Thermophilous oak forests in Slovakia: classification of vegetation and an expert system

Teplomilné doubravy na Slovensku: klasifikace vegetace a expertní systém

Katarína Hegedüšová[1], Hubert Žarnovičan[2], Róbert Kanka[3], Róbert Šuvada[4], Jozef Kollár[3], Dobromil Galvánek[1] & Jan Roleček[5,6]

[1]*Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, SK-845 23, Bratislava, Slovakia, e-mail: katarina.hegedusova@savba.sk;* [2]*Department of Environmental Ecology and Landscape Management, Faculty of Natural Sciences, Comenius University, Mlynská dolina, Ilkovičova 6, SK-842 15 Bratislava, Slovakia, e-mail: hubert.zarnovican@uniba.sk;* [3]*Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, SK-814 99 Bratislava, Slovakia, e-mail: Robert.Kanka@savba.sk, J.Kollar@savba.sk;* [4]*State Nature Conservancy of the Slovak Republic, Administration of the Slovenský kras National Park, Hámosiho 188, SK-049 51 Brzotín, Slovakia, e-mail: robert.suvada@sopsr.sk;* [5]*Institute of Botany of the Czech Academy of Sciences, Department of Paleoecology, Lidická 25/27, CZ-602 00 Brno, Czech Republic, e-mail: honza.rolecek@centrum.cz;* [6]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic*

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Deciduous thermophilous oak forests (phytosociological class *Quercetea pubescentis*) are among the most species-rich and most endangered forest communities in central Europe. Thanks to the varied topography, bedrock, biogeographical influences and rather well-preserved semi-natural and near-natural forest vegetation, Slovakia harbours a diverse heritage of thermophilous oak forests. Here we present a revised and unified syntaxonomic classification of Slovak thermophilous oak forests. Although several national classification systems were proposed previously, the new system has the advantage that it is based on the results of numerical analysis of a large dataset of 1131 relevés and reflects modern syntaxonomic concepts. A representative dataset, compiled from the Slovak Vegetation Database and unpublished sources, was selected based on the relative representation of diagnostic species of the *Quercetea pubescentis* class in the relevés. The final classification was produced using beta-flexible clustering and modified TWINSPAN in JUICE software. Resulting clusters were assigned to phytosociological alliances and associations, whose nomenclature was checked for compliance with the International Code of Phytosociological Nomenclature. An expert system including formal definitions based on the Cocktail algorithm and a dichotomous identification key were created and may be used for the assignment of new relevés to the defined associations. Eleven associations were distinguished and classified to three alliances. The alliance *Quercion pubescenti-petraeae* includes the associations *Lithospermo purpurocaerulei-Quercetum pubescentis*, *Seslerio albicantis-Quercetum pubescentis*, *Fraxino orni-Quercetum pubescentis* and *Euphorbio-Quercetum*. The alliance *Aceri tatarici-Quercion* includes the associations *Quercetum pubescenti-roboris* and *Convallario-Quercetum roboris*. The alliance *Quercion petraeae* includes the associations *Carici fritschii-Quercetum roboris*, *Sorbo torminalis-Quercetum*, *Genisto pilosae-Quercetum petraeae*, *Melico pictae-Quercetum roboris* and *Quercetum petraeo-cerridis*. Short descriptions of associations, summarizing information on their species composition, ecology and distribution, are provided and discussed.

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Detrended Correspondence Analysis revealed a complex gradient structure, separating (i) open oak forests on carbonate bedrock from (ii) oak forests on dry and acidic sites, (iii) oak forests on mesic, moderately base- and nutrient-rich sites and (iv) oak forests on mesic, base- and nutrient-rich sites. Ecological preferences of syntaxa were assessed using ecological indicator values and bioclimatic variables. Conservation value and threats to Slovak thermophilous oak forests are discussed.

Keywords: formalized classification, *Quercetea pubescentis*, Slovakia, syntaxonomy, thermophilous oak forests, vegetation survey

Introduction

Deciduous thermophilous oak forests of the class *Quercetea pubescentis* is a well-defined vegetation type, in which the species composition and ecological properties are transitional between forest and non-forest plant communities of warm and dry habitats. They occur in relatively warm and dry regions of Europe (Kevey 2008, Matuszkiewicz 2008, Čarni et al. 2009, Tzonev et al. 2009, Di Pietro et al. 2010, Roleček 2013, Coldea et al. 2015, Reczyńska 2015, Mucina et al. 2016, Stupar et al. 2016, Goncharenko et al. 2020). In central Europe, they are among the most species-rich (Chytrý et al. 2015) and most endangered types of forest vegetation, with the main threats being inappropriate forest management and successional changes due to the decline in traditional forest use and increased nitrogen deposition (Kwiatkowska & Wyszomirski 1988, Hofmeister et al. 2004, Chytrý et al. 2020).

Slovakia harbours a diverse heritage of thermophilous oak forests thanks to the varied topography, bedrock, biogeographical influences and rather well-preserved semi-natural and near-natural forest vegetation (Stanová & Valachovič 2002). They occur mainly at low and middle altitudes (120–800 m a.s.l.), often in mosaics with dry grasslands (*Festuco-Brometea* class), thermophilous fringe vegetation (*Trifolio-Geranietea sanguinei* class), thermophilous scrub (*Crataego-Prunetea* class), mesophilous forests (*Carpino-Fagetea sylvaticae* class) and in some areas also with calcicolous pine forests (*Erico-Pinetea* class) or acidophilous oak forests (*Quercetea robori-petraeae* class). They are usually dominated by oaks (*Quercus pubescens* agg., *Q. cerris*, *Q. petraea* agg. and *Q. robur* agg.), frequently accompanied by other drought-tolerant heliophilous trees (*Pinus sylvestris*, *Sorbus aria* agg. and *S. torminalis*) and some mesophilous trees (mainly *Acer campestre*, *Carpinus betulus*, *Fraxinus excelsior* and *Tilia cordata*). Species-rich shrub and herb layers are characterized by light-demanding species of warm and dry sites, such as *Anthericum ramosum*, *Dictamnus albus*, *Clinopodium vulgare*, *Cornus mas*, *Galium glaucum*, *Genista pilosa*, *Peucedanum cervaria*, *Potentilla arenaria*, *Prunus spinosa*, *Rhamnus catharticus*, *Teucrium chamaedrys* and *Vincetoxicum hirundinaria*. The variability in species composition is mainly influenced by the base content of the soil and the complex gradient in light availability, soil moisture and soil nutrients (Roleček 2013).

In previous vegetation surveys of Slovakia (Mucina & Maglocký 1984, 1985, Jarolímek et al. 2008), thermophilous oak forests were classified into four alliances (*Quercion pubescenti-petraeae* Br.-Bl. 1932, *Quercion petraeae* Zólyomi et Jakucs ex Jakucs 1960, *Aceri tatarici-Quercion* Zólyomi et Jakucs 1957, *Quercion confertae-cerris* Horvat 1954) and a single order *Quercetalia pubescentis-petraeae* Klika 1933, within the widely conceived class *Querco-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937.

Here, we adhere to the EuroVegChecklist (Mucina et al. 2016), which takes into account the high number of diagnostic species of thermophilous oak forests and classifies them in a separate class *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959. This concept is in accordance with some previous studies (e.g. Doing Kraft 1955, Rodwell et al. 2002, Borhidi et al. 2012, Roleček 2013). This and some other methodological decisions were based on a consensus of a team of authors of the sixth volume of the edition Plant communities of Slovakia (e.g. Kliment & Valachovič 2007, Hegedüšová Vantarová & Škodová 2014), for which our classification was prepared.

The main aims of this study were: i) to prepare a revised and unified classification of thermophilous oak forests in Slovakia, ii) to provide formal definitions of the associations for an expert system and identification key based on the definitions, iii) to evaluate habitat requirements and distribution of the defined associations.

Material and methods

Data preparation

Published relevés in the Slovak Vegetation Database (Hegedüšová 2007, Šibík 2012, EU-SK-001 in the Global Index of Vegetation-Plot Databases) and unpublished relevés in private databases stored using TURBOVEG database software (Hennekens & Schaminée 2001) were used for the classification. The initial dataset contained 15,713 relevés of all types of Slovak forest and scrub vegetation, used for the preparation of the sixth volume of the edition Plant communities of Slovakia. This dataset was processed using JUICE 7.0.194 software (Tichý 2002). Plant nomenclature was harmonized using Marhold & Hindák (1998). Due to differences in taxonomic concepts and precision of species identification between authors of relevés, some species and subspecies were merged into more broadly conceived taxa (Electronic Appendix 1). We excluded taxa determined only to genus level (except *Taraxacum*) and bryophytes and lichens, because they were recorded only by some authors. Records of identical species in different vegetation layers were merged into a single record (at the stage of description of diagnostic, constant and dominant species, the different layers were reinstated). To reduce the negative effect of the variation in plot sizes (Chytrý & Otýpková 2003, Dengler et al. 2009) we excluded relevés with a plot size below 100 m^2, above 650 m^2 and relevés without information on plot size (except the relevés published in significant works before 1970 in which this information is usually missing). We also excluded relevés with a tree layer cover lower than 5% and the cover of *Abies alba*, *Carpinus betulus*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *P. mugo* and *Robinia pseudoacacia* higher than 50%. In the next step, relevés of the *Quercetea pubescentis* class were defined as those in which the percentage cover of diagnostic species of the class was higher than the percentage cover of diagnostic species of the *Carpinion betuli* alliance (*Carpino-Fagetea sylvaticae* class) and *Quercetea robori-petraeae* class, as recognized in the relevant literature (Borhidi & Kevey 1996, Jarolímek et al. 2008, Chytrý 2013, Mucina et al. 2016). Relevés with less than four diagnostic species of the *Quercetea pubescentis* class were excluded. Based on a consensus of the team of authors of the Plant communities of Slovakia, geographical stratification was not carried out due to the low number of relevés available for some forest and scrub vegetation types. After these steps, the final dataset contained 1131 relevés (Fig. 1).

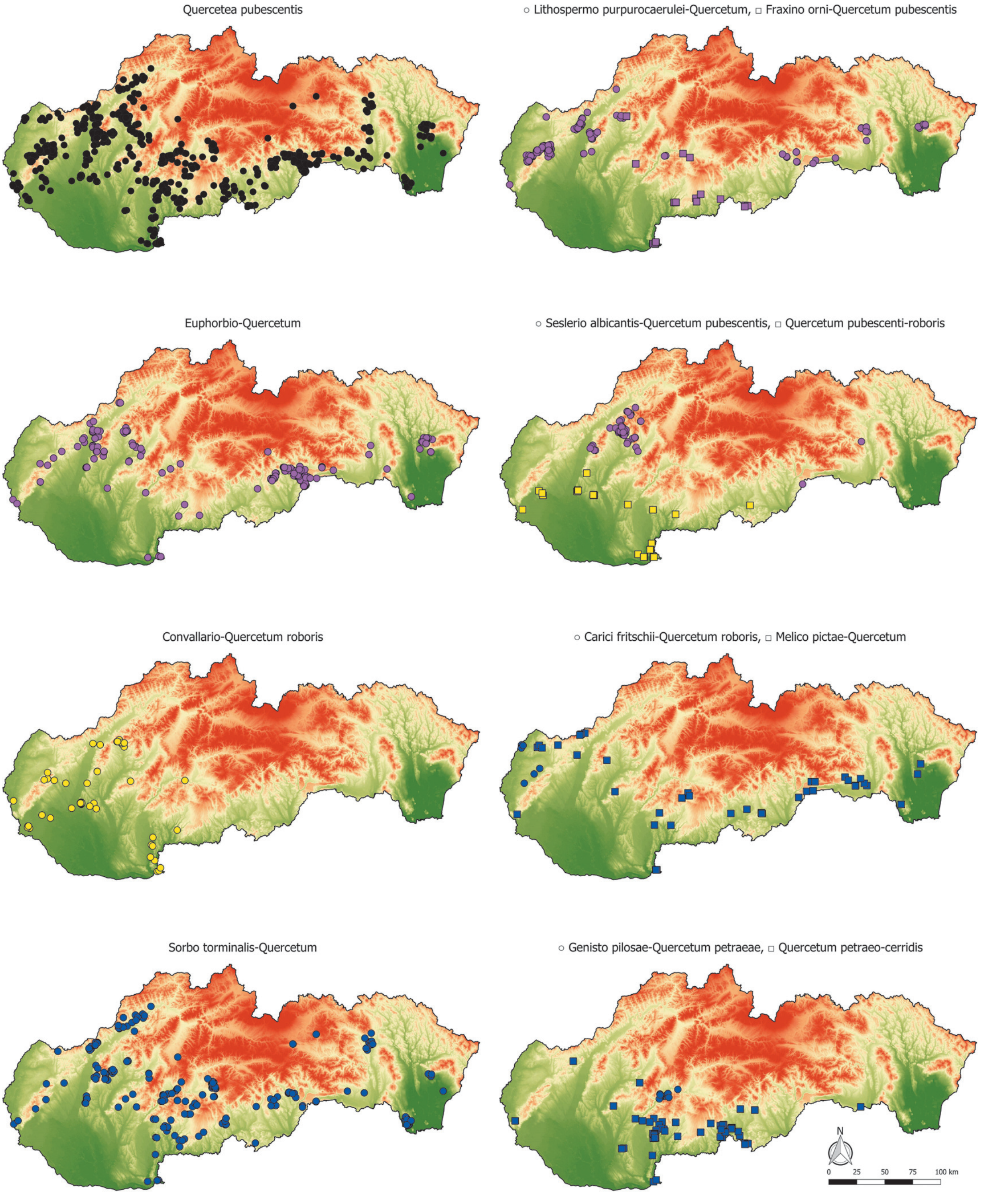

Fig. 1. – Distribution maps of the associations. Black – all relevés analysed; purple – *Quercion pubescenti-petraeae* alliance; yellow – *Aceri tatarici-Quercion* alliance; blue – *Quercion petraeae* alliance.

