Species richness of vertebrates in the Czech Republic

Jarmila KROJEROVÁ-PROKEŠOVÁ[1]*, Miroslava BARANČEKOVÁ[1], Petra ŠÍMOVÁ[2], Miroslav ŠÁLEK[2], Miloš ANDĚRA[3], Vladimír BEJČEK[2], Vladimír HANÁK[4], Lubomír HANEL[5], Stanislav LUSK[1], Blanka MIKÁTOVÁ[6], Jiří MORAVEC[3], Karel ŠŤASTNÝ[2] and Jan ZIMA[1]

[1] *Institute of Vertebrate Biology ASCR, v.v.i., Květná 8, CZ-603 65 Brno, Czech Republic; e-mail: krojerova@ivb.cz*

[2] *Faculty of Environmental Sciences, Czech University of Life Sciences, Kamýcká 129, CZ-165 21 Praha 6, Czech Republic; e-mail: simova@fle.czu.cz*

[3] *Department of Zoology, National Museum (Natural History), Václavské nám. 68, CZ-115 79 Praha, Czech Republic; e-mail: milos_andera@nm.cz*

[4] *Faculty of Science, Charles University, Viničná 7, CZ-128 00 Praha, Czech Republic; e-mail: vhanak@natur.cuni.cz*

[5] *Management of Protected Landscape Area Blaník, Vlašimská 8, CZ-257 06 Louňovice pod Blaníkem, Czech Republic; e-mail: lubomirhanel@seznam.cz*

[6] *Agency for Nature Conservation and Landscape Protection of the Czech Republic, Pražská 155, CZ-500 04 Hradec Králové, Czech Republic; e-mail: blanka.mikatova@nature.cz*

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A b s t r a c t . The species richness of free-living vertebrates was analysed using mapping of occurrence within individual grid squares (12 x 11.1 km) over the territory of the Czech Republic. The data on species distribution were derived from recent distributional atlases published in the last 15 years, and the records originated mostly in the last 20 years. Altogether, 384 species of cyclostomes, bony fishes, amphibians, reptiles, birds and mammals were included in this study and their presence or absence was recorded in 678 grid squares.

The species numbers ascertained in the 523 grid squares situated completely within the Czech Republic varied from 92 to 259 species, with a median of 182 species. The first two principal components explained 44.9 % of the total variance and separated two main habitat gradients based on values of different environmental, topographic, and demographic variables in particular squares. The PC1 represents a gradient from urban habitats at lower altitudes to more homogenous habitats with dominant coniferous forests and meadows situated at higher altitudes. The importance of natural habitats (represented by broad-leaved and mixed forests, as well as by protected areas) and landscape heterogeneity increases along the PC2. Generalized Linear Modelling for each group of vertebrates was fitted using the number of species of individual vertebrate groups as a response variable and the first two principal components as explanatory variables. The species richness of all vertebrate groups except for reptiles is highly dependent on the PC1. The number of fish, amphibian, and bird species in squares decreases with increasing value of the PC1, i.e. it is higher in urban areas at lower altitudes. By contrast, the number of mammal species is higher in uninhabited areas at higher altitudes. The gradient represented by the PC2 is highly significant for species richness of reptiles and mammals, and the number of species of both groups increases with increasing importance of natural habitats.

Key words: mapping squares, species numbers, environmental variables, PCA

Introduction

Data on the species richness of animals, plants and other organisms have been collected during recent centuries all around the world. Detection of causes of the spatial variability in species

* Corresponding author

richness on local, regional and global scales has been of permanent interest to biologists and is still valuable for conservation plans (e.g. Anderson 1984, Owen 1989, Meliadou & Troumbis 1997, Andrews & O'Brien 2000, Kryštufek 2004, Ulrich et al. 2007). For conservation biology it is useful to identify the areas of species concentrations known as hot spots (Myers 1988, 1990). However, detection of species richness patterns is so far feasible only in well-studied organismal groups and within regions where long-term intensive faunistic research has been carried out.

In Europe the knowledge of the distribution of vertebrates is generally good and datasets of records are exceptionally rich and complete. This has enabled publication of synthetic distributional atlases in the major groups of terrestrial vertebrates (e.g. Gasc et al. 1997, Hagemeier & Blair 1997, Mitchell-Jones et al. 1999) as well as setting-up a number of handbooks summarizing current knowledge about individual groups. Consequently, many studies (not only in Europe) have examined patterns of species richness as a suitable biodiversity indicator at different scales (for review e.g. Willig et al. 2003). For evaluation of species richness patterns it is necessary to avoid the influence of different area size as the positive area effect on species richness has been confirmed (Rosenzweig 1992, Anderson & Marcus 1993). Therefore, the equal area of sampling unit is a basic requirement for such studies. Further, richness data should pertain only to ecologically similar taxonomic groups (Andrews & O'Brien 2000).

