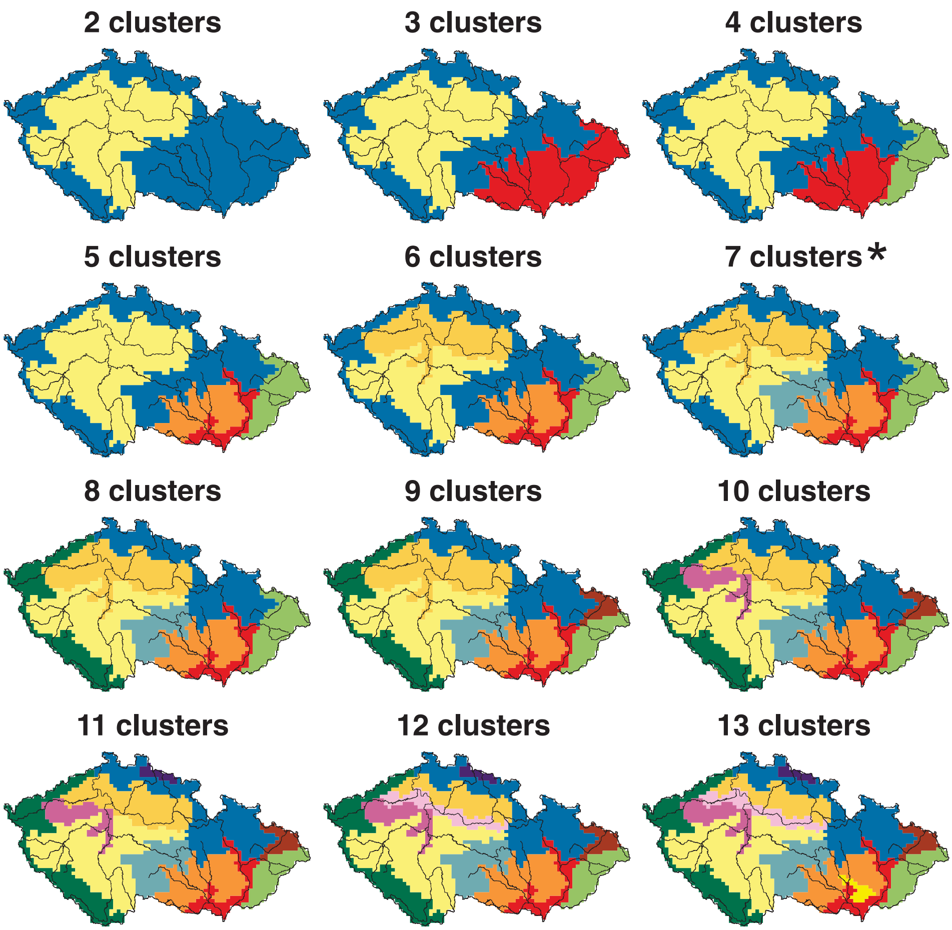

Fig. 6. – Clustering sequence of spatially constrained clustering of natural habitats of the Czech Republic using the β_{sim} dissimilarity measure and Ward's minimum variance method. Asterisk denotes the optimal number of clusters according to the cross-validation procedure.

