

## Calicolous rock-outcrop lime forests of east-central Europe

Vápnomilné skalní lipiny východní části střední Evropy

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We studied the diversity of calicolous rock-outcrop forest vegetation dominated by lime (*Tilia cordata*, *T. platyphyllos* and *T. tomentosa*) in northern Austria, the Czech Republic, southern Poland, Slovakia, northern Hungary and north-western Romania. This vegetation includes species-rich forests with a mixture of mesophilous and thermophilous forest species, dry grassland species and species of rock outcrops. It is classified in the alliance *Melico-Tilion platyphylli* of the order *Aceretalia pseudoplatani* (class *Carpino-Fagetea*). It is rare in the study area, usually occurring on the upper parts of steep rocky slopes with shallow soil on limestone or other types of base-rich bedrock. Since such conditions are unfavourable for the development of closed-canopy zonal forests, numerous light-demanding relict species occur there (e.g. *Dianthus praecox*, *D. spiculifolius*, *Primula auricula*, *Sesleria* spp., *Tephroseria integrifolia* and *Viola jooi*). Based on the results of unsupervised classification using original (n = 118), previously published (n = 87) and unpublished relevés stored in the EVA database (n = 6; thus 211 relevés in total), we distinguished three phytosociological associations: (i) *Tilio platyphylli-Fraxinetum excelsioris* occurring in central Slovakia and northern Hungary, (ii) *Spiraeo chamaedryfoliae-Tilietum cordatae*, a new association recorded in northern and western Romania, and (iii) *Seslerio caeruleae-Tilietum cordatae* occurring in the Czech Republic, northern Austria, northern Hungary, western Slovakia and also in southern Poland, where we recorded this community for the first time in this country. We created an expert system for automatic classification of these forests, which includes formal definitions of the three associations and seven subassociations.

Keywords: *Aceretalia pseudoplatani*, *Carpino-Fagetea*, classification, expert system, forest vegetation, *Melico-Tilion platyphylli*, phytosociology, *Tilia*

### Introduction

Lime (*Tilia*) is a common constituent of central European mesophilous forests. Three species occur there: small-leaved lime (*Tilia cordata*) and large-leaved lime (*Tilia platyphyllos*) are widespread in central Europe, whereas silver lime (*Tilia tomentosa*) is confined to the south-eastern periphery of this area, to the north reaching south-western Ukraine (Meusel & Jäger 1989, Eaton et al. 2016). *Tilia cordata* has the broadest ecological niche of these three species as it occurs in both mesophilous (oak-hornbeam, scree and ravine) and slightly hygrophilous (floodplain) forests. In contrast, *Tilia platyphyllos* inhabits mainly scree and ravine forests. *Tilia tomentosa* tolerates drier conditions, also

occurring in thermophilous oak forests (Borhidi et al. 2013, Coldea et al. 2015). Although being common on flat terrain and gentle slopes, lime often becomes a dominant tree on steeper slopes, where it thrives because of its high tolerance of drought and clonal growth. It frequently forms either multi-stemmed trunks or single-stemmed individuals connected below ground, which enables it to grow on screes and in rock crevices (Radoglou et al. 2009, Logan et al. 2015). Lime is also supported by coppicing, which was practised in more accessible places.

Various types of forest communities with lime can be recognized in central Europe. Most of them belong to scree and ravine (*Aceretalia pseudoplatani*) or oak-hornbeam (*Carpinetalia betuli*) forests. Most of the studies on *Aceretalia pseudoplatani* report lime occurring on nutrient-rich lower parts of slopes, usually in stream valleys at low and middle altitudes, often together with *Acer* spp., *Carpinus betulus*, *Fraxinus excelsior* and *Ulmus glabra* (e.g. Husová 1982, Willner 1996). However, lime can also be found on the steep upper parts of slopes, growing on and among rocks. Such rocky sites with shallow and nutrient-poor soil prevent zonal tree species from attaining dominance. While south-facing rocky slopes are typically covered by dry grasslands or thermophilous oak or pine forests, north-facing rocky slopes are cooler and wetter, thus supporting more mesophilous vegetation, with lime often being the dominant tree. Within *Aceretalia pseudoplatani*, two groups of lime forests are usually distinguished (e.g. Clot 1990, Oberdorfer 1992) with several associations described within each: non-calcicolous lime forests, e.g. *Poo nemoralis-Tilietum cordatae* reported by Firbas & Sigmond (1928) and calcicolous lime forests. The latter can be further divided into nutrient-rich lime forests on lower slopes, e.g. *Aceri-Tilietum* described by Faber (1936), and nutrient-poorer lime forests on upper rocky slopes, usually with a lower amount of soil. In this study, we are interested in the latter, which we refer to as calcicolous (base-rich) rock-outcrop lime forests (hereafter ‘CROLFs’).

CROLF refers to a type of forest vegetation occurring under special environmental conditions. As already mentioned, it is usually found on the upper parts of steep rocky slopes on limestone or, less frequently on other types of base-rich bedrock, such as palaeobasalt, calcareous gneiss, calcareous conglomerate, dolomite and marble. In warm and dry areas, the slope is usually facing north, whereas in cooler areas the aspect may vary. Substrate ranges from solid rock with scattered hollows filled with fine soil to steep loamy or scree slopes with numerous rock outcrops of different sizes. The soil can be found only between rock outcrops; it is usually shallow and nutrient-poor. However, the occurrence of nitrophilous species indicates that soil nutrient content may vary from place to place.

The tree canopy is rather open (usually between 65–80%) in this rocky habitat. At most sites it is dominated by *Tilia cordata* or *T. platyphyllos*, while *T. tomentosa* occurs at several sites in north-western Romania. Other tree species often accompany lime: *Acer platanoides*, *Carpinus betulus* and *Fraxinus excelsior* are among the most frequent, with *Quercus petraea* agg. and *Sorbus aria* agg. being frequently admixed at drier sites. The shrub layer may vary markedly in both the number of species and its total cover, with *Berberis vulgaris*, *Cornus mas*, *Corylus avellana* and *Euonymus verrucosus* being the most frequent species. The herb layer is usually rich in species, containing a mixture of species of mesophilous forests (e.g. *Campanula rapunculoides*, *Carex digitata*, *Fragaria vesca*, *Lactuca muralis*), thermophilous forests (e.g. *Anthericum ramosum*, *Polygonatum*

*odoratum*, *Tanacetum corymbosum*, *Vincetoxicum hirundinaria*) and common species on rock outcrops (e.g. *Arabidopsis arenosa*, *Asplenium ruta-muraria*, *A. trichomanes*, *Hylotelephium maximum*). Species of dry grasslands (e.g. *Allium flavum*, *Carex humilis*, *Melica ciliata*, *Teucrium chamaedrys*) are often present at more open sites in drier areas. Since the prevailing conditions at CROLF sites are unfavourable for the development of zonal forests with a closed canopy, numerous relict species of different periods have been preserved there (e.g. *Aconitum anthora*, *Dianthus praecox*, *D. spiculifolius*, *Draba aizoides*, *Edraianthus graminifolius*, *Erysimum pallidiflorum*, *Primula auricula*, *Saxifraga paniculata*, *Sesleria caerulea*, *S. heuflerana*, *S. rigida*, *Tephroses integrifolia*, *Thalictrum foetidum*, *Viola jooi*). As most of them are light-demanding species, it is highly likely that there has been a continuous existence of a mosaic of open-canopy *Tilia* and *Corylus* woodland and patches of open grassland and rocky habitats since the early Holocene (see e.g. Tallantire 2002, