Numerical classification of oak forests on loess in Hungary, Croatia and Serbia

Numerická klasifikace doubrav na sprašových půdách v Maďarsku, Chorvatsku a Srbsku

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Oak forests on loess are floristically one of the richest types of broadleaved forests and are among the most threatened types of natural habitats in the Carpathian Basin. They are classified in several communities in Hungary, Croatia and Serbia. These syntaxa are distinguished mostly on the basis of traditional phytosociological methods without comparison across a larger geographical scale. The recognition of some of these local syntaxa in the field, therefore, can be difficult, and the application of their names to communities in other areas may be questionable. The goal of this study was to develop an international typology for oak forests on loess based on a numerical analysis. A data set of 437 phytosociological relevés (stands of 12 associations from three countries) was stratified and 270 relevés were analysed using multivariate statistical methods. Six types were distinguished: *Primula vulgaris* type (xero-mesic to mesic sub-Mediterranean closed-canopy oak forests); *Ruscus aculeatus* type (xeric to xero-mesic sub-Mediterranean type); *Vinca herbacea* type (xeric continental open-canopy woodlands); *Pulmonaria mollis* type (xeric to mesic continental closed-canopy forests); *Corydalis cava* type (mesic closed-canopy oak forests in nutrient-rich habitats); and *Stellaria media* type (xeric to mesic oak forests in nutrient-rich habitats). The vegetation types identified are related to syntaxa traditionally recognized by phytosociologists. Our analysis did not support the distinction of some associations with local distributions. The geographical distributions of the two main forest types exhibited a gradient-like pattern in a north-east–south-west direction. The dry continental forest steppe woodland is mainly distributed in the north-eastern part of Hungary, whereas the xero-mesic sub-Mediterranean forests are restricted to the southwestern and southern part of our study area. This pattern corresponds to a climatic gradient from the North Hungarian Mts to north-eastern Croatia and northern Serbia.

K e y w o r d s: *Aceri tatarici-Quercion,* Carpathian Basin, forest steppe, gradient, phytosociology

Introduction

Loess covers large areas in the Carpathian Basin (Niklfeld 1973–1974). Despite this, oak forests on loess are restricted mainly to the transitional zone between lowlands and hilly regions and the foothills of the mountains (Zólyomi 1989, Fekete et al. 2011). These forests grow on chernozem-like soils, which are highly fertile. Palaeoecological data indicate the persistent dominance of temperate deciduous wooded steppe with a varying canopy composition on the Great Hungarian Plain throughout the Holocene (Magyari et al. 2010). Changes in vegetation linked to human intervention (e.g. burning) in the landscape, expansion of weeds and reduction in the arboreal vegetation in the forest-steppe environment are traceable to the Late Neolithic and Early Copper Age (Sümegi et al. 2012). The loss of tree cover during the last two millennia is almost certainly a result of intense agricultural exploitation of the area (Magyari et al. 2010). These forests survived only as fragments, of which many were subject to strong anthropogenic influences (Zólyomi 1957, 1958, Molnár et al. 2000). Stands of these forests may differ substantially due to human management, local conditions, as well as variation in climate and altitude. Tree growth and cover range from small trees and scattered groups of trees on the driest or most disturbed sites to well-developed forests with closed canopy on more favourable sites. There is an extremely high risk that there will be a decline in the floristic richness of the small isolated fragments of forests, especially those at the limits of their geographical range. According to Borhidi & Sánta (1999), species-rich loess oak forests are relicts and worthy of strict protection. In Annex I of the Habitat Directive, these types of forest are designated with the code: 91I0 Euro-Siberian steppe woodlands and forests with *Quercus* spp. and indicated as a priority habitat (http://ec.europa.eu/environment/nature/legislation/habitatsdirective).

Continental xero-thermophilous oak forests in the central and eastern part of Europe were surveyed and first synthesized by Zólyomi (1957, 1958). The communities described were included in the alliance *Aceri tatarici-Quercion* Zólyomi & Jakucs 1957. The southern limit of the distribution of loess oak forests runs across south-western Hungary, north-eastern Croatia and the northern part of Serbia (Horvat et al. 1974, Jakucs 1974, Jovanović 1997). However, there is no unified syntaxonomy of this vegetation type, which hinders cross-border communication. North-eastern Croatia is a part of the Pannonian Plain (Horvat 1954, Ilijanić 1966). The potential vegetation of this transitional forest steppe zone is oak forest on loess belonging to the *Carpinion betuli* alliance (Rauš 1971, 1976). Small fragments of oak forest also occur on the loess plateau on the Bansko hill (Purger & Csiky 2008). These stands are unique in Croatia as some rare continental species occur in them, but their syntaxonomical status is unclear. In northern Serbia (Vojvodina province), the oak forests on loess described by Slavnić (1952) are included in the *Carpinion betuli* alliance (Jovanović et al. 1986a, b). However, the potential natural vegetation of the loess plateau is considered to be a mosaic of forest steppe vegetation belonging to the alliance *Aceri tatarici-Quercion* (Parabućski & Janković 1978, Jovanović 1997). Nevertheless, delimitation of the oak forests on loess assigned to different alliances is not clear. There is a continuous transition within xeric and mesic forest types, in which the composition of the herb layer varies considerably depending on soil moisture, nutrient availability and openness of the canopy (Kevey 2008).

Several different associations of oak forests on loess occur in Hungary, Croatia and Serbia (Table 1). These syntaxa with restricted distributions are distinguished mostly on the basis of traditional phytosociological methods without comparing them with others at a larger geographical scale and thus it is difficult to recognize them in nature. To clarify the syntaxonomical relationships of the communities described, we carried out a classification of forests growing on loess in the three countries. Our objectives were to answer the following questions by using a large international geographically stratified data set: (i) What types of loess oak forest can be distinguished in the study area using multivariate statistical analyses? (ii) What are the differences between these types in terms of diagnostic, dominant and constant species? (iii) What are the differences between these types in terms of ecological features based on indicator values? (iv) Is there a gradient in forest vegetation in these three neighbouring countries? (v) Do the results obtained by multivariate methods correspond with those based on traditional classification?

Material and methods

Study area

Oak forests on loess currently occur in a limited area in Hungary (Zólyomi et al. 2013): in the Gödöllő and Velence hills (Fekete 1965), the North Hungarian Mts, the Mezőföld (Borhidi et al. 2012), the Tolna hills and on the Nyárád-Harkány Plain (Kevey 2008). In Croatia, this type of vegetation occurs in the north-eastern part of the country (Rauš et al. 1985, Franjić et al. 2005) on the western slopes of the Fruška Mts (Rauš 1971), the loess plateau near Đakovo (Rauš 1976) and Bansko hill (Purger & Csiky 2008, Csiky & Purger 2013). In northern Serbia (Vojvodina province) it occurs on lowland loess terraces in the foothills of the Fruška Mts and Titel hill (Jovanović 1997). We analysed a data set from these areas (Fig. 1).

The climate in the study area has a transitional character. In the eastern part of Hungary, it is moderately continental, whereas sub-Mediterranean influences are stronger towards the south and southwest. In addition, the strength of continental and sub-Mediterranean climatic influences changes from year to year (Zólyomi et al. 1997). According to the climatic maps of Hungary (Mersich et al. 2002), the range of the mean annual precipitation increases from 500–550 mm in the central part of the Great Plain to 550–600 mm towards the north-eastern part of Hungary and the Danube region, and even further to 600–700 mm in the South Transdanubian region. The range of the average annual temperature increases from 8–10 °C to 10–12 °C in the same direction. In north-eastern Croatia, the mean annual precipitation amounts to 651 mm, while the average annual temperature is 10.8 °C. This climate is warm-temperate without a drought period. Precipitation is rather evenly distributed throughout the year, with winter being the driest (Seletković & Katušin 1992). The distribution of precipitation in northern Serbia (Vojvodina province) follows a predominantly continental pattern with higher amounts of rainfall in June. In the north-western part of Vojvodina, the mean annual precipitation is 586 mm, but in the hilly regions, such as in the Fruška Mts, it is more than 650 mm. The months with the lowest precipitation are March and October. The mean annual temperature in Vojvodina increases from the north-west (10.7 °C) towards the south-east (11.7 °C).