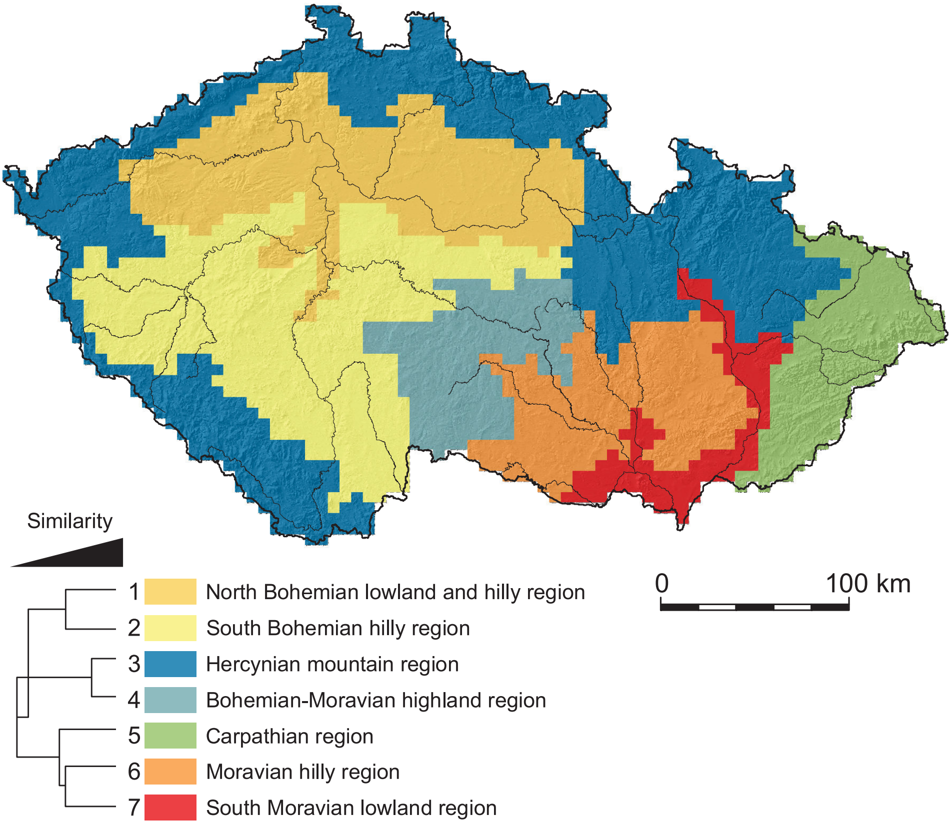

Fig. 7. – Regions of the Czech Republic based on the spatially constrained clustering with the optimal number of seven clusters according to cross-validation procedure. Reversal in the dendrogram is due to spatial constraints.

from a group of clusters 3–7, although their similarity was greater than the similarity within the second group (i.e. between the branch including clusters 3 and 4, and that including clusters 5, 6 and 7).

Cluster 1 (North Bohemian lowland and hilly region), situated in the lowlands and hilly landscapes around the Labe and Ohře rivers, was characterized by dry grasslands (T3.4, T3.3), while cluster 2 (South Bohemian hilly region), representing the hilly landscape of south-central Bohemia, was characterized by acidophilous oak forests (L7.1, L7.2). Cluster 3 (Hercynian mountain region), representing Hercynian mountains, was characterized by montane *Trisetum* meadows (T1.2) and bog spruce forests (L9.2). Cluster 4 (Bohemian-Moravian highland region) was characterized by acidic moss-rich fens (R2.2) and mesotrophic vegetation of muddy substrata (M1.6). Within the branch containing the remaining clusters, cluster 5 (Carpathian region) was separated from the two South Moravian regions (clusters 6 and 7). This region was characterized by the Carpathian and Polonian oak-hornbeam forests (L3.2, L3.3). Cluster 6 (Moravian hilly region), representing the hilly landscape of south-central Moravia, was characterized by acidophilous thermophilous oak forests (L6.5), low xeric scrub (K4) and narrow-leaved dry grasslands

Table 3. – Characteristic habitats in the seven clusters resulting from the spatially constrained clustering, based on the phi coefficient of association (× 1000). See Table 1 for details.

