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# Biogeographical patterns in vertebrate assemblages of the Czech Republic: regional division in the context of species' distributions in Europe

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**Abstract.** This study attempts to explore biogeographical patterns in vertebrate assemblages of the Czech Republic and to delineate faunal biogeographical regions of the country. We focused on native terrestrial species and first explored main gradients in the composition of their assemblages. The first gradient revealed by Principal Coordinate Analysis was best correlated with climatic variables, whereas the second gradient can be ascribed rather to longitude and to the associated habitat change. Using the spatially constrained clustering, the Czech Republic was divided into five cohesive regions and species above-average associated with these regions showed distinct distributions within the European continent. Delineated regions also significantly differed at least in three considered environmental variables. We provided clear evidence that species distribution data gathered by national mapping support main biogeographical patterns suggested by previously published expert-based classifications of the country. We also demonstrated that the fauna of the Czech Republic shows a biogeographical pattern very similar to that showed by natural habitats defined in terms of plant communities. This indicates that both fauna and flora of the Czech Republic yield to the same environmental forces and biogeographical processes such as spreading of faunistic and floristic elements from the adjacent Carpathian Mountains and the Pannonian Basin.

**Key words:** beta diversity, biogeographical regions, spatially constrained clustering, terrestrial vertebrates

## Introduction

Biogeographical regionalizations represent fundamental abstractions of the geographical organisation of life on Earth in response to past or current physical and biological forces (Kreft & Jetz 2010). Traditionally, main attention has been paid to regionalizations at broad spatial scales, especially at the global scale (Sclater 1858, Wallace 1876, Proches 2005, Kreft & Jetz 2010, Holt et al. 2013). These biogeographical regions provided a valuable insight into the broad-scale spatial organisation of world's biota and its evolution. However, delineation of biogeographical units representing regional faunal differences became of special importance also at finer spatial scales, e.g. at a sub-continental level (Heikinheimo et al. 2007,

Rueda et al. 2010, Linder et al. 2012) and at a country-wide perspective (Järvinen & Väisänen 1980, Gonseth et al. 2001, Filipe et al. 2009, Divíšek et al. 2014a). Indeed, such fine-scale regions based on differences in the composition of local assemblages reflect contemporary species distributions, influenced by recent events and processes such as anthropogenic landscape changes rather than deep biogeographical history of a given area and species' evolution. Nevertheless, this does not degrade their value, because understanding of environmental, geographical and historical forces that form the fine-scale biogeographical regions is essential for understanding the biogeographical patterns at broader spatial scales. Moreover, the landscape-level regions represent important baseline

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information not only for scientists but particularly for nature conservation planning and decision making, e.g. for the application of Natura 2000 principles in countries of the European Union. Yet, biogeographical classifications of national territories based on mapped species occurrences and exactly described statistical criteria are still relatively rare, at least in central Europe including the Czech Republic.

Although being a small country in the middle of the European continent (48°33′-51°3′ N, 12°5′-18°52′ E), the Czech Republic represents a very interesting area from the zoogeographical point of view. Firstly, the country's variable environmental conditions and the long history of human impact both entail heterogeneous landscapes with a high diversity of habitat types, which offer conditions suitable for species with different ecological requirements. For example, oak forests and grasslands in warm and dry lowlands provide suitable habitats for sub-mediterranean and pannonian steppe species. On the other hand, mixed and spruce montane forests, so-called "mountain taiga", in cold and humid mountains provide habitats favourable for boreal species. Secondly, these heterogeneous landscapes host a greater part of species occurring in the entire central Europe. For example, ca. 70 % of mammals and birds, ca. 50 % of reptiles and ca. 80 % of amphibians occurring in central Europe occur also in the Czech Republic (IUCN 2012, BirdLife International & NatureServe 2014). Furthermore, the area of the country is well surveyed in terms of species distributions which can be documented by many distribution atlases published since the 1970s (Šťastný et al. 1987, 1996, 2006, Moravec 1994, 2015, Mikátová et al. 2001, Anděra & Gaisler 2012). Thirdly, beside the heterogeneous landscapes and high species richness, the Czech Republic represents an interesting area also in terms of historical biogeography because it is situated at the crossroads of postglacial colonisation routes (Hewitt 2000) and in the proximity to Carpathian refuges, recently proposed for various species (Kotlík et al. 2006, Hofman et al. 2007, Magri 2008, Juřičková et al. 2014). Nowadays, an appreciable number of species reach the western or eastern limits of their ranges in the Czech Republic. Both purely environmental factors and geographical or historical ones, especially faunistic element spreading from adjacent biogeographical provinces, could thus cause important regional differences in the composition of species assemblages across the Czech Republic. This is supported by national expert-based zoogeographical (Mařan 1958), phytogeographical (Skalický 1988) and biogeographical classifications (Culek 1996) which distinguish the Pannonian region in the south-east and the Carpathian region in the east of the Czech Republic. However, these classifications have never been compared with the classification based on the mapped species distributions and formally described classification criteria.

Biogeographical regions were traditionally delineated based on expert knowledge irrespective of spatial scale. However, the recent progress in statistical methods coupled with much more data being available have stimulated the development of statistically derived classifications. These statistical classifications are based on the clustering of sampling units, e.g. grid cells covering the area under study, according to the similarity of their assemblages (Kreft & Jetz 2010). Nevertheless, the similarity between neighbouring grid cells generally decreases towards finer grains as it is directly mathematically related to the local slope of the species-area relationship (Lennon et al. 2001, Šizling et al. 2011). As we decrease the spatial grain, we decrease the number of species, which can be detected in each grid cell due to the uneven species distribution in the landscape and habitat heterogeneity. Therefore, there is high probability that neighbouring grid cells will share a smaller proportion of species than larger ones and consequently they will be less similar. In such a case, the classification process may often lead to spatially discontinuous clusters (see e.g. Pasinelli et al. 2001, Eronen et al. 2011, Divíšek et al. 2014a, 2016), which resemble rather landscape types than distinct cohesive regions *sensu stricto*. To avoid spatially disparate clusters, an incorporation of spatial constraints into the classification process was proposed (Legendre 1987, Legendre & Legendre 2012). In this case, grid cells are clustered according to their similarity but it is allowed to cluster only those cells, which are spatially connected according to the predefined connectivity scheme. This approach may have several advantages. Although the clusters resulting from the spatially constrained clustering are more internally heterogeneous as compared with the unconstrained equivalent, they may be, on the other hand, more readily interpretable (Legendre 1987). This is in accordance with Wallace's (1876) criteria that faunal regions should be similar in area, compact and easy to define. Furthermore, applying the constraint of spatial contiguity to an agglomerative clustering procedure forces different clustering methods to produce approximately the same results (Legendre 1987). Incorporation of spatial constraints was often used in classifications along transects (e.g. Tuomisto et al. 2003) but it is relatively rare in classifications

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focused on the delineation of biogeographical regions (but see e.g. Kupfer et al. 2012). We believe, however, that adding spatial information into the classification of biogeographical regions may help to explore better geographical trends in the species composition of considered area.