Data analysis

To build the classification, we used both agglomerative and divisive classification algorithms. Our aim was to identify robust groups of relevés (i.e. vegetation types) with a coherent species composition, which were interpretable in terms of ecology and distribution, but at the same time respecting traditional concepts of alliances and associations used in central Europe. In the first step, we distinguished the alliances using beta-flexible clustering (beta = –0.25, Bray-Curtis dissimilarity, log-transformed percentage abundances) in PC-ORD 6.0 software (McCune & Mefford 2011). In the second step, we distinguished the associations within each alliance using a modified TWINSPAN algorithm (Roleček et al. 2009), with three pseudospecies cut levels (0, 5, 25%) and with total inertia as a measure of cluster heterogeneity. Coherence of clusters was checked using detrended correspondence analysis (DCA) and their content was evaluated using the analysis of diagnostic, constant and dominant species in JUICE. The diagnostic value of the species was assessed using the phi coefficient based on the fidelity concept (Bruelheide 1995, Sokal & Rohlf 1995, Chytrý et al. 2002). All clusters were virtually standardized to a size equal to 14% of the total data set (Tichý & Chytrý 2006). Fisher's exact test ($P < 0.001$) was used to identify species with a significant link to a particular cluster (Tichý & Chytrý 2006). The critical values for diagnostic species were set as follows: the phi coefficient ≥ 0.20 and frequency ≥ 20%. Species considered constant (frequency ≥ 50%) in two or more clusters were not accepted as diagnostic. Nomenclature of associations and alliances was checked for compliance with the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

We prepared formal definitions of all associations using combinations of Cocktail sociological species groups (Bruelheide 1995, 1997, 2000) and dominant species, following the protocol used in JUICE software (Kočí et al. 2003). Sociological species groups were formed of species with a high co-occurrence rate, evaluated using the phi coefficient. The numbers of species in the groups (three to seven) were set empirically (Kočí et al. 2003). Because some definitions are rather complex, we built a simple dichotomous identification key based on the sociological species groups, which illustrates the relationships between the associations that were identified. Pairwise differences in the defining species groups were also summarized in a table (Electronic Appendix 2).

The main gradients in species composition were analysed using DCA in R package vegan (Oksanen et al. 2013) run from JUICE. Percentage cover values were log-transformed and rare species down-weighted. To assist the ecological interpretation of ordination axes, altitude and unweighted averages of combined Ellenberg and Jurko ecological indicator values (EIVs) for relevés (Jurko 1990, Ellenberg et al. 1992, Šibíková et al. 2010) were projected on the DCA plot. Taxa lacking EIVs were listed in Electronic Appendix 3. Differences in altitude and EIVs were tested using Tukey's HSD for unequal N test, followed by multiple comparisons of the mean ranks in STATISTICA software (StatSoft Inc. 2013).

To show the differences in climatic requirements of the different alliances, 19 bioclimatic variable values were calculated for each relevé from a set of global climate layers WorldClim2 (Fick & Hijmans 2017) with a 30 seconds spatial resolution (~1 km^2). Differences were again tested using Tukey's HSD for unequal N test.


A
B
C
D
E
F
G
H

Fig. 2. – Photographs of representative stands of the Slovak thermophilous oak forest associations: (A) *Lithospermo purpurocaerulei-Quercetum pubescentis*, Vinište Hill, Považský Inovec Mts (photo K. Chytrý, 2020); (B) *Seslerio albicantis-Quercetum pubescentis*, Rokoš Hill, Strážovské vrchy Mts (M. Duchoň, 2011); (C) *Fraxino orni-Quercetum pubescentis*, Skaly Hill, Burda Hills (J. Roleček, 2006), (D) *Euphorbio-Quercetum*, Jankov vŕšok Hill, Strážovské vrchy Mts (M. Duchoň, 2009); (E) *Quercetum pubescenti-roboris*, Belianske kopce Hills, Podunajská pahorkatina Hills (K. Chytrý, 2018); (F) *Convallario-Quercetum roboris*, Dubník Wood, Podunajská pahorkatina Hills (J. Košťál, 2008); (G) *Carici fritschii-Quercetum roboris*, Záhorská nížina (J. Kollár, 2005); (H) *Sorbo torminalis-Quercetum*, Skýcov, Tríbeč Mts (J. Roleček, 2005); (I) *Genisto pilosae-Quercetum petraeae*, Kapitulské bralá Cliffs, Štiavnické vrchy Mts (J. Mertlik, 2016); (J) *Melico pictae-Quercetum roboris*, Nemečky, Podunajská pahorkatina Hills (J. Kollár, 2005); (K) *Quercetum petraeo-cerridis,* Čankov, Podunajská pahorkatina Hills (J. Roleček, 2003).

Information on bedrock and soils was extracted from thematic maps (Hraško et al. 1993, https://apl.geology.sk/gm50js) and the extensive literature on individual sites. As detailed surveys were available only for a minority of sites, the textual descriptions need to be viewed with caution. Soil typology used in the descriptions follows the World Reference Base for Soil Resources (FAO 2015).

To assess the conservation value of the associations, we calculated average numbers of threatened species in their relevés. We also identified threatened species with high frequency or dominance in our dataset; we interpret them as species for which thermophilous oak forests may be an important habitat. Threat status of the species follows recent edition of the Slovak Red List (Eliáš et al. 2015).

Results and discussion

Classification, ordination and ecological relationships

Of the 24 associations previously reported from Slovakia (Jarolímek et al. 2008), 11 were accepted and assigned to three of the four previously reported alliances (see the relationships between previously and presently accepted syntaxa in Electronic Appendix 4). The most xerophilous associations on base-rich soils are grouped in the *Quercion pubescenti-petraeae* alliance (613 relevés); the *Aceri tatarici-Quercion* alliance (104 relevés) includes sub-continental forest-steppe oak forests and the *Quercion petraeae* alliance (414 relevés) includes thermophilous oak forests on neutral to acidic substrata. Distribution maps of the defined alliances and associations are in Fig. 1 and photographs of representative stands in Fig. 2. Diagnostic, constant and dominant species of the associations are summarized in Table 1 and Electronic Appendix 5.

Compositional and ecological relationships between the associations are illustrated using ordination plots (Fig. 3). DCA revealed a rather complex gradient structure in three-dimensional space, resembling the shape of a tetrahedron. One of its vertices is formed by open oak forests on carbonate bedrock (*Lithospermo-Quercetum* and *Seslerio-Quercetum*), separated from the other associations on the first ordination axis. These are differentiated along the second and third ordination axis, with the three remaining vertices formed by oak forests on dry and acidic sites (*Genisto-Quercetum*), mesic, moderately base- and nutrient-rich sites (*Quercetum petraeo-cerridis*) and mesic, base- and nutrient-rich sites (*Convallario-Quercetum*). We assume that the complex structure is the result of at least two phenomena: (i) the composition of Slovak thermophilous oak forests was shaped by several independent ecological gradients; and (ii) several pools of species are present in the vegetation of Slovak thermophilous oak forests and they are largely confined to specific habitats or geographical regions. Consequently, we can distinguish three different associations of dry oak forests on base-rich soils (*Lithospermo-Quercetum*, *Seslerio-Quercetum* and *Quercetum pubescenti-roboris*), depending on habitat conditions and species pools available. Further examples of (at least partly) vicariant associations include *Genisto-Quercetum* and *Sorbo-Quercetum* on dry and acidic sites, *Melico-Quercetum*, *Carici fritschii-Quercetum* and *Quercetum petraeo-cerridis* on semi-open, mesic, moderately base- and nutrient-rich sites, or *Euphorbio-Quercetum* and *Convallario-Quercetum* on base- and nutrient-rich sites. We suggest that this pattern to some extent reflects different evolutionary, refugial and migration histories of different oak forest sites. Some of them apparently harbour relict light-demanding species inherited from cold-tolerant Pleistocene and Early Holocene communities (Roleček 2007b, Chytrý et al. 2010), while others were shaped by postglacial processes, including the spread of sub-Mediterranean and other relatively thermophilous species (Ložek 2007). On the other hand, local co-occurrence patterns of different oak forest associations are usually driven by simple ecological rules (see the scheme in Fig. 4 and differences in EIVs and altitude in Fig. 5).

These rules are also reflected in the differentiation of thermophilous oak forest alliances with respect to climatic conditions (Fig. 6, Electronic Appendix 6). Stands of the *Aceri tatarici-Quercion* alliance occur at sites with the highest annual mean temperature during the warmest and coldest quarters, and lowest annual precipitation. In contrast, stands of the *Quercion pubescenti-petraeae* alliance occur at sites with a lower annual mean

Table 1. – An abridged synoptic table of the associations of the *Quercetea pubescentis* class in Slovakia. Different alliances are separated by vertical lines. Percentage frequency values of diagnostic species (D.S., phi coefficient ≥ 0.20, frequency ≥ 20%, Fisher's exact test P < 0.001, frequency not higher than 50% in more than one association) are shown on a grey background. They are sorted by decreasing fidelity. Diagnostic species with a frequency at least 1.3× higher then in any other association within the alliance are given in bold. Other abundant species (frequency > 35% in the whole dataset) and the remaining *Quercus* species (tree layer) are listed at the bottom of the table. They are sorted by decreasing frequency. *Allium *montanum – A. senescens* subsp. *montanum*, *Poa *scabra – P. pannonica* subsp. *scabra*, *Verbascum *austriacum – V. chaixii* subsp. *austriacum*; (E_3) – tree layer; (E_2) – shrub layer; no information on layer – herb layer and saplings. Association numbers correspond to the numbers in the text and figures. Full synoptic table is provided in Electronic Appendix 9.

Association number Association name abbreviation Alliance name abbreviation	1 LpQp Qpp	2 SaQp Qpp	3 FoQp Qpp	4 EQ Qpp	5 Qpr AtQ	6 CQr AtQ	7 CfQr Qp	8 StQ Qp	9 GpQp Qp	10 MpQr Qp	11 Qpc Qp
Number of relevés	214	139	29	231	32	72	12	231	20	51	100
D.S. *Lithospermo purpurocaerulei-Quercetum pubescentis*											
Erysimum odoratum	**55**	8	0	12	0	0	0	1	0	0	0
Melica ciliata	**45**	10	14	2	3	1	0	0	0	0	0
Scabiosa ochroleuca	**29**	4	3	1	0	0	0	0	0	0	1
Sedum sexangulare	**35**	4	14	2	0	0	0	3	0	0	4
Stachys recta	44	4	34	10	6	0	0	2	0	0	0
Potentilla arenaria agg.	**31**	0	7	1	0	0	0	0	15	0	0
Asperula cynanchica	**44**	21	14	3	0	0	0	1	30	0	1
Allium flavum	**36**	14	17	5	0	0	0	1	0	0	2
Bupleurum falcatum	**40**	21	0	22	0	0	0	3	10	0	0
Arabis turrita	**24**	4	0	6	0	0	0	1	0	0	0
Berberis vulgaris	**33**	11	0	10	3	10	0	1	0	0	0
Sanguisorba minor	**27**	16	3	5	0	0	0	0	0	0	0
Rhamnus cathartica	**44**	20	10	13	16	17	0	3	5	0	4
Acosta rhenana	**21**	0	10	1	0	0	0	0	0	0	0
Origanum vulgare	**43**	12	17	13	16	0	0	11	5	4	9
Jovibarba globifera	**20**	7	3	1	0	0	0	0	0	0	0
Fraxinus excelsior	**46**	10	0	23	6	35	17	17	0	16	5
Berberis vulgaris (E_2)	**21**	10	0	6	0	7	0	0	0	2	0
Anthericum ramosum	**57**	40	34	19	6	1	42	20	20	16	5
Veronica teucrium	**22**	0	3	4	16	1	0	1	0	2	0
Quercus pubescens agg. (E_2)	33	23	34	20	19	3	0	1	0	0	1
Inula conyza	**21**	12	10	7	9	3	0	2	0	0	11
Corylus avellana	**26**	9	7	11	0	10	8	16	0	18	3
D.S. *Seslerio albicantis-Quercetum pubescentis*											
Asperula tinctoria	21	**74**	0	3	0	0	8	1	0	0	0
Potentilla heptaphylla	7	**78**	7	7	19	0	0	2	0	0	3
Leontodon incanus	11	**56**	0	2	0	0	0	0	0	0	0
Hippocrepis comosa	10	**49**	0	4	0	0	0	0	0	0	0
Galium pumilum agg.	1	**33**	0	1	0	0	0	0	0	0	1
Dorycnium pentaphyllum agg.	21	**59**	34	2	0	0	0	2	0	2	17
Acinos alpinus	1	**27**	0	0	0	0	0	0	0	0	0
Chamaecytisus hirsutus	5	**39**	7	8	3	0	0	2	0	8	2
Bromus monocladus	0	**22**	0	1	0	0	0	0	0	0	0
Polygala amara agg.	1	**22**	0	0	0	0	0	0	0	0	0
Lotus corniculatus	14	**40**	17	1	0	0	0	6	0	0	5
Juniperus communis	12	**40**	10	7	0	0	0	3	0	0	13
Teucrium montanum	15	**26**	0	1	0	0	0	0	0	0	0
Thalictrum minus	9	**29**	3	2	9	0	0	0	0	0	1
Leontodon hispidus	9	**30**	0	0	6	0	8	0	0	2	1
Epipactis atrorubens	1	**22**	0	3	3	1	0	0	0	0	0