Cluster		1	2	3	4	5	6	7
No. of grid cells		409	512	733	182	184	239	111
No. of characteristic habitats (including shared habitats)		9	3	5	4	8	3	8
No. of characteristic habitats (not including shared habitats)		6	3	4	3	8	2	6
North Bohemian lowland and hilly region (cluster 1)								
T3.4	Broad-leaved dry grasslands	355	–	–	–	60	136	98
T5.3	*Festuca* sand grasslands	323	–	–	–	–	–	15
L3.1	Hercynian oak-hornbeam forests	299	194	–	–	–	91	–
L6.4	Central European basiphilous thermophilous oak forests	298	–	–	–	6	10	–
T5.2	Open sand grasslands with *Corynephorus canescens*	271	–	–	–	–	–	41
L7.4	Acidophilous oak forests on sand	266	–	–	–	–	–	128
North Bohemian lowland and hilly region and Moravian hilly region (cluster 1 and 6)								
T3.3	Narrow-leaved dry grasslands	351	–	–	–	–	259	159
South Bohemian hilly region (cluster 2)								
L7.2	Wet acidophilous oak forests	116	370	–	–	–	–	–
L7.1	Dry acidophilous oak forests	129	312	–	–	–	13	–
T1.4	Alluvial Alopecurus meadows	40	287	–	–	–	–	–
Hercynian mountain region (cluster 3)								
T1.2	Montane *Trisetum* meadows	–	–	499	–	–	–	–
L9.2	Bog spruce forests	–	–	378	139	–	–	–
L9.1	Montane *Calamagrostis* spruce forests	–	–	298	–	14	–	–
R3.1	Open raised bogs	–	–	255	–	–	–	–
Hercynian mountain region and Bohemian-Moravian highland region (cluster 3 and 4)								
T2.3	Submontane and montane *Nardus* grasslands	–	–	327	321	–	–	–
Bohemian-Moravian highland region (cluster 4)								
R2.2	Acidic moss-rich fens	–	–	193	359	–	–	–
M1.6	Mesotrophic vegetation of muddy substrata	5	25	–	344	–	–	–
R2.3	Transitional mires	–	–	206	332	–	–	–
Carpathian region (cluster 5)								
L3.3	Carpathian oak-hornbeam forests	–	–	–	–	641	242	236
L3.2	Polonian oak-hornbeam forests	–	–	49	–	510	–	102
R1.3	Forest springs with tufa formation	49	–	–	–	420	–	–
R1.1	Meadow springs with tufa formation	10	–	–	–	359	–	–
K2.2	Willow scrub of river gravel banks	–	–	–	–	320	–	21
T1.10	Vegetation of wet disturbed soils	–	13	54	–	315	–	–
M5	*Petasites* fringes of montane brooks	–	–	243	–	292	–	–
T1.3	*Cynosurus* pastures	–	–	168	–	269	–	–
Moravian hilly region (cluster 6)								
L6.5	Acidophilous thermophilous oak forests	145	90	–	–	–	278	–
K4	Low xeric scrub	154	–	–	–	–	264	38
South Moravian lowland region (cluster 7)								
L3.4	Pannonian oak-hornbeam forests	–	–	–	–	–	247	529
T1.7	Continental inundated meadows	75	–	–	–	–	–	388
M7	Herbaceous fringes of lowland rivers	103	–	–	–	–	56	351
L6.3	Pannonian thermophilous oak forests on sand	–	–	–	–	–	–	294
L6.2	Pannonian thermophilous oak forests on loess	–	–	–	–	–	126	288
M2.3	Vegetation of exposed bottoms in warm areas	4	–	–	–	–	15	268
North Bohemian lowland and hilly region and South Moravian lowland region (cluster 1 and 7)								
L2.4	Willow-poplar forests of lowland rivers	305	–	–	–	181	–	627
L2.3	Hardwood forests of lowland rivers	257	–	–	–	154	–	596

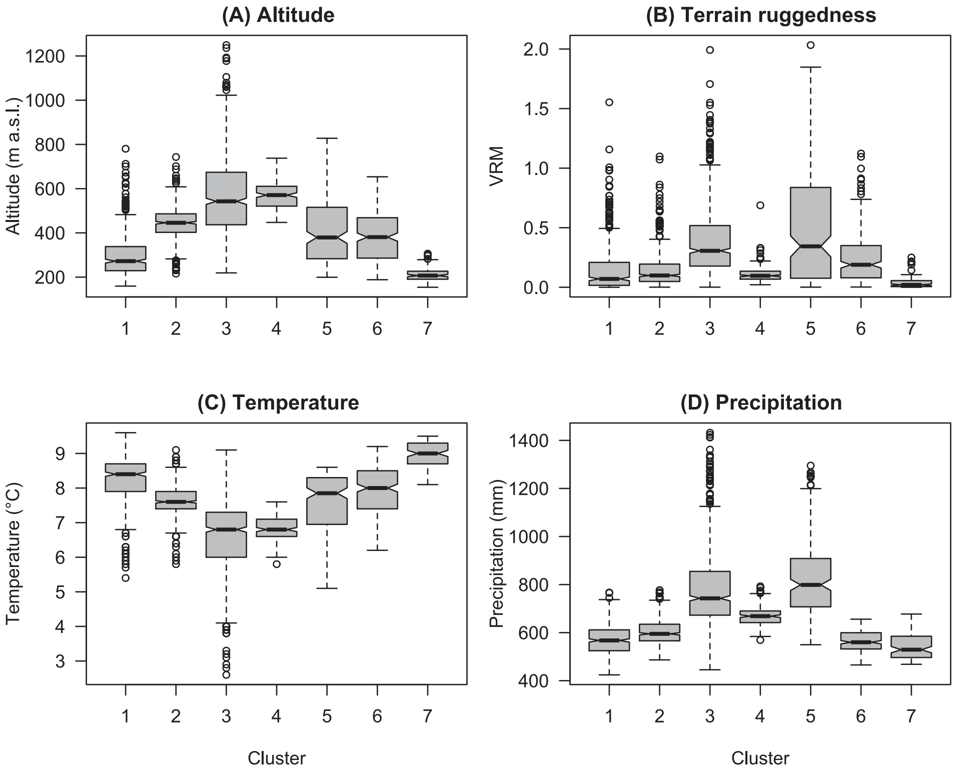

Fig. 8. – Environmental variables for seven regions (clusters) resulting from spatially constrained clustering procedure. 1 – North Bohemian lowland and hilly region; 2 – South Bohemian hilly region; 3 – Hercynian mountain region; 4 – Bohemian-Moravian highland region; 5 – Carpathian region; 6 – Moravian hilly region; 7 – South Moravian lowland region. See Fig. 4 for details.