Vegetation data

In this study, we used a data set of 437 phytosociological relevés of loess oak forests including 312 relevés from Hungary, 55 relevés from Croatia and 70 relevés from Serbia (Table 1). We included in our analysis every available relevé of forests growing on loess up to 300 m a.s.l. and not influenced by ground water or salt accumulation in the soil. This information is provided by the person who collected the data and the selection of the relevés was based on their reports. In cases when no information was available, we drew

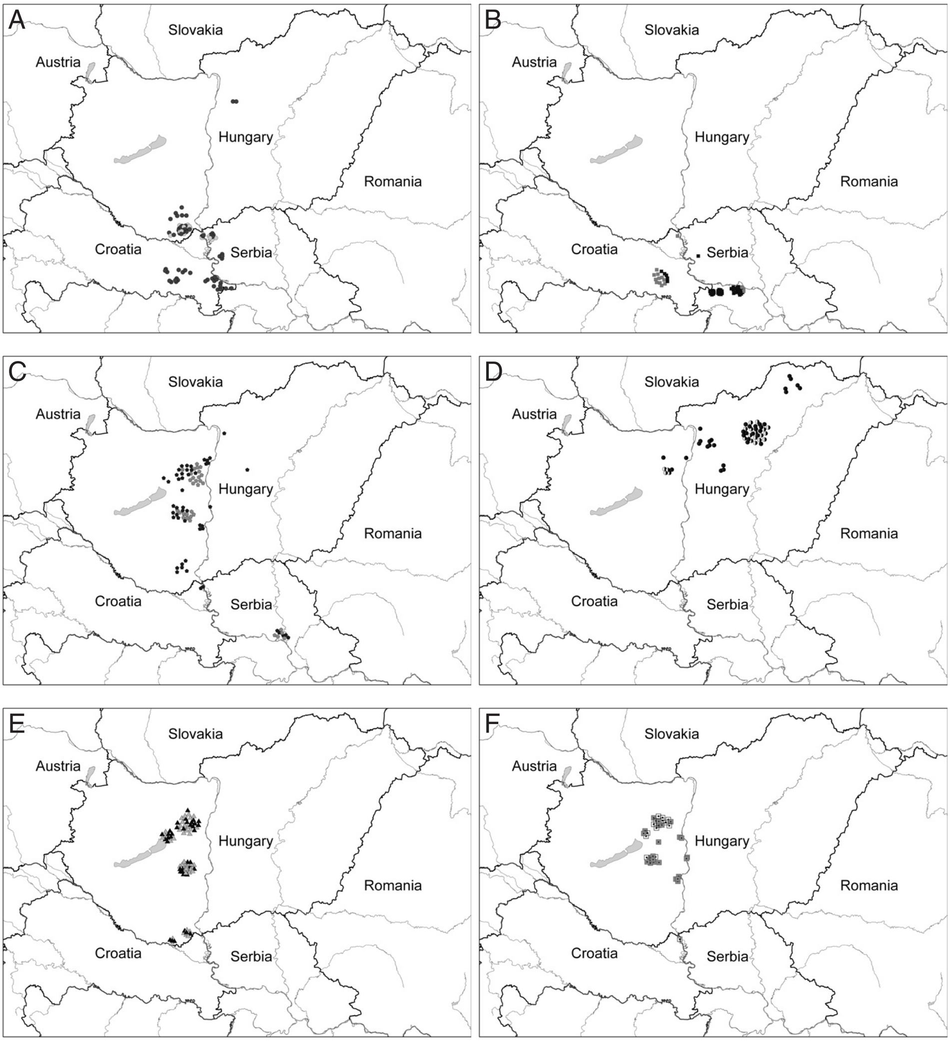

Fig. 1. – Distribution of the different types of oak forests on loess in Hungary, Croatia and Serbia. A – *Primula vulgaris* type, B – *Ruscus aculeatus* type, C – *Vinca herbacea* type, D – *Pulmonaria mollis* type, E – *Corydalis cava* type, F – *Stellaria media* type.

on our own field experience (if the exact location was known), or available geographical information (if the exact location was unknown). The data set was constructed from the relevés of recent field sampling, from the Hungarian phytosociological data base (CoenoDatRef; Lájer et al. 2008) and the literature. Additionally, some unpublished relevés from Hungary (B. Kevey et al., D. Purger), Croatia (J. Csiky et al.) and Serbia (D. Purger, Z. Tomić) were also used (Table 1). We excluded phytosociological tables, in which the rarest species were obviously omitted (e.g. Janković & Mišić 1980; see Lengyel et al. 2012). All relevés were recorded using the Zürich-Montpellier method (Braun-Blanquet 1964, Westhoff & van der Maarel 1978) between 1952 and 2009, and about 65%

Table 1. – Cross-tabulation of the traditional associations with the vegetation types indicated by this analysis. The number of relevés (before/after stratistication) of a traditional association assigned to a particular vegetation type is shown for individual clusters: A – *Primula vulgaris* type, B – *Ruscus aculeatus* type, C – *Vinca herbacea* type, D – *Pulmonaria mollis* type, E – *Corydalis cava* type, F – *Stellaria media* type.

Name of the association	Distribution	No. of relevés	Source	A	B	C	D	E	F
Aceri tatarici-Quercetum roboris Zólyomi 1957	Hungary	33/33	Zólyomi et al. 2013			6	26	1	
Aceri tatarici-Quercetum roboris Zólyomi 1957	Hungary	70/38	Kevey 2008 and unpubl.			35			3
Aceri campestri-Qurcetum roboris Fekete 1965	Hungary	2/2	Fekete 1965	2					
Pulmonario mollis-Quercetum roboris Kevey 2008	Hungary	132/55	Kevey 2008 and unpubl.	4			5	24	22
Corydalido cavae-Carpinetum betuli Kevey 2008	Hungary	60/37	Kevey 2008 and unpubl.	16				16	5
Aceri tatarici-Quercetum roboris Zólyomi 1957	Hungary (Baranya-hills)	11/11	Purger, unpubl.	6		5			
Aceri tatarici-Quercetum roboris Zólyomi 1957	Croatia (Bansko hill)	9/5	Csiky et al., unpubl.	3		2			
Aceri campestri-Quercetum cerris Franjić et al. 2005	Croatia	16/5	Franjić et al. 2005		5				
Carpino betuli-Quercetum roboris (Anić 1959) Rauš 1969 subass. *quercetosum cerris* Rauš 1971	Croatia (Fruška Mts)	14/14	Rauš 1971	14					
Carpino betuli-Quercetum roboris (Anić 1959) Rauš 1969 subass. *quercetosum cerris* Rauš 1971	Croatia (Đakovo)	16/16	Rauš 1976	16					
Carpino betuli-Quercetum roboris (Anić 1959) Rauš 1969 subass. *quercetosum cerris* Rauš 1971	Serbia (Bačka)	5/5	Purger 1993	4		1			
Tilio tomentosae-Quercetum roboris Slavnić 1952	Serbia (Bačka, Srem)	9/5	Slavnić 1952	5					
Fraxino orni-Quercetum virgilianae Gajić 1955	Serbia	6/5	Tomić, unpubl.		5				
Tilio tomentosae-Quercetum cerridis Glišić 1972	Serbia (Fruška Mts)	12/12	Tomić, unpubl.		12				
Quercetum cerridis-virgilianae B. Jov. et E. Vuk. 1977 subass. *typicum* Tomić 1991	Serbia (Fruška Mts)	17/17	Tomić, unpubl.		17				
Pruno mahalebi-Quercetum roboris Tomić 2009	Serbia (Fruška Mts)	11/5	Tomić, unpubl.		5				
Orno-Cotino-Quercetum pubescentis Butorac et al. 2008	Serbia (Titel hill)	10	Butorac et al. 2008			5			
Total no. of relevés		437/270		70	44	54	31	41	30