In this study, we attempt to explore main gradients in the composition of assemblages of terrestrial vertebrates, namely mammals, birds, reptiles and amphibians, native in the Czech Republic and to delineate faunal biogeographical regions of the country. Although the term "biogeographical (or zoogeographical) region" is often understood in relation to global biogeographical divisions, we use it for the regional division of the Czech Republic because its primary purpose is to explore regional differences in the composition of species assemblages. Beside the regional division, we address the following questions: 1) Do these landscape-level regions differ in environmental conditions? 2) What species are associated with these regions? 3) Do these regions differ in broad-scale latitudinal and longitudinal distribution of associated species? 4) What areas in Europe host assemblages similar to those typical of Czech regions? 5) Does this regional division correspond with the previously published expert-based biogeographical classifications of the Czech Republic?

## Material and Methods

### Species data

We used the national distribution atlases of mammals (Anděra & Gaisler 2012), birds (Šťastný et al. 2006), reptiles (Mikátová et al. 2001) and amphibians (Moravec 1994) to compile a database of species occurrences (presence/absence records) in a grid of 628 rectangles (hereafter called grid cells) covering the Czech Republic. Each grid cell spans 10′ of longitude and 6′ of latitude, which represents ca. 12 × 11.1 km (133.2 km$^2$). Because the above-mentioned atlases differ in data collection methods and in the considered time period, we carefully checked the data for mutual comparability. We considered only records since 1980, and the data on reptiles and amphibians were updated according to records gathered by the Agency for Nature Conservation and Landscape Protection of the Czech Republic (http://portal. nature.cz/). We excluded species that are listed in the atlases, but their distribution in the Czech Republic is uncertain and also species that are not native in the country according to Mlíkovský & Stýblo (2006). This selection resulted in 73 out of 89 mammals; 199 out of 215 birds (only records of confirmed and probable breeding were used); 10 out of 11 reptiles and 21 out of 21 amphibians.

### Environmental data

For each grid cell, we calculated mean altitude from the digital elevation model of the Czech Republic (resolution 50 × 50 m). Mean annual temperature and annual precipitation amount were extracted from Climate atlas of Czechia (Tolasz 2007). All grid cells were also characterized by the relative proportion of natural and non-natural habitats. The distribution of natural habitats was obtained from the GIS database of the Agency for Nature Conservation and Landscape Protection of the Czech Republic, which contains a polygon layer of (semi-)natural habitat types defined by Chytrý et al. (2001). We considered only the polygons of well-preserved habitats (first two out of four categories of representativeness). For our purpose, we adopted the classification by Divíšek et al. (2014b) and merged 127 original habitat types into 26 new variables representing zoologically meaningful natural habitats (see Table S1 in Appendix). Because natural habitats cover only a small area in each grid cell, we also used the Corine Land Cover 2000 database (EEA 2010) to characterise the area of each grid cell, which is not covered by natural habitats. We followed the classification by Storch et al. (2003) and combined the original 28 land-cover types recognized in the Czech Republic into 16 classes, which represent land-cover types potentially relevant for the considered taxa (see Table S2 in Appendix). Data were processed in ArcGIS 10.2 software (ESRI 2014).

All 26 natural habitats and 16 land-cover types were used either as explanatory variables in subsequent statistical analyses (if necessary, they were divided to forest and open habitats; see Tables S1 and S2 in Appendix) or in the Principal Component Analysis (PCA) to calculate main habitat gradients in the country. The broken-stick method was used to determine the number of significant PCA axes and it suggested the first and the second axis only. The first axis reflected the change in the composition of both natural habitats and land-cover types (non-natural habitats) but the second axis reflected rather the change in the composition of natural habitats.

### Gradients in the species composition

For each vertebrate group separately and also for all groups together, we calculated pairwise dissimilarities in the species composition between the grid cells using the beta-sim index ($\beta_{sim}$). The advantage of $\beta_{sim}$

is its independence of species richness gradients in the study area (Koleff et al. 2003). This index is used to calculate the compositional dissimilarity between two grid cells as follows:

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

where $a$ is the number of shared species, $b$ is the number of species unique to the first grid cell and $c$ is the number unique to the second grid cell. Values of $\beta_{sim}$ vary from 0 for the identical species composition of two grid cells to 1 for grid cells that do not share any species.

In order to explore main gradients in the composition of vertebrate assemblages of the Czech Republic, we submitted each dissimilarity matrix to the Principal Coordinate Analysis (PCoA). Because the $\beta_{sim}$ index produces a non-Euclidean dissimilarity matrix, it is necessary to apply a correction for negative eigenvalues in PCoA (Legendre & Legendre 2012). We used Cailliez (1983) correction method, which computes the smallest positive number and adds it to each dissimilarity value. Subsequently, we correlated the first and the second PCoA axis with the mean altitude, temperature, precipitation, main habitat gradients in the country and with latitude and longitude.

As the environment also changes with latitude and longitude, we additionally tested the independent effect of geographical position on the species composition using the distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999). This analysis is described in on-line Appendix.

*Classification analysis*

In order to classify the area of the Czech Republic to biogeographical regions based on the distribution of all native terrestrial vertebrates living in the country, we used the above-mentioned corrected dissimilarity matrix calculated from a table of the occurrences of all 303 species in 628 grid cells covering the country's territory. We applied the spatially constrained clustering method which clusters the grid cells according to the similarity of their assemblages, allowing to cluster only those grid cells that are spatially connected according to the predefined connectivity scheme (Legendre & Legendre 2012). Thus, it produces spatially coherent clusters that are well geographically distinguished from each other. Before performing the spatially constrained clustering, it is necessary to determine spatial connections between each pair of grid cells. We used the rook scheme (Fortin & Dale 2005), which considers each grid cell to be connected with four

adjacent grid cells in four cardinal directions (N, E, S, W). According to this criterion, we calculated a binary connectivity matrix comprising 1 for connected grid cells and 0 for unconnected grid cells. Subsequently, both the species dissimilarity matrix (based on $\beta_{sim}$ index) and the connectivity matrix were subjected to the clustering procedure using Ward's algorithm (Ward 1963). Although in subsequent analyses and interpretations we focused primarily on the results of spatially constrained clustering, we show also the results of clustering without spatial constraints for the comparison of these two approaches. Additionally, we performed both types of the classification analysis for each considered vertebrate group separately and results of these classifications can be found in Appendix.

A crucial point in the interpretation of hierarchical clustering results is deciding upon levels to be interpreted. To select an optimum partition level, i.e. the optimum number of clusters, we used the classification crispness method developed by Botta-Dukát et al. (2005). This method dwells on the calculation of fidelity of each species to each cluster, G statistics, which measures species capacity to distinguish the clusters within a given partition. This measure is called "separation power" of species. The higher the average separation powers for all species, the better the clusters can be distinguished by the species, i.e. the better the classification. For details of this method see Botta-Dukát et al. (2005).

*Analysis of clustering results*

To test whether biogeographical regions resulting from the spatially constrained clustering differ significantly in the values of environmental variables, we used a non-parametric Kruskal-Wallis test. This test was performed for each pair of clusters within the partition suggested by the classification crispness method. We also corrected the resulting $P$-values using Benjamini & Hochberg's (1995) method to avoid issues related to multiple testing.

To reveal a "typical assemblage" for each region in an optimum partition, we first determined the association of each species to each cluster using the equalized phi ($\Phi$) coefficient of association (Tichý & Chytrý 2006). The higher the positive values of $\Phi$ were, the higher was the species association with the given region (i.e. high frequency of species' occurrence inside the region but low outside it). $\Phi$ values close to zero suggest no association of the species with the given region, i.e. random distribution. The lower the negative values of $\Phi$ were, the higher was the negative association
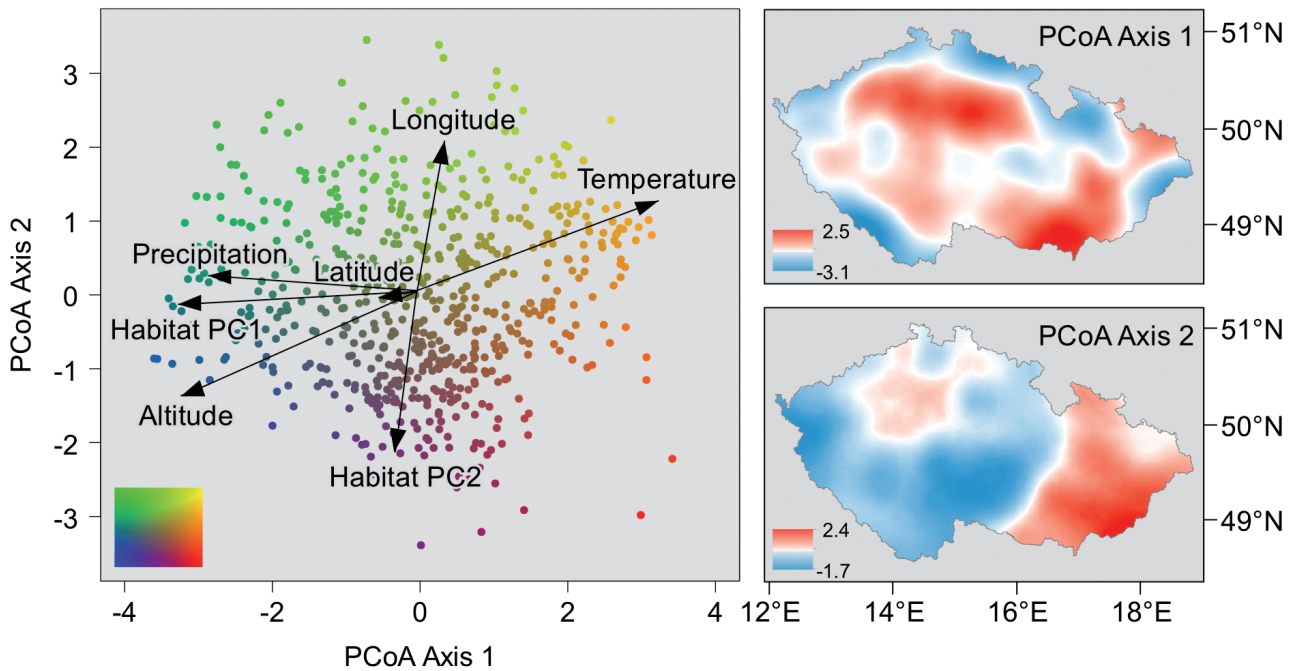
**Fig. 1.** Visualization of main biogeographical gradients in the composition of vertebrate assemblages of the Czech Republic. Diagram on the left shows results of the Principal Coordinate Analysis of the $\beta_{sim}$ dissimilarities in the composition of local assemblages of all native terrestrial vertebrates occurring in the country. Environmental variables and geographical coordinates were passively projected into the diagram. Maps on the right show geographic representation of the first two PCoA axes of species composition. These maps were obtained from the ordinary kriging interpolation using the scores of grid cells on the PCoA axes.
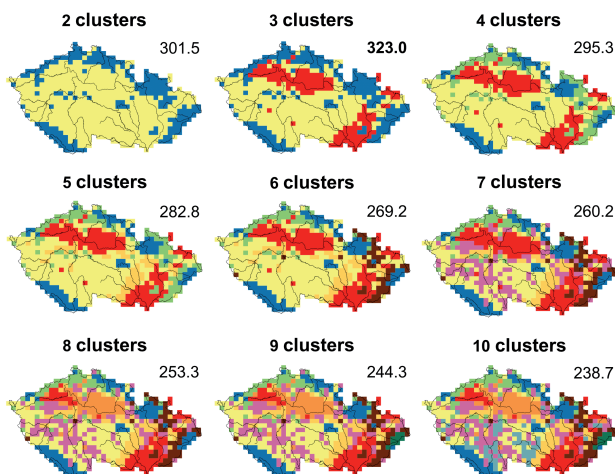


**Fig. 2.** Spatially unconstrained classification of the Czech Republic based on the distributions of all 303 native terrestrial vertebrates occurring in the country. Maps show different levels of the dendrogram, i.e. different partitions from 2 up to 10 clusters. Classification crispness value corresponding to respective partition is shown above each map. The highest value indicating the optimal classification is in bold.

**Fig. 3.** Spatially constrained classification of the Czech Republic based on the distributions of all 303 native terrestrial vertebrates occurring in the country. See Fig. 2 for details.

of the species with the given region (i.e. the species does not occur in the given region, or the frequency of its occurrence in that region is very low compared to the frequency of its occurrence outside the region). We then selected species with above-average positive association ($\Phi$) to a particular region and considered this set of species as a "typical assemblage" for the given region. The European ranges of species belonging to typical assemblages were compared in subsequent biogeographical analyses.

In order to reveal whether the regions differ in species' distributions at a broader spatial scale of the European continent, we first calculated the geographical centre of the distribution of each species in Europe. For this purpose, we considered the area from 11° W to 39°

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1 Hercynian mountain region
2 Carpathian region
3 Bohemian-Moravian hilly and highland region
4 Central Bohemian lowland and hilly region
5 Pannonian region

0        100 km
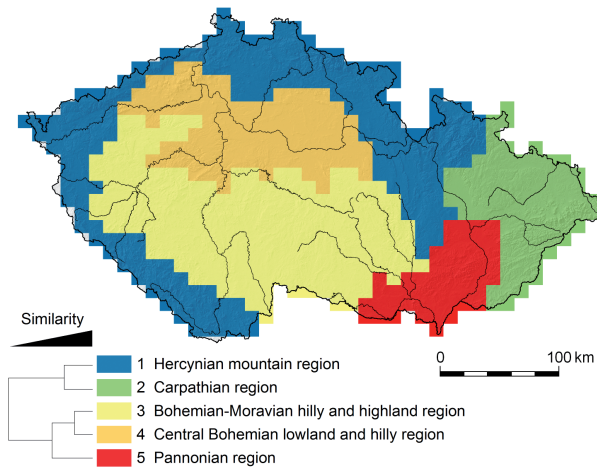
**Fig. 4.** Five regions of the Czech Republic suggested by the classification crispness method. Regions were classified based on the distributions of all 303 native terrestrial vertebrates living in the country.

coordinates showed that the first PCoA axis of each vertebrate group was associated primarily with climatic variables and with the related first habitat gradient (PC1; Table 1 and Fig. 1). On the other hand, the second PCoA axis of all groups was associated rather with longitude and the related second habitat gradient (PC2; Table 1 and Fig. 1). Additional dbRDA tests showed that, after accounting for all environmental factors, the change in the composition of assemblages of all vertebrate groups except reptiles was significantly associated with longitude, whereas latitude was significant for amphibians only (see Table S3 in Appendix).

*Regional division*
As we had expected, the spatially unconstrained clustering produced spatially disparate clusters (Fig.

**Table 1.** Correlations (Spearman correlation coefficients) of the two first PCoA axes with five main environmental gradients in the country and geographical coordinates. Habitat gradients were calculated by the ordination (PCA) of 26 natural habitat types and 16 types of land-cover. The number of significant axes (principal components – PC) was assessed using the Broken-stick method. Bold numbers indicate the strongest correlations.

| | Mammals | | Birds | | Reptiles | | Amphibians | | All | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Altitude | −0.77 | −0.25 | −0.76 | 0.41 | −0.41 | 0.21 | 0.46 | 0.39 | −0.81 | −0.38 |
| Temperature | **0.79** | 0.19 | **0.78** | −0.41 | 0.49 | −0.20 | −0.54 | −0.39 | **0.84** | 0.35 |
| Precipitation | −0.65 | 0.16 | −0.66 | 0.15 | **−0.53** | 0.06 | 0.59 | 0.17 | −0.72 | −0.04 |
| Habitat PC1 | −0.74 | 0.04 | −0.78 | 0.14 | −0.39 | 0.18 | **0.59** | 0.16 | −0.81 | −0.05 |
| Habitat PC2 | −0.19 | −0.51 | −0.15 | **0.46** | −0.19 | 0.15 | −0.06 | **0.40** | −0.16 | **−0.56** |
| Longitude | 0.10 | **0.55** | 0.13 | −0.41 | 0.04 | **−0.22** | 0.04 | −0.26 | 0.10 | 0.50 |
| Latitude | −0.11 | 0.07 | −0.11 | 0.03 | −0.29 | 0.10 | 0.28 | 0.01 | −0.11 | 0.02 |

E and from 34° N to 72° N. Species distributions in Europe were extracted from the IUCN database (IUCN 2012) for mammals, reptiles and amphibians, and from BirdLife International & NatureServe (2014) for birds. For each region of the Czech Republic, we then plotted range coordinates of species belonging to typical assemblage as boxplots. Differences between each pair of regions were tested by Kruskal-Wallis test and resulting *P*-values were adjusted using Benjamini & Hochberg's (1995) correction method. Finally, we also plotted the European distribution of typical assemblages into maps to reveal which areas in Europe host faunal assemblages similar to those occupying the regions delineated in the Czech Republic.

## Results
*Composition of species assemblages*
The correlation of PCoA axes with main environmental gradients in the country and with geographical

2). In this case, the classification crispness method suggested to divide the area of the Czech Republic into three clusters. The hierarchy of the spatially unconstrained classification up to 10 clusters is shown in Fig. 2 and can be compared with the hierarchy of the spatially constrained classification in Fig. 3. In the spatially constrained classification, the classification crispness method suggested to divide the country to five regions (Fig. 4). These regions showed significant differences in the values of environmental variables (Table 2). All regions were significantly different at least in three environmental variables; however, most of them differed in all environmental variables.

*Biogeography of delineated regions*
Using the equalized Φ coefficient, we determined the association of each species with each delineated region and these results can be found in Table S4 in
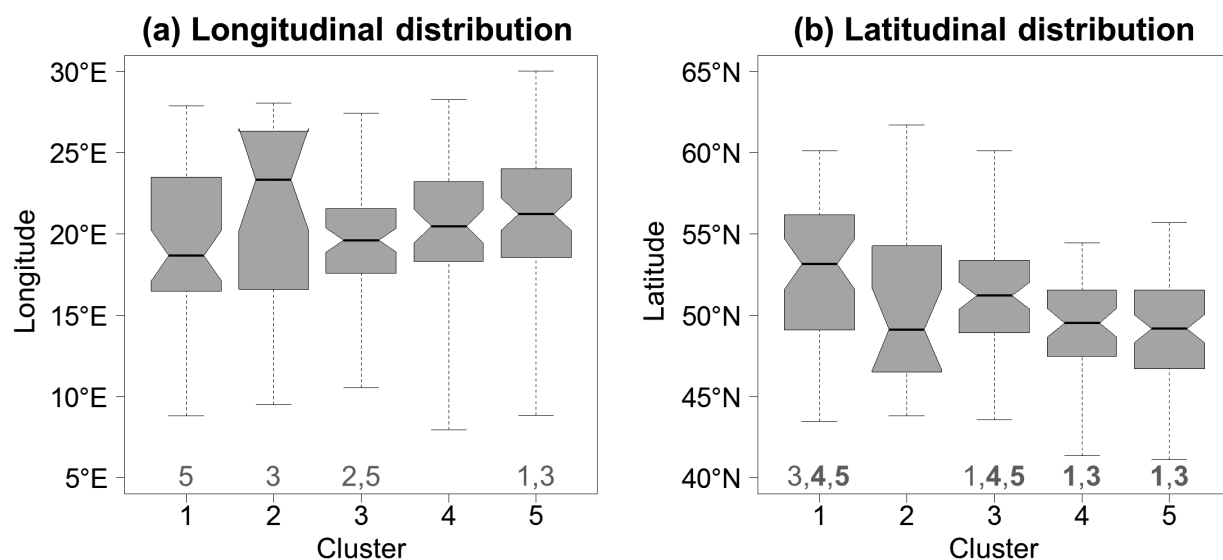
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**(a) Longitudinal distribution**

**(b) Latitudinal distribution**

**Fig. 5.** Boxplots showing longitudinal (a) and latitudinal (b) coordinates of the geographic centres of species' European ranges. For each region, only above-average associated species (according to the equalized phi coefficient of association) were considered. Grey numbers indicate regions with significantly different distributions according to Kruskal-Wallis tests ($P < 0.05$). Differences that were significant after correcting for multiple testing are in bold. 1 – Hercynian mountain region (52 species), 2 – Carpathian region (24 species), 3 – Bohemian-Moravian hilly and highland region (75 species), 4 – Central Bohemian lowland and hilly region (54 species), 5 – Pannonian region (78 species). 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) show the maximum and minimum values.