Association number Association name abbreviation Alliance name abbreviation	1 LpQp Qpp	2 SaQp Qpp	3 FoQp Qpp	4 EQ Qpp	5 Qpr AtQ	6 CQr AtQ	7 CfQr Qp	8 StQ Qp	9 GpQp Qp	10 MpQr Qp	11 Qpc Qp
Number of relevés	214	139	29	231	32	72	12	231	20	51	100
Campanula rotundifolia agg.	9	**32**	0	1	0	0	25	2	0	0	0
Thymus praecox	3	**22**	7	1	0	0	0	0	0	0	3
Primula veris	27	**55**	21	20	34	14	0	8	0	16	5
Epipactis helleborine agg.	9	**32**	7	8	3	6	8	9	0	2	1
Viburnum lantana	34	**45**	3	32	9	29	0	8	0	4	3
Asarum europaeum	10	**30**	0	16	0	17	0	8	0	6	0
Tithymalus epithymoides	25	**40**	21	12	19	3	0	7	10	4	2
Melampyrum cristatum	18	21	0	15	0	0	0	2	0	0	0
Inula hirta	15	22	17	2	3	1	0	4	0	0	2
Fragaria moschata	34	**47**	0	20	44	19	0	39	0	25	30
D.S. *Fraxino orni-Quercetum pubescentis*											
Achillea nobilis	1	0	**45**	1	0	0	0	5	0	0	4
Cota tinctoria	4	0	**38**	1	0	0	0	1	0	0	5
*Poa *scabra*	0	0	**38**	0	0	0	0	1	0	0	9
Festuca pseudodalmatica	1	0	**45**	1	0	0	0	2	20	0	16
Fraxinus ornus (E_3)	6	2	**34**	3	3	1	0	0	0	0	0
Lactuca viminea	2	0	**31**	1	0	0	0	1	10	0	0
Trifolium alpestre	19	29	**83**	20	28	0	42	31	20	22	35
Fraxinus ornus (E_2)	9	4	**34**	3	6	1	0	0	0	4	2
Myosotis arvensis	0	0	**24**	1	3	0	0	3	0	0	0
Carex praecox	4	0	**31**	1	16	0	0	1	0	2	2
Vicia hirsuta	0	0	**28**	2	0	0	0	6	5	0	4
Verbascum phoeniceum	3	0	**24**	1	6	0	0	1	0	6	1
Thymus pannonicus	16	1	**24**	1	0	0	0	0	0	0	0
Ajuga genevensis	19	30	**52**	7	19	6	0	14	20	8	17
Seseli osseum	22	6	**34**	4	0	0	0	1	25	0	12
D.S. *Euphorbio-Quercetum*											
Waldsteinia geoides	5	1	0	**29**	0	6	0	2	0	2	0
Glechoma hederacea agg.	23	4	3	**41**	19	25	0	11	0	12	9
Crataegus laevigata (E_2)	8	14	10	**44**	9	18	0	26	0	20	32
D.S. *Quercetum pubescenti-roboris*											
Cruciata laevipes	1	0	0	2	**50**	19	8	1	0	2	14
Dictamnus albus	15	1	3	5	**47**	22	0	2	0	0	0
Pulmonaria mollis s. lat.	9	9	14	14	**69**	18	0	25	10	25	15
Euonymus europaeus (E_2)	1	0	0	2	**34**	15	0	1	0	10	1
Ranunculus polyanthemos	4	9	3	3	**38**	4	0	6	0	14	4
Allium scorodoprasum	0	0	0	0	**25**	6	0	1	0	0	8
Viola suavis	0	0	3	3	**22**	4	0	1	0	0	0
Inula salicina	1	2	0	1	**22**	1	0	1	0	6	0
Carex michelii	13	28	34	34	**63**	25	0	14	0	24	15
Rhamnus cathartica (E_2)	14	5	3	4	**38**	11	17	3	0	4	10
Vicia pisiformis	0	0	3	1	**22**	1	0	4	0	2	7
Robinia pseudoacacia (E_2)	0	0	3	1	**25**	8	0	2	15	4	3
Vicia cracca agg.	1	0	24	6	**31**	0	0	9	0	10	12
Carex muricata agg.	14	12	31	26	**59**	42	25	23	0	20	47
D.S. *Convallario-Quercetum roboris*											
Viola mirabilis	1	8	0	11	22	**47**	0	2	0	12	3
Acer campestre (E_3)	8	17	24	35	41	**57**	0	13	0	18	2
Clematis vitalba	9	6	3	9	6	**29**	0	6	0	2	1
Alliaria petiolata	17	1	17	33	28	**49**	0	17	0	6	22
Galium odoratum	7	6	0	8	0	**29**	0	20	0	16	3

Association number	1	2	3	4	5	6	7	8	9	10	11
Association name abbreviation	LpQp	SaQp	FoQp	EQ	Qpr	CQr	CfQr	StQ	GpQp	MpQr	Qpc
Alliance name abbreviation	Qpp	Qpp	Qpp	Qpp	AtQ	AtQ	Qp	Qp	Qp	Qp	Qp
Number of relevés	214	139	29	231	32	72	12	231	20	51	100
Geranium robertianum	16	0	0	13	19	**38**	17	14	5	0	20
Convallaria majalis	4	16	0	28	25	**39**	42	19	0	25	2
D.S. *Carici fritschii-Quercetum roboris*											
Festuca rubra agg.	0	1	7	1	0	0	**92**	5	0	20	29
Carex fritschii	0	0	0	0	0	0	**58**	0	0	0	0
Arrhenatherum elatius	13	0	7	4	0	0	**75**	3	10	8	1
Peucedanum oreoselinum	4	0	0	1	13	0	**67**	1	0	8	1
Anthoxanthum odoratum	0	0	0	1	0	0	**58**	2	0	8	4
Frangula alnus (E_2)	1	0	0	0	0	1	**67**	6	0	24	3
Cerastium arvense	0	4	0	1	0	0	**50**	0	0	0	0
Viola canina	0	0	0	0	0	0	**50**	1	0	4	1
Festuca ovina agg.	9	1	3	9	6	0	**75**	6	30	2	10
Iris variegata	6	0	0	0	6	1	**50**	0	0	0	0
Luzula campestris agg.	1	0	7	1	13	0	**67**	8	20	12	13
Carex caryophyllea	1	2	17	1	6	0	**58**	2	0	8	17
Pulmonaria angustifolia	0	0	0	0	0	0	**33**	0	0	0	0
Polygonatum odoratum	40	21	14	19	13	17	**92**	17	45	6	8
Lysimachia vulgaris	1	0	0	0	0	0	**33**	1	0	0	0
Molinia caerulea agg.	0	0	0	0	0	0	**33**	4	0	0	0
Calamagrostis epigejos	1	3	7	1	25	1	**58**	3	5	6	18
Carex pallescens	0	0	0	1	0	0	**42**	2	0	20	5
Mycelis muralis	18	9	0	16	3	15	**67**	26	5	12	13
Agrostis vinealis	0	0	0	0	0	0	**25**	0	0	0	0
Frangula alnus	0	0	0	0	0	0	**33**	5	0	6	4
Hieracium umbellatum	3	2	0	2	0	1	**42**	3	20	6	0
Carex supina	0	0	3	0	0	0	**25**	0	0	0	0
Moehringia trinervia	0	0	0	3	0	8	**42**	8	5	6	22
Thesium linophyllon	3	0	0	0	0	0	**25**	0	10	0	1
Campanula patula	0	0	0	0	0	0	**25**	1	0	8	6
Galium verum agg.	13	2	21	10	25	0	**58**	7	0	33	30
D.S. *Sorbo torminalis-Quercetum*											
Carex digitata	3	5	0	12	0	4	0	**27**	0	10	1
Galium schultesii	9	19	21	42	3	14	0	**62**	40	35	26
Campanula persicifolia	16	27	14	25	38	17	25	**61**	15	41	42
Hypericum montanum	1	5	0	5	0	0	8	**20**	0	10	8
Festuca heterophylla	6	1	24	10	28	6	0	39	10	35	19
D.S. *Genisto pilosae-Quercetum petraeae*											
Linaria genistifolia	19	0	31	1	0	0	0	3	**85**	0	5
Dalanum ladanum	1	0	7	1	0	0	0	3	**65**	0	1
Cardaminopsis arenosa agg.	24	11	28	13	0	0	0	18	**85**	0	6
Steris viscaria	1	0	21	1	6	0	42	17	**85**	12	18
Avenella flexuosa	1	0	0	2	0	0	0	6	**45**	6	0
Pilosella cymosa	5	0	3	1	0	0	0	1	**40**	0	0
Digitalis grandiflora	7	1	7	10	0	6	8	27	**70**	24	11
Rosa canina agg.	5	2	48	42	22	18	0	28	**90**	25	17
Acetosella multifida agg.	1	0	0	0	0	0	8	1	**35**	0	0
Myosotis sylvatica	1	1	0	2	0	0	0	5	**30**	0	0
Fagus sylvatica	15	13	7	9	0	3	0	27	**55**	12	1
Hieracium laevicaule	0	0	0	1	0	0	0	1	**25**	2	0
Polypodium vulgare	1	0	0	5	0	0	0	6	**30**	2	0
Asplenium septentrionale	0	0	0	0	0	0	0	1	**20**	0	0
Verbascum densiflorum	2	0	0	0	0	0	0	1	**20**	0	0

Association number Association name abbreviation Alliance name abbreviation	1 LpQp Qpp	2 SaQp Qpp	3 FoQp Qpp	4 EQ Qpp	5 Qpr AtQ	6 CQr AtQ	7 CfQr Qp	8 StQ Qp	9 GpQp Qp	10 MpQr Qp	11 Qpc Qp
Number of relevés	214	139	29	231	32	72	12	231	20	51	100
Pilosella officinarum	2	15	3	1	0	0	8	2	**30**	0	8
Pseudolysimachion spicatum	12	0	10	1	3	0	8	1	**30**	0	7
Silene vulgaris	13	2	10	10	9	1	0	9	**35**	10	5
Genista tinctoria	21	9	31	13	13	3	17	42	**60**	33	29
D.S. *Melico pictae-Quercetum roboris*											
Ranunculus auricomus agg.	0	0	0	5	0	6	0	15	0	**29**	6
Lysimachia nummularia	0	0	0	0	9	3	0	5	0	**25**	16
Vicia sepium	1	0	0	3	3	8	8	14	0	**25**	5
Viola riviniana	0	1	0	4	13	3	8	16	0	**29**	17
Carpinus betulus (E_3)	7	1	14	33	9	36	0	29	0	**43**	19
Polygonatum multiflorum	1	0	0	11	6	17	0	10	0	**24**	2
Melampyrum pratense	2	17	0	2	0	1	42	20	30	35	0
Scrophularia nodosa	0	0	0	1	13	13	25	16	0	27	6
Viola reichenbachiana	1	11	3	10	9	31	0	27	0	33	15
Serratula tinctoria	1	0	17	3	19	1	25	7	0	29	13
Heracleum sphondylium	0	1	0	13	19	15	0	6	0	**22**	0
D.S. *Quercetum petraeo-cerridis*											
Vicia cassubica	0	0	0	2	16	0	0	6	0	14	**43**
Lychnis coronaria	0	0	7	0	0	0	0	2	0	0	**28**
Veronica officinalis	0	2	3	1	9	4	33	36	20	31	**54**
Torilis japonica	1	0	0	9	9	18	25	14	0	6	**40**
Acer tataricum	1	0	7	3	6	18	0	3	0	16	**26**
Acer tataricum (E_2)	0	0	3	3	6	10	0	2	0	18	23
Pyrus communis agg. (E_2)	10	14	17	16	19	4	0	9	0	14	**34**
*Verbascum *austriacum*	35	35	24	18	41	4	0	17	0	4	**42**
Cerasus avium	7	6	10	20	28	11	25	42	10	37	44
Species diagnostic for two or three associations											
Helianthemum nummularium agg.	**48**	23	3	4	0	0	0	0	0	0	1
Oryzopsis virescens	**48**	32	0	6	3	7	0	0	0	2	0
Campanula glomerata agg.	**30**	21	14	2	0	0	0	2	0	4	2
Inula ensifolia	33	36	7	9	3	1	0	1	0	0	1
Sorbus aria (E_2)	40	**52**	0	16	0	4	0	5	15	4	0
Salvia pratensis	34	35	24	11	9	0	0	1	0	0	1
Sorbus aria (E_3)	28	33	0	8	0	1	0	3	15	0	0
Sesleria albicans	21	**47**	0	1	0	0	0	0	0	0	0
Arabis hirsuta agg.	27	**62**	3	8	3	0	0	3	0	0	1
*Allium *montanum*	**37**	22	3	3	0	0	0	3	**55**	0	8
Pilosella bauhinii	24	44	**72**	5	0	0	8	11	20	6	23
Sorbus torminalis	30	**63**	0	41	3	14	0	31	5	12	8
Sorbus torminalis (E_3)	14	38	3	42	6	18	0	19	0	12	1
Festuca pallens	19	**26**	0	1	0	0	0	0	**50**	0	0
Rosa canina agg. (E_2)	7	9	**48**	28	**44**	8	8	16	**35**	16	10
Campanula bononiensis	12	0	**31**	4	**22**	0	0	1	0	0	0
Campanula rapunculoides	26	25	17	**49**	0	21	0	**42**	15	22	8
Lathyrus vernus	3	3	3	**34**	3	15	0	44	0	37	7
Bromus benekenii	3	9	0	**27**	9	**31**	0	14	0	12	3
Ulmus minor (E_2)	1	0	7	2	**50**	28	0	0	0	0	8
Viola odorata	19	1	10	4	**47**	31	0	3	0	8	2
Ulmus minor (E_3)	0	0	0	1	31	29	0	1	0	2	0
Galium aparine	3	1	38	27	**63**	44	0	20	10	8	25
Arum alpinum agg.	1	0	0	1	28	31	0	1	0	2	0
Polygonatum latifolium	0	0	0	1	28	31	0	1	0	4	3

