Research paper

Comparative study of Central and Eastern European alliances of thermophilous oak forests (*Quercion petraea*, *Betonico-Quercion*, and *Lathyro-Quercion*) within the temperate zone of Europe

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Abstract. In this paper we carried out a comparative analysis of three alliances, namely *Quercion petraea, Betonico-Quercion* and *Lathyro-Quercion*, which span Central and Eastern European thermophilous oak forests. The main goal was to find out floristic and ecological differences as well as to assess specificities in the phytosociological and layer structure across the syntaxa in different regions of Europe. Cluster analysis was performed based on the Bray-Curtis distance matrix and the flexible beta algorithm. A phytoindication method was applied to determine ecological relationships. Variability in the phytosociological structure was studied by shares of species of different classes of vegetation. The layer structure features were investigated by comparing species with the highest constancy value within each layer. Analysis of the distribution boundaries of differentiating species allowed the geographical boundaries of the three identified syntaxa clusters to be delineated. In the phytosociological structure, the greatest differences were found in the proportion of species of *Quercetea pubescentis* and *Brachypodio-Betuletea* classes. The Central and Eastern European syntaxa groups were shown to be significantly different in the constancy-ranked series of major layer-forming species.

Key words: Europe, thermophilous oak forests, syntaxonomy, *Quercion petraea, Betonico-Quercion, Lathyro-Quercion.*

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Introduction

Thermophilous oak forests, traditionally classified within the class *Quercetea pubescentis* Doing Kraft ex Scamoni et Passarge 1959, are of great interest as one of the most floristically rich forest communities in Europe. This specific type of forest vegetation provides habitats for many species of nature conservation importance. Moreover, they mainly grow on the borders of forest and open dryland areas and are vulnerable to anthropogenic impact.

The most typical are communities in Southern and Southeastern Europe (Blasi *et al*., 2004; Sanda *et al*., 2008; Tzonev *et al*., 2009; Čarni *et al*., 2009; Stupar *et al*., 2015; Tzonev *et al*., 2019). They also grow in Cen-

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tral Europe (Zólyomi, 1957; Jakucs, 1961; Mucina *et al*., 1993; Chytrý, 1994; Chytrý & Horák, 1997; Chytrý, 1997; Roleček, 2005; Roleček, 2007; Kevey, 2008; Indreica, 2011; Borhidi *et al*., 2012; Chytrý *et al*., 2013; Hegedüšová *et al*., 2021), extending to northern regions (Libbert, 1933; Oberdorfer, 1992; Kwiatkowska & Solińska-Górnicka, 1993; Jakubowska-Gabara, 2000; Matuszkiewicz, 2007; Kasprowicz, 2010; Brzeg & Wika, 2017). Thermophilous oak forests are also found in Eastern Europe (Morozova, 1999; Bulokhov & Solomeshch, 2003; Goncharenko, 2003; Panchenko, 2013; Semenishchenkov & Poluyanov, 2014; Panchenko, 2015; Goncharenko & Kovalenko, 2019; Kozhevnikova & Prokhorov, 2021), and the most remote region in the Southern Urals (Solomeshch *et al*., 1989; Martynenko *et al*., 2005; Martynenko *et al*., 2008; Mirkin *et al*., 2010).

Moving away from the main Mediterranean centre of diversity toward the north and east, communities lose their typical thermophilous characteristics, while gaining features of those forest vegetation classes for which the climatic conditions are more suitable. Because of this, most of the thermophilous oak forests in the northern part of the temperate zone have a transitional nature, which complicates syntaxonomic decisions.

In Eastern Europe thermophilous (or more accurately the use of the term "xeromesophytic" or "dry-mesic") oak forests demonstrate considerable differences from Central European ones (Semenishchenkov, 2012; Semenishchenkov & Poluyanov, 2014; Goncharenko *et al*., 2020). This led to the allocation of two new Eastern European alliances *Betonico officinalis-Quercion roboris* Goncharenko *et* Semenishchenkov in Goncharenko *et al*. (2020) and *Scutellario altissimae-Quercion roboris* Goncharenko in Goncharenko *et al*. (2020), which are vicariants of *Quercion petraeae* Issler 1931 and *Aceri tatarici-Quercion* Zólyomi 1957, respectively (Goncharenko *et al*., 2020). However, due to the poorly studied area of Eastern Europe, it is unclear where exactly the boundary between the Central and Eastern European alliances lies. The same is true of the eastern boundary of the alliance *Betonico-Quercion*, since further to the east, it is replaced by the alliance *Lathyro pisiformis-Quercion roboris* Solomeshch *et* Grigoriev in Willner *et al*. (2016), with its main distribution in the Southern Urals (Solomeshch *et al*., 1989; Solomeshch *et al*., 1994; Martynenko *et al*., 2008; Willner *et al*., 2016). All of the above shows that the issue of Eastern European thermophilous oak forests is far from clear and thus, further research is still required.