The spatial distribution of biodiversity is heterogeneous. At the macro-scale, several general global patterns of species richness were detected (Gaston 1997, Currie et al. 1999). Latitudinal diversity pattern of species richness has been verified in most of the studies for many groups (for review e.g. Stevens 1989), with a general explanation involving mainly the size of area, climatic conditions and ecosystem productivity (Ehrlich & Wilson 1991, Rosenzweig 1992, Willig et al. 2003). At meso-scales (10^6–10^{10} m^2), vertebrate species richness is expected to correlate mainly with landscape structure and composition (Bell et al. 1991, Kerr & Packer 1997, Fuller et al. 2001) and with disturbance mechanisms (Rundell et al. 1998).

The Czech Republic is situated in Central Europe, which is a region with high species richness of some vertebrate groups, e.g. mammals (Mitchell-Jones et al. 1999, Baquero & Tellería 2001, Kryštufek & Griffiths 2002), but with lower species richness of other groups, e.g. reptiles (Meliadou & Troumbis 1997). It is an inland country covering an area of 78.866 km^2. Its surface has mainly the character of highlands (39 %) and uplands (30 %), with the elevation range varying from 115 m to 1.602 m a.s.l. Most of the area (67 %) is situated at altitude up to 500 m.

The Czech Republic represents a traditionally and thoroughly studied area in respect of vertebrate biology. During recent decades, detailed handbooks of most vertebrate groups were compiled and published (Baruš & Oliva 1992a,b, 1995, Hudec 1983, 1994, Hudec & Šťastný 2005, Anděra & Horáček 2005). The available distributional data for animals, particularly for vertebrates, are abundant and they are usually arranged and presented in the standard grid system (Buchar 1982). Using this grid system, distributional data on mammals (Anděra & Hanzal 1995, 1996, Anděra 2000, Anděra & Beneš 2001, 2002, Anděra & Červený 2004, Hanák & Anděra 2005, 2006, Anděra & Hanák 2007), birds (Šťastný et al. 2006), reptiles (Mikátová et al. 2001), amphibians (Moravec 1994), and cyclostomes and bony fishes (Hanel & Lusk 2005) were published. In respect of the unique uniformity and completeness of the published distributional datasets, this study is aimed to summarize the records on the occurrence of vertebrates in the Czech Republic and to examine the species richness patterns in dependence on various environmental, topographic and demographic variables.

Methods

Vertebrate occurrence was mapped using grid squares (more precisely trapeziums) of 10' east longitude x 6' north latitude. The squares defined by meridians and parallels are naturally of variable size increasing slightly from northwest (130.6 km^2) to southeast (136.6 km^2). The approximate size of a square in the Czech Republic is 12 x 11.1 km (average area 133.5 km^2). The standard grid system consists of 678 squares, some of them situated behind the borders or only partially situated within the Czech Republic. To eliminate the area effect, only squares with 100% of their surface inside the Czech Republic were chosen, making a total of 523 squares used for analysis. A very small variability between square areas (± 3 km^2) was considered negligible with regard to the overall square size and no correction was considered to be necessary.

All maps of species richness for individual vertebrate groups were created in ArcGis 9.1 using the background *shp layer of squares from the JanMap application (freeware Janitor J/2, provided by the CENIA GIS Laboratories, http://janitor.cenia.cz).

Original primary presence data of individual species were obtained from the published atlases that report verified records only (Moravec 1994, Anděra & Hanzal 1995, 1996, Anděra 2000, Anděra & Beneš 2001, 2002, Mikátová et al. 2001, Anděra & Červený 2004, Hanák & Anděra 2005, 2006, Hanel & Lusk 2005, Šťastný et al. 2006, Anděra & Hanák 2007). These data originated from recording conducted during the last 50 years; however, the records have mostly been made in the last 20 years and in some groups (e.g. birds) the recording period is rather short and well defined. In addition, the occurrence of species recorded in the Czech Republic after publication of the atlases was taken into account (Piálek et al. 2000). The distribution records of mammals and amphibians were updated according to data published on www.biolib.cz. Altogether 384 species (both autochthonous and introduced) were included in this study (2 cyclostomes, 61 bony fishes, 21 amphibians, 11 reptiles, 201 birds, 88 mammals). The cyclostomes and bony fishes were pooled subsequently as fishes, and their permanent as well as temporary occurrence was considered. In birds, only breeding species (with confirmed, probable, and possible breeding) were taken into consideration; winter, autumn, and spring migrants were not included in the analysis. In bats, summer as well as winter occurrence in squares was used. For other mammals, as well as for fishes, reptiles and amphibians only the simple presence/absence data in individual squares were available.