Appendix. Species above-average associated with the delineated regions (i.e. typical assemblages) revealed mostly distinct distributions in Europe (Fig. 5). Generally, the longitudinal distribution of species above-average associated with the Carpathian (cluster 2) and Pannonian region (cluster 5) tended slightly eastwards, whereas the distribution of species above-average associated with the Hercynian mountain region (cluster 1) and the Bohemian-Moravian hilly and highland region (cluster 3) tended rather westwards (Fig. 5a). The latitudinal distribution of species above-average associated with the Hercynian mountain region (cluster 1) tended considerably northwards, whereas species of the Central Bohemian lowland and hilly region (cluster 4) and the Pannonian region (cluster 5) tended significantly southwards (Fig. 5b).

According to IUCN maps, faunal assemblages typical of the Hercynian mountain region (cluster 1) occur in the mountains of central Europe, i.e. in the Alps or the Tatra Mountains (Fig. 6a). The Carpathian region (cluster 2) hosts probably the most distinct assemblages, which occur in the Carpathians only (Fig. 6b). Both the Bohemian-Moravian hilly and highland region (cluster 3) and the Central Bohemian lowland and hilly region (cluster 4) contain faunal assemblages similarly distributed across Europe (Fig. 6c, d). However, the distribution of assemblages

typical of the Central Bohemian lowland and hilly region (cluster 4) tends more south-eastwards (Fig. 6d). Assemblages typical of the Pannonian region (cluster 5) occur in the western part of the European steppe zone, i.e. in the Pannonian Basin and from central Ukraine to Moldova (Fig. 6e).

## Discussion

In this study, we attempted at providing the first statistical regional division of the Czech Republic based on the current distributions of terrestrial vertebrates native in the country. We used two contrasting methods to classify the area of the Czech Republic, spatially unconstrained and spatially constrained clustering. While the former produces internally homogeneous but spatially disparate clusters, the latter yields spatially coherent but internally less homogeneous regions. Each of these methods has some advantages and disadvantages depending on questions asked and purpose of classification.

On the one hand, if the aim is to improve understanding of purely ecological patterns, the unconstrained classification is preferable because it identifies areas with similar faunal assemblages irrespective of their location. Furthermore, it may also provide an insight into the beta diversity pattern. If the resulting clusters are scattered in spatially discontinuous patches, it is probable that the faunal composition of a pair of
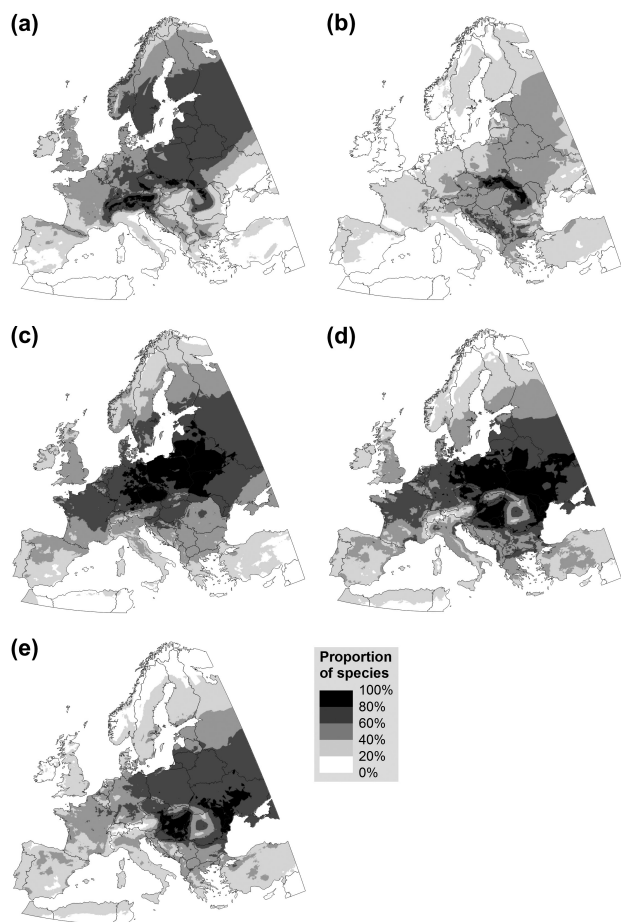
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**Fig. 6.** European distribution of species above-average associated (according to the equalized phi coefficient of association) with particular region: (a) Hercynian mountain region (cluster 1; 52 species), (b) Carpathian region (cluster 2; 24 species), (c) Bohemian-Moravian hilly and highland region (cluster 3; 75 species), (d) Central Bohemian lowland and hilly region (cluster 4; 54 species), (e) Pannonian region (cluster 5; 78 species). Colour scale shows the proportion (%) of above-average associated species, i.e. what areas in Europe host faunal assemblages typical of delineated regions.

**Table 2.** Results of the Kruskal-Wallis tests for each pair of delineated regions showing which pairs significantly differ in selected environmental variables (\*\*\* $P < 0.001$, \*\* $P < 0.01$, \* $P < 0.05$, [NS] not significant). $P$-values were adjusted using the Benjamini & Hochberg's (1995) correction method. See also Fig. S13 in Appendix for boxplots illustrating environmental differences of delineated regions. 1 – Hercynian mountain region, 2 – Carpathian region, 3 – Bohemian-Moravian hilly and highland region, 4 – Central Bohemian lowland and hilly region, 5 – Pannonian region. Proportion of forest and open habitats in each grid cell was calculated based on combination of CORINE 2000 Land Cover data and natural habitat data (see Methods and Tables S1 and S2 in Appendix).