Association number Association name abbreviation Alliance name abbreviation	1 LpQp Qpp	2 SaQp Qpp	3 FoQp Qpp	4 EQ Qpp	5 Qpr AtQ	6 CQr AtQ	7 CfQr Qp	8 StQ Qp	9 GpQp Qp	10 MpQr Qp	11 Qpc Qp
Number of relevés	214	139	29	231	32	72	12	231	20	51	100
Ulmus minor	1	0	0	2	28	33	0	1	0	0	7
Chaerophyllum temulum	0	0	0	8	25	**33**	0	1	0	8	2
Quercus robur agg. (E_2)	0	0	0	1	**38**	7	17	2	0	**35**	0
Prunus spinosa (E_2)	8	5	0	14	**75**	14	0	10	0	37	**49**
Agrimonia eupatoria	8	2	21	10	**53**	3	0	2	0	10	**33**
Hypericum hirsutum	0	0	0	2	**31**	11	0	5	0	10	**31**
Rosa gallica	1	1	17	3	**22**	3	0	3	0	6	**22**
Quercus robur agg.	0	1	0	1	9	13	**67**	2	0	49	0
Potentilla alba	0	0	0	1	0	1	**50**	5	0	33	10
Agrostis capillaris	1	0	0	0	6	0	**83**	5	10	22	37
Rubus sect. *Rubus*	6	1	3	3	13	13	**58**	17	15	22	41
Luzula luzuloides	0	0	0	3	0	1	0	45	**90**	22	3
Quercus petraea agg. (E_2)	1	5	21	18	19	6	8	48	60	29	40
Carex montana	5	17	0	16	6	11	8	39	0	**57**	9
Cruciata glabra	5	1	3	42	3	7	0	55	30	43	49
Hieracium sabaudum	3	25	17	16	19	4	8	53	15	31	49
Fragaria viridis	14	4	**34**	4	**31**	6	0	0	0	10	**31**
Quercus cerris (E_2)	2	12	**45**	6	**41**	7	0	7	0	22	**63**
Other abundant species											
Vincetoxicum hirundinaria	89	94	28	76	47	50	58	50	60	29	40
Veronica chamaedrys agg.	26	44	79	65	69	29	83	85	95	80	81
Cornus mas (E_2)	88	88	34	89	44	71	0	21	0	27	10
Tithymalus cyparissias	83	67	76	39	63	19	92	32	40	35	76
Quercus petraea agg. (E_3)	7	23	38	65	47	51	25	100	100	39	69
Clinopodium vulgare	50	13	14	62	78	36	100	67	15	55	73
Ligustrum vulgare (E_2)	35	58	34	67	94	58	17	40	5	41	75
Ligustrum vulgare	47	51	28	68	34	72	25	48	5	47	45
Acer campestre	52	34	45	69	72	81	8	48	0	31	37
Pyrethrum corymbosum	52	61	38	72	41	22	0	50	10	37	27
Poa nemoralis	19	5	45	35	84	49	17	87	95	67	77
Crataegus monogyna (E_2)	58	63	48	55	53	54	0	26	0	29	45
Teucrium chamaedrys	88	96	79	37	28	0	50	17	25	0	33
Quercus pubescens agg. (E_3)	86	91	59	58	41	18	0	2	0	0	4
Melica uniflora	36	35	10	64	53	64	0	40	5	25	21
Brachypodium sylvaticum	28	54	10	39	47	78	83	34	0	31	50
Melittis melissophyllum	27	58	7	48	25	36	0	52	0	35	25
Crataegus monogyna	58	49	24	44	41	57	8	26	0	18	20
Fragaria vesca	18	21	10	58	6	18	58	57	20	67	46
Poa pratensis agg.	28	45	72	33	88	6	83	26	40	41	81
Geum urbanum	37	9	21	43	88	76	25	31	10	45	51
Quercus petraea agg.	5	12	31	38	31	25	17	82	100	24	53
Cornus mas	63	62	14	52	6	43	0	16	0	20	4
Brachypodium pinnatum	57	67	38	41	44	13	33	24	0	20	9
Astragalus glycyphyllos	14	29	34	41	50	21	0	60	10	27	56
Viola hirta	47	49	21	27	69	46	0	19	0	31	60
Acer campestre (E_2)	28	14	31	47	84	68	0	34	0	31	42
Dactylis polygama	16	21	34	51	56	31	58	48	25	31	38
Securigera varia	69	58	69	23	28	11	8	25	20	4	23
Lathyrus niger	1	14	10	47	47	28	0	69	0	53	41
Quercus cerris (E_3)	12	35	79	27	75	63	0	24	0	20	94
Quercus robur agg. (E_3)	1	1	0	2	53	51	92	6	0	69	2

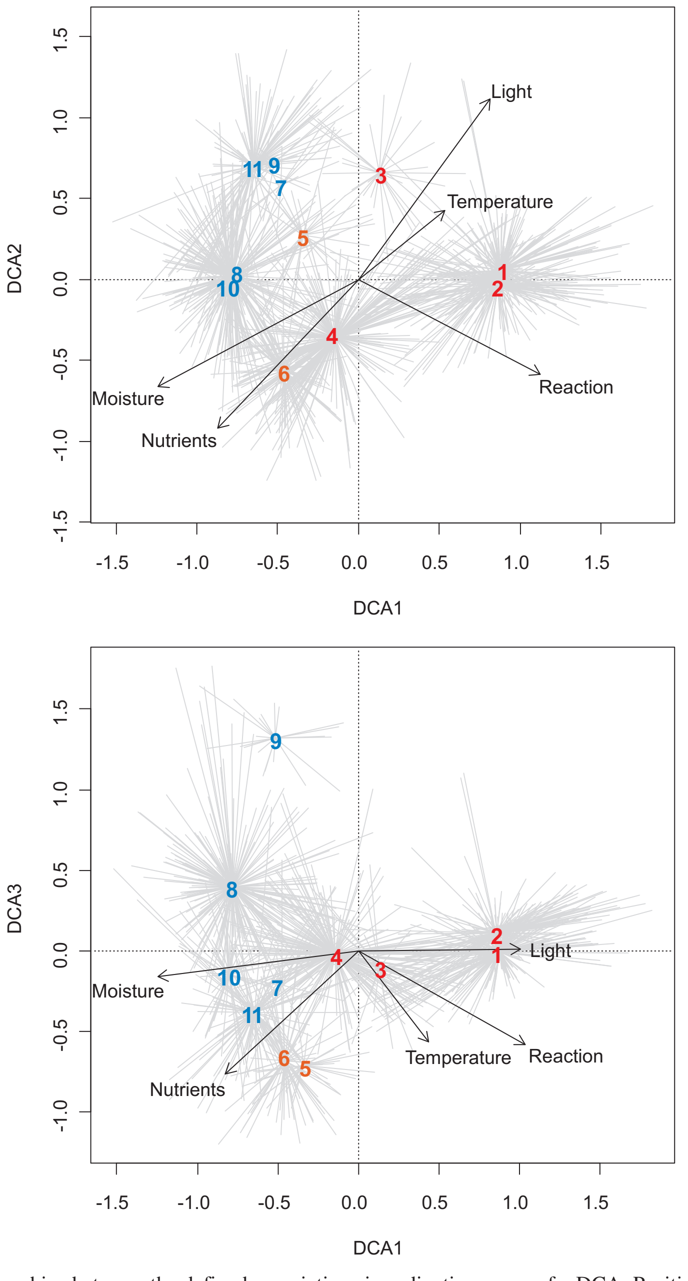

Fig. 3. – Relationships between the defined associations in ordination space of a DCA. Positions on the first and second (top) and first and third (bottom) ordination axes are shown. Arrows are passively projected vectors of EIVs. Numerals denote centroids of clusters formed by relevés classified to the same association. Shared colours indicate associations classified to the same alliance. Grey lines connect centroids with individual relevés. Association codes: 1 – *Lithospermo purpurocaerulei-Quercetum pubescentis*, 2 – *Seslerio albicantis-Quercetum pubescentis*, 3 – *Fraxino orni-Quercetum pubescentis*, 4 – *Euphorbio-Quercetum*, 5 – *Quercetum pubescenti-roboris*, 6 – *Convallario-Quercetum roboris*, 7 – *Carici fritschii-Quercetum roboris*, 8 – *Sorbo torminalis-Quercetum*, 9 – *Genisto pilosae-Quercetum petraeae*, 10 – *Melico pictae-Quercetum roboris*, 11 – *Quercetum petraeo-cerridis*.

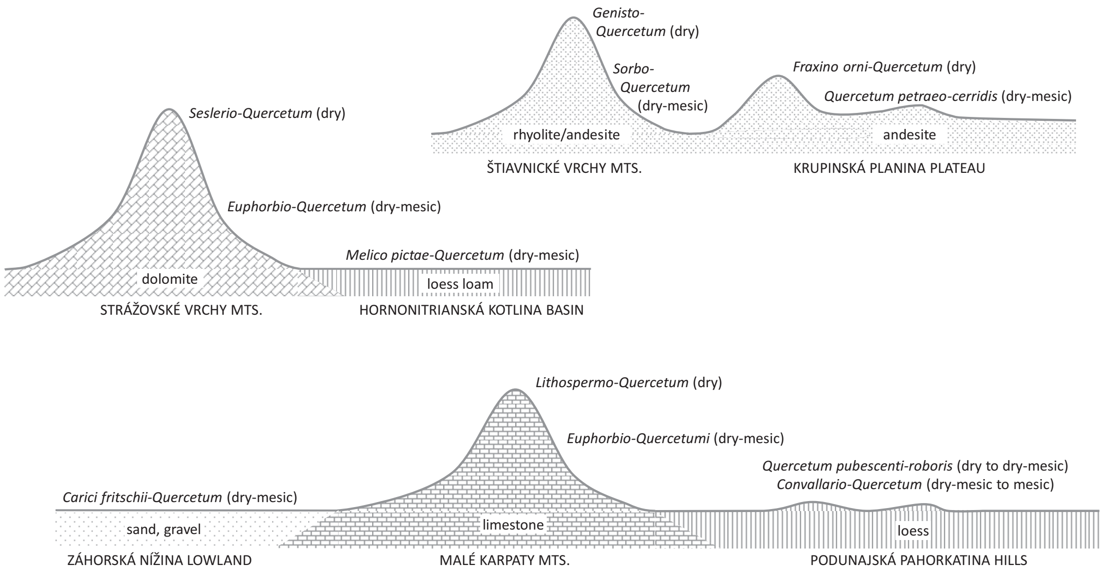

Fig. 4. – A simplified scheme of a typical position of defined associations in the Slovak landscapes.

temperature and the highest amount of precipitation. Vegetation of the *Quercion petraeae* alliance mostly occurs in areas with intermediate values of precipitation and temperature; however, during the coldest quarter, the lowest temperatures are recorded there.

Characteristics of syntaxa

Full syntaxonomic scheme and its comparison with the previously accepted one is provided in Electronic Appendix 4. Information on structure, composition, ecology and syntaxonomy of the distinguished associations is provided below. We do not provide detailed characteristics of higher syntaxa, which would largely repeat information available elsewhere (e.g. Willner & Grabherr 2007, Roleček 2013) and will be provided in the upcoming sixth volume of the monograph Plant communities of Slovakia.

Quercion pubescenti-petraeae **alliance**

Diagnostic species (sorted by decreasing fidelity; E_3 – tree layer; E_2 – shrub layer; no layer information – herb layer and saplings): *Carex humilis*, *Quercus pubescens* agg., *Quercus pubescens* agg. (E_3), *Erysimum odoratum*, *Teucrium chamaedrys*, *Asperula tinctoria*, *Helianthemum nummularium* agg., *Bupleurum falcatum*, *Arabis hirsuta* agg., *Sesleria albicans*, *Leontodon incanus*, *Pimpinella saxifraga*, *Sorbus aria* (E_2), *Hippocrepis comosa*, *Asperula cynanchica*, *Inula ensifolia*, *Allium flavum*, *Sanguisorba minor*, *Sorbus aria*, *Salvia pratensis*, *Stachys recta*, *Melica ciliata*, *Melampyrum cristatum*, *Oryzopsis virescens*, *Cornus mas* (E_2), *Teucrium montanum*, *Sorbus aria* (E_3), *Campanula glomerata* agg., *Dorycnium pentaphyllum* agg., *Scabiosa ochroleuca*, *Arabis turrita*, *Galium glaucum*, *Quercus pubescens* agg. (E_2), *Potentilla arenaria* agg.,

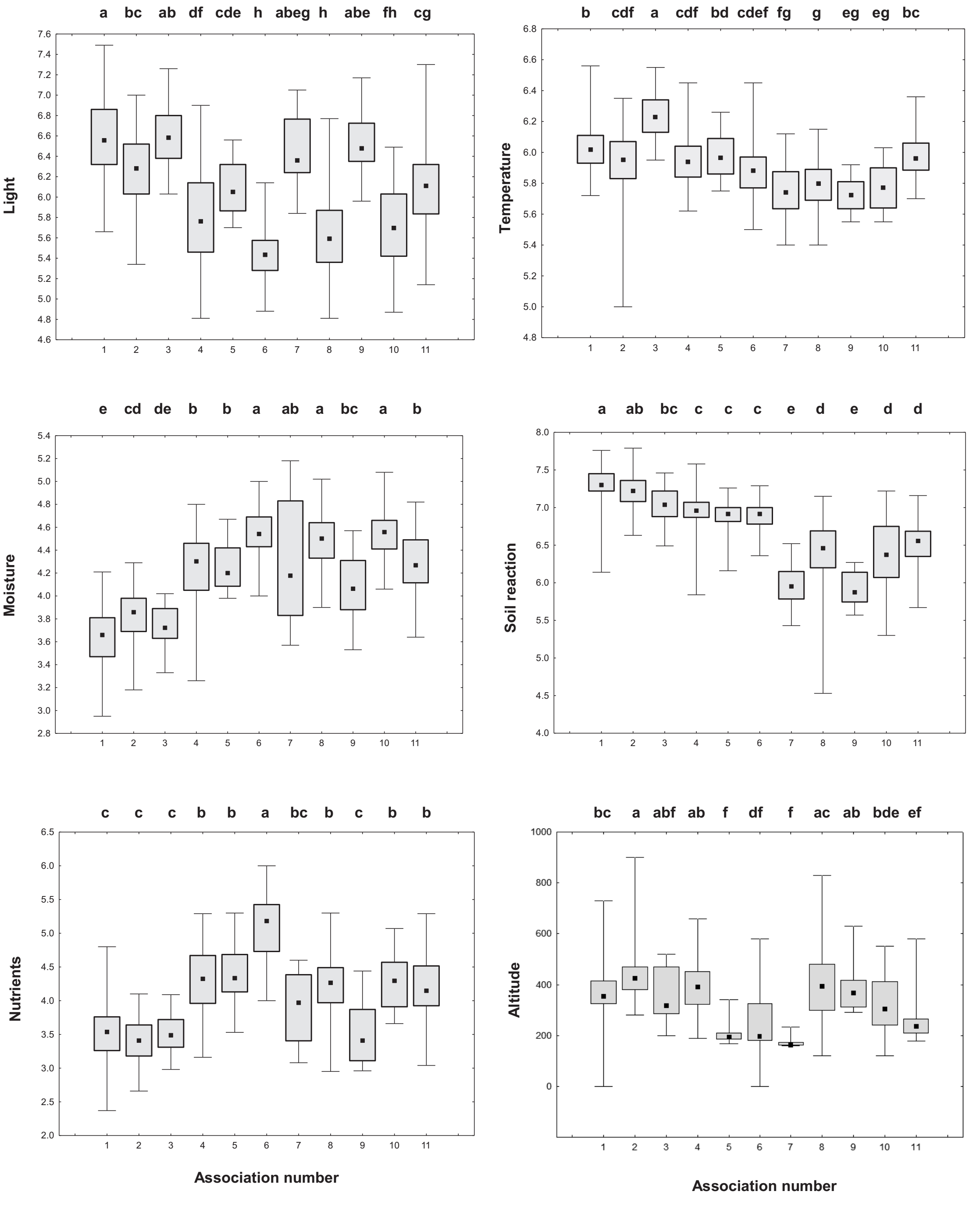

Fig. 5. – Differences in EIVs and altitude of the defined associations. Medians, lower and upper quartiles and 5th and 95th percentiles are shown. Significant differences (ANOVA, Tukey's HSD for unequal N test and multiple comparison tests of the mean ranks, $P < 0.01$) are marked by different letters above the boxes. Association numbers (1–11) correspond to numbers in the text, Table 1 and Figure 3.