In this study, we focus on a comparative analysis of Central European, Eastern European and South Uralian alliances, namely *Quercion petraea*, *Betonico-Quercion* and *Lathyro-Quercion*. These alliances are almost uniform in zonal conditions and extend along a continentality gradient. Our study was also inspired by new data published, in particular from Slovakia (Hegedüšová *et al*., 2021) and poorly studied eastern territories, including Kazakhstan (Kozhevnikova & Prokhorov, 2021). As for the easternmost *Lathyro-Quercion* alliance, a considerable number of associations are usually described as new (Martynenko *et al*., 2005; Martynenko *et al*., 2008; Mirkin *et al*., 2010). Given the remote and isolated location of the Southern Urals, this is quite reasonable. So we also included them in our comparative study.

The aims of the present study were: 1) to perform a formal classification of syntaxa of the Central European, Eastern European and South Uralian groups, taking into account new data from the Southern Urals, Kazakhstan and Central Europe; 2) to determine the main ecological gradients underlying their differentiation; 3) to identify the specificities of the phytosociological structure of syntaxa, taking into account their ecotonic nature in syntaxonomic terms; 4) to carry out a comparative analysis of the main layer-forming species, which are also habitat-forming, significantly influencing the growth of other species.

Material and Methods

For further analysis, we selected 28 syntaxa that are representative of three alliances *Quercion petraea*, *Betonico-Quercion* and *Lathyro-Quercion* (10, 10 and 8 syntaxa, respectively). Data on their species composition, ecological characteristics and geographic location are taken from synoptic tables given in publications (for a list of publications see the Reference section and Table S1). Taxa names were unified according to the Euro+Med resource (www.emplantbase.org). Mosses and lichens were excluded because they were not recorded in all publications.

To perform a formal classification, the synoptic data matrix (syntaxa in columns and species in rows) is subjected to cluster analysis, taking into account the logarithmically transformed values of species constancies. A Bray-Curtis distance matrix and a flexible beta algorithm (with beta = -0.25), which are very popular and well-proven in phytosociological studies, were used for agglomeration (Bray & Curtis, 1957; Lance & Williams, 1967; Legendre & Legendre, 2012). The resulting groups (clusters) of syntaxa at higher levels were compared with the original classification given by the authors at the level of alliances.

To understand the ecological drivers underlying syntaxa differentiation, we conducted the non-metric multidimensional ordination, or NMDS, (Kruskal, 1964) and tested the relationship between ordination axes and environmental variables (Legendre & Legendre, 2012). The environmental variables were obtained using the phytoindication method, which was performed using the Didukh ecological scales (Didukh, 2011). Vectors of the environmental variables were projected into the ordination space using the environmental variable fitting function, or *envfit*, from the *vegan* package (Oksanen *et al*., 2018). To show the differences between the groups of syntaxa, mean values of the environmental variables were calculated for each group and differences in the means were checked using the Tukey's HSD test in R software.

Given that thermophilous oak forests are a heterogeneous group especially in the northern part of their distribution range, we measured the affinity to different vegetation classes using the proportions of diagnostic species in the species composition of each syntaxon. The EuroVegChecklist served as a basis for the species-to-class classification (Mucina *et al*., 2016). The proportion of diagnostic species of different vegetation classes was used to reveal major phytosociological differences between Central and Eastern European syntaxa.

To discover the peculiarities of the layer structure of the thermophilous oak forests in different regions of Europe, we compared the species of the highest frequency in each of the main layers, namely tree, shrub and herbaceous layers. The average value of species constancy in the groups of syntaxa identified by the cluster analysis was first calculated. Then the species were ranked according to the value of average constancy and the five topmost species (conventionally defined threshold) in each layer were tabulated for comparison.

Results and Discussion

Formal classification

According to the results of the agglomerative cluster analysis, 28 analyzed syntaxa (see Table S1) were divided into three groups, conventionally designated as A, B, C (Figure 1). The cluster A united Central European syntaxa (1–10). The cluster B consists of Eastern European syntaxa with the main distribution in the Middle Russian Upland (11–20). The cluster C unites the South Uralian group of syntaxa (21–28).