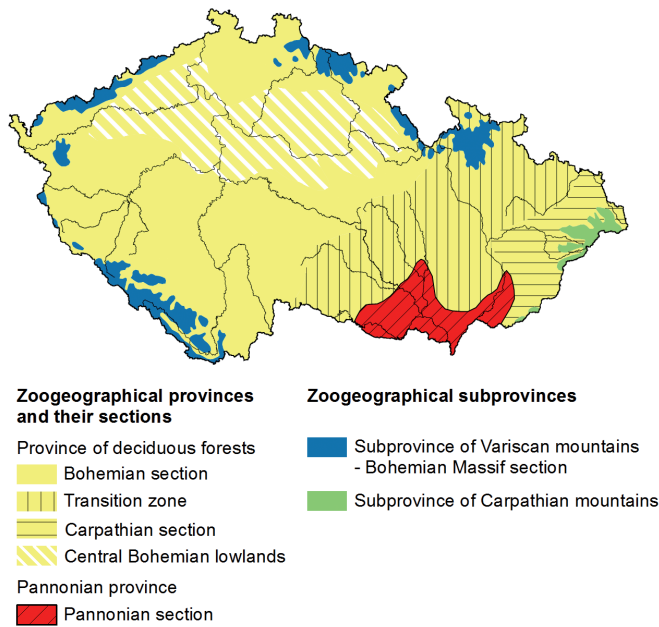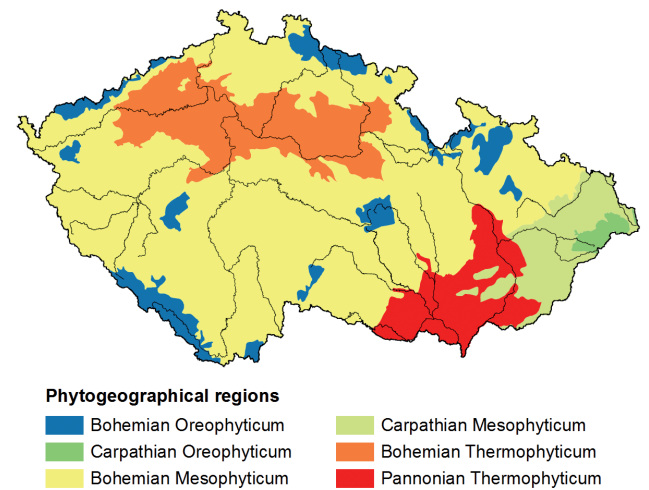| | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| Altitude | | | | |
| 1 | 31.7\*\*\* | 18.3\*\*\* | 153.5\*\*\* | 112.1\*\*\* |
| 2 | | 12.5\*\*\* | 43.4\*\*\* | 58.3\*\*\* |
| 3 | | | 165.3\*\*\* | 114.8\*\*\* |
| 4 | | | | 16.2\*\*\* |
| Temperature | | | | |
| 1 | 41.8\*\*\* | 61.9\*\*\* | 172.0\*\*\* | 117.8\*\*\* |
| 2 | | 4.3\* | 52.6\*\*\* | 71.4\*\*\* |
| 3 | | | 140.8\*\*\* | 112.4\*\*\* |
| 4 | | | | 27.3\*\*\* |
| Precipitation | | | | |
| 1 | 0.0[NS] | 175.3\*\*\* | 154.9\*\*\* | 103.5\*\*\* |
| 2 | | 110.2\*\*\* | 108.2\*\*\* | 82.2\*\*\* |
| 3 | | | 18.5\*\*\* | 31.8\*\*\* |
| 4 | | | | 6.6\* |
| Forest habitats | | | | |
| 1 | 6.0\* | 70.0\*\*\* | 87.6\*\*\* | 45.0\*\*\* |
| 2 | | 4.9\* | 25.4\*\*\* | 14.4\*\*\* |
| 3 | | | 30.9\*\*\* | 14.1\*\*\* |
| 4 | | | | 0.3[NS] |
| Open habitats | | | | |
| 1 | 6.3\* | 60.6\*\*\* | 58.4\*\*\* | 52.6\*\*\* |
| 2 | | 10.2\*\* | 18.0\*\*\* | 24.0\*\*\* |
| 3 | | | 8.3\*\* | 16.6\*\*\* |
| 4 | | | | 2.8[NS] |
| Natural habitats | | | | |
| 1 | 0.1[NS] | 128.9\*\*\* | 42.8\*\*\* | 9.8\*\* |
| 2 | | 70.3\*\*\* | 25.5\*\*\* | 6.0\* |
| 3 | | | 12.7\*\* | 16.8\*\*\* |
| 4 | | | | 2.6[NS] |

neighbouring grid cells is not similar. Relatively low similarity in the composition of faunal assemblages in the Czech Republic was documented by Divíšek et al. (2014b) who showed that, at this spatial scale, only about 15-29 % of variation in the species composition is spatially structured. It may indicate discontinuous environmental conditions in heterogeneous landscape or a considerable degree of landscape fragmentation. Nevertheless, the spatial discontinuity of clusters may be ascribed also to the scale of observation (Divíšek et al. 2016). On the other hand, if the aim is to divide the study area into a few regions with relatively uniform biota (e.g. for nature conservation purposes or for a comparison with expert-based classifications), the spatially constrained method can be preferred. Spatial information incorporated into the classification

process can help to better explore regional differences in the species composition, especially when important geographical gradients exist within the area considered. In our study, ordination results provided direct evidence of strong geographical gradient, primarily longitudinal, existing in the faunal composition of the Czech Republic, which could not be explained by
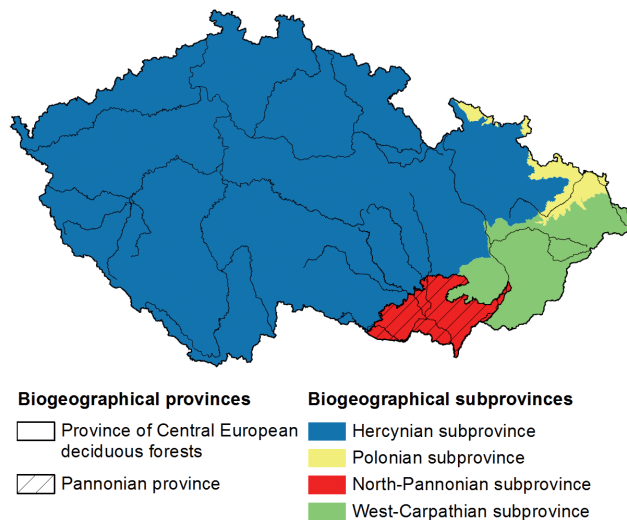
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**(a) Zoogeographical classification by Mařan (1958)**



**Zoogeographical provinces and their sections**

Province of deciduous forests
- Bohemian section
- Transition zone
- Carpathian section
- Central Bohemian lowlands

Pannonian province
- Pannonian section

**Zoogeographical subprovinces**
- Subprovince of Variscan mountains - Bohemian Massif section
- Subprovince of Carpathian mountains

**(b) Phytogeographical classification by Skalický (1988)**



**Phytogeographical regions**
- Bohemian Oreophyticum
- Carpathian Oreophyticum
- Bohemian Mesophyticum
- Carpathian Mesophyticum
- Bohemian Thermophyticum
- Pannonian Thermophyticum

