



Thermophilous oak forests of the steppe and forest-steppe zones of Ukraine and Western Russia

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Abstract

We present a formal classification of thermophilous oak forests of the steppe and forest-steppe zones of Ukraine and Russia. Using 45 sources (synoptic tables; some from Central and Western Europe were also included for comparative purposes), we classified the data using cluster analyses, followed by post-classification tools aimed at formal identification of the optimal number of clusters and fidelity-based table sorting. Db-RDA ordination and a CART were used to identify the lead putative climatic drivers of the vegetation patterns. Of the six clusters identified by our classification procedures, two clusters are interpreted here as new alliances (*Betonico-Quercion*, *Scutellario-Quercion*). Some new associations classified into these alliances were also either validated or described as new. We further show that the *Quercion petraeae* is of heterogeneous nature and the position of the units previously classified as the *Potentillo albae-Quercion* should be re-evaluated. NMDS was used to analyse the patterns of the phytocoenologic elements (diagnostic species of relevant syntaxonomic classes) in the six clusters. This analysis revealed that the classification of the Ukrainian and Russian thermophilous oak forests into the *Quercetea pubescentis* class is untenable and remains open to further scrutiny.

Keywords *Aceri tatarici-Quercion* · *Betonico officinalis-Quercion roboris* · Eastern Europe · *Quercetea pubescentis* · *Quercion petraeae* · *Scutellario altissimae-Quercion roboris* · Thermophilous oak forests

Abbreviations

CART	Classification and Regression Tree
db-RDA	Distance-based Redundancy Analysis
NMDS	Non-metric Multidimensional Scaling

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Introduction

Thermophilous (and sub-thermophilous) deciduous oak forests are an important vegetation type dominating southern regions of Europe. They are very abundant especially on the Balkan Peninsula (Čarni et al. 2009; Tzonev et al. 2009; Stupar et al. 2015), in Italy (Blasi et al. 2004; Pietro et al. 2010), France (Treiber and Remmert 1998; Bœuf 2010), and northern Spain (Rivas-Martínez et al. 2001). In Central and Western Europe they occur scattered and occupy topographically (and meso-climatically) favourable habitats in Poland (Kwiatkowska and Solińska-Górnicka 1993; Jakubowska-Gabara 2000; Matuszkiewicz 2007; Kasprowicz 2010), Germany (Oberdorfer 1992), Czechia and Slovakia (Chytrý 1997; Chytrý and Horák 1997; Roleček 2007, 2013), Austria (Mucina et al. 1993), Hungary (Zólyomi 1957; Jakucs 1961; Borhidi 2003; Kevey 2008; Borhidi et al. 2012; Zólyomi et al. 2013; Lendvai et al. 2014; Horváth et al. 2017), and Romania (Sanda et al. 2008; Indreica 2011). These forests also occur in Eastern Europe (Ukraine, Russia, and Belarus), however here they remain poorly studied. The vegetation map of Europe (Bohn et al.

2004) failed to feature these forests in Eastern Europe, and interestingly, also in Germany.

In Eastern Europe, the syntaxonomy of these forest communities remains controversial. Ukrainian and Russian phytosociologists classify the thermophilous oak forests in two alliances, namely the *Quercion petraeae* Issler 1931 (syn. *Potentillo albae-Quercion* Jakucs in Zólyomi 1967) and the *Aceri tatarici-Quercion* Zólyomi 1957. The *Quercion petraeae* comprises Central European thermophilous acidophilous oak forests (Mucina et al. 2016), and apparently the distribution area of this alliance does not reach Ukraine and Western Russia. Earlier essential phytogeographical distinction between Central and Eastern European thermophilous forest types has been noted by Semenishchenkov (Semenishchenkov 2012; see also Bulokhov and Semenishchenkov (2013)). These authors pointed upon that the Eastern European oak forests show a general decrease of species richness and of representation of Central European species, absence of submediterranean floristic elements and increase of boreal elements instead. The only oak species in Eastern Europe is *Quercus robur*. The other alliance, the *Aceri tatarici-Quercion* (Zólyomi 1957; see also Mucina et al. 2016) has been coined for both the Pontic and Pannonian regions, however, the identity of these forests in Ukraine and Southern Russia remains contentious.

The aim of the study is to contribute to solving the problem of identity of the thermophilous oak forests of the steppe and forest-steppe zones of Ukraine and Russia. Here we present results of a formalised classification of the relevant syntaxa, using selected syntaxa of Central and Western Europe for

comparative purposes. We shall also demonstrate that the forests from Ukraine and Western Russia cannot be included into any of the known alliances. Considering the wide geographical coverage of the comparative material, we use climatic data to assist our analyses seeking putative drivers of the differences between the Eastern European and other oak forests.

Material and methods

Study region

The vegetation plot data used in this study cover published material featuring thermophilous oak forests of wide geographical coverage (Fig. 1). In Ukraine and Russia these forests occur in the forest-steppe zone as well as within the steppe zone. For comparative purposes, we have also included data from Poland, Germany, Czechia, Slovakia, Hungary and Romania (Table S1).

According to Köppen-Geiger climate classification, the Ukrainian and Russian parts of the study region correspond to the *Dfb* (warm-summer humid continental) climate type (Kottek et al. 2006). The western regions experience milder climate of the *Cfb* (temperate oceanic) and the southernmost locations have the *Dfa* (hot-summer humid continental) type. The Ukrainian and Russian oak forests experience much lower winter temperatures and larger temperature span (difference between the coldest and hottest months).

Most of the studied area is found between elevations of 100 to 700 m. More elevated are the western locations on the

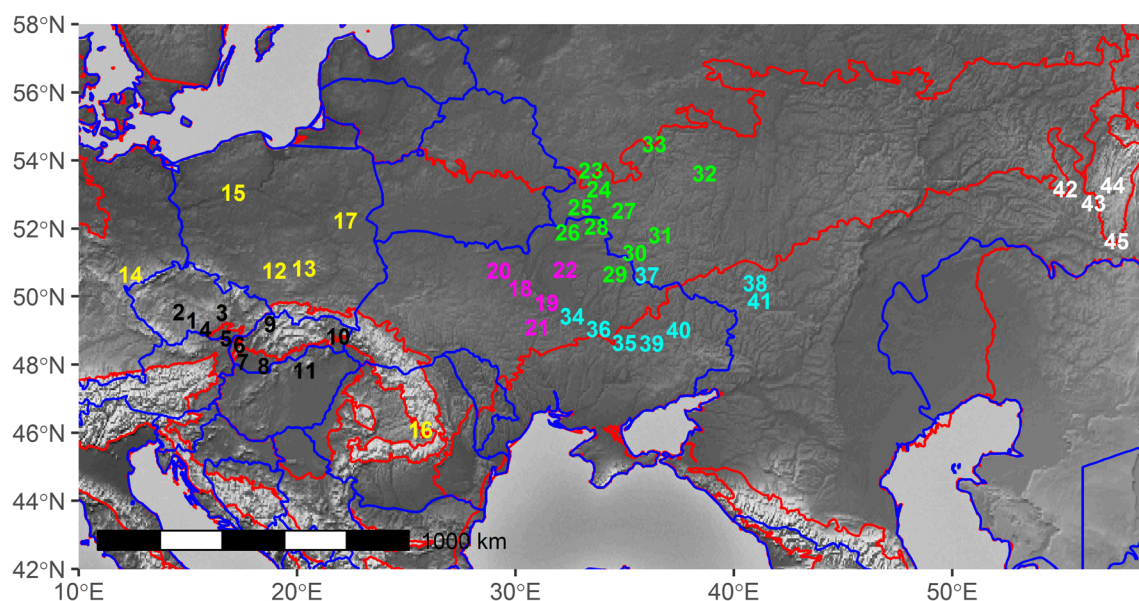


Fig. 1 Distribution of the studied thermophilous oak forests. The red lines are the boundaries of the biogeographical regions (European Environmental Agency 2016). The blue lines are the state boundaries drawn by Natural Earth Database (<http://www.naturalearthdata.com>).

The numbers represent the local/regional synoptic datasets (see Table S1), colour-coded to represent clusters revealed by our analyses: Cluster A – black, B – yellow, C – pink, D – green, E – cyan, F – white

Carpathians and the easternmost in the Southern Urals. In the Eastern European section of the study area, the elevations span merely 100 to 300 m above sea level. Within the study area, there are several geographic barriers, mainly stretching in meridional manner. The most apparent barriers, coinciding with borders of some floristic provinces, are the river valleys of the Dniester, Dnieper, and Volga as well as the mountain ranges of the Carpathians and of the Southern Urals.

Data collection and collation

We have collected 45 local/regional data sets (tables) of the targeted thermophilous oak and some related xeromesophytic pine-oak forest communities (Table S1). These are so called *phytocoenon [synoptic] tables* according to Westhoff & van der Maarel (1978, p. 322) as they are local/regional oak forest assemblages; 24 of those come from Ukraine and Western Russia. We refrained from including the submediterranean Crimean thermophilous forests because of their disparate floristic composition and genesis (Didukh 1996).