Table 4. – Percentage areas of the main geological formations in clusters resulting from spatially constrained clustering. 1 – North Bohemian lowland and hilly region; 2 – South Bohemian hilly region; 3 – Hercynian mountain region; 4 – Bohemian-Moravian highland region; 5 – Carpathian region; 6 – Moravian hilly region; 7 – South Moravian lowland region. See Fig. 4 for details.

Geological formations	Cluster						
	1	2	3	4	5	6	7
Proterozoic and Palaeozoic rocks	17.1	81.0	72.7	98.2	1.9	58.4	3.2
Cretaceous sediments	31.6	6.5	12.8	0.7	0.1	0.7	–
Upper Tertiary and Quaternary sediments	37.8	12.1	11.7	0.8	30.9	29.4	86.9
Carpathian flysch sediments	–	–	–	–	65.7	9.9	8.5
Tertiary volcanic rocks	7.7	–	1.0	–	0.7	–	–
Limestone and calcareous sediments	5.8	0.4	1.7	0.2	0.7	1.2	1.4
Serpentines	–	–	0.1	0.1	–	0.4	–

(T3.3). Cluster 7 (South Moravian lowland region) represents floodplains along the Morava and Dyje rivers with characteristic hardwood and willow-poplar forests (L2.3, L2.4). For each cluster, the characteristic habitats, identified using the phi coefficient of association, are summarized in Table 3.

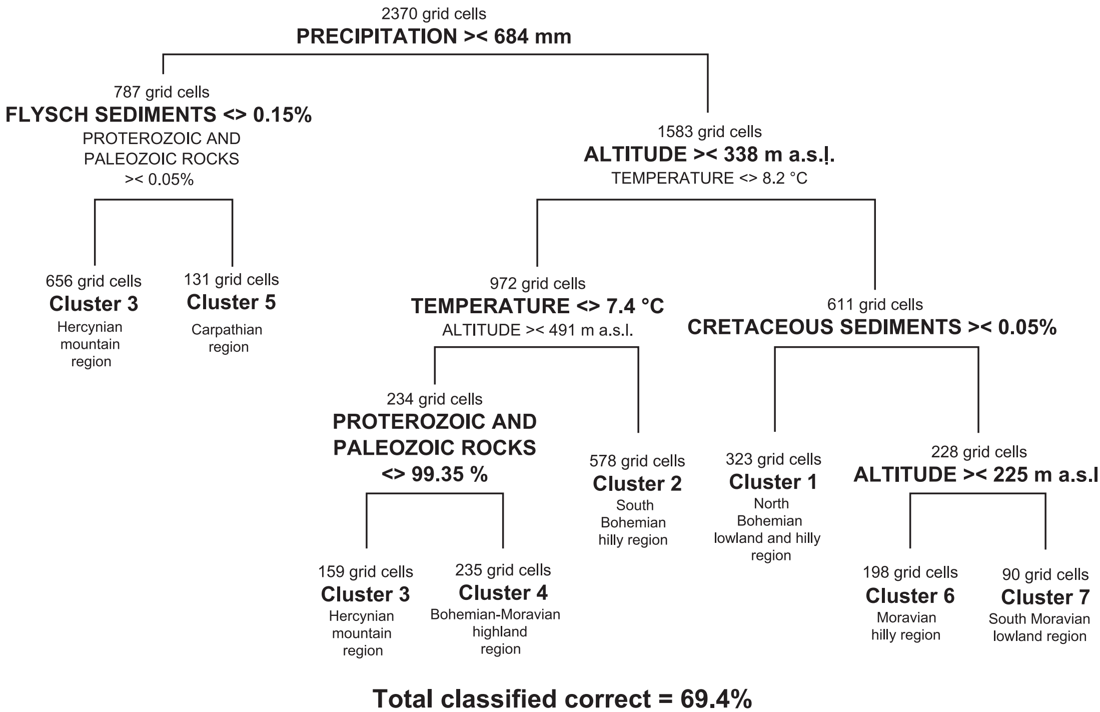

Fig. 9. – Classification tree describing the separation of the seven regions (clusters) resulting from spatially constrained clustering in terms of abiotic factors. See Fig. 5 for details.