**(c) Biogeographical classification by Culek (1996)**



**Biogeographical provinces**
- Province of Central European deciduous forests
- Pannonian province

**Biogeographical subprovinces**
- Hercynian subprovince
- Polonian subprovince
- North-Pannonian subprovince
- West-Carpathian subprovince

**(d) Classification based on natural habitats by Divíšek et al. (2014)**



**Regions of natural habitats**
- North Bohemian lowland and hilly region
- South Bohemian hilly region
- Hercynian mountain region
- Bohemian-Moravian highland region
- Carpathian region
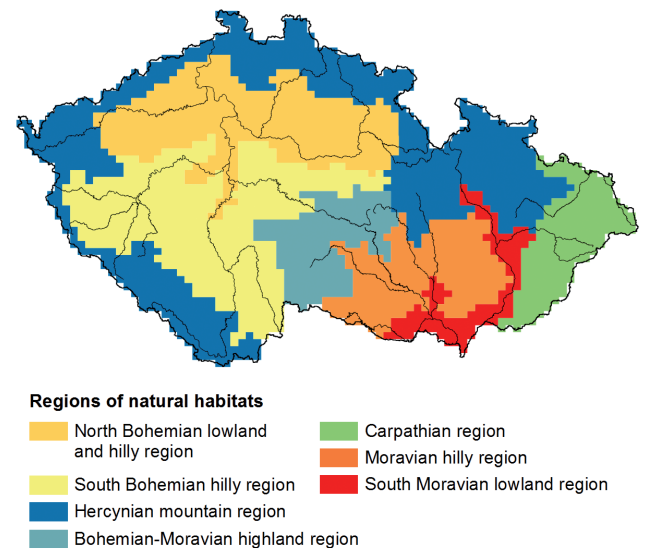- Moravian hilly region
- South Moravian lowland region

**Fig. 7.** Three expert-based classifications (a, b, c) and one statistically derived classification (d) of the Czech Republic. Regions of natural habitats (d) are based on the distribution of 127 natural habitat types defined in the Catalogue of Habitats of the Czech Republic (Chytrý et al. 2001). Classification was done using the spatially constrained Ward's clustering of the $\beta_{sim}$ dissimilarity matrix. Note, that natural habitats were mapped in finer spatial resolution of 5′ of longitude and 3′ of latitude (ca. 6 × 5.6 km), i.e. in grid cells corresponding with the quarters of grid cells used in this study.

the considered environmental factors. This pattern, which was documented also by Storch et al. (2003), can be largely ascribed to the biogeographical history and position of the Czech Republic within Europe (Pokorný et al. 2015a). According to the theory of postglacial range expansions, the area of central Europe was, after the end of the last (Vistulian) glaciation, colonized by species from different glacial refuges situated in south-eastern and south-western Europe. Thus, some species reach limits of their ranges in central Europe nowadays, e.g. European hedgehog (*Erinaceus europaeus*) and northern white-breasted hedgehog (*E. roumanicus*), and several hybridization zones of closely related species (or subspecies) go in the latitudinal direction just across the Czech Republic (Hewitt 2000). However, the biogeographical boundary between the Bohemian Hercynides and the Western Carpathians can be attributed rather to

differences in environmental conditions during the last glacial, which supported the existence of so-called "cryptic refuges" in the Western Carpathians and consequently different faunal development in both areas (Horáček 2000, Pokorný et al. 2015a). Besides, the east-west gradient in the faunal composition of central Europe might have been influenced by the intensity of human impact. It was documented for example that the degree of deforestation, woodland fragmentation and modification of forest composition is probably the main reason why the species richness of woodland avifauna increases from Great Britain across central European plains to western Russia (Tomiałojć 2000).

All regions we identified in the country significantly differ in environmental conditions. However, some of them may rather reflect geographical gradients, which could be formed either by historical or relatively recent events and processes. The Hercynian mountain region includes, beside typical central European mixed forests at lower altitudes, also extrazonal patches of boreal coniferous forest (taiga) and tundra at the highest altitudes (Chytrý 2012). These habitats provide conditions suitable for some rare bird species (or subspecies) which are characteristic for European mountain ranges, e.g. Alpine accentor (*Prunella collaris*), boreal zone of Europe, e.g. western capercaillie (*Tetrao urogallus*), or arctic tundra, e.g. bluethroat (*Luscinia svecica svecica*). On the other hand, some species occurring in avian assemblages of the highest European mountains, e.g. wallcreeper (*Tichodroma muraria*), are missing. In the case of mammals, this region is occupied mainly by mammal species typical of European broadleaved forests whereas, similarly to birds, mammals typical of the highest altitudes of the Alps and the Tatra Mountains, e.g. Alpine marmot (*Marmota marmota*), are missing or current populations are not indigenous, e.g. chamois (*Rupicapra rupicapra*). Only few species of reptiles and amphibians tolerating cold climatic conditions are associated with this region, e.g. common European adder (*Vipera berus*), viviparous lizard (*Zootoca vivipara*) or Alpine newt (*Ichthyosaura alpestris*). Taken together, species associated with this region are adapted to environmental conditions occurring in the Alpine or Boreal environmental zones of Europe identified by Metzger et al. (2005).

The Carpathian region identified in the eastern Czech Republic is probably the most heterogeneous region as to species' European distributions, because it includes species occupying different latitudes in Europe, i.e. species with northern ranges as well as species with south-eastern ranges (Fig. 5b). On the other hand, this region comprises a considerable proportion of more easterly-distributed species, especially those occurring primarily on the Balkan Peninsula, e.g. forest dormouse (*Dryomys nitedula*), and in the Carpathians; however, only Carpathian newt (*Lissotriton montandoni*) is the Carpathian sub-endemic species. The mapping of species' European distributions showed that the Carpathian Mountains represent the only area in Europe, which hosts more than 80 % of species above-average associated with the Carpathian region of the Czech Republic. This region is characteristic also by the occurrence of large carnivores, i.e. Eurasian lynx (*Lynx lynx*), brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*), but the presence of the latter two species in this region largely depends on the immigration of individuals from Slovakia where these species survived even at their lowest extent during the 1950-1970s (Chapron et al. 2014). Delineation of the Carpathian region within the Czech Republic is supported also by the distribution of recently distinguished slow worms *Anguis fragilis sensu stricto* occurring in western and central Europe and *A. colchica* distributed from the eastern Czech Republic and the Baltic region eastward to northern Iran (Gvoždík et al. 2010). Although we followed the former taxonomy (e.g. Arnold 2002) and considered *A. colchica* and *A. fragilis* as one species occurring across the entire area of the country (Mikátová et al. 2001), the currently known distribution of *A. colchica* in the Czech Republic corresponds well with the delineation of the Carpathian region (Moravec 2015). Considerable distinctiveness of the Carpathian fauna and flora in the eastern Czech Republic, which was documented also by other classifications (Mařan 1958, Skalický 1988, Culek 1996, Divíšek et al. 2014a), may be largely ascribed to geographical and namely historical factors. It was documented for example that during the full glacial and late glacial, mountain valleys of the north-western Carpathians might have supported taiga or hemiboreal forests (Jankovská & Pokorný 2008, Kuneš et al. 2008) or even the patches of broadleaved forest vegetation (Willis & van Andel 2004). By contrast, the landscape of Bohemia tended to be generally treeless, with an occasional occurrence of woodland patches (Kuneš et al. 2008). Thus, forest habitats in the Western Carpathians probably enabled some forest animal species to survive the Last Glacial Maximum in refuges directly in central Europe. Full glacial refuges in the Carpathian Mountains are well documented e.g. for bank vole (*Clethrionomys glareolus*; Kotlík et al. 2006) or yellow-bellied toad

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(*Bombina variegata*; Hofman et al. 2007). All these factors (environmental, geographical and historical) support the uniqueness of Carpathian assemblages.