of them were recorded during the last two decades (1990–2009). The plot size varied between 100 and 1600 m^2. The data were stored in the TURBOVEG database (Hennekens & Schaminée 2001). In order to correct for oversampling, the data set was stratified (Knollová et al. 2005) both geographically (using strata of 0.28° × 0.32° approximate extent) and syntaxonomically (using author's association assignments for definition of strata). From each stratum, five relevés were chosen using the HCR resampling method (Lengyel et al. 2011), applying Sørensen index as the distance measure and 10,000 trials. This selection yielded a total of 270 phytosociological relevés, which were directly used in the analyses. Nomenclature is used according to Király (2009). The data on the occurrence of *Quercus* species were lumped as follows: *Quercus robur* agg. (incl. *Quercus robur* s. str., *Q. pedunculiflora*, *Q. crassiuscula*, *Q. pilosa*), *Quercus petraea* agg. (incl. *Q. petraea* s. str., *Q. dalechampii*, *Q. polycarpa*), *Q. pubescens* agg. (incl. *Q. pubescens* s. str., *Q. virgiliana*), *Q. frainetto*, *Q. cerris* (incl. *Q. austriaca*) and the introduced *Q. rubra*. The list of merged species names is available from the authors upon request.

Data analysis

In order to reduce statistical noise in our data, the variables for classification were the significant metric ordination axes instead of species (Gauch 1982, Botta-Dukát et al. 2005). Principal coordinates analysis (PCoA) was performed using Sørensen index as the distance measure. Only axes with eigenvalues higher than expected by chance determined from the broken stick distribution (Legendre & Legendre 1998) were considered significant. Then, relevés were classified by Ward's agglomerative method using Euclidean distances between coordinates of relevés. The optimal level of this hierarchical classification was identified by the Optimclass method (Tichý et al. 2010) using recommended $P < 10^{-6}$ and $P < 10^{-9}$ thresholds of Fisher's exact test. Species fidelities towards clusters were expressed by the phi coefficient (Chytrý et al. 2002) for equal group sizes (Tichý & Chytrý 2006). The threshold of fidelity was set to phi = 0.35, but only species showing a non-random distribution (Fisher's exact test: $P < 0.0001$) across clusters were considered as diagnostic species. Frequent and dominant species were also determined for each cluster. Species occurring at > 40% frequency in a cluster were included in the group of frequent species. Dominant species were defined as those that reach 5% total cover in 10% of the relevés in a cluster. This procedure resulted in clusters that we consider representatives of oak forest types on loess. However, the applied HCR resampling method may introduce systematic errors, if clusters are related to environmental variables or their distribution is plotted on a map (Lengyel et al. 2011). Thus, for mapping purposes, relevés excluded from hierarchical classification were assigned to the clusters using the composite index (van Tongeren et al. 2008) and these assigned relevés were also plotted on distribution maps.

Climatic data for relevé locations were downloaded from the WorldClim database (Hijmans et al. 2005; http://www.worldclim.org). The climate elements considered were monthly precipitation and mean, minimum and maximum temperature. Mean annual temperature, mean annual precipitation and mean indicator values (Borhidi 1995) calculated for the relevés were passively projected onto the ordination diagram.

Distribution of the mean indicator values of relevés within different clusters were compared in box plots. Clusters were also compared based on the distribution of the indicator values (moisture demand, nutrient demand and continental vs Mediterranean character) of faithful species.

To check the accuracy of traditional syntaxonomical classification, the results of the numerical analyses were compared using cross tabulation to the currently accepted classification of oak forests on loess (e.g. Jovanović 1997, Vukelić & Rauš 1998, Trinajstić 2008, Borhidi et al. 2012).

Results and discussion

Classification of relevés

The first six axes of the principal coordinates ordination had higher eigenvalues than expected by chance and were therefore used as input variables for the classification. These axes captured 47.4% of the total variation in species composition. The Optimclass method indicated the six-group level as the best interpretable classification using a threshold of $P < 10^{-6}$ (Fig. 2). The two-cluster level proved to be optimal at the stricter ($P < 10^{-9}$) setting. The differences in diagnostic, dominant and constant species between the types distingushed are presented in the synoptic table (Table 2).

Cluster A: *Primula vulgaris* type. The *Primula vulgaris* type is characterized by 15 diagnostic species (Table 2) that are mostly mesic and nutrient-demanding plants (Table 3). It comprises xero-mesic to mesic closed oak forests growing either on the plains or in shady, humid valleys and slopes of low hills, particularly on deep soils. The dominant trees are usually *Quercus robur* and *Q. cerris* with an admixture of mesic species of trees (e.g. *Carpinus betulus*, *Cerasus avium*). The herb layer is characterized also by mesic species, such as *Carex sylvatica*, *Viola reichenbachiana*, *Galium odoratum*, *Stellaria holostea*, *Allium ursinum* and several taxa with a sub-Mediterranean distribution e.g. *Asperula taurina* subsp. *leucanthera*, *Euphorbia amygdaloides* and *Scutellaria altissima*.

Cluster B: *Ruscus aculeatus* type. The *Ruscus aculeatus* type encompasses xeric to xero-mesic sub-Mediterranean oak forests, which differ from the previous type in the more frequent occurrence of thermophilous and heliophilous species (Table 3), e.g. *Quercus pubescens*, *Fraxinus ornus*, *Cornus mas*. It is distinguished by four diagnostic species: *Tilia tomentosa*, *Ruscus aculeatus*, *Rosa arvensis* and *Hedera helix.* In our analysis, all relevés recorded in stands in the Fruška Mts were classified in the same type regardless of their previous syntaxonomical assignment (Table 1).

Cluster C: *Vinca herbacea* type. The *Vinca herbacea* type represents the dry continental forests with open canopy. It is distinguished by 50 diagnostic species (Table 2), of which 90% are xerophilous (drought-tolerant) species adapted to dry or semi-dry habitats (e.g. *Aster linosyris*, *Campanula bononiensis*, *Peucedanum cervaria*, *P. alsaticum*), and only 4% of them prefer damp soils (Table 3). About 38% of them are continental and sub-continental floristic elements (e.g. *Adonis vernalis*, *Ajuga laxmannii*, *Euphorbia glareosa*, *Vinca herbacea*), while 14% belong to the group of sub-Mediterranean floristic elements (e.g. *Colutea arborescens*, *Teucrium chamaedrys*, *Vincetoxicum hirundinaria*). A large number of heliophilous species in the herb layer, which are typical of dry grasslands and forest margins (*Festuca* spp., *Inula conyza*, *Thalictrum minus*), are faithful to this type. This species-rich steppe woodland with a distinctly open tree canopy contains the oak species: *Quercus robur* agg., *Q. pubescens* agg. and *Q. cerris*. *Acer campestre*, *A. tataricum*, and *Ulmus minor* form a lower canopy layer. The usually dense shrub layer consists of *Ligustrum vulgare*, *Prunus spinosa*, *Crataegus monogyna*, *Viburnum lantana*,