The approximate geographical positions of the source data sets (Fig. 1) were established either by using GPS data on position of relevés (if given in the respective sources) or indirectly by consulting the notes on distribution of the syntaxa as given in the original sources.

The reasons for using synoptic tables, instead of relevé data follow the arguments as presented by Matevski et al. (2018). The local/regional synoptic tables summarise local/regional vegetation patterns at the level of associations (or subassociations) and reflect both unique ecological patterns (and drivers) as well as past florogenetic processes. Further, in this study we focus on high-rank syntaxa and have no intention to revise syntaxonomy at the association level. Using synoptic tables further allows re-using published material presenting only simplified frequency-class values. In such cases, when the synoptic tables were presented in classical (Braun-Blanquet 1964) constancy-class categories, we have recoded the categories as follows: V – 90 %, IV – 70 %, III – 50 %, II – 30 %, I – 10 %.

The syntaxonomic nomenclature follows the EuroVegChecklist (Mucina et al. 2016). All references to articles of the Code of Phytosociological Nomenclature correspond to the third edition of the ICPN (Weber et al. 2000). We unify the taxonomic concepts and species nomenclature using the Euro+Med (<http://www.emplantbase.org>). because of disparate origins (and associated local taxonomic and nomenclature preferences) of the data sources used. The taxonomic crosswalk between the original and current concepts is featured in Table S2. Here we have also highlighted those taxonomic concepts which that deviate from the Euro+Med; those exceptions were largely motivated by current molecular-phylogenetic knowledge that has not find its way to Euro+Med yet. Non-vascular plants and fungi were excluded from our analyses because of poor balance of their coverage across the sources used.

Data analyses

The synoptic table sources (with constancy values coded in percentages) were summarised in a master synoptic data matrix (further SDM). The SDM was submitted to a two-step transformation: a log-transformation on species constancy data, followed by Hellinger normalisation. The log-transformation was aimed at reducing the right-skewed distribution of species constancy data. The Hellinger normalisation overcomes the so-called ‘double-zero problem’ that emerges when grossly unequally long vectors (e.g. two synoptic columns having disparate total number of species) are being compared using resemblances such as Euclidean Distance (Legendre and Gallagher 2001; Legendre and De Cáceres 2013).

The transformed and normalised SDM was subjected to hierarchical cluster analysis using the Ward’s method (also known as Incremental Sum of Squares Method), which produces compact, even-sized clusters and is not sensitive to chaining effect (Granato and Ares 2013). This clustering method was found to produce cluster-combination outcomes very similar to widely used average-link clustering or similar similarity-optimizing methods such as beta-flexible (e.g. Mucina 1982; Lötter et al. 2013; Tsakalos et al. 2018). The clustering was performed using the *hclust* function of the package *stats* in R (<https://www.r-project.org>). The dendrogram of the Ward’s clustering was then iteratively tested to establish the optimal final number of clusters by using the Silhouette (Halkidi et al. 2001; Rendón et al. 2011) and the OptimClass (in OptimClass-1 mode, see Tichý et al. 2010) approaches. These are based on different initial assumptions – on maximizing the geometric criterion of cluster distinguishability by the distance matrix (Aho et al. 2008) and on maximizing the number of faithful species.

Construction of the synoptic table

The columns (original synoptic tables) in the SDM were re-ordered to follow the order of the classified objects in the dendrogram of the clustering analysis.

The sorting of species in the SDM was carried out on basis of fidelity of species to the identified clusters. The faithful species were identified not only for individual clusters, but also for cluster combinations using the *multipatt* analysis (De Cáceres et al. 2010, 2012). We used its implementation in the *indicspec* package for R software (De Cáceres and Legendre 2009). The *multipatt* analysis was performed using the IndVal index (Dufrêne and Legendre 1997) in its group-equalised modification (De Cáceres et al. 2010).

Post-classification analyses

To understand the main gradients in floristic composition, the non-metric multi-dimensional scaling (NMDS);

McCune et al. 2002; Legendre and Legendre 2012) was performed. NMDS was carried out using the Kruskal's (1964) original monotone regression to minimize the stress and two dimensions were selected into which the dissimilarity matrix was scaled down in multidimensional space. To explain the axes of ordination in syntaxonomic terms we superimposed (as covariables) information on the proportion of species diagnostic in selected different classes of vegetation, namely *Brachypodio pinnati-Betuletea pendulae*, *Carpino-Fagetea sylvaticae*, *Festuco-Brometea*, *Molinio-Arrhenatheretea*, *Quercetea pubescentis*, *Quercetea roboris-petraeae*, *Crataego-Prunetea*, *Trifolio-Geranietea sanguinei*. The species typical of anthropogenic classes (*Artemisietea vulgaris*, *Epilobietea angustifolii*, *Robinietea*) were summarised as category 'ANT'. The relationship between axes of the NMDS and these variables was evaluated by the multiple regression approach and passively projected onto the ordination space. Ordination and fitting calculations were performed using the functions *metaMDS* and *envfit* from the *vegan* package (Oksanen et al. 2019).

In species-to-class classification, we followed the EuroVegChecklist (EVC; Mucina et al. 2016), corrected in cases when a species showed deviating phytosociological link and supplemented by species not featured by the EVC. This information is given in the Column B in Table S3. Since many of the species are affiliated with several classes of vegetation, the frequencies obtained for each class were normalised by dividing by the total sum of the frequencies per syntaxon (synoptic column). These data, structured per class, are collected in Table S4.

Bioclimatic analyses: Searching for drivers of the vegetation patterns

We used the database of bioclimatic variables of Hijmans et al. (2005) to characterise the climatic differences between the

studied vegetation types and to identify putative climatic drivers of the vegetation patterns. Considering that the locations of some syntaxa were only approximate, buffered means with a radius of 20 km were calculated for each bioclimatic variable (Table S4) using the QGIS software, ver. 2.18 (<http://qgis.org>).

Distance-based Redundancy Analysis (db-RDA; Legendre and Legendre 2012) has been selected to carry out a constrained ordination on climatic data. Our choice was motivated by the ability of this technique to handle dissimilarity matrices derived from pre-transformed data. The bioclimatic analyses involved two steps: (1) first we tested the models using a complete list of BioClim variables (bio1–bio19; Table S4), followed by (2) second step involving a reduced list of variables after a variable-selection analysis was performed. The variable reduction was performed, aiming at overcoming the multicollinearity issue and simplification of the model selecting the most important of bioclimatic variables while maintaining a high degree of explained variation. The calculations were carried out using the functions *dbRDA* (for constrained ordination) and *ordiR2step* (for variable selection) from the R package *vegan* (Oksanen et al. 2019).

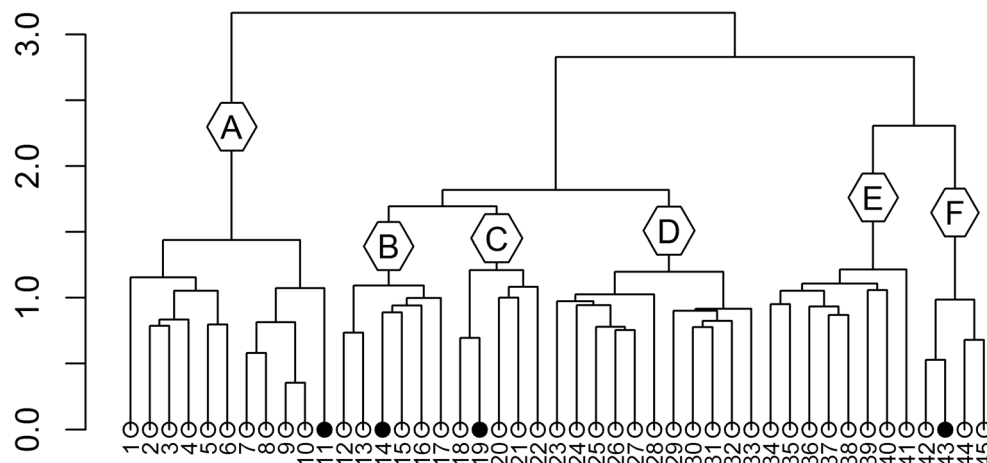
The CART (Classification and Regression Tree) method (Breiman et al. 1984) was applied to build a binary decision tree revealing the hierarchy of the most polarising climatic variables in the universe defined by syntaxa revealed by the clustering.

Results

Classification patterns

The classification of the studied oak forests revealed six clusters (Fig. 2) as identified by both the Silhouette statistics based on the Hellinger distance matrix (Fig. S1) and the OptimClass analysis with the threshold of Fisher's criterion set to 0.001 (Fig. S2).