The fauna of the Bohemian-Moravian hilly and highland region is largely similar to that of the Central Bohemian lowland and hilly region, as these two regions share a high proportion of species. Therefore, the distribution of assemblages typical of these two regions considerably overlaps in Europe, particularly within an area roughly corresponding to the continental environmental zone (Metzger et al. 2005). However, assemblages of the Bohemian-Moravian hilly and highland region tend to occur more to the north and at higher altitudes, while assemblages of the Central Bohemian lowland and hilly region tend more to the south-east and to lower elevations. Distinctiveness of the Bohemian-Moravian hilly and highland region is supported by the occurrence of species associated with wetlands and water bodies. In the Medieval and early Modern Period, systems of fishponds were built in southern Bohemia and in the Bohemian-Moravian Highlands. At present, these fishpond and wetland areas represent hotspots of amphibian and namely avian diversity in the Czech Republic (Krojerová-Prokešová et al. 2008).

The landscape of the Central Bohemian lowland and hilly region is similar to the Pannonian region. In the driest and warmest parts (with total annual precipitation amount below 525 mm and mean annual temperature over 8.25 °C; Chytrý 2012), both regions were occupied by forest-steppe habitats even in the period of maximum Holocene afforestation immediately before the Neolithic (Kuneš et al. 2015, Pokorný et al. 2015b). Since that period, landscapes of the two regions have been continually deforested and transformed into so-called "cultural steppes". However, there are only small patches of steppe habitats today whereas a predominant part of these regions is occupied by agricultural landscape. Although the relative extent of open habitats immediately before the Neolithic Period is unknown, it is believed that these habitats and subsequent anthropogenic landscape changes might have allowed several species that were dominant in glacial assemblages, e.g. common vole (*Microtus arvalis*), to survive in the Czech Republic until present days. On the other hand, landscape changes associated with early Neolithic farming (i.e. deforestation and formation of a "cultural steppe") are traditionally mentioned as a reason for the colonisation of the Czech territory by apochoric thermophilous species of open habitats which are not known from glacial

assemblages. However, new fossil records indicate that some of these species, e.g. garden dormouse (*Eliomys quercinus*) or bicoloured shrew (*Crocidura leucodon*), colonized central Europe probably already in the Early Holocene, thus without any causal relation to anthropogenic landscape changes (Horáček et al. 2014). Nowadays, both the Central Bohemian lowland and the Pannonian region host central European fauna associated with agricultural landscape which contains patches of lowland (forest-)steppe habitats and oak-hornbeam forests.

Despite the above-mentioned similarities with the Central Bohemian lowland and hilly region, the Pannonian region hosts one of the most distinct faunal assemblages within the Czech Republic. It includes species whose distribution in Europe tends south-eastwards or eastwards, either those with historically regressing ranges, e.g. common stonechat (*Saxicola torquatus*), or the recently expanding taxa, e.g. Syrian woodpecker (*Dendrocopos syriacus*). Besides, it also hosts a high proportion of species which are rare in the Czech Republic, e.g. soprano pipistrelle (*Pipistrellus pygmaeus*), European bee-eater (*Merops apiaster*), green lizard (*Lacerta viridis*) or Danube crested newt (*Triturus dobrogicus*). Whereas the Central Bohemian lowland and hilly region represents a relatively small isolated area of lowland forest-steppe habitats surrounded by montane forest habitats, the Pannonian region is a part of the continuous forest-steppe area that extends from Hungary through eastern Austria and south-western Slovakia to southern Moravia (Chytrý 2012). A faunal assemblage similar to that occupying the Pannonian region can be found, indeed, in the central part of the Pannonian Basin but also in south-west Ukraine and Moldova. This pattern corresponds well to that found by Storch & Šizling (2002) for rare bird species. They demonstrated that birds, which are rare in the Czech Republic are more frequent in the south-eastern and north-eastern part of central Europe, while common birds occur in almost entire central Europe except its southernmost part. Generally, rare species of the Czech Republic are those occupying high mountain elevations (including the Western Carpathians) and those occupying (semi-)open habitats in lowlands especially in the Pannonian region.

We want to emphasize that the regionalization proposed in this study is based on current species distributions resulting from the interplay of natural factors and human activities such as habitat modification, landscape fragmentation etc. These distributions may thus change over a relatively short time. For example,

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there were 62 mammal species occurring in the Czech Republic at the beginning of the 20th century, while 89 species occurred there at the beginning of the 21st century (Anděra & Gaisler 2012). However, we believe that the proposed regional division based on the distribution data gathered by national mappings does not represent only a short-time pattern, because it is largely similar to the main biogeographical pattern suggested by the former expert-based classifications of the country (Fig. 7a-d). Although there are differences in the number of regions and exact localization of their borders, the general pattern is roughly the same. All previous divisions identified the distinct so-called Pannonian and Carpathian regions as well as differences between higher and lower altitudes. The largest difference can be found in comparison with the biogeographical division of the Czech Republic by Culek (1996), where Bohemian lowlands are not distinguished from the Hercynian subprovince at the hierarchical level of subprovinces but only in finer subdivision. We demonstrated that the fauna of terrestrial vertebrates of the Czech Republic shows a biogeographical pattern very similar to that showed by natural habitats defined in terms of plant communities (Divíšek et al. 2014a). This indicates that similar environmental forces and biogeographical processes such as the spreading of faunistic and floristic elements from the adjacent Carpathian Mts. and Pannonian Basin drive both fauna and flora of the Czech Republic. Concluding we want to emphasize that the present study does not aim to provide better solutions or even to replace the previous expert-based biogeographical classifications of the Czech Republic, but rather to provide a useful and statistically based insight into biogeographical patterns in this country in addition to the previous classifications.

## Acknowledgements

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**Supplementary online material**

Appendix – supporting information (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/divisek_et_al._appendix_supporting_information.docx).