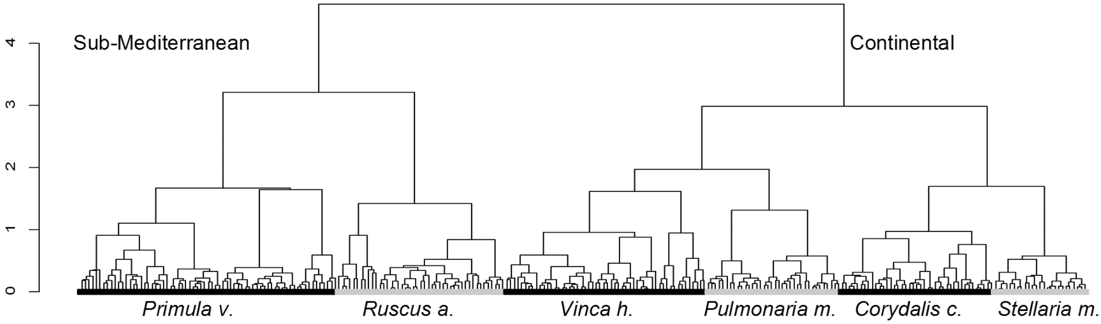

Fig. 2. – Dendrogram of relevés of oak forests analysed. A – *Primula vulgaris* type, B – *Ruscus aculeatus* type, C – *Vinca herbacea* type, D – *Pulmonaria mollis* type, E – *Corydalis cava* type, F – *Stellaria media* type.

Euonymus verrucosus and *E. europaeus*. The common herbaceous species include forest steppe plants, such as *Brachypodium pinnatum*, *Buglossoides purpurocaerulea*, *Carex michelii*, *Dictamnus albus*, *Inula germanica* and *Vincetoxicum hirundinaria.*

Cluster D: *Pulmonaria mollis* type. The semi-dry to mesic continental forests of the *Pulmonaria mollis* type is distinguished in the current analysis by 16 species (Table 2). These are species mainly typical of the south-east European dry oak forests (*Quercetea pubescentis-petraeae*) and many of them are continental floristic elements. This forest type is characterized by a closed canopy and a rich, but moderately dense shrub layer in which xerophilous (*Viburnum lantana*, *Euonymus verrucosus*, *Cornus mas*) and rather mesic (*Ligustrum vulgare*, *Crataegus laevigata*, *Euonymus europaeus*) species co-occur. The herbaceous layer is characterized by a predominance of xero-mesic forest species, such as *Iris variegata, Doronicum hungaricum*, *Pulmonaria mollis* and *Carex michelii*. Mesic species (e.g. *Elymus caninus*, *Bromus benekenii*, *Anemone ranunculoides*, *Viola cyanea*) are common, and some of them may even be abundant. Among the diagnostic species, the high percentage of species with continental ranges indicates the affinity of this type to the forests of the East European forest steppe.

Cluster E: *Corydalis cava* type. The *Corydalis cava* type represents mesic closed oak forests in nutrient-rich habitats. It is distinguished by 17 faithful species (Table 2), of which 13 are plants typical of soils rich in mineral nitrogen, or are indicators of fertile soils (Table 3), e.g. *Corydalis cava* and *C. pumila*. About half of the faithful species are adapted to slightly damp or moist, well aerated soils that do not dry out (e.g. *Mercurialis perennis*). One diagnostic plant (*Helleborus dumetorum*) is a Mediterranean floristic element. The herb layer of this forest is usually dominated by mesophytes (Table 2).

Cluster F: *Stellaria media* type. The *Stellaria media* type is characterised by 19 faithful species (Table 2). It comprises xeric to mesic closed oak forests growing in shady and humid sites in nutrient-rich habitats. The high abundance of nitrophytes (e.g. *Sambucus nigra*, *Viola odorata*, *Geranium robertianum*) indicates eutrophic soil and/or disturbance (Table 3). Nutrient accumulation is often caused by the invasion of *Robinia pseudoacacia*. The disturbance of oak forests in nutrient-rich habitats is indicated by the occurrence of a large number of ubiquist and forest weeds.

Table 2. – Percentage constancy values of species in each of the six vegetation types (columns) and their corresponding fidelity values. Species with phi > 0.35 are arranged in order of decreasing fidelity values and are marked with grey shading. Species with phi < 0.35, but with a frequency of at least 50% in some of the clusters are listed at the bottom of the table.

	Cluster A		Cluster B		Cluster C		Cluster D		Cluster E		Cluster F	
Primula vulgaris	51	0.66	0	---	0	---	0	---	2	---	0	---
Viola reichenbachiana	74	0.64	0	---	0	---	3	---	29	---	4	---
Carex sylvatica	62	0.64	11	---	0	---	0	---	7	---	0	---
Circaea lutetiana	51	0.62	0	---	0	---	0	---	7	---	0	---
Asarum europaeum	39	0.57	0	---	2	---	0	---	0	---	0	---
Anemone nemorosa	25	0.44	2	---	0	---	0	---	0	---	0	---
Euphorbia amygdaloides	26	0.43	4	---	0	---	0	---	0	---	0	---
Galium odoratum	52	0.42	18	---	0	---	0	---	32	---	0	---
Dentaria bulbifera	25	0.41	0	---	0	---	0	---	5	---	0	---
Stellaria holostea	59	0.40	38	---	2	---	0	---	34	---	0	---
Carpinus betulus	75	0.40	40	---	0	---	22	---	63	---	0	---
Asperula taurina subsp. *leucanthera*	25	0.39	7	---	0	---	0	---	0	---	0	---
Pulmonaria officinalis	30	0.38	0	---	2	---	6	---	0	---	8	---
Scutellaria altissima	19	0.37	0	---	0	---	0	---	2	---	0	---
Cerasus avium	54	0.35	36	---	7	---	6	---	17	---	8	---
Tilia tomentosa	45	---	93	0.66	2	---	0	---	12	---	12	---
Ruscus aculeatus	16	---	60	0.64	0	---	0	---	0	---	0	---
Rosa arvensis	9	---	44	0.56	0	---	0	---	0	---	0	---
Hedera helix	45	---	78	0.50	13	---	0	---	27	---	4	---
Teucrium chamaedrys	0	---	0	---	76	0.63	42	---	0	---	0	---
Festuca valesiaca agg.	0	---	0	---	72	0.60	36	---	2	---	4	---
Achillea millefolium agg.	0	---	0	---	54	0.59	8	---	2	---	4	---
Fragaria viridis	0	---	0	---	52	0.53	11	---	0	---	12	---
Galium mollugo agg.	3	---	0	---	70	0.53	22	---	10	---	24	---
Adonis vernalis	3	---	0	---	59	0.53	33	---	0	---	0	---
Medicago falcata	0	---	0	---	37	0.52	6	---	0	---	0	---
Peucedanum alsaticum	0	---	0	---	37	0.52	6	---	0	---	0	---
Centaurea scabiosa s.l.	0	---	0	---	30	0.51	0	---	0	---	0	---
Falcaria vulgaris	0	---	0	---	39	0.51	6	---	0	---	4	---
Elymus hispidus	0	---	0	---	35	0.50	6	---	0	---	0	---
Bromus inermis	0	---	0	---	37	0.50	8	---	0	---	0	---
Salvia pratensis	0	---	0	---	33	0.49	6	---	0	---	0	---
Melica transsilvanica	0	---	0	---	35	0.46	3	---	0	---	8	---
Galium verum	6	---	0	---	39	0.46	11	---	0	---	0	---
Securigera varia	0	---	0	---	52	0.45	28	---	0	---	12	---
Euphorbia cyparissias	10	---	4	---	70	0.44	50	---	5	---	20	---
Vinca herbacea	1	---	0	---	56	0.44	33	---	0	---	16	---
Potentilla recta	0	---	0	---	22	0.44	0	---	0	---	0	---
Inula ensifolia	0	---	0	---	22	0.44	0	---	0	---	0	---
Arabis hirsuta	0	---	0	---	31	0.43	3	---	0	---	8	---
Thlaspi perfoliatum	1	---	0	---	39	0.43	8	---	0	---	12	---
Anthericum ramosum	0	---	0	---	31	0.42	6	---	2	---	4	---
Salvia nemorosa	0	---	0	---	24	0.41	0	---	0	---	4	---
Colutea arborescens	3	---	0	---	31	0.41	6	---	5	---	0	---
Ajuga laxmannii	1	---	0	---	30	0.41	6	---	0	---	4	---
Agrimonia eupatoria	7	---	0	---	44	0.40	19	---	2	---	8	---
Eryngium campestre	0	---	0	---	19	0.40	0	---	0	---	0	---
Erysimum diffusum	0	---	0	---	19	0.40	0	---	0	---	0	---
Euphorbia glareosa	0	---	0	---	19	0.40	0	---	0	---	0	---