Fig. 2 Dendrogram of the cluster analysis of the studied oak forests showing six clusters (A through F; for the identification of the clusters see caption of Fig. 1). Holotypes of the *Aceri tatarici-Quercion* (11), *Convallario majalis-Quercion roboris* (19), *Potentillo albae-Quercion* (14), and *Lathyro pisiformis-Quercion roboris* (43) are marked as full circles



The classification pattern revealed by the clustering was translated into a synoptic table using the *IndVal* analysis and *multipatt* species sorting (Table 1; for the full version see Table S3).

Geographic distribution and bioclimatic analysis

The six clusters identified by clustering form compact geographic groupings (see Fig. 1). The only exception is exemplified by syntaxon no. 16.

The db-RDA model (Fig. 3) with a full set of bioclimatic variables was highly significant ($p < 0.001$) and all 19 BioClim variables explain 56.3 % of total variation. This ratio of the contribution suggests that the vegetation patterns in the studied forests are largely structured by climatic variables.

The ordination model with a reduced set of variables is also significant ($p < 0.001$). Eight out of 19 bioclimatic variables selected relate to temperature (bio1, bio3, bio4, bio5, bio6, bio11) and two (bio8, bio19) feature aspects of both temperature and precipitation. The proportion of variation explained by the eight bioclimatic variables was 38.1 %. The constrained Axis 1

explains about 30 % of the fitted variance reflected by constraints, and 11 % of the total variance. The eigenvalue (2.95) of the first constrained axis is 2.15 times more than the eigenvalue (1.37) of first unconstrained axis, implying that unconstrained axes reflect residual variation after constrained ones.

CART analysis (Fig. 4) also features six terminal nodes, putatively corresponding to six clusters of the classification analysis. The purity of the terminal leaves of the CART model is high as the values range from 0.71 to 1.00 (maximal purity). This suggests that there are clear climatic differences between the studied clusters. Some of the bioclimatic variables (bio1, bio4, bio5) have been shown as important also by the *ordiR2step* variable selection algorithm. The bio4 variable is recognised as the single most significant one as it separates two cluster groups, namely (A, B) from (C through F). The bio1 variable suggest separation of the clusters A and B at 8.2 °C of average annual temperature, while the cluster F is shown to diverge at threshold of 5.1 °C. Climatic conditions of cluster D are different by showing the maximum temperature of warmest month below 24.4 °C.

Table 1 Shortened differentiating table of the studied oak forests. Column “Diag” corresponds to the groups of species as revealed by the *multipatt* sorting

Clusters	A	B	C	D	E	F	Diag
Number of syntaxa	11	6	5	11	8	4	
<i>Ligustrum vulgare</i>	V	II			I		A
<i>Festuca stricta</i> subsp. <i>sulcata</i>	V	I			I		A
<i>Lembotropis nigricans</i>	IV						A
<i>Melica uniflora</i>	IV						A
<i>Verbascum chaixii</i> s. l.	IV						A
<i>Fragaria moschata</i>	V			I			A
<i>Teucrium chamaedrys</i>	V		II				A
<i>Luzula campestris</i>	IV			I			A
<i>Cornus mas</i>	IV						A
<i>Dictamnus albus</i>	IV						A
<i>Robinia pseudoacacia</i>	IV						A
<i>Carex caryophylla</i>	IV	I		I			A
<i>Sorbus torminalis</i>	III	I					A
<i>Symphytum tuberosum</i>	III	I					A
<i>Viburnum lantana</i>	III				I		A
<i>Lactuca quercina</i>	IV			I	I		A
<i>Arrhenatherum elatius</i>	III			I			A
<i>Quercus cerris</i>	III	I					A
<i>Rosa gallica</i>	III	I					A
<i>Anemone nemorosa</i>		V					B
<i>Juniperus communis</i>	I	V		I			B
<i>Viola reichenbachiana</i>	II	V					B
<i>Luzula pilosa</i>		V	II	II			B
<i>Fagus sylvatica</i>	I	IV					B
<i>Sanicula europaea</i>	I	V		I			B
<i>Euphorbia angulata</i>	I	IV					B

Table 1 (continued)

Clusters	A	B	C	D	E	F	Diag
<i>Festuca amethystina</i>	I	IV					B
<i>Hypericum montanum</i>	II	V		I			B
<i>Campanula glomerata</i>	I	V		II			B
<i>Melampyrum polonicum</i>			IV				C
<i>Allium oleraceum</i>	I			V	I		D
<i>Ranunculus acris</i>				IV			D
<i>Epilobium angustifolium</i>				III			D
<i>Paris quadrifolia</i>				III			D
<i>Leucanthemum vulgare</i>	I			III			D
<i>Thalictrum aquilegifolium</i>		I		III			D
<i>Dryopteris carthusiana</i>		I	II	IV			D
<i>Trifolium montanum</i>	I			III			D
<i>Campanula patula</i>		I	II	III			D
<i>Prunella vulgaris</i>		I		III	I		D
<i>Centaurea jacea</i>	I	I		III	I		D
<i>Scutellaria altissima</i>					IV		E
<i>Lamium maculatum</i>				II	IV		E
<i>Crataegus rhipidophylla</i> agg.		I		III	V		E
<i>Acer tataricum</i>	II		V	II	V		E
<i>Aconogonon alpinum</i>						V	F
<i>Galatella sedifolia</i> subsp. <i>biflora</i>						V	F
<i>Geranium pseudosibiricum</i>						V	F
<i>Klasea radiata</i> subsp. <i>gmelinii</i>						V	F
<i>Bupleurum longifolium</i>		I				V	F
<i>Seseli libanotis</i>					I	V	F
<i>Lathyrus rotundifolius</i>						IV	F
<i>Valeriana wolgensis</i>						IV	F
<i>Vincetoxicum albobianum</i>						IV	F
<i>Rosa majalis</i>				II		V	F
<i>Caragana frutex</i>					II	V	F
<i>Carex pediformis</i> s. l.					II	V	F
<i>Lathyrus pisiformis</i>		I		II	I	V	F
<i>Aconitum anthora</i> s. l.	I			I	II	V	F
<i>Viola collina</i>	I	II		I		V	F
<i>Bistorta officinalis</i>				I		IV	F
<i>Quercus petraea</i> agg.	V	V					AB
<i>Crataegus monogyna</i> agg.	V	V					AB
<i>Peucedanum cervaria</i>	V	V		II			AB
<i>Hieracium murorum</i> s. l.	V	V		I			AB
<i>Hieracium sabaudum</i>	V	III					AB
<i>Rubus fruticosus</i> agg.	V	III					AB
<i>Ajuga reptans</i>	V	V		II			AB
<i>Melittis melissophyllum</i>	IV	IV					AB
<i>Vicia cassubica</i>	III	V		II			AB
<i>Festuca heterophylla</i>	IV	II					AB
<i>Hieracium lachenalii</i>	IV	III					AB
<i>Prunus avium</i>	IV	II			I		AB
<i>Lactuca muralis</i>	IV	IV	II	I	I		AB
<i>Galium intermedium</i>	III	V		I			AB
<i>Festuca ovina</i>	IV	III		II			AB
<i>Carex michelii</i>	V	I		II	IV		AE
<i>Euonymus europaeus</i>	IV	I	II	II	IV		AE
<i>Vicia pisiformis</i>	IV			I	II		AE
<i>Hypericum hirsutum</i>	IV			I	II		AE
<i>Bromopsis benekenii</i>	IV			I	II		AE
<i>Ulmus minor</i> s. l.	III			I	II		AE
<i>Pulmonaria angustifolia</i>	II	IV		V			BD
<i>Deschampsia cespitosa</i>		III		IV			BD
<i>Taraxacum officinale</i> agg.		III		V	II		BD
<i>Ranunculus auricomus</i> agg.	II	IV		IV			BD

Table 1 (continued)