Values for environmental, topographic, and demographic variables in individual squares were acquired using spatial analysis in GIS. Calculated variables were specified to involve the main habitat types in the Czech Republic. Some of them also reflect the extent of anthropogenic utilisation of the environment and the presence of natural biotopes valuable for nature protection. Also altitude was used as an important environmental factor. The proportion of basic land-cover types in squares was calculated using vector data of Corine LandCover (European Commission 1994) (the smallest mapping unit of 1 ha). Based on these data the Shannon diversity index (DIV) of the original land-covers was calculated for each square (Magurran 1988). Other variables were included using the

Table 1. List of abbreviations for vertebrate groups and environmental, topographic, and demographic variables.

Abbreviation	Explanation	Data Source
FISH	number of fish species in square	Hanel & Lusk 2005
AMPH	number of amphibian species in square	Moravec 1994
REPT	number of reptile species in square	Mikátová et al. 2001
BIRD	number of bird species in square	Šťastný et al. 2006
MAM	number of mammal species in square	Anděra et al. 1995–2007
CIT	urban fabric (in % of area)	Corine LandCover (1.1)
IND	industrial, commercial and transport units (in % of area)	Corine LandCover (1.2)
POP	human population density (per 1 km^2)	ArcCR500
ROAD	presence of important barriers expressed as the lengths of highways in square (km/km^2)	ArcCR500
ARA	arable land (in % of area)	Corine LandCover (2.1)
MEAD	meadows and pastures (in % of area)	Corine LandCover (2.3)
WAT	water bodies (in % of area)	Corine LandCover (5.1.1, 5.1.2)
STREAM	density of water streams (the length of streams per 1 ha not considering their width and flow rate)	ArcCR500
CON	coniferous forest (in % of area)	Corine LandCover (3.1.2)
NATFOR	broad-leaved and mixed forest, transitional woodland shrub (in % of area)	Corine LandCover (3.1.1, 3.1.3, 3.2.4)
DIV	landscape heterogeneity – Shannon's diversity index (counted using all classes distinguished in Corine at the most detailed level)	Corine LandCover
NAT	natural biotopes valuable for natural protection defined as small-scale protected areas and Sites of Community Importance – Natura 2000 (in % of area)	ANCLP
ALT	mean altitude of square	ArcCR500

digital vector database ArcCR500, water utilisation information system HEIS and data of the Agency for Nature Conservation and Landscape Protection of the Czech Republic (ANCLP). All variables used are listed in Table 1.

To reduce co-linearity and the numbers of explanatory variables presented to multivariate models (Currie et al. 1999), we employed the values of Spearman correlation coefficients (Table 2) to exclude the factors that may be considered replaceable by a single underlying predictor. As a result, we excluded the proportions of arable land in the squares (ARA) from further analyses. Although the arable land dominates in the Czech Republic and forms large uniform units, it is highly negatively correlated with the two another important predictors – proportion of coniferous forests (CON), i.e. dominant habitat in some parts of the country, and landscape heterogeneity (DIV).

The effects of particular variables were estimated using the first two principal components from a Principal Component Analysis (PCA) describing the complex landscape structures in respective grid squares. We standardized the variables by norm (i.e. the square root of the sum of squares of the values) producing the required PCA on a matrix of correlations. We present the cumulative fit of each predictor referring to its tightness to principal components. Minimum difference between values of PC1 and PC2 indicates a

Table 2. Spearman's correlation coefficients reflecting relationships between environmental variables evaluated in this study.