Characteristics of the abiotic environment of individual regions are summarized in Fig. 8 and proportions of geological formations within clusters are listed in Table 4. Classification trees revealed that separation of the regions corresponded mainly to annual precipitation (split value 684 mm at the first node; Fig. 9). The following nodes were split according to the proportion of flysch sediments and altitude. Lower nodes of the classification tree were split by mean annual temperature, proportion of Cretaceous sediments, Proterozoic and Palaeozoic rocks and altitude. The optimal tree for spatially constrained clusters had eight terminal nodes and correctly classified 69.4% of the grid cells.

Discussion

The maps presented in this study are the first attempts to provide a statistical classification of the Czech landscape based on the distribution of natural and semi-natural habitat types. As habitat types are defined based on plant communities (Chytrý et al. 2010), their diversity is not only a surrogate for vegetation diversity, but also for the diversity of plant species and, to a considerable degree, the diversity of animals and other heterotrophic organisms. The advantage of habitats over land-cover data from remote sensing is that the former provide a much finer resolution of biodiversity patterns, which cannot be achieved by remote sensing. A disadvantage is that any mapping of large extent and fine resolution such as the Czech habitat mapping project (Härtel et al. 2009) requires involvement of many field mappers, who introduce some degree of inconsistency due to the unavoidable subjectivity of expert decisions. Still we believe that the unified mapping legend (Chytrý et al. 2001), standardized mapping protocols (Guth & Kučera 2005) and centralized coordination of the Czech mapping project (Härtel et al. 2009) provide data that are sufficiently robust for the purpose of deriving habitat-based landscape types and regions at a national scale.

In statistically derived landscape classifications, segregation of grid cells into different clusters depends on the dissimilarity in their habitat compositions, measured by a dissimilarity index. However, this dissimilarity is influenced by differences in habitat richness across the study area (Lennon et al. 2001, Kreft & Jetz 2010), which is on average higher in areas with few habitat types, and this may influence the classification results. Examples of areas in the Czech Republic with a high number of natural habitat types include the Křivoklátsko region south-west of Prague or southern Bohemia, where topographically heterogeneous landscapes with deeply incised river valleys host a high number of different habitats (Zelený & Chytrý 2007, Chytrý 2012). In contrast, intensively cultivated lowlands of southern Moravia, industrially transformed landscape of the Mostecká Basin or uniform landscape of the Nízký Jeseník Mountains are examples of habitat-poor regions. Theoretically, such habitat-poor areas might be divided into more landscape types than habitat-rich areas due to high habitat turnover, but this is not the case in our study because we used the β_{sim} dissimilarity index, which quantifies habitat turnover independently of the variation in habitat richness (Lennon et al. 2001, Koleff et al. 2003, Baselga et al. 2007). Therefore, we believe that our landscape classification reflects pure habitat turnover across the Czech Republic and not differences in habitat richness resulting from either ecological processes or uneven survey effort.

In this study we used two contrasting methods to classify landscape, unconstrained and spatially constrained clustering. While the former produces internally homogeneous but spatially disparate landscape types, the latter yields spatially coherent but internally less homogeneous regions. Each of these methods has some advantages and disadvantages depending on the questions asked and the purpose of the landscape classification. If the aim is to improve understanding of ecological patterns, unconstrained classification is preferable, because it indicates which landscape sections are similar irrespective of their location; it may identify isolated areas of a particular landscape type located far from the main area of its distribution. Unconstrained classification also provides insights into the habitat beta-diversity pattern in the Czech Republic. If resulting clusters are scattered in spatially discontinuous patches, it is probable that the habitat composition of a pair of neighbouring grid cells is not similar. This may indicate discontinuous environmental conditions in heterogeneous landscapes or a considerable degree of landscape fragmentation at least in some parts of the Czech Republic. However, spatial discontinuity of clusters resulting from unconstrained clustering is also affected by the grid resolution used in the analysis, because similarity between grid cells increases with coarsening of spatial resolution (Lennon et al. 2001, Gaston et al. 2007, Keil et al. 2012). If a fine spatial grain is used, clusters may not be spatially coherent due to low similarity of neighbouring grid cells and weak relationship between similarity of pairs of grid cells and their geographical distance. On the other hand, if the aim is to divide a landscape into a few regions with relatively uniform biota for the purpose of survey or management planning, the spatially constrained method may be preferred. Spatial constraints may also serve as surrogates for migration constraints and results of classification may thus improve understanding of biogeographical patterns in the country flora. For example, vegetation may be physiognomically similar in both the western and eastern parts of the Czech Republic, but its species composition may differ considerably.