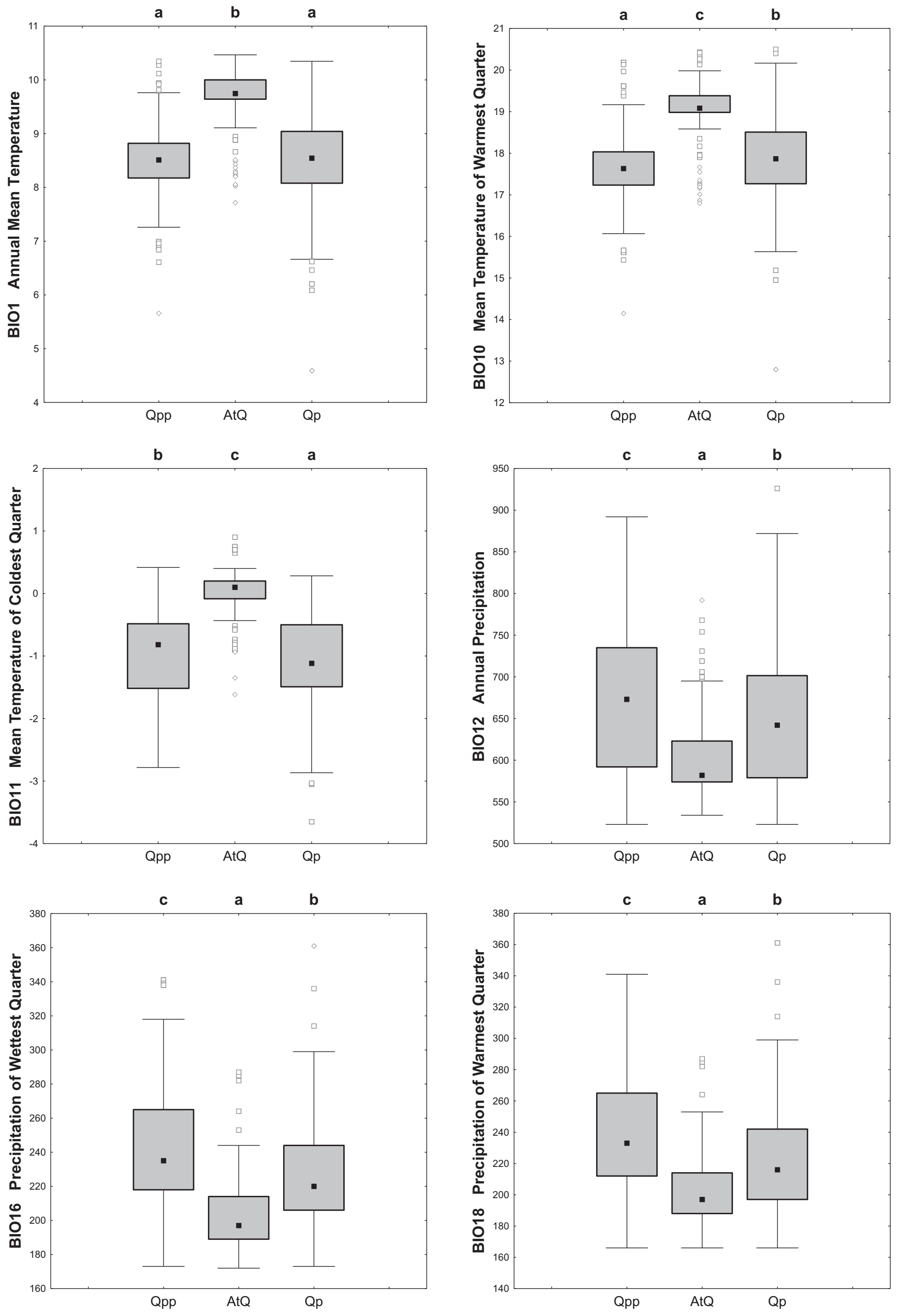

Fig. 6. – Differences in particular bioclimatic variables associated with the defined alliances. Qpp – *Quercion pubescenti-petraeae*, AtQ – *Aceri tatarici-Quercion*, Qp – *Quercion petraeae*. Medians, lower und upper quartiles, non-outlier range, outliers and extreme values are shown. Significant differences (ANOVA, Tukey's HSD for unequal N test and multiple comparison tests of the mean ranks, $P < 0.05$) are marked by different letters above the boxes.

Anthericum ramosum, *Jovibarba globifera*, *Potentilla heptaphylla*, *Galium mollugo* agg., *Anthyllis vulneraria*, *Cornus mas*, *Acosta rhenana*, *Medicago falcata*, *Cerasus mahaleb*, *Brachypodium pinnatum*, *Sedum sexangulare*, *Securigera varia*, *Thymus pannonicus*, *Cerasus mahaleb*, *Galium pumilum* agg., *Allium senescens* subsp. *montanum*, *Aconitum anthora*, *Vincetoxicum hirundinaria*, *Festuca pallens*, *Juniperus communis*, *Acinos alpinus*, *Chamaecytisus hirsutus*, *Campanula rotundifolia* agg., *Asplenium ruta-muraria*, *Lotus corniculatus*, *Achillea millefolium* agg., *Bromus monocladus*, *Polygala amara* agg., *Sorbus torminalis*, *Viola collina*, *Thymus pulegioides*, *Genista pilosa*, *Cotoneaster tomentosus*, *Tithymalus epithymoides*, *Thymus praecox*, *Pilosella bauhinii.*

1. *Lithospermo purpurocaerulei-Quercetum pubescentis* – dry oak forests on carbonate bedrock

D e s c r i p t i o n: Open to semi-open stands on extremely warm and dry sites. The tree layer (mean cover close to 50%) is dominated by *Quercus pubescens* agg., sometimes also *Q. cerris* and *Q. petraea* agg., frequently with an admixture of *Fraxinus excelsior*, *Sorbus aria*, *S. torminalis* and *Tilia cordata*. The shrub layer is usually species-rich and is dominated by light-demanding species (mostly *Berberis vulgaris*, *Cornus mas*, *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare*, *Quercus pubescens* agg., *Sorbus aria* agg.). Frequently there is an admixture of the mesophilous species *Acer campestre* and *Corylus avellana*. The herb layer is variable in both abundance and number of species, but species-rich stands prevail. The most frequent dominants are drought-tolerant graminoids (*Brachypodium pinnatum*, *Carex humilis*, *Festuca rupicola*, *Melica ciliata*, *Oryzopsis virescens* and *Sesleria albicans*), together with herbs characteristic of *Festuco-Brometea* and *Trifolio-Geranietea* classes, such as *Anthericum ramosum*, *Galium glaucum*, *Inula ensifolia*, *Teucrium chamaedrys*, *Tithymalus cyparissias* and *Vincetoxicum hirundinaria.*

E c o l o g y: Occupy extremely warm and dry sites, often in a fine-scale mosaic of forests, thermophilous scrub and fringe communities. Usually occur on moderate to very steep sun-exposed slopes (mean slope 25°) with south and south-west orientations. The most frequent soils are Rendzic and Lithic Leptosols developed over limestones and less often dolomites.

D i s t r i b u t i o n: Scattered in lower mountain ranges (mean altitude 380 m a.s.l.) with carbonate rocks on southern periphery of the Carpathians, both in western and eastern Slovakia, mainly in Malé Karpaty Mts, Považský Inovec Mts, Strážovské vrchy Mts, Slovenský kras Karst, Čierna hora Mts and Vihorlat Mts, rarely elsewhere.

Syntaxonomy:

Association name: *Lithospermo purpurocaerulei-Quercetum pubescentis* Michalko 1957
Orig. (Michalko 1957, p. 69): Asociácia *Quercus pubescens-Lithospermum purpureo-coeruleum*
Nomenclatural type: Michalko (1957): Table 4, rel. 7, lectotypus hoc loco
Synonyms: *Quercetum lanuginosae pannonicum* Dostál 1933 p. p. (§34a); *Dictamno-Sorbetum* Knapp 1942 p. p. (§1); *Pruno mahaleb-Quercetum pubescentis* Jakucs et Fekete 1957 (§3f), *Carici-Quercetum virgilianae* (Klika 1951) Miadok 1980 prov., nom. ined. (§1), *Pruno mahaleb-Quercetum pubescentis* Jakucs et Fekete ex Jakucs 1961 (syntax. syn); *Asplenio cuneifolii-Quercetum petraeae* Chytrý et Horák 1997 p. p. (syntax. syn.), *Quercetum pubescentis praecarpaticum* subass. with *Cotinus coggygria* Futák 1947 p. p. (incl.), *Quercetum pubescentis praecarpaticum* sensu Futák 1947 p. p., non Klika 1937 (pseudonym)

2. *Seslerio albicantis-Quercetum pubescentis* – dealpine oak forests on carbonate bedrock

D e s c r i p t i o n: Open to semi-open stands on moderately warm and dry sites. The tree layer (mean cover 60%) is usually dominated by *Q. pubescens* agg., often of dwarfed growth, with admixture of *Fagus sylvatica*, *Quercus cerris*, *Q. petraea* agg., *Pinus sylvestris*, *Sorbus aria* agg. and *S. torminalis*. The shrub layer is poorly to moderately developed and mostly dominated by *Cornus mas*. There is often an admixture of *Crataegus monogyna*, *Ligustrum vulgare* and *Sorbus aria* agg. The herb layer is usually well developed and species-rich, with a characteristic mixture of montane species (e.g. *Acinos alpinus*, *Carduus glaucinus*, *Carex alba*, *Hippocrepis comosa*, *Leontodon incanus*, *Phyteuma orbiculare*, *Polygala amara* agg., *Pulsatilla subslavica* and *Sesleria albicans*) and species of warm and dry sites, often near the northern limit of their distribution in Slovakia (Galvánek 1998). Drought-tolerant heliophilous graminoids (*Brachypodium pinnatum*, *Carex humilis*, *Sesleria albicans*) usually dominate. A relatively mesophilous character is reflected in a higher frequency of species such as *Brachypodium sylvaticum*, *Galium mollugo* agg., *Melittis melissophyllum*, *Hieracium murorum*, *Primula veris* and *Symphytum tuberosum* agg.

E c o l o g y: Occupy moderately warm and dry sites on the upper parts of moderate to steep slopes (mean 23°) with south, south-east and south-west orientations. The most frequent soil is shallow Rendzic Leptosol developed over dolomite, on extreme slopes also over limestone. Sometimes they descend to inversion valleys, where they grow on relatively deeper and heavier soils in contact with beech forests.

D i s t r i b u t i o n: Restricted to middle altitudes (mean 430 m a.s.l.) of Strážovské vrchy and Považský Inovec Mts in western Slovakia, where forest-steppe and high-montane species pools meet. Less typical stands lacking many diagnostic species can exceptionally be found elsewhere.

Syntaxonomy:

Association name: *Seslerio albicantis-Quercetum pubescentis* Chytrý 1994
Orig. (Chytrý 1994, p. 123): *Seslerio albicantis-Quercetum pubescentis* ass. nova
Nomenclatural type: Chytrý (1994): Table 1, rel. 34, holotypus
Synonyms: *Seslerio-Quercetum pubescentis* Futák 1960 (§1), *Quercetum pubescentis praecarpaticum* sensu Futák 1947 p. min. p. non Klika 1937 (pseudonym)

3. *Fraxino orni-Quercetum pubescentis* – dry oak forests on intermediate igneous bedrock

D e s c r i p t i o n: Open to semi-open stands on extremely warm and dry sites on intermediate igneous bedrock. The tree layer (mean cover near 60%) is often dwarfed and is mostly dominated by oaks (*Quercus cerris*, *Q. pubescens* agg. and *Q. petraea* agg.), in a few sites also by *Fraxinus ornus*, which has its ecological optimum in Slovakia in this vegetation type. In the shrub layer, *Acer campestre*, *Euonymus verrucosus*, *Fraxinus ornus*, *Ligustrum vulgare* and *Quercus pubescens* agg. prevail. The herb layer is species-rich, though somewhat poorer than in the two previous associations, and is dominated by light-demanding and semi-shade-tolerant grasses (*Festuca pseudodalmatica*, *Poa pannonica* subsp. *scabra*, *P. pratensis* agg., in some places also *Brachypodium pinnatum*), while *Carex praecox*, *Festuca heterophylla* and *Poa nemoralis* are present in more closed stands on deeper soils. The occurrence of species of dry grasslands and rocky outcrops on intermediate igneous rocks (*Achillea nobilis*, *Carduus collinus*, *Cota tinctoria*, *Lactuca viminea*, *Pilosella bauhinii*) is characteristic.

E c o l o g y: Occupy moderate to very steep slopes (mean 28°), mostly with south, south-east, south-west and west exposures. The most common soils are Haplic and Rendzic Leptosols on igneous rocks, mostly andesite and andesitic tuff.

D i s t r i b u t i o n: Best developed at *locus classicus* (Burda Hills), scattered in low volcanic mountain ranges (mean altitude 360 m a.s.l.) in the warm and dry southern part of central Slovakia (Krupinská planina Plateau, Cerová vrchovina Mts), rare elsewhere.

Syntaxonomy:

Association name: *Fraxino orni-Quercetum pubescentis* Klika 1938
Orig. (Klika 1938, p. 454): Die *Quercus pubescens-Fraxinus ornus* Assoziation
Nomenclatural type: Klika (1938): Table 3, rel. 3, lectotypus hoc loco
Synonyms: Type *Fraxinus ornus-Quercus pubescens* Roleček 2007b (§1, 3c)

4. *Euphorbio-Quercetum* – dry-mesic oak forests on base-rich bedrock

D e s c r i p t i o n: Mostly semi-open to closed stands representing the least specific and most mesophilous communities of the alliance. The tree layer (mean cover near 70%) is dominated by *Quercus petraea* agg. or *Q. pubescens* agg. and less frequently *Q. cerris*, with *Acer campestre* and *Sorbus torminalis* as the most frequent admixture. The development of the shrub and herb layer is negatively related to the tree cover. The most common species of shrubs are *Cornus mas*, *Crataegus monogyna* and *Ligustrum vulgare*, which are often accompanied by species of oak-hornbeam forests (*Carpinion betuli*). In the herb layer, species from several ecological groups are combined. The most frequent dominant is a shade-tolerant grass *Melica uniflora*, while in open stands the forest-steppe species *Brachypodium pinnatum*, *Lithospermum purpurocaeruleum* and *Vincetoxicum hirundinaria* are abundant. Mesophilous and nitrophilous species (*Brachypodium sylvaticum*, *Campanula rapunculoides*, *Cruciata glabra*, *Dactylis polygama*, *Galium schultesii*, *Geum urbanum*, *Glechoma hirsuta*, *Mercurialis perennis* and *Waldsteinia geoides*) are also frequent.