	Cluster A		Cluster B		Cluster C		Cluster D		Cluster E		Cluster F	
Chamaecytisus austriacus	0	---	0	---	24	0.39	6	---	0	---	0	---
Stachys recta	0	---	0	---	41	0.39	28	---	0	---	4	---
Ranunculus polyanthemos	0	---	0	---	33	0.39	11	---	0	---	8	---
Hypericum perforatum	7	---	0	---	56	0.39	33	---	2	---	24	---
Galium glaucum	0	---	0	---	30	0.39	6	---	0	---	8	---
Poa pratensis agg.	1	---	0	---	52	0.38	47	---	2	---	8	---
Filipendula vulgaris	0	---	0	---	46	0.38	47	0.39	0	---	0	---
Campanula bononiensis	0	---	0	---	56	0.38	14	---	17	---	40	---
Arrhenatherum elatius	0	---	0	---	17	0.38	0	---	0	---	0	---
Calamagrostis epigeios	1	---	0	---	19	0.38	0	---	0	---	0	---
Peucedanum cervaria	0	---	0	---	39	0.37	28	---	5	---	0	---
Inula conyza	1	---	0	---	20	0.37	3	---	0	---	0	---
Plantago media agg.	0	---	0	---	19	0.36	3	---	0	---	0	---
Chrysopogon gryllus	0	---	0	---	15	0.36	0	---	0	---	0	---
Hypericum elegans	0	---	0	---	15	0.36	0	---	0	---	0	---
Viola ambigua	0	---	0	---	15	0.36	0	---	0	---	0	---
Aster linosyris	0	---	0	---	15	0.36	0	---	0	---	0	---
Allium sphaerocephalon	0	---	0	---	15	0.36	0	---	0	---	0	---
Brachypodium pinnatum	0	---	0	---	57	0.35	42	---	15	---	28	---
Inula germanica	0	---	0	---	20	0.35	6	---	0	---	0	---
Melica altissima	0	---	0	---	4	---	36	0.51	2	---	0	---
Lathyrus niger	4	---	2	---	9	---	58	0.50	24	---	0	---
Muscari botryoides	3	---	0	---	0	---	33	0.49	2	---	0	---
Quercus petreaea agg.	14	---	9	---	2	---	64	0.47	34	---	4	---
Vicia pisiformis	0	---	0	---	0	---	25	0.47	0	---	0	---
Inula salicina	0	---	0	---	11	---	36	0.45	2	---	0	---
Pulmonaria mollis	9	---	0	---	24	---	75	0.45	41	---	28	---
Acer tataricum	55	---	40	---	30	---	92	0.43	29	---	16	---
Iris variegata	1	---	0	---	17	---	42	0.41	7	---	4	---
Vicia cassubica	0	---	0	---	0	---	19	0.41	0	---	0	---
Iris graminea	1	---	0	---	0	---	28	0.40	7	---	0	---
Hieracium racemosum	1	---	0	---	2	---	25	0.40	2	---	0	---
Tanacetum corymbosum	0	---	0	---	39	---	53	0.40	10	---	8	---
Betonica officinalis	0	---	0	---	28	---	39	0.38	0	---	4	---
Crataegus laevigata	9	---	7	---	0	---	31	0.36	5	---	0	---
Corydalis pumila	1	---	0	---	22	---	0	---	83	0.62	36	---
Mercurialis ovata	12	---	0	---	0	---	0	---	41	0.51	0	---
Corydalis cava	43	---	4	---	6	---	42	---	90	0.51	28	---
Bromus ramosus	19	---	0	---	6	---	39	---	71	0.51	4	---
Viola mirabilis	4	---	0	---	2	---	0	---	39	0.47	8	---
Chaerophyllum temulum	16	---	0	---	33	---	0	---	80	0.45	68	---
Viola odorata	16	---	0	---	7	---	8	---	51	0.45	8	---
Helleborus dumetorum	3	---	0	---	19	---	3	---	56	0.44	28	---
Gagea lutea	4	---	0	---	0	---	0	---	29	0.42	4	---
Galeopsis pubescens	3	---	0	---	0	---	3	---	24	0.40	0	---
Ranunculus ficaria	57	---	7	---	30	---	58	---	95	0.39	60	---
Poa nemoralis	3	---	0	---	22	---	69	---	80	0.39	52	---
Campanula trachelium	12	---	2	---	4	---	3	---	37	0.39	4	---
Glechoma hirsuta	14	---	22	---	9	---	14	---	51	0.38	0	---
Anemone ranunculoides	20	---	2	---	9	---	0	---	51	0.38	28	---
Rumex sanguineus	38	---	0	---	0	---	6	---	44	0.37	0	---
Fraxinus excelsior	14	---	0	---	11	---	17	---	56	0.37	32	---
Celtis occidentalis	3	---	0	---	48	---	6	---	12	---	88	0.63
Ballota nigra	4	---	0	---	50	---	31	---	20	---	92	0.56