	CIT	IND	ARA	NATFOR	MEAD	WAT	CON	DIV	ROAD	STREAM	NAT	ALT	POP
CIT	1.00	0.59	0.29	0.12	-0.37	0.11	-0.56	0.09	0.43	0.04	0.04	-0.63	0.78
IND	0.59	1.00	0.11	0.13	-0.11	0.16	-0.33	0.18	0.38	-0.03	0.09	-0.38	0.64
ARA	0.29	0.11	1.00	-0.49	-0.64	0.08	-0.60	-0.71	0.09	-0.07	-0.31	-0.52	0.17
NATFOR	0.12	0.13	-0.49	1.00	0.12	-0.09	-0.16	0.61	0.07	0.03	0.40	-0.17	0.02
MEAD	-0.37	-0.11	-0.64	0.12	1.00	-0.06	0.45	0.53	-0.26	0.21	0.12	0.57	-0.18
WAT	0.11	0.16	0.08	-0.09	-0.06	1.00	-0.14	0.09	0.20	0.10	0.06	-0.19	0.09
CON	-0.56	-0.33	-0.60	-0.16	0.45	-0.14	1.00	0.14	-0.29	0.15	-0.05	0.78	-0.36
DIV	0.09	0.18	-0.71	0.61	0.53	0.09	0.14	1.00	0.08	0.16	0.24	0.13	0.15
ROAD	0.43	0.38	0.09	0.07	-0.26	0.20	-0.29	0.08	1.00	-0.10	0.09	-0.34	0.33
STREAM	0.04	-0.03	-0.07	0.03	0.21	0.10	0.15	0.16	-0.10	1.00	0.08	0.18	0.04
NAT	0.06	0.08	-0.31	0.40	0.12	0.06	-0.05	0.24	0.09	0.08	1.00	-0.05	0.05
ALT	-0.63	-0.38	-0.52	-0.17	0.57	-0.19	0.78	0.13	-0.34	0.18	-0.05	1.00	-0.41
POP	0.78	0.64	0.17	0.02	-0.18	0.09	-0.36	0.15	0.33	0.04	0.05	-0.41	1.00

tight association to the PC1, whereas increasing difference between PC1 and PC2 values indicates a link to the PC2. The effects of the first two principal components (PC1, PC2) on species richness of vertebrate groups (classes) were then tested using General Linear Modelling (GLM). The significances of either PC1 or PC2 were controlled for the effect of the PC2 or PC1, respectively, being fitted as the second in the model. Before all procedures, the data was log-transformed to approach normality. All statistical analyses were performed using STATISTICA 8 and CANOCO (ter Braak & Šmilaeur 2002).

Results and Discussion

The species richness in individual systematic groups and in all vertebrates is shown in Figs 1–6. The number of species of all vertebrates found in individual grid squares varied from 92 to 259, with a median of 182 species. The median number of species recorded in a square was 24 in fishes, 8 in amphibians, 5 in reptiles, 110 in birds, and 38 in mammals. The highest diversity of vertebrates was found in two squares: square number 7166 situated in the SE part of the country (southern Moravia, area of the Pálava Protected Landscape Area and the Lednice region) with 259 vertebrate species, and square number 5645 in the NW part of the country (northern part of the Doupovské hory Mts and the adjacent valley of the Ohře River) with 254 vertebrate species. The lowest diversity, 92 species, was found in square number 5650 near the Mšené Lázně village, Litoměřice region, in the NW part of the country.

The first two principal components explained 44.9% of the total variance (Table 3, Fig. 7). The PC1 represents a gradient from urban habitats at lower altitudes to more homogenous habitats with dominant coniferous forests and meadows situated at higher altitudes. The importance of natural habitats (represented by broad-leaved and mixed forests, and protected areas) and landscape heterogeneity increases along the PC2. This may indicate that these environmental gradients (variation in altitude and urbanisation) represent two important drivers of spatial distribution of species richness in the Czech Republic.

The fit of habitat gradients with species richness in individual vertebrate groups is shown in Table 4. The gradient of the PC1 is highly significant for species richness in all the

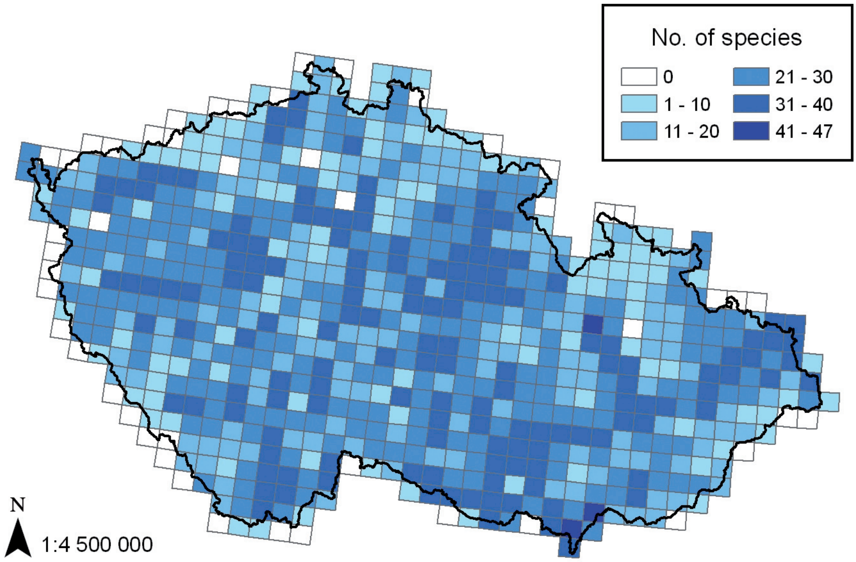

Fig. 1. Species richness of cyclostomes and bony fishes in the Czech Republic.