E c o l o g y: Occupy mostly sun-exposed slopes. Compared to the previous three associations, the slopes are less steep (mean close to 20°). More often found on the colder, north-east and west-facing slopes, plateaus and foothills. The most common soils are Rendzic and Lithic Leptosols developed over different kinds of base-rich hard-rock bedrock, mainly limestones, less often dolomites, intermediate igneous rocks (mainly andesites) and calcareous sandstones (flysch).

D i s t r i b u t i o n: Broadly distributed in lower mountain ranges (mean altitude 400 m a.s.l.) on the southern periphery of the Carpathians, on both sedimentary and igneous rocks, in western, central and eastern Slovakia.

Syntaxonomy:

Association name: *Euphorbio-Quercetum* Knapp ex Hübl 1959
Orig. (Hübl 1959, p. 142): *Euphorbio-Quercetum* Knapp 1944
Nomenclatural type: Hübl (1959): p. 138, rel. 9, lectotypus (designated by Wallnöfer in Mucina et al. 1993)
Synonyms: *Euphorbio-Quercetum vindobonense* Knapp 1944 (§1, 34a), *Torilido-Quercetum* Blažková (1989) 1997 (syntax. syn.), *Avenello-Quercetum* Miadok 1980 prov., nom. ined. (§1, §3b), *Lithospermo-Quercetum virgillianae* (Klika 1951) Miadok 1980 prov., nom. ined. (§1), *Quercetum virgilianae* Šomšák et Háberová 1979 (§3b), *Corno-Quercetum* auct. non Máthé et Kovács 1962 (pseudonym), *Lithospermo-Quercetum petraeae* auct. bohem. non Br.-Bl. 1932 (pseudonym)

Aceri tatarici-Quercion alliance

Diagnostic species (sorted by decreasing fidelity; E_3 – tree layer; E_2 – shrub layer; no layer information – herb layer and saplings): *Ulmus minor* (E_3), *Arum alpinum* agg., *Ulmus minor* (E_2), *Polygonatum latifolium*, *Ulmus minor*, *Quercus robur* agg. (E_3), *Viola mirabilis*, *Chaerophyllum temulum*, *Cruciata laevipes*, *Euonymus europaeus* (E_2), *Viola odorata*, *Dictamnus albus*, *Geum urbanum*, *Acer campestre* (E_3), *Urtica dioica*, *Galium aparine*, *Acer campestre* (E_2), *Corydalis cava*, *Lithospermum purpurocaeruleum*, *Stachys sylvatica*, *Euonymus europaeus*, *Robinia pseudoacacia*, *Vinca minor*, *Quercus cerris* (E_3), *Sambucus nigra*, *Roegneria canina*, *Allium scorodoprasum*, *Asparagus officinalis*, *Robinia pseudoacacia* (E_2), *Brachypodium sylvaticum*, *Acer campestre*, *Alliaria petiolata*, *Quercus robur* agg. (E_2), *Viola suavis*, *Clematis vitalba.*

5. *Quercetum pubescenti-roboris* – dry oak forests on deep base-rich soils

D e s c r i p t i o n: Open to semi-open stands, forest openings and margins bordering dry grasslands. The tree layer (mean cover close to 70%) is dominated by *Quercus cerris*, *Q. pubescens* agg. or *Q. robur* agg. There is often an admixture of mesophilous trees such as *Acer campestre* and *Carpinus betulus*. *Acer tataricum*, sometimes considered a characteristic component (Zólyomi 1957), reaches its distributional limit in western Slovakia and is rare there. The shrub layer is usually well developed, species-rich and formed by a mixture of thermophilous and mesophilous species (mainly *Cornus mas*, *Euonymus europaeus*, *E. verrucosus*, *Ligustrum vulgare*, *Prunus spinosa*, *Rosa canina* agg., *Swida sanguinea* and *Viburnum lantana*). The herb layer is usually species-rich and dominated by both heliophilous and shade-tolerant grasses (mainly *Brachypodium pinnatum*, *B. sylvaticum*, *Poa nemoralis*, *P. pratensis* agg., *Melica uniflora*). An abundant occurrence of drought-tolerant species of dry grasslands and thermophilous forest fringes on base-rich soils (e.g. *Adonis vernalis*, *Betonica officinalis*, *Carex michelii*, *Dictamnus albus*, *Geranium sanguineum*, *Inula salicina*, *Lithospermum purpurocaeruleum*, *Pulmonaria mollis* s. lat.) is characteristic.

E c o l o g y: Occupy mostly flat or mildly undulating topography (mean slope 10°) in warm and dry lowlands with deep soils. The most common soils are Chernozems, Phaeozems and Luvisols over soft base-rich bedrock, mostly loess. Because such sites are fertile and usually suitable for closed-canopy forests, open vegetation depends on regular canopy thinning and is currently preserved only in small fragments, mostly along forest roads and in dynamic forest-grassland mosaics. The spread of the invasive tree, *Robinia pseudoacacia,* is another significant threat (Vítková et al. 2017, Medvecká et al. 2018).

D i s t r i b u t i o n: Rare and endangered vegetation type, distributed in warm and dry lowlands and their peripheries (mean altitude 200 m a.s.l.). Characteristic of the Pannonian region, it is presently confined to a few sites in Podunajská pahorkatina Hills (e.g. Martinský les Wood near Senec, Belianské kopce Hills near Štúrovo) and less typical stands occur elsewhere.

Syntaxonomy:

Association name: *Quercetum pubescenti-roboris* (Zólyomi 1957) Michalko et Džatko 1965
Orig. (Michalko & Džatko 1965, p. 67): *Quercetum pubescentis-roboris*

Nomenclatural type: Zólyomi et al. (2013): p. 173, rel. 9, neotypus hoc loco
Synonyms: *Acereto tatarici-Quercetum pubescentis-roboris* Zólyomi 1957 (§34c), *Quercetum cerris roboretosum* Osvačilová 1956 (incl.), *Lithospermo-Quercetum* („*Querceto-Lithospermetum*“) sensu Jurko 1958 non Michalko 1957 (pseudonym), *Corno-Quercetum* sensu auct. non Máthé et Kovács 1962 (pseudonym)

6. *Convallario-Quercetum roboris* – dry-mesic oak forests on deep base-rich soils

Description: Semi-open to closed stands of the most mesophilous thermophilous oak forests in Slovakia. The tree layer (mean cover close to 70%) is dominated by *Quercus cerris*, *Q. petraea* agg. or *Q. robur* agg. and rarely *Q. pubescens* agg. Frequently there is an admixture of the mesophilous species *Acer campestre*, *Carpinus betulus* and *Ulmus minor*. The shrub layer is mostly well developed, with a high frequency of *Acer campestre*, *Cornus mas*, *Crataegus monogyna* and *Ligustrum vulgare*. The cover and composition of the herb layer is affected by the availability of soil nutrients and canopy cover. Semi-open stands and stands connected to dry grasslands harbour some non-forest and semi-shade species (e.g. *Carex michelii*, *Dictamnus albus*, *Lithospermum purpurocaeruleum*, *Vincetoxicum hirundinaria*), while these species are rare in closed stands, where shade-tolerant mesophilous and nitrophilous species prevail (e.g. *Arum alpinum*, *Bromus benekenii*, *Convallaria majalis*, *Geum urbanum*, *Viola mirabilis*). Mesophilous grasses (mainly *Brachypodium sylvaticum* and *Melica uniflora*) dominate here, together with the herbs *Lithospermum purpurocaeruleum* and, in some stands, *Polygonatum latifolium*. Transitions to oak-hornbeam forests (*Carpinion betuli*) and alluvial forests (*Fraxino-Quercion roboris*) are common, while in more open places rarely borders with *Quercetum pubescenti-roboris.* Non-native and invasive species, such as *Robinia pseudoacacia*, *Solidago canadensis*, *S. gigantea* and *Stenactis annua*, may spread in places significantly affected by human activities (Medvecká et al. 2018).

Ecology: Occupy mostly flat or mildly undulating topography (mean slope nearly 10°) in warm and dry lowlands with deep soils. The most common soils are Chernozems, Phaeozems and Luvisols over soft base-rich bedrock (mostly loess), and in alluvia also Fluvisols; less typical stands on Rendzic Lithosols.

Distribution: Scattered in warm and dry lowlands and its peripheries (mean altitude 260 m a.s.l.). Characteristic of the Pannonian region, mainly Podunajská pahorkatina Hills and the Podunajská rovina Plain, rare on the Východoslovenská rovina Plain. Less typical stands, transitional to *Euphorbio-Quercetum*, occur on slopes of adjacent mountain ranges.

Remark: This association was originally described from sandy soils. A synthetic study of Roleček (2007b) however showed that lowland closed-canopy oak forests are very similar on all substrates. The specificity of different substrates is more pronounced only when the tree layer is open and substrate-specific heliophilous species are present in the herb layer.

Syntaxonomy:

Association name: *Convallario-Quercetum roboris* Soó (1958) 1971
Orig. (Soó 1971, p. 173): *Convallario-Quercetum roboris* s. str. (*tibiscense* Soó l. c.)
Nomenclatural type: Soó (1943): tab. 2, rel. 17, lectotypus hoc loco
Synonyms: *Convallario-Quercetum roboris* Soó (1934) 1957 (§1), *Convallarieto-Quercetum tibiscense* Soó 1958 (§34a), *Quercetum roboris convallariosum* Soó 1937 (§3d), *Quercetum roboris convallarietosum* Soó 1943 (incl.), *Convallarieto-Quercetum roboris* 1958 s. l. (Hauptassoziation)

***Quercion petraeae* alliance**

Diagnostic species (sorted by decreasing fidelity; E_3 – tree layer; E_2 – shrub layer; no layer information – herb layer and saplings): *Luzula luzuloides*, *Veronica officinalis*, *Cruciata glabra*, *Quercus petraea* agg. (E_2), *Hieracium sabaudum*, *Quercus petraea* agg., *Steris viscaria*, *Festuca rubra* agg., *Agrostis capillaris*, *Quercus petraea* agg. (E_3), *Veronica chamaedrys* agg., *Poa nemoralis*, *Genista tinctoria*, *Galium schultesii*, *Carpinus betulus* (E_2), *Ajuga reptans*, *Digitalis grandiflora*, *Potentilla alba*, *Hypericum montanum*, *Lychnis coronaria*, *Melampyrum pratense*, *Cerasus avium*, *Fragaria vesca*, *Calamagrostis arundinacea*, *Hieracium lachenalii*, *Frangula alnus* (E_2), *Campanula persicifolia*, *Festuca heterophylla*, *Vicia cassubica*, *Frangula alnus*, *Solidago virgaurea*, *Carex montana*, *Hieracium murorum*, *Lathyrus niger*, *Cerasus avium*, *Carex pallescens.*

7. *Carici fritschii-Quercetum roboris* – dry-mesic oak forests on deep sandy soils

D e s c r i p t i o n: Include both open low-growing stands and semi-open tall stands. The tree layer (mean cover near 55%) is mostly dominated by *Quercus robur* agg. and less often by *Q. petraea* agg., sometimes with an admixture of *Pinus sylvestris*, which is native in the area of distribution of this association (Jamrichová et al. 2019). The shrub layer is poorly developed, with high frequency of *Frangula alnus*, along with *Crataegus* spec. div. and saplings of *Tilia cordata*. The herb layer often lacks a clear dominant, although *Festuca ovina* agg. (usually *F. guestfalica*) is more abundant on drier sites and *Convallaria majalis* and *Molinia caerulea* agg. (usually *Molinia arundinacea*) are increasingly present at mesic to intermittently wet sites. Characteristic species include light-demanding species preferring or tolerant of dry sandy soils, including *Carex fritschii*, *Cerastium arvense*, *Iris variegata*, *Peucedanum oreoselinum*, *Polygonatum odoratum* and *Vincetoxicum hirundinaria*. Common grassland species (*Agrostis capillaris*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Festuca rubra*, *Luzula campestris* agg., *Poa pratensis* agg., *Viola canina*) are also well-represented. At moister sites there is an increasing presence of species of *Molinion* meadows (*Potentilla alba*, *Serratula tinctoria*), hygrophilous species (*Deschampsia cespitosa*, *Lysimachia vulgaris*) and forest nitrophytes (*Moehringia trinervia*, *Mycelis muralis*, *Scrophularia nodosa*).

E c o l o g y: Occupy flat to slightly undulating topography (mean slope 1%) on sandy and gravel terraces, alluvial fans and aeolian sands. The most common soils are acidic Arenosols in relatively dry sites and Umbrisols in depressions with relatively high content of organic matter and high groundwater level (Jenčo et al. 2018). The composition of the tree layer is influenced by past disturbance regimes (Jamrichová et al. 2019).

D i s t r i b u t i o n: Confined to Záhorská nížina Lowland (mean altitude 175 m a.s.l.), an important refugium of psammophilous plant communities. This region is adjacent to the *locus classicus* of the association on the right bank of the Morava River in the Czech Republic (Chytrý & Horák 1997) and to the Marchfeld region in Austria, where thermophilous oak forests on sand are classified as *Arrhenatherum-Quercus robur*-Gesellschaft (Willner & Grabherr 2007).

R e m a r k: This association was previously assigned to the *Aceri tatarici-Quercion* alliance (Chytrý 1997, Chytrý & Horák 1997, Jarolímek et al. 2008, Roleček 2013). Based on its similarity in terms of species composition with some other associations of the *Quercion petraeae* alliance, such as presence of acidophilous species and absence of many species of mesophilous forest, we classify it within the latter alliance.