The clusters of syntaxa coincide with the division into the alliances of *Quercion*

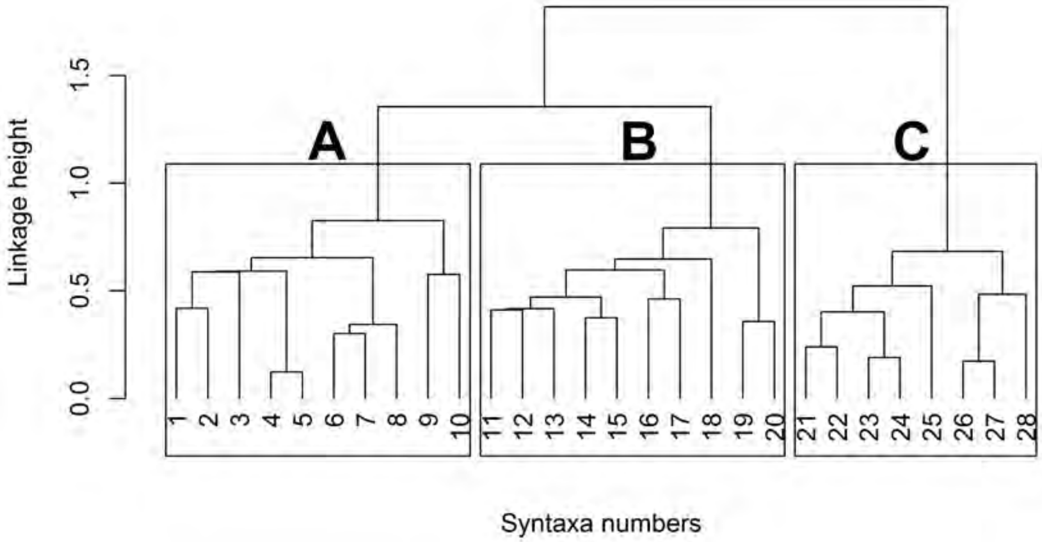

Figure 1. Cluster analysis dendrogram of the syntaxa of thermophilous oak forests. Syntaxa numbers are the same as in Table S1.

petraeae (A), *Betonico-Quercion* (B), *Lathyro-Quercion* (C). This proves the essential differences in species composition between the Eastern European and Central European thermophilous oak forests (Semenishchenkov, 2012; Semenishchenkov & Poluyanov, 2014; Goncharenko *et al.*, 2020). In addition, the Eastern European group was divided into two parts, namely the cluster B, which occupies an intermediate position between A and C, and the cluster C from the Southern Urals. If we take into account the agglomeration at higher levels, cluster B is still closer to cluster A from Central Europe than to cluster C, which is geographically and floristically distant.

According to the cluster analysis results, the geographic boundaries of cluster B proved wider than previously assumed (Goncharenko *et al.*, 2020). Cluster B also included associations from Central Ukraine, in particular *Digitali grandiflorae-Quercetum roboris* (11, Figure 1). This extends the notion about the western border of the *Betonico-Quercion* alliance further west including regions of Central Ukraine in the Dnieper basin (Goncharenko & Kovalenko, 2019). As for syntaxa from Kazakhstan (19 and 20, Figure 1), they also joined the *Betonico-Quercion* alliance (cluster B). This differs from the authors' original treatment of these associations because the association *Astragalo ciceri-Quercetum roboris* (19) was assigned to the *Betonico-Quercion* alliance, but the association *Sanguisorbo officinalis-Quercetum roboris* (20) was classified into another alliance *Lathyro-Quercion* (Kozhevnikova & Prokhorov, 2021). Such a discrepancy may be explained by the inclusion in cluster C (21–28, Figure 1) of specific associations from the Southern Urals with a high content of mountain species. This increased the distance between clusters B and C, and hence lead to the accession of associations from Kazakhstan to the closer cluster B. However, the associations from Kazakhstan (19 and 20) occupy a transitional position in floristic respect between the *Betonico-Quercion* and the *Lathyro-Quercion*, as will be shown later.

Floristic comparison of clusters of syntaxa

The floristic differentiation of Central and Eastern European forests is multilevel (Table S2). It is based on 5 groups (blocks) of differential species. In addition to groups A, B, and C, whose species are concentrated in a single cluster, there are groups AB and BC the species of which overlap pairs of clusters, specifically A + B and B + C, respectively. The group ABC consists of common species for all three groups of syntaxa. Each of the mentioned groups is supported by a significant number of differentiating species.

The multilevel floristic differentiation is explained by the presence of not only local ecological but geographical reasons. Group A (*Quercion petraeae*) concentrates the species associated with Central Europe. The most prominent representatives are such species as *Quercus petraea* (Mattuschka) Liebl., *Ligustrum vulgare* L., *Lembotropis nigricans* (L.) Griseb., *Melittis melissophyllum* L., *Symphytum tuberosum* L., *Festuca heterophylla* Lam., *Melica uniflora* Retz., *Sorbus torminalis* (L.) Crantz. and others. Most of them in Ukraine have their eastern distribution border in the basins of the Dniester and South Bug rivers (Meusel *et al.*, 1965; Meusel & Jäger, 1992). But on the other hand, cluster B (*Betonico-Quercion*) already includes syntaxa from Central Ukraine in the Dnieper basin. Taking both facts into account, we may assume that the boundary between the alliances *Quercion petraeae* and *Betonico-Quercion* runs along the eastern boundary of the above-listed Central European species and in coincidence with the boundary of the Central European floristic province in western Ukraine (Meusel & Jäger, 1992).