Irrespective of the method used, the results agree with previous phytogeographical, zoogeographical and biogeographical classifications of the Czech Republic in that the coarse-scale pattern is driven mainly by altitude (differentiation into mountain areas, mid-altitude areas and dry and warm lowland/colline landscapes) and differences between the Bohemian Massif and Carpathians. The classifications we derived from the habitat data closely match the phytogeographical division of the Czech Republic (Skalický 1988, see also Kaplan 2012), which distinguishes the mountain areas (Oreophyticum), mid-altitude areas (Mesophyticum) and low-altitude areas (Thermophyticum), and within each of them, it separates a western (Hercynian, Bohemian Massif) subunit from an eastern (Carpathian and Pannonian) subunit (Fig. 10A). Our spatially unconstrained clustering indicates that in terms of habitats, the Hercynian-Carpathian difference is strongest at mid-altitudes, whereas the mountain and lowland areas are similar between the western and eastern parts of the Czech Republic. In the mountain areas, the main division is not between the Bohemian Massif and Carpathians but between the highest mountains along the state border and lower mountain ranges. Spatially unconstrained clustering also did not suggest a differentiation of low-altitude areas into Bohemian Thermophyticum and Pannonian Thermophyticum, as suggested by Skalický (1988). Instead, both of these regions were separated into lowland areas along large rivers and warm and dry hilly landscapes, which respectively correspond to lowland and colline altitudinal belts as defined by Skalický (1988, see also Chytrý 2012). However, this discrepancy does not mean that the phytogeographical division of Skalický (1988) is wrong. This expert-based division considered distribution of different vegetation types, but the main focus was on the distributions of plant species. Although most habitats in the Bohemian and Pannonian low-altitude landscapes belong to the same types, their species composition may differ considerably due to migration constraints, which support the division of these two regions. Such migration constraints may be suggested by our spatially constrained clustering results, in which lowlands of the Czech Republic were separated into the North Bohemian lowland and hilly region, which corresponds well with the Bohemian Thermophyticum, and two South Moravian regions (Moravian hilly region and South Moravian lowland region), which represent the Pannonian Thermophyticum.

Habitat-based classifications do not entirely support the division of the Czech Republic into four biogeographical subprovinces (Hercynian, North-Pannonian, West-Carpathian and Polonian) as proposed by Culek (1996). Although the difference between the Bohemian Massif and Carpathians was identified by our classifications, they provided weak support for the separate Polonian subprovince, proposed by Culek (1996) for the lowlands and foothill areas of the north-east of the Czech Republic. The Polonian subprovince or its equivalent is also not distinguished by other biogeographical landscape classifications of the Czech Republic. In the classifications presented here a region corresponding to it appeared only in the partition with eight (nine) clusters in an unconstrained (constrained) classification. This subprovince is very poorly supported by patterns in the distributions of flora and vegetation (Chytrý 2012, Kaplan 2012), and is mainly based on the concept of Polonian oak-hornbeam forests (Moravec et al. 2000), used in the Habitat Catalogue