Syntaxonomy:

Association name: *Carici fritschii-Quercetum roboris* Chytrý et Horák 1997
Orig. (Chytrý & Horák 1997, p. 211): *Carici fritschii-Quercetum roboris* ass. nova
Nomenclatural type: Chytrý & Horák (1997): p. 206, tab. 2, rel. 49, holotypus

8. *Sorbo torminalis-Quercetum* – dry-mesic oak forests on acidic bedrock

Description: Mostly semi-open and relatively tall stands, but open and dwarf stands are also represented. The tree layer is usually dominated by *Quercus petraea* agg., which is often the only species present. Sometimes it is accompanied by other heliophilous or mesophilous trees, mainly *Acer campestre*, *Carpinus betulus*, *Quercus cerris* and *Sorbus torminalis*. The shrub layer is often poorly developed and consisting of saplings, but species such as *Corylus avellana*, *Crataegus* spec. div., *Ligustrum vulgare* and *Cornus mas* may be present, particularly on rich soils. The herb layer is usually dominated by the acid-tolerant grass *Poa nemoralis* and on rich sites also by *Melica uniflora*. Less often *Carex montana*, *Festuca heterophylla* or *Galium schultesii* dominate, while on the nutrient-poorest sites *Luzula luzuloides* may prevail. The species composition is a mixture of species of thermophilous forests, fringes and grasslands (e.g. *Astragalus glycyphyllos*, *Campanula persicifolia*, *Clinopodium vulgare*, *Lathyrus niger*, *Pyrethrum corymbosum*, *Tithymalus cyparissias*, *Trifolium alpestre*, *Vincetoxicum hirundinaria*), acidophytes and acid-tolerant species (*Genista tinctoria*, *Hieracium lachenalii*, *H. murorum*, *H. sabaudum*, *Luzula luzuloides*, *Veronica officinalis*) and often also mesophilous forest species (e.g. *Dactylis polygama*, *Fragaria vesca*, *Galium schultesii*, *Symphytum tuberosum* agg., *Viola reichenbachiana*).

Ecology: Occupies dry-mesic sites, mostly on slopes moderately exposed to sun (mean slope close to 20°), at higher altitudes and in regions with a relatively moist climate also on steep slopes. This vegetation may be considered transitional between *Genisto pilosae-Quercetum* on the driest acidic sites and *Melico pictae-Quercetum* on flat, slightly richer sites (Fig. 3). The most common soils are rather shallow, moderately acidic Cambisols and, on steep slopes, acidic Leptosols.

Distribution: Broadly distributed in low mountain ranges on the southern periphery of the Carpathians, at higher altitudes (mean 400 m a.s.l.) than other associations of the *Quercion petraeae* alliance. Rare in regions with carbonate bedrock. Well-developed stands rich in acidophytes, characteristic of regions with crystalline bedrock (e.g. Bohemian Massif; Roleček 2013), are rarely recorded in Slovakia.

Remark: This association includes many relevés originally classified in the *Festuco heterophyllae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1964 association from the *Carpinion betuli* alliance (Neuhäusl & Neuhäuslová-Novotná 1964, 1967, Jarolímek et al. 2008). A similar vegetation type is broadly distributed in Slovakia, however, its species composition is transitional between the classes *Carpino-Fagetea*, *Quercetea pubescentis* and *Quercetea robori-petraeae* (Roleček 2005, Novák et al. 2020). Relevés with the highest numbers of heliophilous and thermophilous species fall within the range of variation of *Sorbo torminalis-Quercetum* and partly also that of the *Melico pictae-Quercetum roboris* associations.

Syntaxonomy:

Association name: *Sorbo torminalis-Quercetum* Svoboda ex Blažková 1962
Orig. (Blažková 1962, p. 231): *Torminaleto-Quercetum* (Svoboda 1955) Samek 1955
Nomenclatural type: Blažková (1962): 263–265, rel. 6, lectotypus (designated by Chytrý 1997)
Synonyms: *Torminarieto-Quercetum* Svoboda 1955 (§2b), *Asplenio cuneifolii-Quercetum petraeae* Chytrý et Horák 1997 p. p. (syntax. synonym), *Festuco heterophyllae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1964 p. p. (syntax. synonym), *Corno-Quercetum* Jakucs et Zólyomi ex Máthé et Kovács 1962 sensu auct. non Máthé et Kovács 1962 p. p. (pseudonym)

9. *Genisto pilosae-Quercetum petraeae* – dry oak forests on acidic bedrock

Description: Open dwarf oak stands with a tree layer composed of *Quercus petraea* agg. and a minor admixture of other species, e.g. *Sorbus aria* agg. Its cover does not exceed 70% and it may drop below 50% on extreme sites. The shrub layer is often poorly developed or missing and *Rosa canina* agg. is the most frequent species other than saplings (*Quercus petraea* agg., *Carpinus betulus*, *Fagus sylvatica*). The herb layer is usually dominated by acidophilous graminoids (*Avenella flexuosa*, *Luzula luzuloides*) and the dwarf shrub *Genista pilosa*. The most characteristic components of the herb layer are light-demanding acidophilous and acid-tolerant species of rocky grasslands and skeletal soils (e.g. *Acetosella vulgaris* agg., *Allium montanum*, *Cardaminopsis arenosa* agg., *Festuca pallens*, *Dalanum ladanum*, *Linaria genistifolia*, *Pilosella cymosa*, *P. officinarum*, *Polypodium vulgare*). More widely tolerant species of dry grasslands, thermophilous oak forests and their fringes (e.g. *Digitalis grandiflora*, *Galium glaucum*, *Genista tinctoria*, *Hylotelephium maximum*, *Hypericum perforatum*, *Polygonatum odoratum*, *Steris viscaria*, *Vincetoxicum hirundinaria*, *Veronica chamaedrys* agg.) and some mesophilous forest species are also present.

Ecology: Occupy warm and very dry sites on convex relief, rocky ridges and steep slopes with south, south-west to west exposure (mean slope 35°), where the soils are acidic, nutrient-poor, shallow and skeletal Leptosols over base-poor igneous rocks (rhyolite).

Distribution: Confined to the north-western part of Štiavnické vrchy Mts (e.g. Kapitulské bralá Cliffs) at altitudes between 290 and 630 m a.s.l. May occur also in Tríbeč Mts (Husová 1967), however, the available relevés were classified among acidophilous oak forests (*Quercetea robori-petraeae* class) in our analysis.

Syntaxonomy:

Association name: *Genisto pilosae-Quercetum petraeae* Zólyomi et al. ex Soó 1963
Orig. (Soó 1963, p. 136): *Genisto pilosae-Quercetum petraeae* Zólyomi-Jakucs-Fekete 58, Tallós 60, Jakucs 61, 62, Soó 61, 62, Horánszky ined.
Nomenclatural type: Fekete (1956): 357–362, rel. 5, lectotypus (designated by Pallas 1996)
Synonyms: *Genisto pilosae-Quercetum petraeae* Zólyomi et al. in Zólyomi et Jakucs 1957 (§2b), *Asplenio cuneifolii-Quercetum petraeae* Chytrý et Horák 1997 p. p. (syntax. synonym)

10. *Melico pictae-Quercetum roboris* – dry-mesic oak forests on deep heavy soils

Description: Mostly semi-open tall stands dominated by *Quercus robur* agg. At some sites *Q. petraea* agg. and *Q. cerris* are admixed or even dominate, along with *Acer campestre*, *Carpinus betulus*, *Sorbus torminalis* and *Tilia cordata*. The shrub layer is usually rather well developed and species-rich and, besides saplings, is mostly composed of mesophilous species (e.g. *Corylus avellana*, *Frangula alnus*, *Ligustrum vulgare*, *Swida sanguinea*). Some heliophilous and drought-tolerant species (*Cornus mas*, *Crataegus* *monogyna*, *Prunus spinosa*, *Rosa* spec. div.) may also be present. The herb layer is most often dominated by the forest-steppe sedge *Carex montana*, but mesophilous forest grasses *Poa nemoralis* and *Melica uniflora* may also prevail. A combination of mesophilous species (e.g. *Fragaria vesca*, *Lysimachia nummularia*, *Ranunculus auricomus* agg., *Symphytum tuberosum* agg., *Vicia sepium*, *Viola riviniana*, juveniles of *Viburnum opulus*) and species of intermittently wet grasslands and mesic steppe meadows (most often *Betonica officinalis*, *Carex tomentosa*, *Filipendula vulgaris*, *Potentilla alba*, *P. erecta*, *Pulmonaria mollis* s. lat. and *Serratula tinctoria*) is characteristic. They are accompanied by broadly distributed thermophytes and acidophytes. Dry grassland species are rare compared to *Quercetum petraeo-cerridis*.

E c o l o g y: Occupy mesic sites with deep soils in flat or slightly inclined relief (mean slope 7%); mostly in basins, foothills, peripheries of large lowlands and also plateaus. The soils are usually deep, heavily textured, moderately acidic to neutral Stagnosols, Luvisols and Cambisols over loess, loess loam and other substrates rich in clay. They often exhibit a fragipan subsurface soil horizon (Smeck & Ciolkosz 1989) that restricts soil water flow and root penetration.

D i s t r i b u t i o n: Scattered in moderately warm regions in the transitional zone between the Carpathian and Pannonian regions (mean altitude 330 m a.s.l.), rare elsewhere. The best developed stands were recorded in Hornonitrianská kotlina, Pliešovská kotlina and Košická kotlina Basins and in Východoslovenská pahorkatina Hills.

Syntaxonomy:

Association name: *Melico pictae-Quercetum* (Mikyška 1944) Klika 1957
Orig. (Klika 1957, p. 579): As. *Quercus robur-Melica picta*, popsaná Mikyškou 1943 [described by Mikyška 1943]
Nomenclatural type: Mikyška (1944): Tab. 7, rel. 17, lectotypus hoc loco
Synonyms: *Quercus robur* (*sessilis*) – *Melica picta* Mikyška 1944 (§34c), *Frangulo alnae-Quercetum petraeae-roboris* J. Michalko 1986 (§34c), *Frangulo alni-Quercetum roboris-petraeae* J. Michalko 1991 (§34c), *Molinio arundinaceae-Quercetum* Samek 1962, *Serratulo-Quercetum* Mráz 1963 (syntax. synonym), *Potentillo albae-Quercetum* auct. non Libbert 1933 (pseudonym), *Carici montanae-Quercetum petraeae* Gergely 1962 non Gergely 1962 p. p. (pseudonym)

11. *Quercetum petraeo-cerridis* – dry-mesic Turkey oak forests

D e s c r i p t i o n: Mostly semi-open stands dominated by *Quercus cerris*, usually with an admixture of *Q. petraea* agg. Among other species, only *Carpinus betulus* is relatively frequent. The shrub layer has variable cover and is composed of saplings, along with heliophilous shrubs (e.g. *Acer campestre*, *A. tataricum*, *Crataegus laevigata*, *C. monogyna*, *Ligustrum vulgare*, *Prunus spinosa*, *Pyrus communis*, *Rosa* spec. div.); in previously grazed sites *Juniperus communis* occurs. The herb layer is usually dominated by the heliophilous grasses *Festuca rupicola* and *Poa pratensis* agg., the broadly tolerant forest grass *Poa nemoralis* and sometimes also tall herb of semi-open habitats *Vicia cassubica*. Characteristic components of this association are sub-Mediterranean species (e.g. *Calamintha menthifolia*, *Lychnis coronaria*, *Potentilla micrantha*, *Silene viridiflora*), but some of them are rare in Slovakia. Broadly distributed species of open and semi-open habitats, preferring or tolerating non-carbonate substrates, are common (e.g. *Agrimonia eupatoria*, *Astragalus glycyphyllos*, *Clinopodium vulgare*, *Dianthus armeria*, *Hypericum hirsutum*, *Rosa gallica*, *Trifolium alpestre*, *Verbascum* *austriacum*, *Vincetoxicum hirundinaria*, *Viola hirta*). Acidophytes, forest mesophytes and species of intermittently wet soils are also present.

E c o l o g y: Occupy relatively mesic and moderately dry sites, usually with flat topography or on moderate slopes (mean slope 10°). On steep slopes with well-developed forest-steppe vegetation they are replaced by open-canopy stands of the *Fraxino orni-Quercetum pubescentis* association. The soils are mostly deep, heavy and moderately acidic up to acidic Luvisols, Stagnosols and Cambisols over loess, loess loam and slope deposits derived from volcanic bedrock such as andesite and andesitic tuff. They are often wet during the spring and dry in summer.

D i s t r i b u t i o n: Scattered in low volcanic mountain ranges and adjacent basins and lowlands (mean altitude 250 m a.s.l.) in warm and dry southern parts of central Slovakia (Cerová vrchovina Mts, Juhoslovenská kotlina Basin, Krupinská planina Plateau, Podunajská pahorkatina Hills, Štiavnické vrchy Mts).

Syntaxonomy:

Association name: *Quercetum petraeo-cerridis* Soó ex Máthé & Kovács 1962
Orig. (Máthé & Kovács 1962, p. 319): *Quercetum petraeae-cerris* Soó 1957
Nomenclatural type: Máthé & Kovács (1962): Table 3, rel. 2, lectotypus hoc loco designatus.
Synonyms: *Quercetum petraeae-cerris* Soó 1957 (§1, §2b), *Quercetum petraeae-cerris pannonicum* Soó (1957) 1963 (§34a), *Querceto-Potentilletum albae* Zólyomi 1950 p. p. (§10b, §31); *Potentillo albae-Quercetum petraeae-cerris* Zólyomi 1957 (§34c), *Quercus sessilis-Festuca heterophylla* ass. Domin, 1931 (syntax. synonym), *Poo scabrae-Quercetum* (Magyar 1933) Neuhäusl et Neuhäuslová-Novotná 1964 (syntax. synonym)

Diversity and syntaxonomic revision

We distinguished 3 alliances and 11 associations of thermophilous oak forests in Slovakia, which is considerably less than the 4 alliances and 24 associations previously reported (Jarolímek et al. 2008). There are several reasons for this reduction. First, the previous list was conceived as a compilation of associations reported from Slovakia and was not based on a critical review. Therefore, redundancies, overlaps and inconsistencies in association concepts were inherent in this list. Second, our system is based on associations defined by a significant number of diagnostic species, which differ also in habitat requirements and/or geographical distribution (Willner 2006). Local vegetation types with characteristic combinations of species, lacking more broadly valid diagnostic species (e.g. *Poo nemoralis-Quercetum dalechampii* Šomšák et Háberová 1979), were not considered as associations. Third, to link the Slovak system of syntaxa to those of the surrounding countries, we adopted some new, often broader concepts of syntaxa. Fourth, based on a critical revision, some previously reported associations were classified in different higher syntaxa (e.g. *Seslerio heuflerianae-Tilietum* Miadok 1980 within the *Tilio-Acerion* Klika 1955 alliance) or are now considered to be absent in Slovakia (e.g. *Cotino-Quercetum pubescentis* Soó (1931) 1932). These differences are summarized in Electronic Appendix 4. The most prominent difference is the exclusion of a whole alliance *Quercion confertae-cerris* Horvat 1954. Currently, the name *Quercion confertae* Horvat 1958 is used for this alliance distributed mainly in the central Balkans (Mucina et al. 2016), southern Hungary (Borhidi et al. 2012) and southern Romania (Coldea et al. 2015). As many of its characteristic sub-Mediterranean species are absent in Slovakia, we did not accept it in our survey.