Cluster B (*Betonico-Quercion*) occupies an intermediate position between the Central European *Quercion petraeae* and the South Uralian *Lathyro-Quercion* groups, as indicated by the presence of the species groups AB and BC (Table S2). Similarly to group A, there are many species restricted in their eastern distribution in groups B and AB. The main reason for this is the increasing continentality of climate. These include species like *Allium oleraceum* L., *Anthericum ramosum* L., *Carex montana* L., *Potentilla alba* L., *Lathyrus niger* (L.) Bernh., *Serratula tinctoria* L. and others. Their eastern distribution boundaries are mostly confined to the Volga basin (Meusel *et al.*, 1965; Meusel & Jäger, 1992). Following the species of Group A, these seem to represent the «second wave», but they do not reach the Southern Urals and therefore are absent from the syntaxa of *Lathyro-Quercion* (Table S2).

Although associations from Kazakhstan joined the *Betonico-Quercion* alliance (Figure 1), they have a transitional character between the alliances *Betonico-Quercion* and *Lathyro-Quercion* (columns 19 and 20, Table S2). Taking into account the aforesaid, we can assume that the boundary between the alliances *Betonico-Quercion* and *Lathyro-Quercion* approximately runs through the Volga valley. Further accumulation of material from continental regions of Russia and Kazakhstan will bring more clarity in this question.

Restrictions on the distribution of eastern species in the reverse western direction are much less expressed. Most of the differentiators of groups C and BC are also found in Ukraine and other European countries. However, the differential species in these groups are associated with other habitats, mainly the meadow-steppe and steppe, due to which they have much less constancy in the composition of thermophilous oak forests.

Thus, there are two trends revealed in Table S2. In the eastward spreading, there are climatic constraints due to harsh continental conditions and especially low winter temperatures, to which western thermophilous species are not adapted. Conversely, in the opposite western direction, restrictions on the distribution of species of groups B and BC are less pronounced, which is explained by a milder climate of Central Europe and therefore, coenotic and edaphic constraints prevail.

Ordination and ecological relationships

In the ordination space, three groups of thermophilous oak forests syntaxa extend mainly along the first axis. The Central Eu-

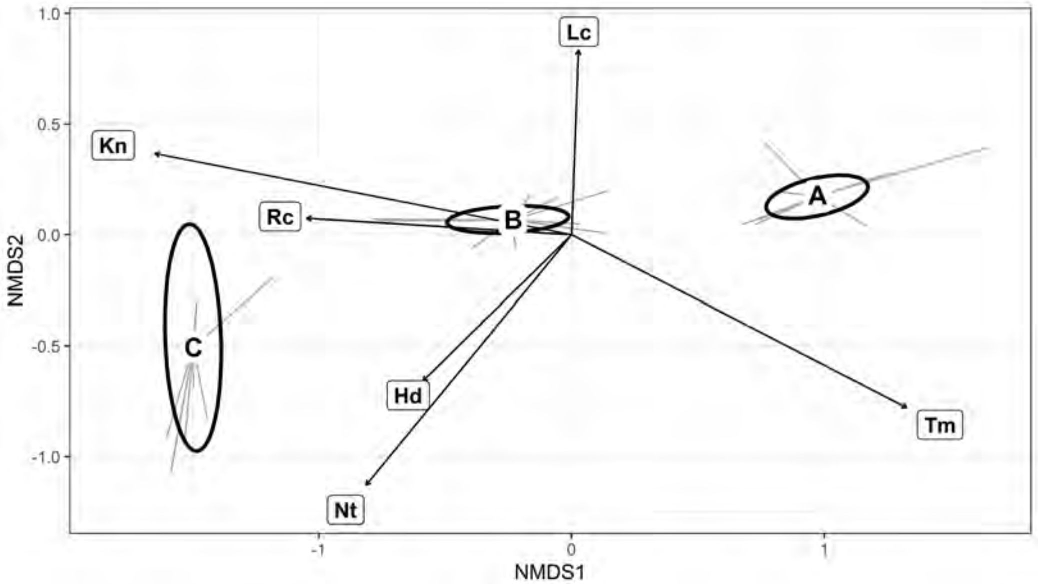

Figure 2. Ordination diagram of groups of syntaxa of thermophilous oak forests and projection of phytoindicational variables. Hd – moisture, Rc – soil acidity, Nt – soil nitrogen, Lc – light regime, Tm – temperature, Kn – continentality. Letters A, B and C correspond to the groups of syntaxa in Figure 1.

ropean (A) and the South Uralian (C) clusters are located at opposite ends (Figure 2).