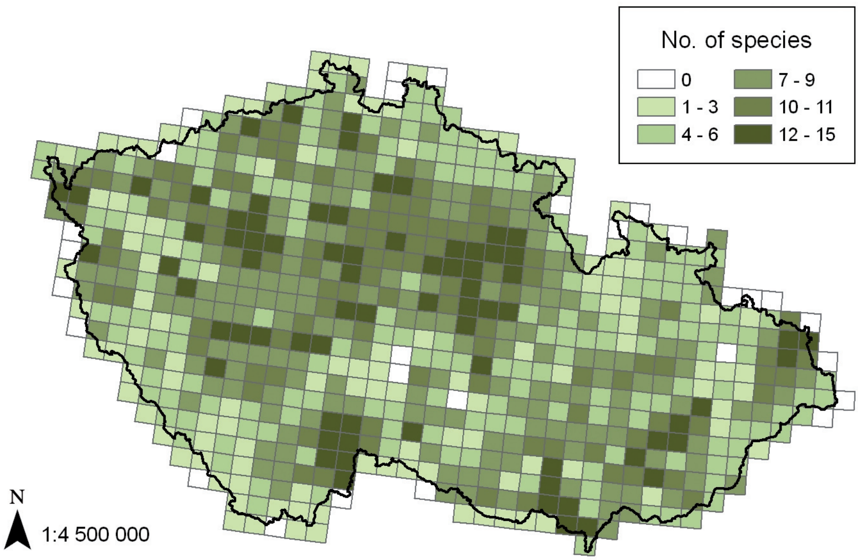

Fig. 2. Species richness of amphibians in the Czech Republic.

vertebrate groups except for reptiles (fishes, amphibians, mammals: $p<0.001$; birds: $p<0.01$). The number of fish, amphibian, and bird species in squares decreases with the increasing value of the PC1, i.e. it is higher in urban areas at lower altitudes according to character loadings. By contrast, the number of mammal species is higher in uninhabited areas at higher altitudes. The gradient of the PC2 is highly significant for species richness of reptiles

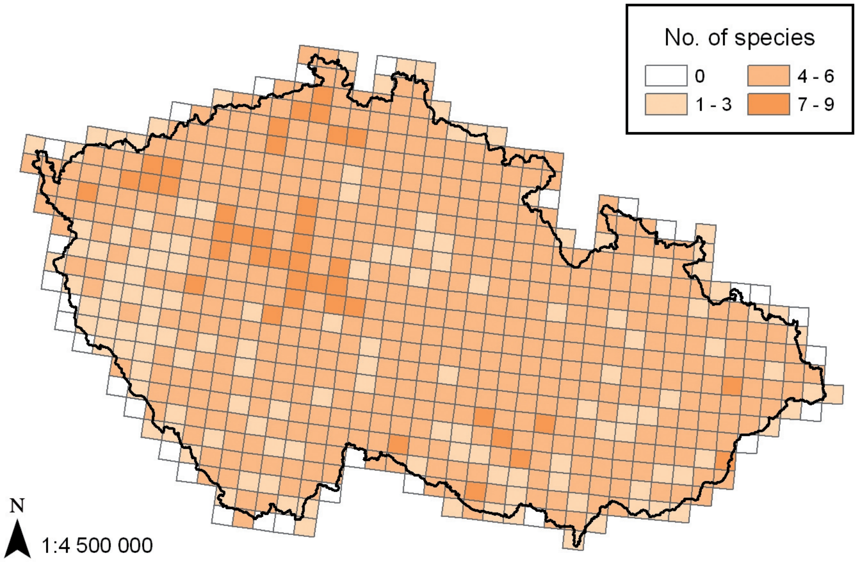

Fig. 3. Species richness of reptiles in the Czech Republic.