Clusters	A	B	C	D	E	F	Diag
<i>Schedonorus giganteus</i>		II		IV	I		BD
<i>Lysimachia vulgaris</i>	I	II		IV			BD
<i>Laserpitium latifolium</i>		II		III			BD
<i>Knautia arvensis</i>	I	II	II	IV			BD
<i>Potentilla erecta</i>	I	III		III			BD
<i>Vaccinium myrtillus</i>	I	V	II	II			BD
<i>Galeopsis bifida</i>				IV		V	DF
<i>Geranium sylvaticum</i>				IV		V	DF
<i>Heracleum sphondylium</i> s. l.	II	I		V	I	V	DF
<i>Prunus padus</i>	I	I		IV	I	V	DF
<i>Viola canina</i> s. l.	II	I		IV	I	V	DF
<i>Elytrigia repens</i>	I		II	IV	I	III	DF
<i>Vicia sylvatica</i>				III	I	IV	DF
<i>Thalictrum minus</i>	I			III	I	IV	DF
<i>Euphorbia esula</i> s. l.	I		II	III		II	DF
<i>Pimpinella saxifraga</i>	V	IV		V			ABD
<i>Serratula tinctoria</i>	V	V		IV			ABD
<i>Potentilla alba</i>	IV	V	II	V			ABD
<i>Agrostis capillaris</i>	IV	IV	II	V			ABD
<i>Carex montana</i>	IV	V	II	IV	I		ABD
<i>Securigera varia</i>	V	III	II	IV	I		ABD
<i>Galium mollugo</i>	III	II		V	I		ABD
<i>Melampyrum pratense</i>	IV	IV		II			ABD
<i>Festuca rubra</i>	III	IV	II	IV			ABD
<i>Carex pallescens</i>	II	III		IV			ABD
<i>Anthoxanthum odoratum</i>	IV	II		III			ABD
<i>Molinia caerulea</i>	II	II		IV			ABD
<i>Viola riviniana</i>	III	III		II			ABD
<i>Pulmonaria obscura</i>		I	II	V	V	III	DEF
<i>Aegopodium podagraria</i>		II		V	IV	V	DEF
<i>Campanula trachelium</i>	II	I		IV	IV	IV	DEF
<i>Polygonatum multiflorum</i>	I	I	II	IV	IV	II	DEF
<i>Phlomis tuberosa</i>	II			II	III	V	DEF
<i>Ulmus glabra</i>	I			I	III	V	DEF
<i>Bromopsis inermis</i>	I			IV	II	II	DEF
<i>Campanula persicifolia</i>	V	V	V	V	II	II	ABCD
<i>Trifolium alpestre</i>	V	V	IV	V			ABCD
<i>Ranunculus polyanthemus</i>	V	V	IV	V			ABCD
<i>Geranium sanguineum</i>	IV	V	V	V			ABCD
<i>Anthericum ramosum</i>	IV	V	IV	IV			ABCD
<i>Genista tinctoria</i>	V	IV	III	IV			ABCD
<i>Platanthera bifolia</i> agg.	V	III	III	V			ABCD
<i>Pinus sylvestris</i>	III	V	V	IV		II	ABCD
<i>Peucedanum oreoselinum</i>	III	IV	V	III	I		ABCD
<i>Campanula rotundifolia</i>	II	II	III	III			ABCD
<i>Primula veris</i> s. l.	V	V	II	V	II	V	ABDF
<i>Brachypodium pinnatum</i>	V	IV		IV	I	V	ABDF
<i>Calamagrostis epigejos</i>	IV	III		V		IV	ABDF
<i>Digitalis grandiflora</i>	IV	V	II	III		V	ABDF
<i>Calamagrostis arundinacea</i>	III	V	II	V		V	ABDF
<i>Vicia sepium</i>	II	IV		V	I	IV	ABDF
<i>Filipendula vulgaris</i>	V	II	II	IV	II	V	ABDF
<i>Tanacetum corymbosum</i>	V	I	II	IV	II	V	ABDF
<i>Silene viscaria</i>	IV	I		III	I	II	ABDF
<i>Moehringia trinervia</i>	II	III	II	V	I	II	ABDF
<i>Rubus saxatilis</i>		V	V	V		V	BCDF
<i>Pteridium aquilinum</i>		V	V	V	I	III	BCDF
<i>Sorbus aucuparia</i>	I	V	V	V	II	V	BCDF
<i>Galium boreale</i>	I	V	II	V	I	V	BCDF
<i>Solidago virgaurea</i>	II	V	IV	V	I	V	BCDF

Table 1 (continued)

Clusters	A	B	C	D	E	F	Diag
<i>Viburnum opulus</i>	I	V	IV	V	II	III	BCDF
<i>Betula pendula</i>	II	IV	IV	V	II	III	BCDF
<i>Rubus idaeus</i>	I	IV	III	IV		III	BCDF
<i>Populus tremula</i>	I	III	V	V	II		BCDF
<i>Lilium martagon</i>	II	V	II	IV		III	BCDF
<i>Convallaria majalis</i>	V	V	V	V	V		ABCDE
<i>Pyrus communis</i> s. l.	V	V	V	V	V		ABCDE
<i>Corylus avellana</i>	IV	V	V	V	II		ABCDE
<i>Galium aparine</i>	V	II	III	III	IV		ABCDE
<i>Cornus sanguinea</i>	IV	IV	II	II	IV		ABCDE
<i>Torilis japonica</i>	V	II	II	II	II		ABCDE
<i>Malus sylvestris</i> s. l.	I	III	III	IV	III		ABCDE
<i>Geum urbanum</i>	V	V	V	V	V	V	ABCDEF
<i>Quercus robur</i>	V	V	V	V	V	V	ABCDEF
<i>Veronica chamaedrys</i>	V	V	V	V	IV	V	ABCDEF
<i>Dactylis glomerata</i> s. l.	V	IV	IV	V	V	V	ABCDEF
<i>Poa nemoralis</i> s. l.	V	IV	IV	V	V	V	ABCDEF
<i>Betonica officinalis</i>	V	V	V	V	III	V	ABCDEF
<i>Melica nutans</i>	V	V	V	V	III	V	ABCDEF
<i>Polygonatum odoratum</i>	V	V	V	IV	IV	V	ABCDEF
<i>Hypericum perforatum</i>	V	V	IV	V	IV	III	ABCDEF
<i>Carex muricata</i> agg.	V	II	III	V	V	V	ABCDEF
<i>Clinopodium vulgare</i>	V	V	IV	V	III	III	ABCDEF
<i>Euonymus verrucosus</i>	V	II	V	V	V	III	ABCDEF
<i>Fragaria vesca</i>	V	V	IV	V	II	V	ABCDEF
<i>Hylotelephium telephium</i> agg.	V	V	III	IV	II	V	ABCDEF
<i>Scrophularia nodosa</i>	V	III	II	V	V	IV	ABCDEF
<i>Stellaria holostea</i>	III	II	V	V	V	V	ABCDEF
<i>Tilia cordata</i>	III	III	V	IV	IV	V	ABCDEF
<i>Viola hirta</i>	V	I	II	V	IV	V	ABCDEF
<i>Achillea millefolium</i> agg.	V	III	III	V	II	IV	ABCDEF
<i>Origanum vulgare</i>	IV	II	IV	IV	III	V	ABCDEF
<i>Silene nutans</i>	V	II	III	IV	II	V	ABCDEF
<i>Rhamnus cathartica</i>	V	V	II	II	III	V	ABCDEF
<i>Galium verum</i>	IV	II	V	IV	II	IV	ABCDEF
<i>Urtica dioica</i>	III	III	V	IV	II	V	ABCDEF
<i>Geranium robertianum</i>	V	I	II	III	II	III	ABCDEF
<i>Carex digitata</i>	II	IV	IV	III	II	III	ABCDEF

Discussion

Geographic and bioclimatic differentiation of the clusters

The formation of geographically distinct groupings (Fig. 1) corresponding to the clusters obtained by the classification based on floristic criteria (Fig. 2) points upon the dominant regional nature of the delimited syntaxa. Clusters A and B (Fig. 1) represent the Central European syntaxa of thermophilous oak forests (Chytrý and Horák 1997; Jakubowska-

Gabara 2000; Roleček 2005; Kasprowicz 2010; Brzeg and Wika 2017). Cluster C consists of syntaxa described in Central Ukraine in the forest-steppe part of the Dnieper valley (Bajrak 1996; Shevchyk et al. 1996; Gayova and Korotchenko 2013). Cluster F is distinctly geographically isolated, and it comprises the steppic oak forests of the Southern Urals (Solomeshch et al. 1989, 1994; Martynenko et al. 2005, 2008; Mirkin et al. 2008, 2010) – the easternmost occurrence of this type of oak forests on European scale. The syntaxa from Ukraine and Western Russia constituted the Clusters D and E; they are characteristic of the Sarmatian (D) and