The first axis is most correlated with the continentality variable *Kn*, followed by the temperature variable *Tm* (Table S3). As mentioned, the increasing continentality of climate may explain the distribution limitations of many thermophilous species towards the east (groups A and AB, Table S2). Edaphic factors, namely soil nitrogen, light regime and moisture, are related more to the second axis (Table S3). A different tendency for the soil acidity vector *Rc*, which differs from the directions of other vectors of edaphic factors, could be explained by the confinement of thermophilous oak forests to the carbonate substrates, as noted by many authors (Table S1).

Based on the comparison of mean values and results of Tukey’s HSD test, we observed significant differences in the continentality variable *Kn* in all three groups (Figure 3f).

The mean values of *Kn* indicator form a monotonic increasing series (39.4, 41.7, 44.0 for clusters A, B, and C, respectively; see Table S4). For other variables, such as soil acidity and nitrogen, significant differences in group means are observed only for the outermost clusters, namely Central European A and South Uralian C, while the intermediate cluster B has no significant differences (shared letters ‘ab’ above Figure 3b, 3c). On the contrary, the two Eastern European clusters B and C are similar concerning the temperature variable, while the cluster A differs from both (letter ‘b’ above Figure 3e). This is explained by the fact that the syntaxa of the cluster A concentrate much more thermophilous species. There are no significant differences in the moisture and light indicators (Figure 3a, 3d), as thermophilous oak forests are similar in this respect in all studied regions.

Comparison of phytosociological structure

Although thermophilous oak forests are formally categorised within the class *Quercetea pubescentis*, they are not typical in northern regions where they grow out-