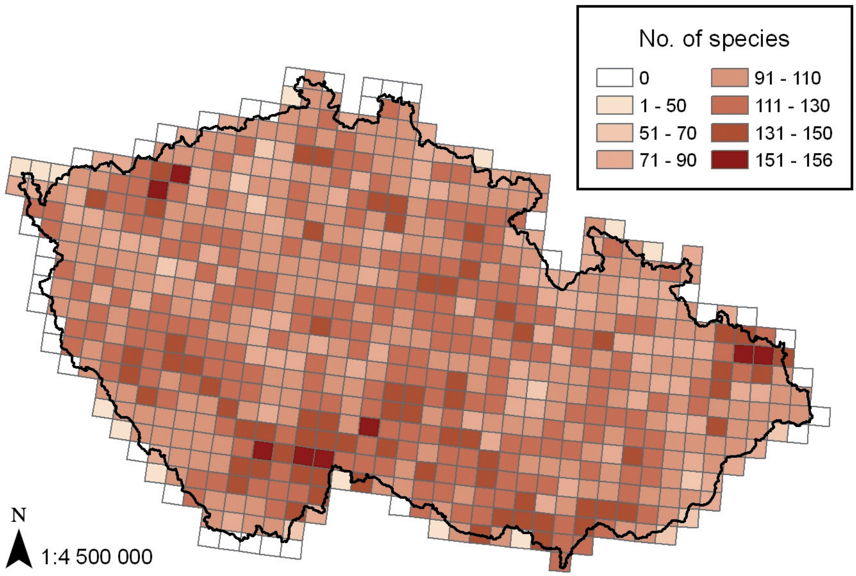

Fig. 4. Species richness of birds (breeding occurrence) in the Czech Republic.

and mammals ($p<0.001$), and the number of species in both the groups increases with the area and the influence of natural habitats. On the other hand, the number of fishes decreases with higher proportion of natural habitats ($p<0.05$). We are aware that these conclusions stem basically from correlations between animal occurrences and habitat variables and they do not necessarily reflect causality.

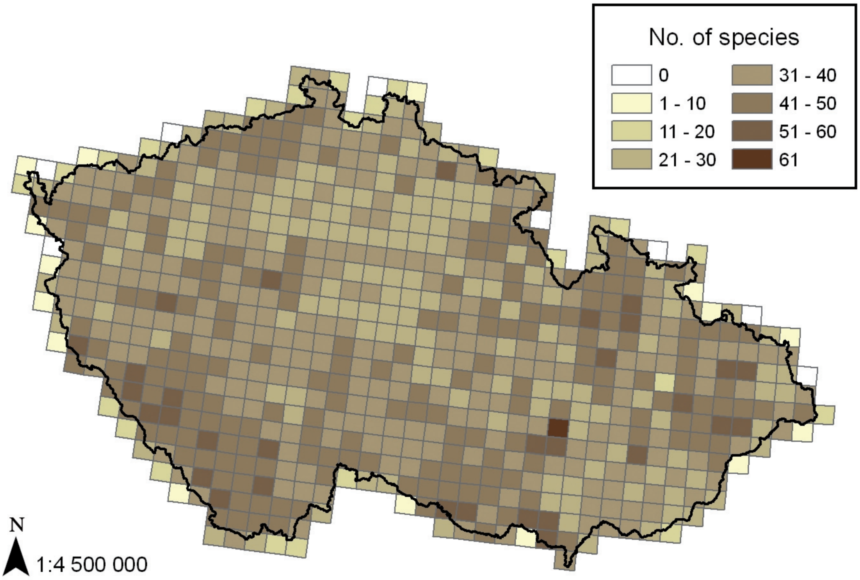

Fig. 5. Species richness of mammals in the Czech Republic.

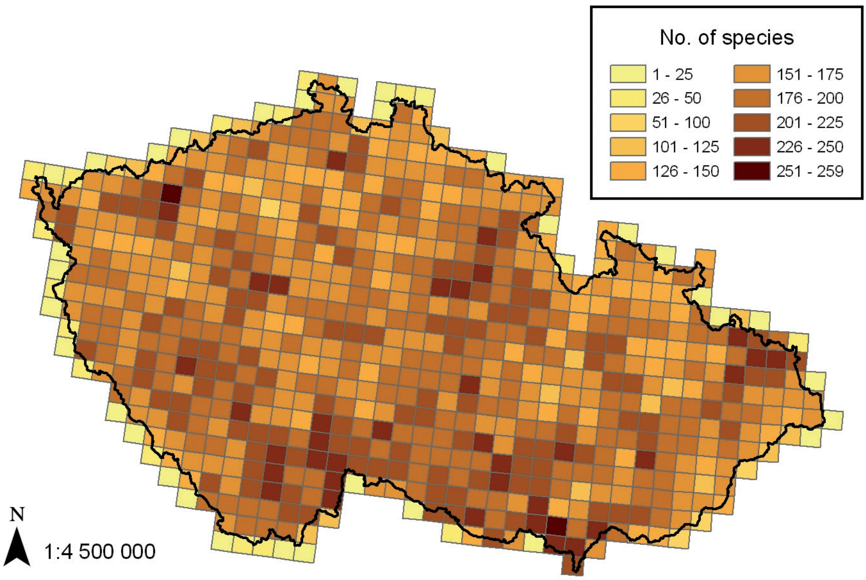

Fig. 6. Species richness of vertebrates in the Czech Republic.