	Cluster A		Cluster B		Cluster C		Cluster D		Cluster E		Cluster F	
Cannabis sativa	0	---	0	---	20	---	0	---	2	---	48	0.50
Chelidonium majus	1	---	0	---	13	---	0	---	34	---	60	0.49
Ornithogalum umbellatum	0	---	0	---	33	---	0	---	27	---	64	0.48
Anthriscus cerefolium	4	---	0	---	44	---	8	---	27	---	72	0.47
Stellaria media agg.	1	---	2	---	31	---	11	---	37	---	68	0.44
Physalis alkekengi	1	---	0	---	17	---	0	---	27	---	52	0.43
Parietaria officinalis	3	---	0	---	4	---	0	---	12	---	36	0.42
Lapsana communis	22	---	0	---	22	---	36	---	68	---	84	0.42
Urtica dioica	33	---	0	---	31	---	6	---	51	---	76	0.41
Fallopia dumetorum	16	---	0	---	54	---	64	---	76	---	96	0.40
Sambucus nigra	46	---	9	---	35	---	28	---	54	---	88	0.40
Bromus sterilis	3	---	0	---	33	---	8	---	15	---	52	0.38
Viola hirta	29	---	4	---	63	---	28	---	32	---	80	0.37
Alliaria petiolata	22	---	2	---	57	---	69	---	41	---	88	0.37
Solanum dulcamara	0	---	0	---	6	---	3	---	0	---	24	0.37
Galium aparine	28	---	13	---	54	---	50	---	49	---	88	0.37
Viola cyanea	14	---	0	---	67	---	69	---	73	---	92	0.35
Ligustrum vulgare	80	---	78	---	89	---	100	---	83	---	80	---
Crataegus monogyna	91	---	71	---	89	---	92	---	100	---	100	---
Brachypodium sylvaticum	62	---	40	---	57	---	56	---	100	---	88	---
Euonymus europaeus	72	---	38	---	78	---	89	---	73	---	100	---
Ulmus minor	74	---	33	---	78	---	42	---	63	---	100	---
Geum urbanum	78	---	27	---	63	---	78	---	98	---	100	---
Acer campestre	94	---	84	---	52	---	94	---	98	---	76	---
Polygonatum latifolium	61	---	0	---	70	---	89	---	83	---	96	---
Quercus cerris	80	---	78	---	43	---	78	---	90	---	24	---
Veronica hederifolia	33	---	11	---	52	---	56	---	85	---	88	---
Prunus spinosa	43	---	4	---	80	---	69	---	51	---	88	---
Dactylis glomerata agg.	32	---	38	---	74	---	75	---	85	---	60	---
Rosa canina agg.	29	---	4	---	85	---	61	---	54	---	64	---
Geranium robertianum	55	---	11	---	28	---	44	---	83	---	80	---
Quercus pubescens agg.	7	---	49	---	81	---	78	---	27	---	60	---
Viburnum lantana	28	---	40	---	59	---	31	---	54	---	80	---
Euonymus verrucosus	16	---	20	---	63	---	72	---	49	---	80	---
Quercus robur	78	---	11	---	26	---	69	---	76	---	52	---
Fraxinus ornus	17	---	73	---	50	---	31	---	51	---	40	---
Cornus sanguinea	70	---	31	---	46	---	58	---	41	---	32	---
Rhamnus catharticus	17	---	11	---	69	---	47	---	15	---	68	---
Cornus mas	28	---	60	---	37	---	11	---	68	---	28	---
Buglossoides purpurocaerulea	32	---	27	---	57	---	67	---	59	---	44	---
Clinopodium vulgare	7	---	0	---	67	---	58	---	27	---	28	---
Clematis vitalba	52	---	11	---	48	---	11	---	61	---	52	---
Arum maculatum agg.	49	---	4	---	6	---	11	---	59	---	32	---
Dictamnus albus	3	---	0	---	54	---	58	---	12	---	28	---
Robinia pseudoacacia	16	---	2	---	37	---	14	---	15	---	56	---
Lactuca quercina	0	---	0	---	20	---	36	---	46	---	56	---
Carex michelii	3	---	0	---	56	---	42	---	15	---	40	---
Pyrus pyraster	19	---	2	---	31	---	53	---	22	---	24	---
Sedum maximum	9	---	0	---	44	---	53	---	12	---	28	---
Elymus caninus	13	---	0	---	6	---	53	---	41	---	36	---
Campanula persicifolia	3	---	0	---	43	---	25	---	29	---	52	---
Fragaria vesca	46	---	4	---	7	---	50	---	22	---	8	---
Veronica chamaedrys agg.	38	---	0	---	39	---	50	---	24	---	8	---

Table 3. – Phytogeographical and ecological characteristics of the different clusters of the oak forests analysed in terms of distribution types and ecological indicator values of their diagnostic species based on Borhidi values (1995): percentage of species with a continental (Con) or sub-Mediterranean (Med) distribution, share of plants of dry (W 1–4) and wet (W 6–7) habitats, and nutrient poor- (N 1–4) and nutrient rich (N 6–9) soils. A – *Primula vulgaris* type, B – *Ruscus aculeatus* type, C – *Vinca herbacea* type, D – *Pulmonaria mollis* type, E – *Corydalis cava* type, F – *Stellaria media* type.

Type	No of diagnostic species	Con (%)	Med (%)	W 1–4 (%)	W 6–7 (%)	N 1–4 (%)	N 6–9 (%)
A	15	7	33	0	67	0	60
B	4	0	25	0	0	0	25
C	50	38	14	90	4	88	6
D	16	44	0	44	6	87	0
E	17	0	6	6	59	12	76
F	19	5	21	21	37	11	74

Comparison of types based on indicator values

The box plots reveal there are big differences in almost all of the indicator values for the *Primula vulgaris* type (cluster A) and *Vinca herbacea* type (cluster C). In the other types, there is a gradual shift in Borhidi's temperature values (TB), soil reaction values (RB) and climatic continentality values (CB) (Fig. 3A, C, F). There is also a gradual shift in Borhidi's moisture values (WB) from the wettest *Primula vulgaris* type to the driest *Vinca herbacea* type. The clusters form two levels with regard to Borhidi's nutrient availability values (NB) (Fig. 3B). The average nutrient availability values for *Primula vulgaris*, *Corydalis cava* (cluster E) and *Stellaria media* types (cluster F) are higher than those for the *Ruscus aculeatus*, *Vinca herbacea* and *Pulmonaria mollis* types. Based on Borhidi's light availability values (LB) (Fig. 3D, E), the *Vinca herbacea* type is characterized by the highest and the *Primula vulgaris*, *Ruscus aculeatus* and *Corydalis cava* types by the lowest values. The *Pulmonaria mollis* and *Stellaria media* types are characterized by an intermediate level of light availability. This pattern corresponds to the different degree of openness of the forest canopy in the various forest types. Indicator values WB, NB, LB, RB and CB were projected onto the ordination diagram with significant ($P < 0.005$) fit and are correlated with both ordination axes, whereas TB is correlated with only the second axis. The relative position of the groups on the ordination diagram (Fig. 4) supports the importance of moisture, nutrient and light availability, continentality and soil reaction gradients in determining species composition.

Clusters were also related to macroclimatic variables from the Worldclim data set. On the ordination diagram, the fitted mean annual temperature runs in a direction opposite to that of the mean indicator values for temperature (TB). We presume that this is an artifact, which reveals the limitations of using TB values. Higher mean temperatures during the vegetation period are associated with continental-type loess forest (*Vinca herbacea* type), whereas warm winter weather is linked to the sub-Mediterranean type (*Primula* and *Ruscus* types; Fig 4).

Spatial pattern in the oak forest vegetation in the study area

The geographical distribution of the relevés indicates the presence of a gradient stretching from the North Hungarian Mts to north-eastern Croatia and northern Serbia. Relevés of