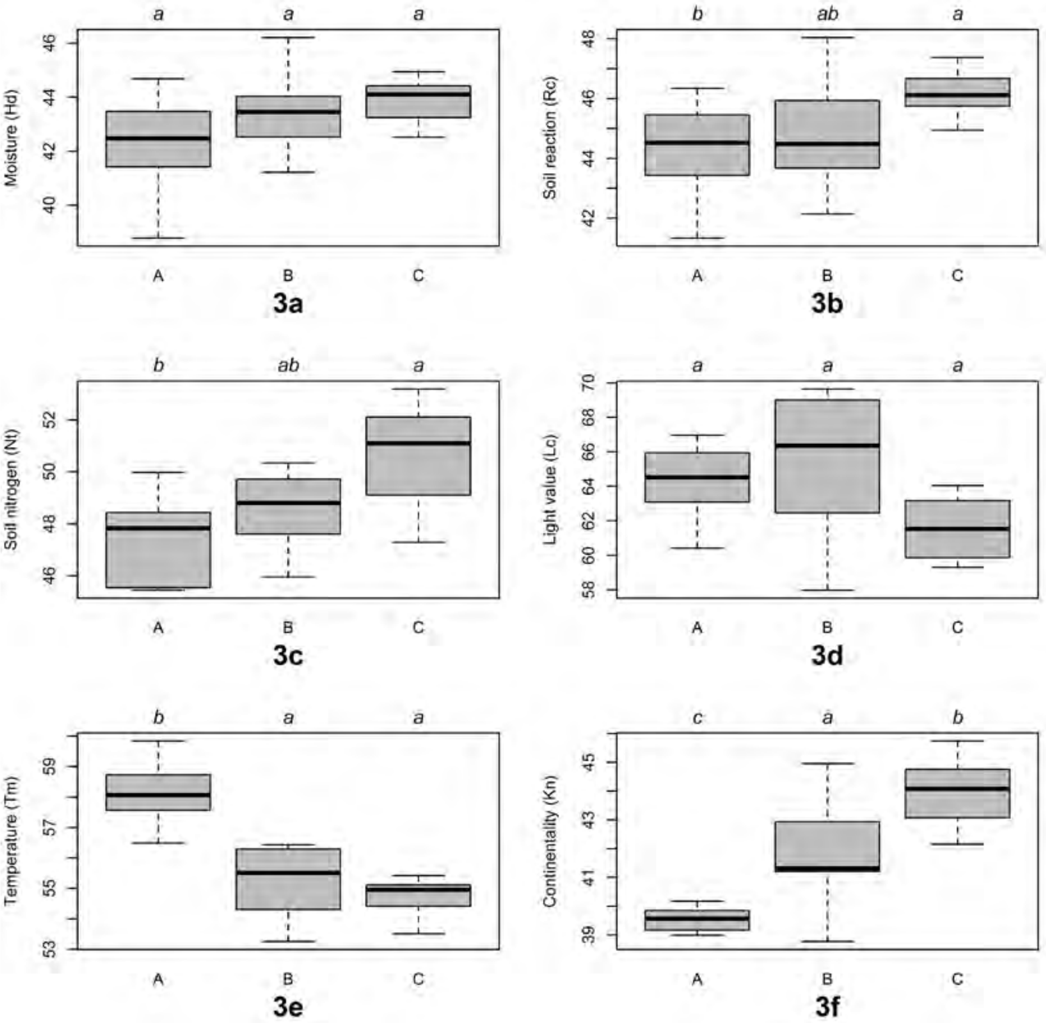

Figure 3. Boxplots showing differences in mean values of phytoindicational variables calculated for three groups of thermophilous oak forests syntaxa. Group labels are provided below each figure and correspond to Figure 1. Italic letters above the figures indicate the Tukey's HSD results.

side the climatic optimum. So their species composition is a phytosociological admixture of species of different vegetation classes. A comparison of the phytosociological structure of the studied syntaxa showed that they affiliate to four forest vegetation classes (*Quercetea pubescentis, Quercetea robori-petraeae, Carpino-Fagetea, Brachypodio-Betuletea pendulae*), three classes of herbaceous vegetation (*Festuco-Brometea, Molinio-Arrhenatheretea*, and *Trifolio-Geranietea*), and a class of xerophytic shrub vegetation (*Crataego-Prunetea*) (Table 1).

The shares of species of some classes vary within a narrow range, and this may be both in low numbers, e.g., as for the class *Crataego-Prunetea*, RHA (0.01–0.06), and in relatively high numbers, e.g., as for *Trifolio-Geranietea*, GER (0.18–0.26, Table 1). The high richness of *Trifolio-Geranietea* species can be explained by the growth of the communities in light and warm habitats optimal for this class.

Table 1. Shares of diagnostic species of different vegetation classes in the syntaxa of thermophilous oak forests. Groups A, B, and C correspond to those identified by the cluster analysis (Figure 1). Syntaxa numbers are the same as in Table S1. Designations of the vegetation classes: PUB – *Quercetea pubescentis*, FAG – *Carpino-Fagetea*, QUE – *Quercetea robori-petraeae*, BRA – *Brachypodio-Betuletea pendulae*, FES – *Festuco-Brometea*, GER – *Trifolio-Geranietea*, MOL – *Molinio-Arrhenatheretea*, RHA – *Crataego-Prunetea*.

Syntaxa num.	Group of syntaxa	PUB	FAG	QUE	BRA	FES	GER	MOL	RHA
1	A	0.16	0.22	0.09	0.07	0.10	0.22	0.09	0.05
2	A	0.14	0.19	0.06	0.06	0.20	0.23	0.06	0.05
3	A	0.16	0.24	0.06	0.05	0.16	0.19	0.10	0.05
4	A	0.14	0.25	0.06	0.06	0.11	0.21	0.12	0.05
5	A	0.14	0.19	0.05	0.05	0.21	0.21	0.10	0.04
6	A	0.16	0.20	0.09	0.08	0.09	0.24	0.09	0.06
7	A	0.17	0.19	0.08	0.07	0.10	0.26	0.06	0.06
8	A	0.11	0.14	0.09	0.08	0.17	0.21	0.15	0.05
9	A	0.11	0.09	0.12	0.07	0.29	0.22	0.05	0.04
10	A	0.12	0.17	0.08	0.07	0.19	0.25	0.07	0.05
11	B	0.16	0.14	0.08	0.12	0.14	0.21	0.15	0.01
12	B	0.14	0.13	0.08	0.11	0.17	0.24	0.12	0.03
13	B	0.14	0.19	0.06	0.08	0.16	0.21	0.10	0.05
14	B	0.12	0.15	0.04	0.10	0.15	0.24	0.16	0.04
15	B	0.15	0.12	0.06	0.10	0.18	0.20	0.15	0.03
16	B	0.12	0.21	0.11	0.13	0.07	0.19	0.17	0.01
17	B	0.10	0.11	0.10	0.11	0.16	0.20	0.22	0.01
18	B	0.16	0.23	0.11	0.11	0.06	0.18	0.14	0.01
19	B	0.08	0.11	0.04	0.11	0.26	0.21	0.15	0.04
20	B	0.08	0.12	0.04	0.12	0.23	0.20	0.19	0.02
21	C	0.05	0.19	0.07	0.28	0.10	0.20	0.16	0.01
22	C	0.05	0.20	0.06	0.20	0.13	0.20	0.12	0.04
23	C	0.08	0.19	0.06	0.20	0.12	0.23	0.12	0.01
24	C	0.08	0.19	0.06	0.19	0.10	0.22	0.10	0.05
25	C	0.08	0.15	0.05	0.22	0.15	0.22	0.13	0.01
26	C	0.07	0.16	0.05	0.22	0.18	0.21	0.11	0.01
27	C	0.08	0.22	0.05	0.20	0.11	0.19	0.11	0.04
28	C	0.08	0.16	0.05	0.19	0.16	0.19	0.13	0.03
Average by Group A		0.14	0.19	0.08	0.07	0.16	0.22	0.09	0.05
Average by Group B		0.14	0.16	0.08	0.11	0.14	0.21	0.15	0.02
Average by Group C		0.07	0.17	0.05	0.19	0.15	0.21	0.13	0.02