Despite the reduction to eleven associations, our analysis confirmed that Slovakia harbours a diverse heritage of thermophilous oak forests. For comparison, in the Czech

Republic and Poland, where similar association concepts are used, eight and five associations are reported, respectively (Matuszkiewicz 2008, Roleček 2013, Reczyńska 2015).

Formalized classification

For the first time we provide formal definitions for all associations of thermophilous oak forests in Slovakia (Electronic Appendices 6 and 8). The definitions are based on logical combinations of dominant species and 21 newly compiled sociological species groups (Table 2), reflecting the co-occurrence patterns in the dataset analysed. Definitions were assembled with the aim to correctly classify as many relevés of oak forests as possible. They classify 36.8% of relevés in our dataset, a value almost identical to that reported by Roleček (2007a) for Czech formal definitions. Out of this number, 83.6% are classified to identical associations as in our numerical classification. The relevés that do not conform to the definition of any association may be classified using the FPFI index (Kočí et al. 2003, Tichý 2005) within the expert system.

The definitions are in several cases rather complex (they include up to 19 members) and are therefore more suitable for the classification within the expert system than for illustration of the floristic composition of the associations (Roleček 2007a). For this reason, we further provide an identification key of associations based on sociological species groups used in formal definitions, which captures the essence of the classification. Although inevitably simplistic, we believe that the logical structure of the key will make it a useful tool. Moreover, differences between associations in the presence of sociological species groups are summarized in Electronic Appendix 2.

Conservation value and threats

Thermophilous oak forests belong to the NATURA 2000 priority habitats (91H0 – Pannonian woods with *Quercus pubescens*, 91I0 – Euro-Siberian steppe oak woods, 91M0 – Pannonian-Balcanic turkey oak-sessile oak forests). They provide important refugia for plant species of high conservation value. On average, the highest numbers of threatened species were recorded in *Seslerio-Quercetum*, *Fraxino-Quercetum* and *Quercetum pubescenti-roboris* associations. *Seslerio-Quercetum* is an extraordinary community also in other respects; while oak forests on dolomite are known also from other countries in central Europe (e.g. Hungary; Suba et al. 1982), the total species composition of the Slovak stands is well-differentiated and points to specific genesis of vegetation at the interface of the high Carpathians and the Pannonian region (Futák 1960). Another specific community with a restricted distribution is *Carici fritschii-Quercetum*, which is confined to sandy soils along the lower Morava River in Slovakia and the Czech Republic (Roleček 2004, Roleček et al. 2017).

Among the threatened species, the relevés analysed included high numbers of the endangered *Arabis pauciflora* (mainly in *Seslerio-Quercetum*) and *Carex fritschii* (in *Carici fritchii-Quercetum*) and vulnerable *Cotinus coggygria* (in *Lithospermo-Quercetum* and *Seslerio-Quercetum*), *Iris variegata* (mainly in *Carici fritchii-Quercetum*), *Medicago prostrata* (in *Fraxino-Quercetum* and *Lithospermo-Quercetum*), *Daphne cneorum* and *Thlaspi montanum* (both in *Seslerio-Quercetum*).

The main threats to Slovak thermophilous oak forests (Galvánek 1998, Kanka 2001, Ružičková 2003, Hrabovský et al. 2007, Roleček 2007b, Medvecká et al. 2018) are similar

Table 2. – Sociological species groups used in Cocktail definitions and in the identification key of associations. Numbers in parenthesis indicate the minimum number of species in the group that have to be present in a relevé for the group to be considered present.

Group name	Included species
Carex fritschii	*Carex fritschii*, *C. supina*, *Cerastium arvense*, *Iris variegata*, *Melampyrum subalpinum*, *Peucedanum oreoselinum* (2)
Dictamnus albus	*Carex michelii*, *Dictamnus albus*, *Lithospermum purpurocaeruleum* (2)
Erysimum odoratum	*Asperula cynanchica*, *Erysimum odoratum*, *Helianthemum nummularium* agg., *Melica ciliata*, *Potentilla arenaria* agg., *Sanguisorba minor* (3)
Festuca heterophylla	*Campanula persicifolia*, *Carex montana*, *Festuca heterophylla*, *Lathyrus niger* (2)
Festuca rupicola	*Agrimonia eupatoria*, *Festuca rupicola*, *Fragaria viridis*, *Poa pratensis* agg. (2)
Galium glaucum	*Carex humilis*, *Galium glaucum*, *Inula ensifolia*, *Teucrium chamaedrys* (2)
Galium odoratum	*Asarum europaeum*, *Bromus benekenii*, *Galium odoratum*, *Pulmonaria officinalis* agg. (2)
Galium schultesii	*Cruciata glabra*, *Galium schultesii*, *Lathyrus vernus*, *Stellaria holostea* (2)
Hieracium murorum	*Hieracium lachenalii*, *H. murorum*, *H. sabaudum* (2)
Linaria genistifolia	*Dalanum ladanum*, *Genista pilosa*, *Linaria genistifolia* (2)
Luzula luzuloides	*Avenella flexuosa*, *Calamagrostis arundinacea*, *Luzula luzuloides*, *Melampyrum pratense* (2)
Lychnis coronaria	*Calamintha menthifolia*, *Lychnis coronaria*, *Potentilla micrantha*, *Silene viridiflora*, *Vicia cassubica* (2)
Mercurialis perennis	*Campanula trachelium*, *Glechoma hirsuta*, *Mercurialis perennis*, *Waldsteinia geoides* (2)
Phlomis tuberosa	*Adonis vernalis*, *Inula germanica*, *Lavatera thuringiaca*, *Phlomis tuberosa* (2)
Poa scabra	*Achillea nobilis*, *Cota tinctoria*, *Festuca pseudodalmatica*, *Lactuca viminea*, *Poa pannonica* subsp. *scabra* (2)
Polygonatum latifolium	*Allium scorodoprasum*, *Arum alpinum*, *Cruciata laevipes*, *Polygonatum latifolium*, *Ulmus minor* (2)
Pulmonaria mollis	*Betonica officinalis*, *Filipendula vulgaris*, *Inula salicina*, *Potentilla alba*, *Pulmonaria mollis* s. lat., *Ranunculus polyanthemos*, *Serratula tinctoria* (2)
Quercus cerris	*Colutea arborescens*, *Crataegus monogyna*, *Prunus spinosa*, *Quercus cerris* (3)
Quercus pubescens	*Cornus mas*, *Fraxinus ornus*, *Quercus pubescens* agg., *Viburnum lantana* (2)
Sesleria albicans	*Acinos alpinus*, *Asperula tinctoria*, *Hippocrepis comosa*, *Leontodon incanus*, *Polygala amara* agg., *Sesleria albicans* (3)
Vincetoxicum hirundinaria	*Anthericum ramosum*, *Polygonatum odoratum*, *Pyrethrum corymbosum*, *Vincetoxicum hirundinaria* (2)

to those in surrounding countries (see e.g. Chytrý et al. 2019): inappropriate forest management and successional changes, either due to the abandonment of traditional management (coppicing, forest grazing, litter raking) or human induced changes in the environment (particularly through nitrogen deposition and intensive game keeping). The spread of both native and non-native species (e.g. *Arrhenatherum elatius*, *Calamagrostis epigejos*, *Impatiens parviflora*, *Phytolacca americana*, *Solidago gigantea*), including trees and shrubs (e.g. *Acer campestre*, *Ailanthus altissima*, *Carpinus betulus*, *Fraxinus ornus*, *Prunus serotina*, *Robinia pseudoacacia*, *Syringa vulgaris*) and the deliberate planting of economic species of trees (mainly *Pinus sylvestris*, *P. nigra*, *Quercus cerris* and *Robinia pseudoacacia*) alter habitat conditions and limit the occurrence of light-demanding species characteristic of thermophilous oak forests. Suitable conservation measures include restoration, or imitation, of traditional management (e.g. canopy thinning, grazing and mowing of the understorey, prescribed burning and creation of small treeless patches) and removal of problematic species.

A simplified dichotomous identification key of associations based on sociological species groups used in Cocktail definitions

1a Groups *Quercus pubescens* or *Quercus cerris* present; usually dominated by *Quercus pubescens* or *Q. cerris*; if dominated by other species of oak, then dry grassland or forest fringe species preferring base-rich soils are present in the understorey 2
1b Groups *Quercus pubescens* and *Quercus cerris* absent; usually dominated by *Quercus petraea* or *Q. robur* 8
2a Group *Erysimum odoratum* present; usually on extremely warm and dry sites on limestone ***Lithospermo purpurocaerulei-Quercetum pubescentis***
2b Group *Erysimum odoratum* absent 3
3a Group *Sesleria albicans* present; usually on less warm and less dry sites on dolomite ***Seslerio albicantis-Quercetum pubescentis***
3b Group *Sesleria albicans* absent 4
4a Group *Poa scabra* present; usually on extremely warm and dry sites on intermediate igneous bedrock ***Fraxino orni-Quercetum pubescentis***
4b Group *Poa scabra* absent; usually on less warm and less dry sites 5
5a Group *Polygonatum latifolium* present; usually in lowlands with loess bedrock 6
5b Group *Polygonatum latifolium* absent; usually on slopes, foothills and plateaus in hilly landscapes with hard-rock bedrock 7
6a Groups *Phlomis tuberosa* or *Pulmonaria mollis* present; usually semi-open stands rich in dry grassland or forest fringe species ***Quercetum pubescenti-roboris***
6b Groups *Phlomis tuberosa* and *Pulmonaria mollis* absent; usually more closed stands less rich in dry grassland and forest fringe species ***Convallario-Quercetum roboris***
7a Group *Quercus cerris* present; usually on intermediate igneous bedrock; nitrophytes less abundant ***Quercetum petraeo-cerridis***
7b Group *Quercus cerris* absent; usually on other hard rocks; nitrophytes often abundant ***Euphorbio-Quercetum***
8a Group *Linaria genistifolia* present; on warm and dry sites with shallow acidic soils in Štiavnické vrchy Mts ***Genisto pilosae-Quercetum petraeae***
8b Group *Linaria genistifolia* absent 9
9a Group *Carex fritschii* present; on deep sandy soils in Záhorská nížina Lowland ***Carici fritschii-Quercetum roboris***
9b Group *Carex fritschii* absent 10
10a Group *Pulmonaria mollis* present; usually dominated by *Quercus robur* or *Q. petraea*; mostly on deep, heavy, moderately base-rich soils in basins, foothills and lowlands ***Melico pictae-Quercetum roboris***
10b Group *Pulmonaria mollis* absent; usually dominated by *Quercus petraea*; mostly on shallow acidic soils in hilly landscapes ***Sorbo torminalis-Quercetum***

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Souhrn

Teplomilné dubové lesy řazené do fytocenologické třídy *Quercetea pubescentis* patří k druhově nejbohatším a zároveň nejohroženějším lesním společenstvům ve střední Evropě. Díky členitému reliéfu, pestrému geologickému podloží, rozmanitým biogeografickým vlivům a poměrně dobře zachované polopřirozené a přírodě blízké lesní vegetaci se na Slovensku dodnes nachází pestrá škála teplomilných doubrav. V předkládané studii přinášíme jejich revidovaný syntaxonomický přehled, formalizovanou klasifikaci a expertní systém. Oproti předchozím publikovaným klasifikacím jsou naše výsledky založeny na numerické analýze velkého souboru dat (1131 vegetačních snímků) a jsou v souladu s moderními syntaxonomickými koncepty. Analyzovaný datový soubor jsme sestavili ze snímků obsažených ve Slovenské vegetační databázi a z dosud nepublikovaných snímků na základě relativního zastoupení diagnostických druhů třídy *Quercetea pubescentis*. Při tvorbě klasifikace jsme použili aglomerativní i divizivní metody, přičemž naším cílem bylo identifikovat opakující se skupiny snímků s charakteristickým druhovým složením, interpretovatelné z hlediska ekologie a rozšíření, které zároveň pokud možno respektují tradiční pojetí syntaxonů ve střední Evropě. Rozlišené vegetační typy jsme na základě zastoupení diagnostických, konstantních a dominantních druhů zařadili do svazů a asociací, jejichž nomenklaturu jsme uvedli do souladu s Mezinárodním kódem fytocenologické nomenklatury. Pro přiřazení nových snímků k definovaným asociacím jsme vytvořili dichotomický určovací klíč a expertní systém, zahrnující formální definice asociací založené na algoritmu Cocktail. Rozlišili jsme celkem 11 asociací rozdělených do tří svazů. Svaz *Quercion pubescenti-petraeae* zahrnuje asociace *Lithospermo purpurocaerulei-Quercetum pubescentis*, *Seslerio albicantis-Quercetum pubescentis*, *Fraxino orni-Quercetum pubescentis* and *Euphorbio-Quercetum.* Svaz *Aceri tatarici-Quercion* zahrnuje *Quercetum pubescenti-roboris* a *Convallario-Quercetum roboris*. Svaz *Quercion petraeae* zahrnuje *Carici fritschii-Quercetum roboris*, *Sorbo torminalis-Quercetum, Genisto pilosae-Quercetum petraeae*, *Melico pictae-Quercetum roboris* a *Quercetum petraeo-cerridis*. Krátké popisy asociací obsahují informace o jejich druhovém složení, ekologii a rozšíření. K vizualizaci hlavních gradientů v druhovém složení jsme použili DCA. Stanovištní nároky syntaxonů jsme vyhodnotili pomocí ekologických indikačních hodnot a bioklimatických proměnných. Diskutujeme také význam slovenských teplomilných doubrav z hlediska ochrany přírody a uvádíme hlavní zdroje jejich ohrožení.

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