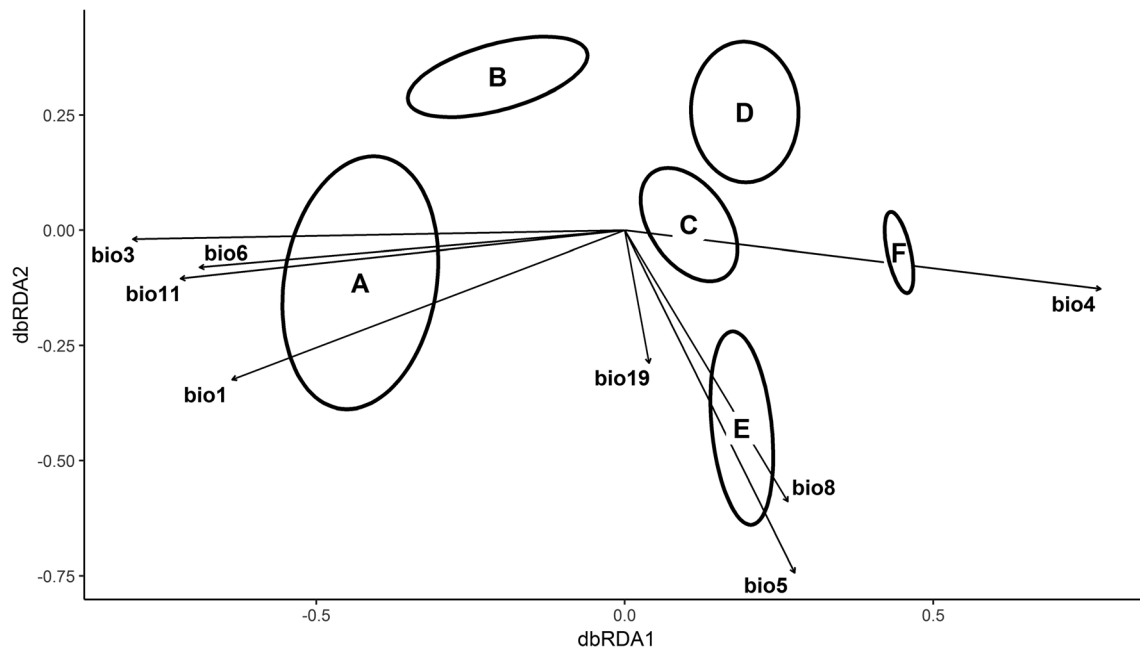


Fig. 3 Distance-based Redundancy Analysis of the studied oak forests using a reduced number of bioclimatic variables. bio1 – annual mean temperature, bio3 – isothermality, bio4 – temperature seasonality (standard deviation *100), bio5 – max temperature of warmest month, bio6 –

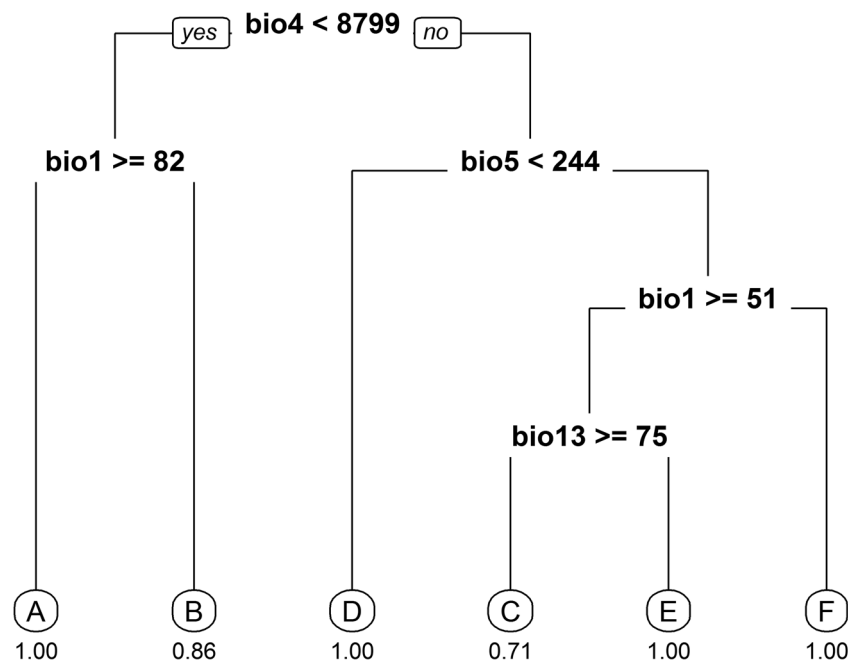
min temperature of coldest month, bio8 – mean temperature of wettest quarter, bio11 – mean temperature of coldest quarter, bio19 – precipitation of coldest quarter

Pontic (E) regions, respectively, hence corroborating the Meusel et al.'s (1965) biogeographic regionalisation scheme.

The db-RDA Axis 1 (Fig. 3) is associated with variables (bio3 and bio4) that are compounds of climate continentality, reflecting the amplitudes and the variation in temperatures accordingly. Clusters A (in mild and climate of southern regions of Central Europe) and F (in continental climate in the Southern

Urals) span the thermic continentality gradient. Thus, in the western, subatlantic regions of the study area the isothermality (bio3) range is 29 – 31 (Table S4), while it is lower (23 – 24) in the eastern, continental regions. Temperature seasonality (bio4/100) differences are even more striking, showing values of 71 – 79 and 127 – 133 for the clusters A and F, respectively. The relationship between the db-RDA Axis 1 (Fig. 3) and

Fig. 4 A CART tree of showing the discrimination of the studied forest by the bioclimatic variables (A – F are the codes of the clusters as in Fig. 2). bio1 – annual mean temperature, bio4 – temperature seasonality, bio5 – max temperature of warmest month, bio13 – precipitation of wettest month. The values of the variables bio1 and bio5 should be divided by 10 to feature Celsius degrees



bioclimatic variables such as bio6 (min temperature of coldest month) and bio11 (mean temperature of coldest quarter) indicates that it is the critically low winter temperatures that might be the main limiting factor in the distribution of the thermophilous flora in continental climate. The db-RDA Axis 2 spans the northern clusters B (Polish) and D (Sarmatian) and the southern cluster E (Pontic). The latter axis is associated with variables bio5 and bio8, which vary along the north-south gradient, reflecting change in temperature.

The outlying position of the syntaxon 16 (Fig. 1), representing the Transylvanian record (Indreica 2011) of the *Potentillo albae-Quercion*, which appears to be geographically remote from the core distribution of this alliance (mainly Poland), might be caused by aberrant soil conditions. We suggest that more phytosociological data from various substrates from Transylvania might throw more light on this problem.

Syntaxonomic interpretation of the classification analysis

Cluster A. *Quercetalia pubescentis*

Cluster A differs from others in presence of submediterranean, thermophilous elements such as *Cornus mas*, *Dictamnus albus*, *Ligustrum vulgare*, *Sorbus torminalis*, *Symphytum tuberosum*, and *Viburnum lantana* that point out upon the affiliation of this cluster with the class *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959 (the order *Quercetalia pubescenti-petraeae* Klika 1933). Cluster A comprises two subclusters A1 (columns 1 – 6) and A2 (columns 7 – 11) with the latter typically containing communities with thermophilous tree species such as *Quercus cerris* and *Q. pubescens* (Table S3). Further, within the cluster A, there are two groups syntaxa; the columns 1, 2, 3, 9, 10 (Table S1) used to be classified by their authors in the *Quercion petraeae* while the columns 4, 5, 6, 7, 8 (Table S1) represent the *Aceri tatarici-Quercion* (Zólyomi 1957; Chytrý and Horák 1997; Roleček 2005). The latter alliance is typically Pannonian and thermophilous while the *Quercion petraeae* seems mainly to be of Hercynian distribution and more acidophilous. This is indicated by the occurrence of *Anthoxanthum odoratum*, *Campanula rotundifolia*, *Festuca ovina*, *Galium pumilum*, and *Hieracium maculatum* (see Table S3), and shows floristic similarity to the oak forests of the subatlantic Central and atlantic Western Europe, including also the protologue of the alliance *Quercion petraeae* (Issler 1931). In a recent interpretation by Mucina et al. (2016), the *Quercion petraeae* alliance is syntaxonomically heterogenous as it appears (Fig. 2) that the holotype of the *Potentillo albae-Quercion* Libbert 1933 (considered as synonym of the *Quercion petraeae* in Mucina et al. 2016) has been segregated into another cluster (B), containing sources classified as the *Potentillo albae-Quercetum*.

Associations represented in our analyses:

Quercion petraeae Issler 1931

Genisto pilosae-Quercetum petraeae Zólyomi, Jakucs et Fekete ex Soó 1963

Sorbo torminalis-Quercetum Svoboda ex Blažková 1962

Potentillo albae-Quercetum sensu auct. czech. et slovak., non *Potentillo albae-Quercetum* Libbert 1933

Aceri tatarici-Quercion Zólyomi 1957

Aceri tatarici-Quercetum pubescentis-roboris Zólyomi 1957

Carici fritschii-Quercetum roboris Chytrý et Horák 1997

Convallario-Quercetum roboris Soó (1939) 1957

Quercetum pubescenti-roboris (Zólyomi 1957) Michalko et Džatko 1965

Cluster B. *Potentillo albae-Quercion*

All syntaxa in Cluster B were identified as the association *Potentillo albae-Quercetum petraeae* Libbert 1933 (Table S1). The species composition of this association contains less thermophilous species of southern provenience when compared to the Cluster A. Cluster B shows, to an extent, floristic similarity with oak-dominated communities of the class *Quercetea robori-petraeae* as it supports many acidophilous species (e.g. *Maianthemum bifolium*, *Potentilla erecta*, *Rubus saxatilis*, *Vaccinium myrtillus*, and *Veronica officinalis*). The *Potentillo albae-Quercetum* occurs typically on slightly acidic, clay-rich soils (Kasprowicz 2010). The similarity of clusters A and B, both occurring in Central Europe, is confirmed by the significant AB species group, consisting of 20 species (Table S3). There are Central European species in this group (*Festuca heterophylla*, *Hieracium lachenalii*, *H. sabaudum*, *Melittis melissophyllum*, *Quercus petraea* etc.), which differentiate the Cluster B from the more eastern Clusters C and D, but are common to the communities of the Cluster A. The other species (*Anemone nemorosa*, *Euphorbia angulata*, *Festuca amethystina*, *Juniperus communis* etc.) are concentrated only in the B *multipatt* group (16 species), supporting identity of the cluster B. Our analyses suggest that both the relationship between the *Quercion petraeae* and the *Potentillo albae-Quercion* as well as classification of these two alliance concepts within the *Quercetalia pubescenti-petraeae* should be critically revisited.