While similar in the sense that all syntaxa are a phytosociological mixture of species in which no single vegetation class plays a dominant role, they nevertheless differ in the proportions in which species of the different classes are combined in the different regions. Major differences between Central European and Eastern European forests are mainly observed not concerning a single class, but if we take into account the proportions of species of the classes *Quercetea pubescentis / Brachypodio-Betuletea*, PUB/BRA. The first class is more represented in the western syntaxa of cluster A, and the number of species of the second class increases significantly in the eastern syntaxa of cluster C from the Southern Urals. The ratio PUB/BRA of these two classes forms the following series: 0.14/0.07 = 2.14 in cluster A, 0.14/0.11 = 1.27 in cluster B, and 0.07/0.19 = 0.38 in cluster C. Thus, the phytosociological structure of thermophilous oak forests display patterns associated with the proximity of the region to the climatic optimum of one or another class. Thus, the class *Quercetea pubescentis* has a Mediterranean centre of the climatic optimum (Jakucs, 1960) and the class *Brachypodio-Betuletea* has the south Siberian centre of diversity (Ermakov *et al*., 1991). Most likely in the northern regions, thermophilous oak forests represent an aggregate type syntaxonomically, so the question of their placement into only one of the forest vegetation classes cannot be solved. This problem will be explained by the complexity of the classification of ecotone vegetation types and should be considered concerning individual syntaxa.

Comparison of the most constant layer-forming species

In addition to floristic, ecological and phytosociological differences between the three groups of thermophilous forests discussed in the previous sections, there is a differentiation in the lists of the main layer-forming species. In Table 2 species that are ranked by the constancy value in each of the clusters A, B and C form a diagonal-like pattern in three main layers.

Table 2. Species with the highest scores of average constancy in each cluster of syntaxa of thermophilous oak forests. Five topmost species are shown in each cluster. The numbers represent ranks and the upper indexes are percentages of the average constancy of the species.

Species (grouped by the layers)	Clusters of syntaxa		
	A	B	C
Tree layer			
Quercus petraea	1^{80}		
Carpinus betulus	2^{45}		
Prunus avium L.	3^{28}		
Quercus robur	4^{26}	1^{98}	1^{88}
Betula pendula		2^{40}	5^{7}
Pinus sylvestris	5^{18}	3^{34}	
Pyrus communis		4^{33}	
Tilia cordata			2^{58}
Ulmus glabra			4^{44}
Acer platanoides		5^{27}	3^{53}
Shrub layer			
Ligustrum vulgare	1^{46}		
Crataegus monogyna Jacq.	2^{41}		
Acer campestre L.	3^{27}		
Lembotropis nigricans	4^{27}		
Prunus spinosa L.	5^{25}		
Euonymus verrucosus Scop.		1^{49}	2^{48}
Frangula alnus		2^{48}	
Sorbus aucuparia		3^{44}	
Cytisus ruthenicus		4^{36}	
Corylus avellana L.		5^{30}	
Prunus padus L.			1^{52}
Caragana frutex			3^{47}
Prunus fruticosa			4^{44}
Rhamnus cathartica L.			5^{40}
Herbaceous layer			
Veronica chamaedrys	1^{79}	2^{62}	
Poa nemoralis	2^{73}		5^{76}
Clinopodium vulgare	3^{52}	4^{54}	

Species (grouped by the layers)	Clusters of syntaxa		
	A	B	C
Euphorbia cyparissias L.	4^{50}		
Vincetoxicum hirundinaria Medik.	5^{50}		
Betonica officinalis		1^{64}	
Convallaria majalis		3^{57}	
Poa angustifolia L.		5^{53}	
Origanum vulgare			1^{84}
Stellaria holostea			2^{83}
Brachypodium pinnatum			3^{80}
Rubus saxatilis L.			4^{77}

In the western syntaxa of cluster A, the most constant species are *Quercus petraea* and *Carpinus betulus* L. in the tree layer. Moving eastward, in cluster B, they are replaced by *Quercus robur* L. with *Betula pendula* Roth. In cluster B the role of *Pinus sylvestris* L., *Pyrus communis* L., *Acer platanoides* L. is also increasing (Table 2). In cluster C, the species *Quercus robur* comes first, followed by the species *Tilia cordata* Mill., which has the second rank. Such species as *Acer platanoides* and *Ulmus glabra* Huds. have also significant participation, occupying the third and fourth ranks, respectively, in the communities from the Southern Urals.