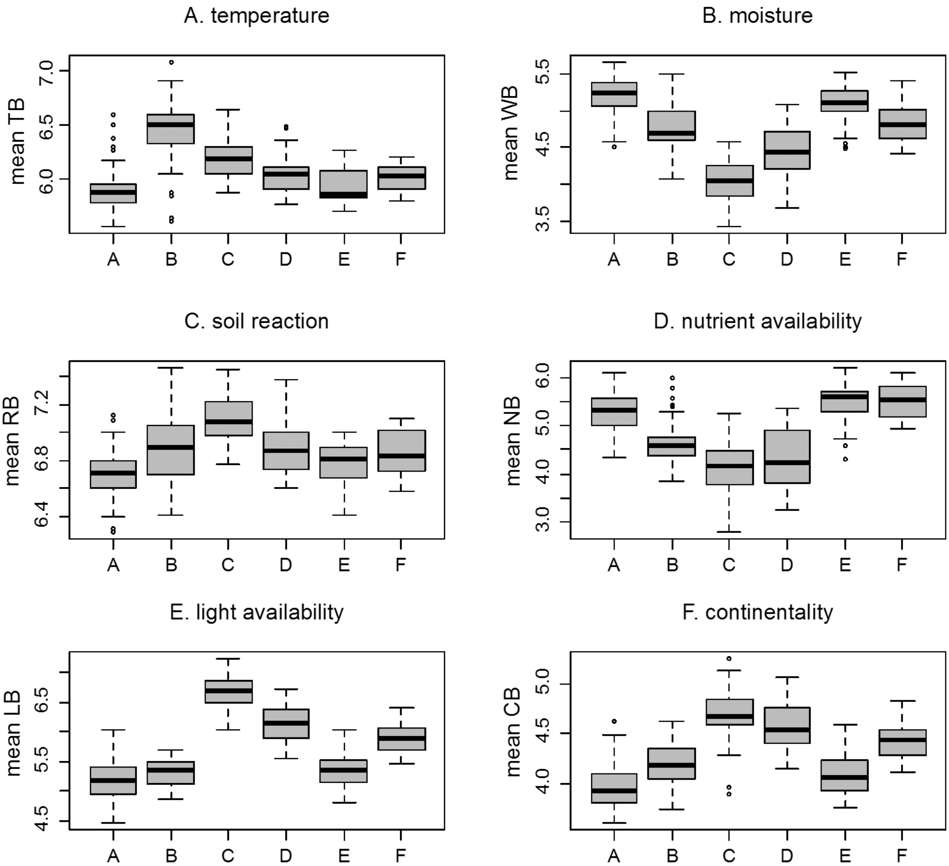

Fig. 3. – Box plots of indicator values of oak forest clusters for mean (A) temperature, (B) moisture, (C) soil reaction, (D) nutrient status, (E) light availability, and (F) continentality. TB – Borhidi's temperature values, WB – Borhidi's moisture values, RB – Borhidi's soil reaction values, NB – Borhidi's nutrient demand values, LB – Borhidi's light demand values, CB – Borhidi's climatic continentality values.

the continental steppe woodland are mainly distributed over a large area in Hungary from the foothills of the North Hungarian Mts and Baranya hills in southern Hungary (Fig 1C, D), whereas those of the xero-mesic sub-Mediterranean types are restricted to the southwestern and southern part of the Carpathian Basin (Fig. 1A, B). Samples representing the dry to mesic closed oak forests in nutrient-rich habitats occur in between the other two (Fig. 1E, F). The forests at the ends of this climatic gradient markedly differ in habitat conditions and floristic composition. The mean annual precipitation within the range of the continental forest steppe woodlands (*Vinca* and *Pulmonaria* types) and the sub-Mediterranean forest type (*Primula* and *Ruscus* types) is 500–600 mm and 600–700 mm, respectively. The average annual temperature in the distribution area of the continental type (8–10 °C) also differs from that of the sub-Mediterranean type (10–12 °C). The climatic differences are associated with qualitative and quantitative changes in the frequency of floristic elements. For example, continental species (e.g. *Ajuga laxmannii*, *Vinca herbacea*, *Adonis vernalis*) are rarer or play a minor role in the southern part, while species with

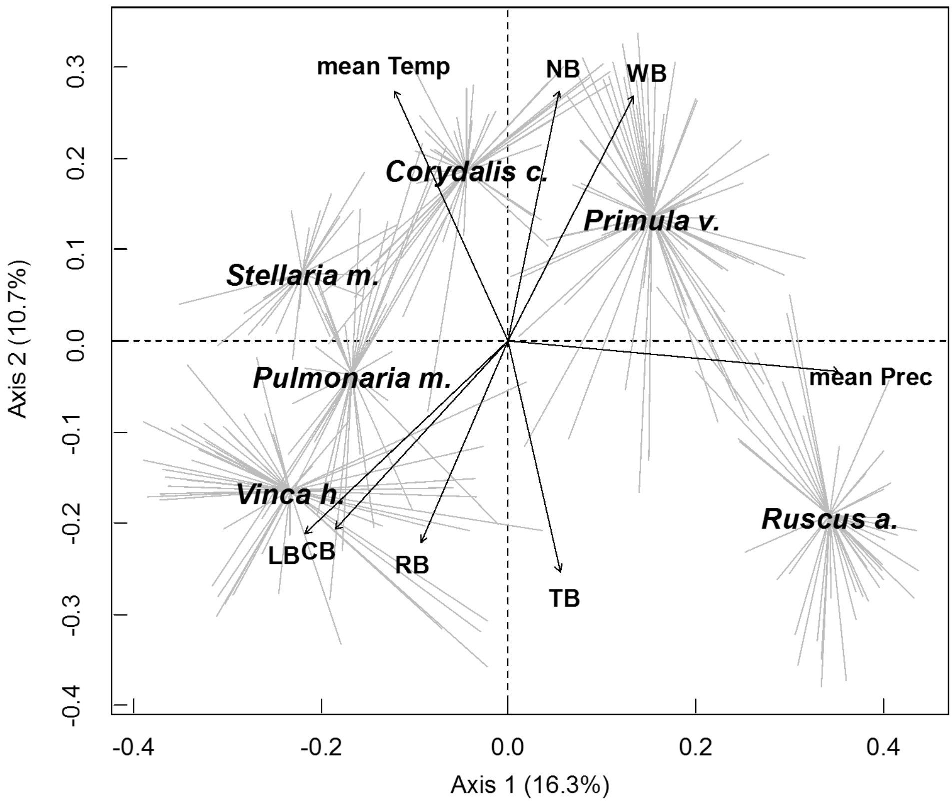

Fig. 4. – Result of the principal coordinates analysis (PCoA) plotted in the form of a spider diagram with 'legs' joining relevés that belong to the same cluster (the 'body'). A – principal coordinates ordination diagram with spider plot of the clusters; B – ordination diagram and spider plot with passively projected mean indicator values; C – ordination diagram and spider plot with passively projected mean values for precipitation (Prec) and temperature (Temp).

sub-Mediterranean distributions (e.g. *Quercus cerris*, *Q. frainetto*, *Q. pubescens*, *Hedera helix*, *Ruscus aculeatus*, *Tilia tomentosa*) occur more frequently and/or abundantly there.

Relation of the distinguished types to syntaxa described in the phytosociological literature

Our results suggest that the oak forests on loess studied in Hungary, Croatia and Serbia may represent at least five syntaxonomical units, while the sixth unit could not be interpreted coenologically. These units are phytosociologically heterogeneous, composed of relevés representing different associations. The analysis did not support uniqueness and distinctness of narrow-range associations and subassociations. Many of the local associations overlapped with other earlier described ones. This suggests that they should be united to form broader associations. The discrepancy between the number of units identified and the number of previously described associations in the study area indicates the need for a thorough nomenclatural revision.

The floristic composition and ecological features of the *Primula* type distinguished by our analysis are in accordance with the description of several communities (Table 1). Nevertheless, we propose that this complex be treated as an association with the name *Tilio tomentosae-Quercetum roboris* Slavnić 1952, which is a valid name with priority. This association, which is formally described by Slavnić (1952, 1954) as occurring on loess terraces in the southern part of the Pannonian plain in Vojvodina (Serbia), is broadly accepted by Serbian phytocoenologists (e.g. Parabućski & Janković 1978, Jovanović 1997, Tomić 2004).

The *Ruscus* type comprises oak forests in the southern part of the study area with a contrasting and often ambiguous syntaxonomical status (Table 1). Franjić et al. (2005) suggest that some xero-mesic forests may have developed from mesic forests of the *Carpinion betuli* alliance via anthropogenic degradation. Although almost all of the oak communities growing in the Fruška Mts were placed in the order *Quercetalia pubescentis* Br.-Bl. (1931) 1932 (see Janković & Mišić 1980, Parabućski et al. 1986), some were referred to the alliance *Quercion farnetto* Horvat 1954 and the rest to *Quercion pubescentis-petraeae* Br-Bl. 1932 (Rauš 1971, Tomić 1991). Syntaxonomical position of this type is not clear. Therefore, for a unifying nomenclature, further comparison of forests on other substrates at larger scales is needed.