Association represented in our analyses:

Potentillo albae-Quercetum Libbert 1933

Cluster C. *Convallario majalis-Quercion roboris*

Cluster C comprises mixed oak-pine dry to mesic forests on sandy (so called ‘boreal’) river terraces. Most of the syntaxa of this cluster have been classified as belonging to the alliance *Convallario majalis-Quercion roboris* described from Central Ukraine (Kaniv Nature Reserve) on the boreal terrace of the Dnieper River (Shevchyk et al. 1996). The floristic composition of the communities of this alliance suggest an ecotonal position as the species pool is combined from three sources, namely species of the classes *Carpino-Fagetea* (the prevalent element), *Quercetea pubescentis*, and *Quercetea roboris* (Table S4). The absence of the *Vaccinio-Piceetea* species is associated with drier climate conditions of the forest-steppe zone than in the boreal zone – the core of the distribution of the latter class. A share of the *Quercetea roboris* species indicates acidic soils, which is also pointing upon a similarity with the Cluster B. The syntaxa of the Cluster C differ from the Cluster B in the absence of many Central European elements, usually typical of the acidophilous *Quercus petraea* forests. Cluster C has very few character species (Table 1), and most of the differentiating ones have a wide European range, being absent only in the Cluster F. If we compare Clusters C and D, they appear to some extent similar due to light-demanding and drought-tolerant species. The great differences between these clusters are found in soil conditions. The oak forests of the Cluster C are associated with poor sod-podzolic sandy soils and there is always pine in the tree layer. The presence of acidophytes and absence of nutrient-demanding species such as *Carex montana*, *Potentilla alba*, *Pulmonaria angustifolia* and others, is typical of oak forests on richer and heavier soils.

Associations represented in our analyses:

Clinopodio vulgaris-Quercetum roboris I. Solomakha,
Senchylo & Vorobyov 1996

Daphno cneori-Quercetum roboris Goncharenko in
Goncharenko et al. 2020 (for the valid description of
this association see below)

Melico nutantis-Quercetum roboris Shevchyk &
V. Solomakha 1996

Convallario majalis-Quercetum roboris sensu Shevchyk
& V. Solomakha 1996, non *Convallario majalis-*
Quercetum roboris Soó (1939) 1957

Pteridio aquilini-Quercetum roboris Bajrak 1996

Cluster D. *Betonico officinalis-Quercion roboris*

(for the valid description of this alliance see below)

This cluster comprises syntaxa of subxerophilous to mesic species-rich oak forests in the Sarmatian Floristic Province, distributed in the forest-steppe zone and in the southern regions of the forest zone (Fig. 1). These forests prefer sandy

soils of river terraces containing water-retaining layers of loam and clay and linked to depressions filled with heavy soils.

In the tree layer of these forests oak clearly dominates. Unlike the Central European communities, the only oak species found here is *Quercus robur*, most often represented by the late-flowering var. *tardiflora* Czern. *Acer platanoides*, *Betula pendula*, *Pinus sylvestris*, *Populus tremula*, *Pyrus communis*, and *Tilia cordata* are the other tree species occurring in these communities, albeit inferior in heights and frequency. Closeness of tree canopy ranges between 50 and 80 %. In contrast to the monospecific tree layer, shrub layer is species-rich – perhaps a result of low canopy closure. The shrub layer (1 – 40 %) contains (listed in descending order of frequency): *Frangula alnus*, *Sorbus aucuparia*, *Euonymus verrucosus*, *Corylus avellana*, *Viburnum opulus*, *Cytisus ruthenicus*, *Rhamnus cathartica*, *Prunus padus*, *Acer tataricum*. Herb layer is also floristically rich (53 species on 100 m² plot; Panchenko 2015). There are many grasses (*Agrostis capillaris*, *Brachypodium pinnatum*, *Calamagrostis arundinacea*, *C. epigejos*, *Dactylis glomerata*, *Melica nutans*, *Poa angustifolia*, *P. nemoralis*), associated with nemoral and subboreal elements such as *Convallaria majalis*, *Galium boreale*, *Pteridium aquilinum* and *Rubus saxatilis*. The herb-layer physiognomy is shaped by xeromesophilous, light-demanding herbs, many of them typical of the *Trifolio-Geraniea* (up to 21 %; Table S4). Presence of the steppe elements (typical of the class *Festuco-Brometea*) is also high and increases (up to 17 %; Table S4) especially in communities on soils developing over carbonate bedrocks (chalk, marl, limestone).

The forests of this type do not occupy large areas and do not show distinct dominants in the herbaceous layer. They were poorly studied by the Soviet Geobotanical School and they were reported at best as ‘*Quercetum herbosum*’ without describing the intricate herbaceous layer in detail. Since the early nineties of the last century, these forests became a subject of studies based on floristic-sociological approach (Bulokhov 1989; Bulokhov and Solomeshch 2003; Goncharenko 2003; Semenishchenkov and Panchenko 2012; Semenishchenkov and Teleganova 2013; Semenishchenkov and Poluyanov 2014; Panchenko 2015). These studies have not, however, clarified the syntaxonomic position in relations to similar Central and Western European oak forest syntaxa summarised under the concept of the *Quercion petraeae* (see Mucina et al. 2016 for extensive synonymy).

Our study (Fig. 2) provides evidence that part of the studied Ukrainian and Russian oak forests have been segregated into a cluster D, clearly different from those of Central Europe (clusters A and B). And this separation is well supported by its position in the used phytogeographical framework (Fig. 1) as well as in species composition (Table 1, Table S3). Therefore, we interpret this cluster as a new alliance – the *Betonico officinalis-Quercion roboris*. The western limits of

the alliance distribution roughly correspond to the eastern limit of *Quercus petraea* distribution in Ukraine (Meusel et al. 1965, Map 122a), while the other limits (northern, southern and eastern) coincide with the distribution range of *Potentilla alba* (Meusel et al. 1965, Map 214d) in Ukraine, Russia, and Belarus.

Associations represented in our analyses:

- Chamaecytiso ruthenici-Quercetum roboris*
Semenishchenkov and Poluyanov 2014
- Galio tinctoriae-Quercetum roboris* Goncharenko 2003
- Lathyro nigri-Quercetum roboris* Bulokhov and
Solomeshch 2003
- Potentillo albae-Quercetum* sensu Morozova 1999, non
Potentillo albae-Quercetum Libbert 1933
- Pyro pyrastris-Quercetum roboris* Semenishchenkov and
Poluyanov 2014

Cluster E. *Scutellario altissimae-Quercion roboris* (for the valid description of this alliance see below)

Cluster E comprises sub-xerophilous oak forests of the Pontic region of Ukraine and Southern Russia, occurring in the steppe zone and southern part of the forest-steppe zone. These forests are supported by fertile dark grey soils or podzolized chernozems in neutral or slightly base-rich soil status. The parent rock is loess or sedimentary products of weathering chalk (Central Russian Upland) or of sandstones (Donetsk Ridge).

Stands of these forests have one tree layer, composed of *Quercus robur* (10 – 18 m tall) and complemented by broad-leaved nutrient-demanding species such as *Acer platanoides*, *Fraxinus excelsior*, *Pyrus communis*, *Tilia cordata*, and *Ulmus minor*. The ‘northern’ elements, including *Betula pendula*, *Pinus sylvestris*, and *Populus tremula* are absent. The shrub canopy is closed (30 – 50 %) and species-rich. The cover of the herbaceous layer varies greatly, and it is species-poorer than in the *Betonico-Quercion*.

In countries of the former Soviet Union, these forests have been extensively studied by forest typologists (e.g. Vorobyov 1953; Pogrebnyak 1955; Bellegard 1971). Usually they had been designated as ‘steppic’ or ‘bayrack’ forests and classified as the *Querceta (roboris) lithospermosa* or the *Querceta (roboris) melicosa (pictae)* (Bradis 1971). The term ‘bayrack’ (ravine) forest is associated with the growing of forests of this type on the slopes of ravines in the forest-steppe zone. More detailed information on the structure of communities can be found in Gryn’ (1940), Kotov and Karnaukh (1940), Posokhov (1965), Bradis (1971), Bajrak (1996), Nazarenko and Kuzemko (2011), Sokolova (2011), Semenishchenkov and Poluyanov (2014), and Vorobyov et al. (2017).