Differences in the main layer-forming species extend to all main layers. The species *Ligustrum vulgare* is the most constant species in the shrub layer of the Central European cluster A. The composition of the shrub layer of cluster B is more acidophilous, including such species as *Frangula alnus* Mill., *Sorbus aucuparia* L., *Cytisus ruthenicus* Wol. The constancy of species such as *Caragana frutex* (L.) C. Koch, *Prunus fruticosa* Pall. etc. in the shrub layer of cluster C is explained by the formation on the border with petrophytic steppe communities in the Southern Urals (Table S1).

One of the most characteristic features of thermophilous oak forests is a floristically rich herbaceous layer. Although it usually has no clearly expressed dominants, there is also a differentiation in the herbaceous layer, similar to that in the tree and shrub layers. The most constant species in cluster A are *Veronica chamaedrys* L., *Poa nemoralis* L., *Clinopodium vulgare* L. (Table 2). In the Eastern European cluster B they are replaced by *Betonica officinalis* L., *Veronica chamaedrys*, *Convallaria majalis* L., and in cluster C the most constant are species like *Origanum vulgare* L., *Stellaria holostea* L., *Brachypodium pinnatum* (L.) Beauv. (Table 2).

Two factors seem to play a major role in the succession of major layer-forming species. The first one is the degree of tolerance of species to climate continentality, and the second reason is in contact with what types of vegetation the thermophilous oak forests form in each region. Although the species listed in Table 2 are not exclusive to just one of the clusters, their constancies vary greatly depending on whether the climatic conditions are optimal or not for one or another species. This causes a change in the constancy-ranked series of the layer-forming species, as shown in Table 2. Regarding the role of surrounding communities, this environment is different in different regions of Europe, as the ecological conditions and predominant substrates on which communities are formed change, too.

Conclusion

In this study, we conducted a comparison of thermophilous oak forests in the northern part of their distribution, where they are the most problematic from a syntaxonomic point of view. A cluster analysis of syntaxa, including new data from Central and Eastern Europe, confirms the presence of three geographically and floristically distinct groups, corresponding to the level of alliances. Moreover, Eastern European forests were divided into two groups, namely the *Betonico-Quercion* centred on the Middle Russian Upland and the *Lathyro-Quercion* confined to the Southern Urals.

Analysis of the distribution boundaries of differentiating species in groups A and AB, as well as B and BC, allowed us to preliminarily outline the boundaries of the three European alliances. The boundary between the alliances *Quercion petraeae* and *Betonico-Quercion* roughly coincides with the boundary of the Central European floristic province. At least parts of Central Ukraine in the Dnieper basin belong to the *Betonico-Quercion* alliance, where many Central European species have already disappeared. The analysis of the species composition of differential groups B and BC indicates a boundary between the alliances *Betonico-Quercion* and *Lathyro-Quercion* in the Volga River basin, and syntaxa from Kazakhstan occupy an intermediate position between them. Further accumulation of material, especially from poorly studied continental regions of Russia, is necessary to clarify this question.

According to the results of ordination analysis, the leading factor influencing the division of the three identified groups of thermophilous oak forests is the increasing continentality of the climate towards the east. Edaphic factors also play an obvious role but concerning the differentiation of syntaxa at a lower, local level. Comparison of the mean values showed significant differences between all groups of thermophilous oak forests by the continentality variable, while only the extreme groups, namely the Central European *Quercion petraeae* and the South Uralian *Lathyro-Quercion*, differ in soil acidity and nitrogen indicators.

In the phytosociological structure, species of the *Quercetea pubescentis* class are not the dominant group in any of the syntaxa groups. Significant factors that determine the features of the phytosociological structure of syntaxa of a particular region are the location relative to the climatic optimum of various vegetation classes, as well as the composition of the surrounding vegetation types with which thermophilous oak forests border in different regions. The greatest differences in the phytosociological structure of the three studied groups of syntaxa are observed in the ratio of the shares of *Quercetea pubescentis* and *Brachypodio-Betuletea* species, i.e., classes that are polar concerning the continentality of climate.

The Central European and Eastern European thermophilous oak forests are also differentiated by the main layer-forming species, and this applies to all layers, including tree, shrub and herbaceous layers. The extent to which climatic conditions are optimal for particular layer-forming species causes their variation from west to east and, consequently, leads to differences in the constancy-ranked series of layer-forming species as well as the physiognomy and habitats of communities.

Supplements (Tables S1, S2, S3, S4) **are on the webpage:** https://mi.emu.ee/et/teadusinfo/metsanduslikud-uurimused/contents/2021/vol-75/

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