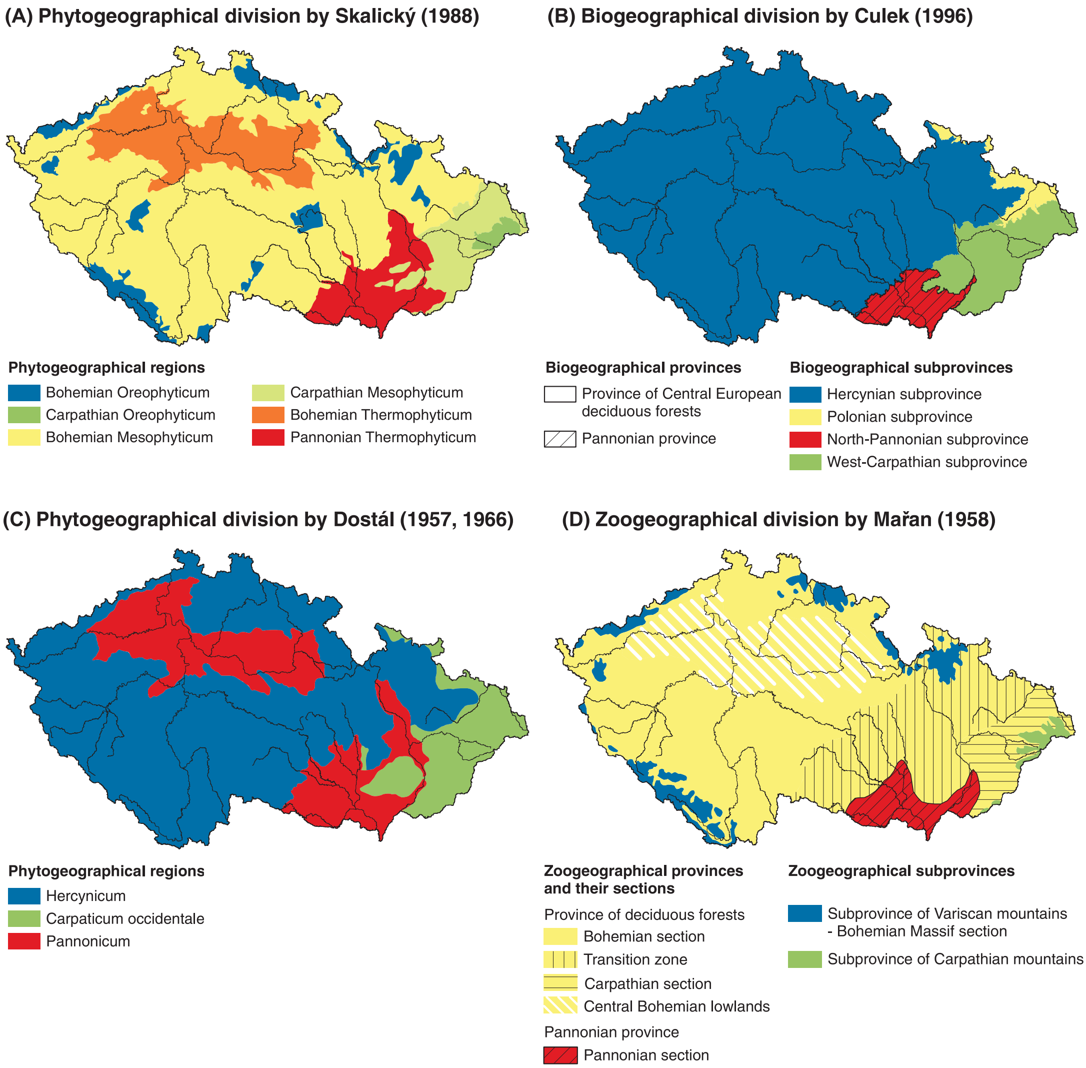

Fig. 10. – Expert-based biogeographical divisions of the Czech Republic.

(Chytrý et al. 2001) and thus present in our input data. However, a distinct unit of the Polonian oak-hornbeam forests in the Czech Republic is not supported by an analysis of vegetation-plot data (Knollová & Chytrý 2004), therefore it was not included in the new national vegetation classification (Chytrý 2013). No other vegetation/habitat types have a distribution matching that of the putative Polonian oak-hornbeam forests. Consequently, the concept of a Polonian subprovince in the Czech Republic requires critical re-evaluation. The North-Pannonian subprovince proposed by Culek (1996) in the south-eastern part of the Czech Republic is well separated in our habitat-based classification from adjacent Hercynian and West-Carpathian subprovinces, but as discussed above, it appears to be very similar to the dry and warm areas in northern, central and eastern Bohemia, which were classified as part of a Hercynian subprovince by Culek (1996). Our spatially unconstrained classification kept these dry and warm areas in Bohemia in the same cluster as those in southern Moravia, however, both regions were divided into lowland landscapes, mainly including river corridors and adjacent areas, and dry hilly (colline) landscapes. These colline landscapes, with some areas of adjacent or embedded lowland landscape, closely correspond to the areas of the forest-steppe biome as delineated by Chytrý (2012). Of the other areas of azonal biomes, our unconstrained habitat-based classification recognizes the mountain (spruce) taiga biome, roughly corresponding to mountain landscapes. In contrast, it does not recognize the lowland (pine) taiga biome (Chytrý 2012, Novák et al. 2012) and the tundra biome (Soukupová et al. 1995), perhaps partly because of their small size and patchy occurrence within the landscape matrix dominated by other biomes and partly due to poor development of these azonal biomes in the Czech Republic, with absence of some habitats that are typical of these biomes elsewhere.

Our landscape classification may also be compared with the older phytogeographical (Dostál 1957, 1966; Fig. 10C) and zoogeographical classifications (Mařan 1958; Fig. 10D). The former is similar to our spatially constrained classification as it distinguishes two separate lowland regions (both belonging to the Pannonicum), Hercynian mountains and highlands (Hercynicum), and the Carpathian region (Carpathicum occidentale). Nevertheless, Dostál's (1957, 1966) classification does not differentiate the South Bohemian region of the Hercynicum occurring at low altitudes, which was separated from the rest of the Hercynicum in our spatially constrained habitat-based classification (see Fig. 6 and dendrogram in Fig. 7).