The syntaxonomic identity of this alliance has been obscured for a long time because authors uncritically followed

the original Zólyomi’s (1957, Table on pages 412 – 421) delimitation of the *Aceri tatarici-Quercion*. Zólyomi (l.c.) described several geographical variants of this ‘*Aceri tatarici-Quercetum*’ of which several are from outside of the Pannonian Basin. One of the subunits – the ‘*Aceri tatarici-Quercetum roboris (rossicum)*’ – is based on data from Gryn’ (1940) as well as Kotov and Karnaukh (1940) of the oak forests of the Donetsk Ridge. The Zólyomi’s broad concept of the ‘*Aceri tatarici-Quercetum*’ has not been confirmed by our analyses since the Pannonian and the Pontic oak forests have been separated into different clusters (A: Pannonian and E: Pontic). The former is clearly affiliated with the *Querceta pubescentis*; the latter is described here as a new alliance – the *Scutellario altissimae-Quercion roboris*.

Forests of this type have a scattered distribution confined to uplands (Podil’s’ka Vysochyna, Donetsk Ridge, Central Russian Upland) and therefore they are often called ‘top-of-hill’ (in Ukrainian ‘nagorniy’) forests. Across their distribution area, they are strongly anthropogenically transformed.

Kleopov (1933, 1990) attempted to explain the gradients in the floristic composition of the oak forests in florogenetic terms and discerned six geographic types calling them *moldavicum*, *thraico-borysthenicum*, *donetzcicum*, *tanaiticum*, *volgense*, and *praeuralense*. The forests of the southwest Ukraine and of Moldova still contain some floristic elements typical of the submediterranean regions (*Asparagus tenuifolius*, *Cornus mas*, *Cotinus coggygria*, *Coronilla elegans*, *Melica uniflora*, *Polygonatum latifolium*, *Staphylea pinnata* etc.). The orests of the Donetsk Ridge are enriched in species with a circum-pontic distribution (*Arum elongatum*, *Dentaria quinquefolia*, *Laser trilobum*, *Lysimachia verticillata*, *Physospermum cornubiense*, *Scilla sibirica*, *Symphytum tauricum*, *Veronica umbrosa*, *Vincetoxicum scandens* etc.). East of the Volga, submediterranean elements disappear from these forests. The Volga hence plays a role of an important geographical barrier having impact on the oak-forest differentiation in Eastern Europe (Gribova et al. 1980; Kleopov 1990).

The distribution range of the alliance *Scutellario-Quercion* can be roughly delimited as follows: the western border of the alliance coincides with the eastern border of the distribution of *Quercus petraea* in Ukraine (Meusel et al. 1965, Map 122a). The northern distribution limit is delineated by the northern limits of *Aegonychon purpureocaeruleum* (Meusel et al. 1965, Map 363a) and *Melica picta* (Meusel et al. 1965, Map 39d), while the eastern limit may extend up the Volga River. In the southern of forest-steppe ecotone, the ranges of the *Betonico-Quercion* and the *Scutellario-Quercion* alliances partially overlap, but they are separated by different soils and topographic conditions and usually do not border each other. The former alliance is more connected with the gentle relief of river terraces with sandy soils, while the latter is confined to elevated, rugged watershed relief supporting heavier soils, and eroded slopes of river valleys and gullies.

Associations represented in our analyses:

- Aegonycho purpureocaerulei-Quercetum roboris* Bajrak 1996
Caragano fruticis-Aceretum tatarici Nazarenko and Kuzemko 2011
Fritillario ruthenici-Quercetum roboris Onyschenko, Dyakova et Karpenko ex Goncharenko in Goncharenko et al. 2020 (for the validation of this association see below)
Vicio pisiformis-Quercetum roboris Semenishchenkov and Poluyanov 2014
Violo hirtae-Quercetum roboris Vorobyov et al. 2017
Melampyro nemorosi-Carpinetum betuli sensu Lyubchenko et al. 1997, non *Melampyro nemorosi-Carpinetum betuli* Passarge 1957

Cluster F. *Lathyro pisiformis-Quercion roboris*

This alliance represents steppic oak forests of the Southern Urals (Solomeshch et al. 1989, 1994; Martynenko et al. 2005, 2008; Mirkin et al. 2008, 2010; Willner et al. 2016). They occur in form of small-sized and scattered patches, at elevations spanning 300 and 500 m (rarely as low as 250 m or as high as 600 m). Usually they are found on a strongly dissected relief occupying the tops of ridges and upper parts of the well-insulated south-facing slopes with inclination from 5° to 30°, and in some cases up to 40°. They are also found on the steep slopes of the mountain river valleys of the Southern Urals, in particular the Belaya River. Substrates supporting these forests are classified as grey-forest soils, shallow, rocky, over calcareous substrates (limestones, lime-rich sandstones and shales).

The authors characterise the species composition of these forests as transitional between forest and steppe vegetation and therefore some steppic elements (e.g. *Caragana frutex*, *Cerasus fruticosa*) commonly occur in these forests. A distinctive feature of the xero-mesophilous steppic oak forests of the Southern Urals is the presence of Siberian elements such as *Cacalia hastata*, *Carex macrourea*, *Cicerbita uralensis*, *Hieracium albocostatum*, and *Lathyrus litvinovii* (Solomeshch et al. 1994).

The syntaxonomic position of this unit remains controversial. Mucina et al. 2016 classified this alliance in the *Quercetalia pubescenti-petraeae* Klika 1933. This solution is no longer tenable as the *Quercetalia pubescentis* elements are virtually missing here. Some authors preferred classification of this alliance in the order *Fagetalia sylvaticae* (Mirkin et al. 2008, 2010). In the ground layer, these oak forests are floristically similar to the hemiboreal class *Brachypodio pinnati-Betuletea pendulae*, yet they are distinguished by the absence of *Pinus sylvestris*, *Betula pendula*, and *Larix sibirica*, typical of the hemiboreal class (Ermakov et al. 1991). Due to steppic species composition of the communities, these forests also differ from the nemoral

forests in the same region which motivated some authors (e.g. Martynenko et al. 2005; Willner et al. 2016) to classify the *Lathyro-Quercion* in the order *Quercetalia pubescenti-petraeae*. It appears that the classification of this alliance into any of the known syntaxonomic orders remains ambivalent.

Associations represented in our analyses:

- Brachypodio pinnati-Quercetum roboris* Grigoriev in Solomeshch et al. 1989
Filipendulo vulgaris-Quercetum roboris Martynenko et al. 2008
Omphaloido scorpioidis-Quercetum roboris Martynenko et Solomeshch in Martynenko 2009

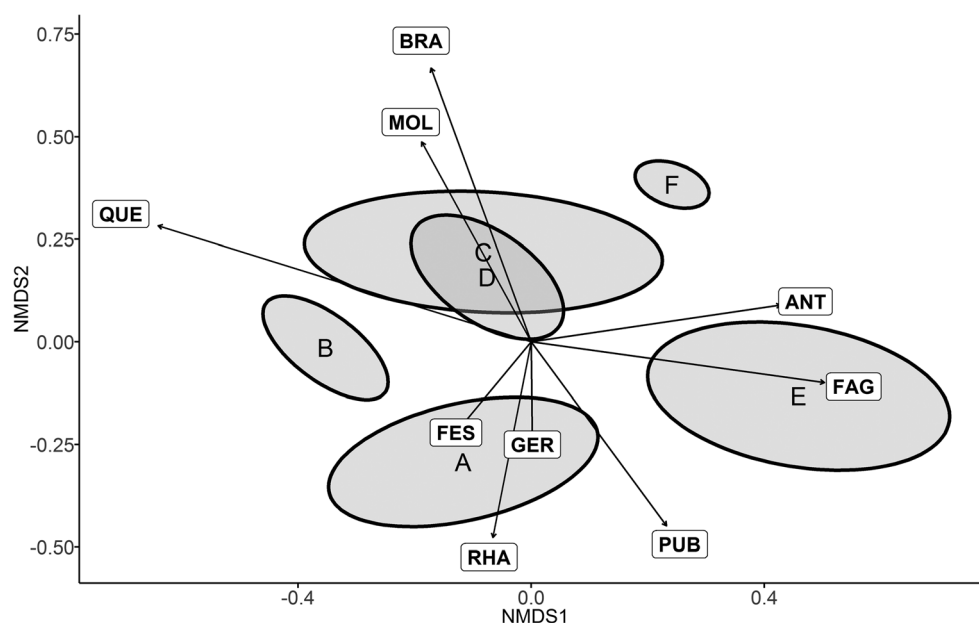
Position of the Ukrainian and Russian oak forests in large-scale perspective

Thermophilous oak forests of the steppe and forest-steppe zones of Ukraine and Russian Federation have been a subject of floristic-sociological studies following Braun-Blanquet approach since the 90s (Bulokhov and Solomeshch 1991; Shevchyk et al. 1996), however, their syntaxonomic position remained unclear. Although some alliances were described in this region (e.g. *Convallario-Quercion*, *Lathyro-Quercion*), the authors of them preferred using concepts coined in other parts of Europe (*Quercion petraeae*, *Potentillo albae-Quercion*, *Aceri tatarici-Quercion*). Due to lack of data and synthetic studies, the classification of these forests into syntaxonomic orders and classes remains problematic. The solution of classifying the known alliances into the *Quercetalia pubescentis* (Mucina et al. 2016) was then naturally poorly informed.