Within the models made for individual vertebrate groups, the highest percentage of variance explaining the species richness was detected for amphibians (multiple R-adjusted = 0.135, i.e. significant gradient of PC1 explains 13.5% of variance) and mammals (multiple R-adjusted = 0.121, i.e. significant gradients of PC1 and PC2 explain 12.1% of variance). The proportion of explained variance is relatively low. However, it is necessary to consider that

Table 3. Cumulative fits of environmental variables expressed as fractions of variances defined by the two principal components PC1 and PC2. The PC2 column exhibits the amount of variance explained by the PC1 and PC2 together. Small difference between PC1 and PC2 indicates a tight association to the PC1, increasing difference refers to a link with the PC2.

	PC1	PC2
PCA		
Eigenvalues	3.23	2.17
Proportion of variance	0.27	0.18
Cumulative fit		
ALT	1.000	1.000
ROAD	0.070	0.070
STREAM	0.041	0.041
POP	0.025	0.026
WAT	0.040	0.043
CITY	0.217	0.220
IND	0.112	0.117
CON	0.631	0.645
MEAD	0.264	0.291
DIV	0.011	0.083
NATFOR	0.006	0.326
NAT	0.163	0.942

each vertebrate class is highly heterogeneous containing number of species with different and sometimes even antagonistic habitat preferences (e.g. mountain vs. lowland species). This heterogeneity decreases the percentage of explained variance even in subordinate taxa and its influence increases with grouping them into higher taxonomic group.

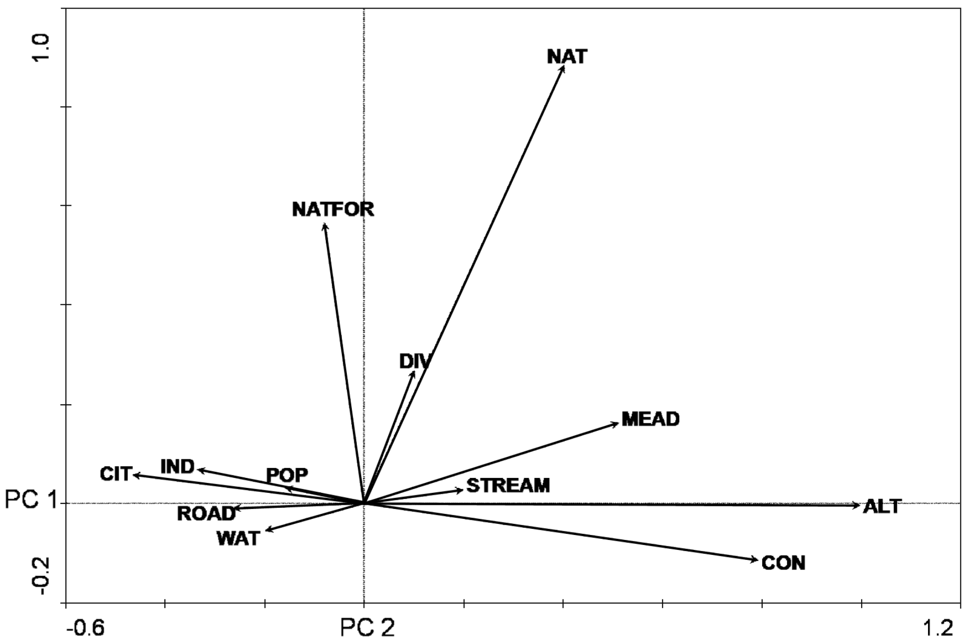

Fig. 7. Principal components analysis showing the vectors of environmental variables.

Table 4. Fit of habitat gradients expressed by the relationships between PC1 and PC2 and number of species in particular vertebrate groups; t – t-statistics, β – regression coefficient (slope) of given variable in the General Linear Model (GLM), P – significance value. Significant values are given in bold.