Mařan's (1958) classification might in principle be less similar to our results because it is based on the distributions of animals, but it does provide support for many landscape types and regions suggested by our analyses (Fig. 10D). For example the Bohemian Massif section of the Variscan mountain subprovince delineated by Mařan (1958) corresponds well with our mountain landscapes. Also, Mařan's Pannonnian province corresponds to our South Moravian lowland region. It indicates that the distributions of wild animals probably either closely depend on the distributions of habitats and plant communities or that the distributions of both plants and animals depend on the environment and biogeographical context, including similar historical migration routes.

Finally, our results may also be compared with those of Chuman & Romportl (2010) who provided, using GIS and the TWINSPAN classification method, the first statistical landcape classification of the Czech Republic. Their classification is based mainly on abiotic conditions (e.g. altitude, annual precipitation and soil types), land-cover data and the map of reconstructed natural vegetation of the Czech Republic (Mikyška et al. 1968). Although they used a finer spatial resolution of 2 × 2 km and delineated in total 11 landscape types, their results closely match those of our spatially unconstrained classification. However, they did not differentiate separate landscape types at mid-altitudes in the Carpathians, probably because the environmental variables they used did not show any specific difference in this area.

In conclusion, we want to emphasize that the present study does not aim to provide better solutions or even to replace previous landscape or biogeographical classifications of the Czech Republic. There is no single best classification, because each classification differs in its purpose, input variables, their weighting and classification methods used. Instead, we offer a statistical classification in which the procedures and criteria used are clearly described, so that the rationale is easily understandable. We focused on natural habitats, which are an outcome and excellent indicator of environmental conditions and historical biogeographical processes, but nevertheless do not take into account the full ecological and biogeographical complexity of landscapes. Other approaches, based on different data or other classification methods, may identify different spatial patterns and suggest alternative divisions. Although our comparisons with the existing, mainly expert-based, classifications suggest that the main patterns revealed by all the classifications are roughly similar, they differ, especially at fine scales. Identification and explanation of these differences may contribute to a better understanding of the general biogeographical patterns in national territories.

Acknowledgements

We thank the authors of the national Habitat Catalogue for providing the habitat framework, hundreds of experts who mapped the distributions of habitats in the field, Agency for Nature Conservation and Landscape Protection of the Czech Republic for coordinating habitat mapping and providing the habitat distribution database, Lubomír Tichý and David Zelený for discussion on the concept of this paper, Jiří Sádlo and two anonymous referees for helpful comments on a previous version of the manuscript, and Tony Dixon for English proofreading. This study was supported by the Czech Science Foundation (project no. 14-36079G, Centre of Excellence PLADIAS), long-term development support of the Institute of Geonics (RVO: 68145535) and a Specific Research project at Masaryk University (MUNI/A/0952/2013; Analysis, evaluation, and visualization of global environmental changes in the landscape sphere).

Souhrn

Tato studie je prvním pokusem o statistickou klasifikaci krajiny České republiky založenou na analýze biologických dat, konkrétně rozšíření přírodních biotopů definovaných v Katalogu biotopů České republiky (Chytrý et al. 2001), jak byly zaznamenány při národním projektu mapování biotopů (Härtel et al. 2009). Vycházeli jsme ze záznamů o výskytu jednotlivých typů přírodních biotopů v 2370 mapových polích o velikosti 5' zeměpisné šířky × 3' zeměpisné délky. Použitím dvou odlišných klasifikačních metod (neomezenou a prostorově omezenou klasifikací) jsme vymezili sedm typů krajiny a sedm regionů České republiky, které jsme následně charakterizovali souborem abiotických faktorů. Pro každý typ krajiny a region jsme zároveň stanovili charakteristické přírodní biotopy. Výsledky obou použitých metod potvrdily, že biogeografické členění české krajiny závisí hlavně na nadmořské výšce, klimatických faktorech a rozdílech mezi Českým masivem a Karpaty. Obě výsledné klasifikace jsme porovnali s fytogeografickým členěním České republiky (Dostál 1957, 1966, Skalický 1988), biogeografickým členěním (Culek 1996), zoogeografickým členěním (Mařan 1958) a s environmentální klasifikací České republiky (Chuman & Romportl 2010). Předložená klasifikace není chápána jako vylepšení nebo náhrada předchozích klasifikací, protože každá z nich má odlišný účel a vychází z jiných vstupních dat a metodik jejich integrace. Analytický postup její přípravy je však přesně popsán, což umožňuje pochopit její logický základ. Srovnání nové klasifikace s předchozími přispívá k lepšímu pochopení biogeografických zákonitostí území České republiky.

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Received 23 December 2013
Revision received 27 May 2014
Accepted 29 May 2014