Our study has no ambition to clarify the issue of the high-rank classification in full extent as our analyses involve only limited scope of the oak-dominated forests. A more appropriate analysis should include a broad spectrum of the *Quercetalia pubescentis* forests from Western, Central and Southern Europe, as well as oak-hornbeam forests of the *Carpinetalia betuli*, oak forests of the *Quercetalia robori-petraeae* and possibly also of the *Brachypodio-Betuletea*. Such a synthesis is clearly overdue. We do offer, however, insight into the studied Ukrainian-Russian oak forests from the point of view of the composition of phytocoenologic elements (Table S4).

A passive projection of the phytocoenologic elements on an NMDS plane (Fig. 5) suggests that the Cluster A has the highest (of all other cluster involved) share of the *Quercetalia pubescentis* (PUB) and associated thermophilous elements of the *Festuco-Brometea* (FES), *Trifolio-Geranietea* (GER) and *Crataego-Prunetea* (RHA) elements (see also the high values of r^2 of regression in Table S6). The classification of the other alliances (represented by the Clusters B, C, D, E, and F) as belonging to the *Quercetalia pubescentis*, is clearly not supported.

Fig. 5 NMDS-ordination diagram with vectors of phytosociological variables. Ellipses in the diagram correspond to six clusters of thermophilous oak forest (for the cluster codes see Fig. 2). Classes of vegetation: BRA – *Brachypodio pinnati-Betuletea pendulae*, FAG – *Carpino-Fagetea*, FES – *Festuco-Brometea*, GER – *Trifolio-Geranietea*, MOL – *Molinio-Arrhenatheretea*, PUB – *Quercetea pubescentis*, QUE – *Quercetea robori-petraeae*, RHA – *Crataego-Prunetea*, ANT – aggregated category ‘Anthropogenic classes’



The oak forests in North-Central Europe (Clusters B, C, D: *Potentillo-Quercion*, *Convallario-Quercion*, *Betonico-Quercion* respectively) contain many acidophilous species, hence the importance of the *Quercetea robori-petraeae* elements in these clusters. Interestingly, the Cluster C and D also contain high shares of the *Brachypodio-Betuletea* and *Molinio-Arrhenatheretea* classes. The share of the *Carpino-Fagetea* (FAG) in the Cluster E (*Scutellario-Quercion*) may hint at its classification, however we refrain from speculating about this in syntaxonomic meaning. The *Lathyro-Quercion* is not only geographically but also floristically outlying; the phytocoenologic elements point upon its putative position between the classes *Carpino-Fagetea* and *Brachypodio-Betuletea*.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix: Descriptions and validation of new syntaxa

Betonico officinalis-Quercion roboris Goncharenko & Semenishchenkov *all. nov. hoc loco*

Dry-mesic floristic-rich oak forests in the Sarmatian region.

Misapplied names: *Quercion petraeae* sensu *auct. ucrain. et ross.*, non *Quercion petraeae* Issler 1931; *Potentillo albae-Quercion petraeae* sensu *auct. ucrain. et ross.*, non *Potentillo albae-Quercion petraeae* Jakucs in Zólyomi 1967

Holotypus: Galio tinctoriae-Quercetum roboris Goncharenko 2003

Diagnostic taxa: *Quercus robur* *Clematis recta*, *Cytisus ruthenicus* *Ajuga genevensis*, *Allium oleraceum*, *Anthericum ramosum*, *Asperula tinctoria*, *Betonica officinalis*, *Campanula persicifolia*, *Digitalis grandiflora*, *Melampyrum nemorosum*, *Origanum vulgare*, *Potentilla alba*, *Securigera varia*, *Serratula tinctoria*, *Trifolium alpestre*, *Turritis glabra*, *Veronica chamaedrys*, *Vicia sepium*, *Vincetoxicum hirundinaria*, *Viola hirta*

Scutellario altissimae-Quercion roboris Goncharenko *all. nov. hoc loco*

Steppic oak forests in the Pontic region.

Misapplied name: *Aceri tatarici-Quercion* sensu *auct. ucrain. et ross.*, non *Aceri tatarici-Quercion* sensu Zólyomi 1957.

Holotypus: Fritillario ruthenici-Quercetum roboris Onyschenko, Dyakova & Karpenko ex Goncharenko *ass. nov.* (for the valid description of the association see below).

Diagnostic taxa: *Quercus robur* *Acer tataricum*, *Cerasus fruticosa*, *Crataegus rhipidophylla* agg., *Prunus spinosa* subsp. *dasyphylla* *Aegonychon purpureocaeruleum*, *Carex michelii*, *Euphorbia semivillosa*, *Festuca stricta* subsp. *sulcata*, *Melica picta*, *Phlomis tuberosa*, *Scutellaria altissima*, *Vicia pisiformis*, *Vincetoxicum scandens*

Daphno cneori-Quercetum roboris Goncharenko *ass. nov. hoc loco*

Xeromesophytic oak-pine forests on boreal terraces of the Dnieper River of the Central Ukraine.

Incl.: *Convallario majalis-Quercetum roboris daphneosum cneori* Gayova & Korotchenko 2013 (Gayova and Korotchenko 2013, p. 28)

Note: The association typifies pine-oak forests supported by the boreal terraces of the Dnieper River in Central Ukraine (near Cherkassy). (Gayova and Korotchenko 2013) classified this vegetation as the subassociation *Convallario majalis-Quercetum roboris daphneosum cneori*. We suggest that due to distinct floristic composition showing more xerophilous elements (e.g. *Anemone patens*, *Daphne cneorum*, *Dracocephalum ruyschiana*, *Teucrium chamaedrys*) when compared with other associations of the alliance *Convallario majalis-Quercetum roboris* (see columns 18 – 20, Table S3); this syntaxon deserves the rank of an association.

***Scorzonero ensifoliae-Quercetum roboris* Sokolova ex Semenshchenkov ass. nov. hoc loco**

Xeromesophytic oak forests in depressions on sandy terraces (arens) of the Don River in the steppe zone

Synonym: *Scorzonero ensifoliae-Quercetum roboris* Sokolova 2011 nom. inval. (arts. 3b & 5).

Holotypus: Russian Federation, Rostov Region, Tarasovsky District, near Mityakinskaya village; 48.5996° N lat., 39.7182° E long.; Habitat: sandy terrace of the Don River; Relevé area: 225 m². Cover of tree layer: 70 %. Cover of shrub layer: 3 %. Cover of herb layer: 40 %. The species cover-abundance codes follow Braun-Blanquet (1964). Date: 2 August 2009. Author: T. Sokolova.

E₁: *Quercus robur* 4, *Malus sylvestris* +, *Pyrus pyraster* +, *Ulmus minor* +. E₂: *Euonymus verrucosus* 2, *Acer tataricum* +, *Crataegus rhipidophylla* +, *Rosa sp.* +, *Rubus caesius* +. E₃: *Aegopodium podagraria* 3, *Vincetoxicum hirundinaria* 1, *Agrimonia eupatoria* +, *Agrostis tenuis* +, *Arctium nemorosum* +, *Bromopsis inermis* +, *Calystegia sepium* +, *Campanula rapunculus* +, *C. trachelium* +, *Chelidonium majus* +, *Convallaria majalis* +, *Daucus carota* +, *Fragaria viridis* +, *Galeopsis tetrahit* +, *Galium aparine* +, *Geum urbanum* +, *Heracleum sibiricum* +, *Polygonatum odoratum* +, *Pulmonaria obscura* +, *Scorzonera ensifolia* +, *Stellaria media* +, *Trifolium medium* +, *Urtica dioica* +, *Viola suavis* +, *Vincetoxicum scandens* +

***Fritillario ruthenici-Quercetum roboris* Onyschenko, Dyakova et Karpenko ex Goncharenko ass. nov. hoc loco**

Syn.: *Fritillario ruthenicae-Quercetum roboris* Onyschenko, Dyakova & Karpenko 2007 nom. inval. (arts. 3b & 5)

Holotypus: Onyschenko et al. (2007, p. 92, Tab. 1, relevé 1)

These are steppic oak forests on carbonate soils formed over chalk or limestone bedrocks, originally described from

the National Landscape Park “Svyati Gory” in the Donetsk region in Ukraine. This association is possibly identical to the type *Aceri tatarici-Quercetum pubescentis-roboris rossicum* reported by Zólyomi (1957) for the Donetsk Ridge using the data from Ukrainian phytosociologists Gryn’ (1940) as well as from Kotov and Karnaukh (1940).

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