The *Vinca herbacea* type comprises a small group of the original relevés of the *Aceri tatarici-Quercetum.* Zólyomi (1957, 1967) distinguishes several subtypes within this association, such as the subass. *festucetosum* (open), *lithospermetosum* (closed) and *galietosum schultesii* (mesic) (Zólyomi et al. 2013). The *Vinca* type in our analysis corresponds to the description of the open variant of steppe woodland on loess (*Aceri tatarici-Quercetum pubescentis-roboris festucetosum sulcatae*) in Hungary (Zólyomi 1958, 1967, Fekete 1997). Based on the work of Rauš (1971), Trinajstić (1998, 2008) suggests that stands of the association *Aceri tatarici-Quercetum pubescentis-roboris* Zólyomi 1957 do occur in the sub-Pannonian part of eastern Croatia. This opinion has not been confirmed by other phytosociologists (e.g. Vukelić & Rauš 1998). The oak forests with Tatarian maple referred to by Trinajstić (1998, 2008) under the name *Genisto elatae-Quercetum roboris aceretosum tatarici* Rauš 1971 grow in Croatia on alluvial soils on riverbanks (and therefore were not included in this study) and do not conform with stands of the dry continental steppe-forests described by Zólyomi (1957). Our results indicate that there are isolated stands of this dry open continental steppe woodland on Bansko hill in Croatia (Fig. 1C). The polydominant forest stands on the loess plateau on Titel hill (Serbia) formally described as an association under the provisional name *Orno-Cotino-Quercetum pubescentis* Butorac, Igić, Anačkov, Zlatković, Vuković et Boža 2008 (Butorac et al. 2008) also belong here. Among the communities analysed that correspond to the *Vinca herbacea* type, there is no community with a valid name. It seems that the *Vinca herbacea* type distinguished by our analysis could not be identified with *Quercetum pubescenti-roboris* (Zólyomi 1957) Michalko et Džatko 1965 in the strict sense as reported for Slovakia (Roleček 2005). The floristic composition of the dry type of loess oak forests in Slovakia is more similar to that of the *Pulmonaria mollis* type distinguished in this analysis (e.g. *Inula salicina, Pulmonaria mollis, Vicia pisiformis*, etc.). The *Vinca herbacea* type comprises relevés that are mostly recorded in more natural stands with a more pronounced subcontinental and forest-steppe character in floristic composition (e.g. *Ajuga laxmannii*, *Inula germanica*, *Vinca herbacea*). Without further comparative analyses, the syntaxonomical status of this type remains uncertain.

The *Pulmonaria mollis* type comprises relevés recorded in Hungary by Zólyomi and Kevey (Table 1). According to Zólyomi (1967), the typical subassociation of *Aceri tatarici-Quercetum pubescentis-roboris* Zólyomi 1957 (subass. *lithospermetosum*) is characterized by a moderately closed forest canopy. In our analyses, most of Zólyomi's relevés assigned originally to the association *Aceri tatarici-Quercetum pubescenti-roboris* Zólyomi 1957 were classified in the *Pulmonaria* type, including relevés from all three subassociations. In contrast, less than ten percent of the relevés that are classified as closed oak forest on loess and formally described as the association *Pulmonario mollis-Quercetum roboris* Kevey 2008 were included in this cluster. Our results suggest that the *Pulmonaria mollis* type best fits Zólyomi's *Aceri tatarici-Quercetum pubescentis-roboris* Zólyomi 1957, the valid name of which is now *Quercetum pubescenti-roboris* (Zólyomi 1957) Michalko et Džatko 1965 in the broad sense (Chytrý & Horák 1997).

The *Corydalis cava* type includes relevés that are classified into three different associations, and therefore its syntaxonomical status is uncertain (Table 1). One of them is the mesic subassociation of the continental oak forest on loess (subass. *galietosum schultesii*) established by Zólyomi (1967). However, only one of Zólyomi's relevés of this subssociation was classified in this type. In our analysis it was not possible to separate the two rather mesic closed oak forests described by Kevey (2008). This is in line with this author's observation that the phytosociological character of *Pulmonario-Quercetum* is transitional between dry open oak forests on loess and lowland oak hornbeam forests on loess (*Corydalido cavae-Carpinetum betuli* Kevey 2008), which is indicated by the intermediate proportion of species characteristic of dry grassland, xeric oak forests and mesic forests (Kevey 2008, Borhidi et al. 2012, Kevey et al. 2012). We suggest that the latter name for mesic loess oak forests with a closed-canopy in nutrient rich habitats (in the sense of Borhidi et al. 2012) be used despite the obvious absence of a one-to-one correspondence in the two classifications.

The species composition of the *Stellaria media* type seems to be primarily determined by disturbance and therefore stands of considerably different oak forests may be assigned to this type irrespective of their abiotic conditions. This may be particularly apparent in stands that are represented by small and isolated patches in a cultural landscape. There is a continuous transition to other oak forests on loess. The *Corydalis cava* and *Stellaria media* types can be identified as dynamic stages of the main types of loess oak forests and their stands are not necessarily derived from the same phytosociological unit.

There are oak forests of sub-Mediterranean and/or continental character close to the study area in neighbouring countries, e.g. in the Pannonian part of the Czech Republic and Slovakia (Michalko & Džatko 1965, Chytrý 1997, Chytrý & Horák 1997, Roleček 2005, 2007), in Romania (Jakucs et al. 1959, Pascovschi & Doniţa 1967, Fekete 2000), southern Moldova (Borza 1937) and Ukraine (Vakarenko 2009). Their syntaxonomical relationships and nomenclature should be clarified by using data from their entire range including the whole Carpathian Basin. We suggest that the rules and recommendations of the nomenclatural code, particularly those on the legitimacy and priority of names, be closely followed in this process.

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Souhrn

Doubravy na sprašových půdách patří mezi floristicky nejbohatší typy listnatých lesů a jejich přirozené porosty jsou silně ohroženým biotopem Karpatské pánve. Tyto lesy jsou řazeny do několika fytocenologických jednotek s rozšířením v Maďarsku, Chorvatsku a Srbsku, které byly až dosud zpravidla rozlišovány pomocí tradičních fytocenologických metod bez širšího geografického srovnání. Proto se tyto lokálně se vyskytující jednotky v přírodě obtížně rozlišují a přiřazení správných jmen je často nejasné. Cílem práce je vypracovat mezinárodní typologii doubrav vyskytujících se na sprašových půdách. K tomu byla využita numerická analýza 437 fytocenologických snímků z porostů 12 asociací ze tří zemí; po stratifikaci bylo 270 snímků podrobeno mnohorozměrné analýze. Bylo rozlišeno šest typů, s *Primula vulgaris* (xericko-mezické až mezické submediteránní zapojené doubravy), *Ruscus aculeatus* (xerický až xericko-mezický submediteránní typ), *Vinca herbacea* (xerické kontinentální rozvolněné lesy), *Pulmonaria mollis* (xerické až mezické kontinentální zapojené lesy), *Corydalis cava* (mezické zapojené doubravy na živinami bohatých stanovištích) a *Stellaria media* (xerické až mezické doubravy na živinami bohatých stanovištích). Vymezené vegetační typy odpovídají tradičně rozlišovaným syntaxonům, naše analýza nicméně nepotvrdila oprávněnost některých dosud rozlišovaných lokálně rozšířených asociací. Geografické rozšíření dvou hlavních lesních typů se mění na gradientu ze severovýchodu k jihozápadu. Kontinentální porosty lesostepního charakteru na suchých stanovištích jsou nejhojnější v severovýchodním Maďarsku, zatímco xericko-mezické submediterrání lesy jsou omezeny na jihozápadní a jižní část studovaného území. Toto rozšíření odpovídá klimatickým rozdílům mezi Maďarským středohořím na jedné straně a severovýchodním Chorvatskem a severním Srbskem na straně druhé.

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