	FISH			AMPH			REPT			BIRD			MAM		
	t	p	β	t	p	β	t	p	β	t	p	β	t	P	β
PC1	**-7.762**	**<0.001**	**-0.322**	**-8.903**	**<0.001**	**-0.363**	0.064	0.949	0.003	**-2.743**	**0.006**	**-0.120**	**6.738**	**<0.001**	**0.277**
PC2	**-2.271**	**0.024**	**-0.094**	1.956	0.051	0.080	**4.980**	**<0.001**	**0.214**	1.360	0.174	0.059	**5.296**	**<0.001**	**0.218**

Species richness of fishes was mainly correlated with the habitat gradient formed by the PC1. It is interesting that the influence of the density of streams and the area of water bodies is opposite within this gradient (Fig. 7). The area of water bodies is more important with respect to the number of fishes as large water reservoirs are situated at lower altitudes near urban areas and are commercially used for fishing. Here, fish richness and abundance is highly affected by permanent stocking and in seven non-spawning species by re-stocking only. On the other hand, the numerous smaller streams at higher altitudes are species-poor and are suitable for only few fish species (P i v n i č k a 1996).

The amphibians are highly correlated with certain local environmental factors, such as number and distance between small ponds or water quality (H e c n a r & C l o s k e y 1998, R a y et al. 2002). However, the variables derived from GIS environment are limited by the size of the smallest mapping unit, which makes it difficult to detect these local environmental factors and to obtain their relation with amphibian species richness (N o g u e ‘ s - B r a v o & M a r t í n e z - R i c a 2004). Despite these difficulties we were able to detect relation of the number of amphibian species with the gradient represented by PC1. Amphibian species richness was higher at lower altitudes (ALT) and was positively influenced by the presence of rivers and water bodies (WAT). The influence of other factors was possibly less important as the amphibians have relatively small home ranges and they can survive even in limited or fragmented habitats.

The number of reptile species in the Czech Republic, as well as that of amphibians, is low and most of them are present in almost all squares. Their species richness is considerably influenced by the presence or absence of few rare species as *Podarcis muralis* or *Elaphe longissima*. This situation makes it difficult to define precisely the variables affecting species richness of this group. The number of species in reptiles, contrary to amphibians, is correlated to the presence of natural habitats or small-scale protected areas where the rare species could find optimal living microhabitats (N o g u e ‘ s - B r a v o & M a r t í n e z - R i c a 2004). It is interesting that no affect of altitude was detected contrary to other similar studies of herpetofaunal richness patterns (O w e n 1989).

Similarly to fishes, birds are highly affected by the habitat gradient described by the first principal component, and the number of bird species was higher in urban areas at lower altitudes. Many birds are at least tolerant of man-induced changes, and they are often well adapted for life in cities and other synanthropic habitats (e.g. F u c h s et al. 2002).

Altitudinal variation was detected to effect indirectly mammalian distribution and richness (B a d g l e y & F o x 2000) through different climatic conditions that affect primary productivity (P a t t e n 2004). Also the positive relationship between intensity of human occupation and mammalian species richness was detected (N o g u e ‘ s - B r a v o & M a r t í n e z - R i c a 2004). However, the number of mammal species in the Czech Republic tends to be higher in natural non-urban habitats at higher altitudes and is apparently affected by the presence or absence of those species that avoid anthropogenic landscapes. This may be a consequence of lower altitudinal range and moderate variation in climate between various parts of the country.

Patterns of species richness for each vertebrate group in relation to the environmental variables are complex and usually depend on the particular combination of environmental factors (Owen 1989). The existence of numerous species in a hot spots area may result from the presence of many species of narrow distribution range ("rare", endemic or scarce) but may result also from the presence of widespread species (Meliadou & Troumbis 1997). These two situations are not mutually exclusive. In the Czech Republic the rarity of the vertebrate species is believed to inhere mainly in narrow habitat requirements and low local densities of their populations (cf. Rabinowitz 1981).

It is rather surprising that the number of species tends to be higher in urban areas and lower in regions with relatively well-preserved natural ecosystems and landscapes. This could result from a bias in the sampling procedure and indicate that the sampling intensity could be higher in more accessible and highly populated areas similarly to findings of Nogue's-Bravo & Martínez-Rica (2004). On the other hand, certain types of synanthropic habitats may have become suitable for various wildlife terrestrial species, supposedly because of the increased availability of food resources and possibilities to escape hunting pressures.

We are aware of several drawbacks related to the datasets used. The distributional data are not simply comparable between aquatic and terrestrial species and the completeness of datasets may not be the same among individual groups as well as among various regions of the country. Some bias could also result from ecological and behavioural differences between individual taxa within each group that are not equally influenced by the variables (e.g. bats vs. other mammal species). The accuracy of habitat satellite mapping with the smallest mapping unit of one hectare could bias the values of variable in particular squares. Nevertheless, these problems can obviously influence the results only regionally, in certain quadrate grids, and the overall picture may be considered reliable. The methodical problems and gaps in datasets should be removed or diminished in further research.

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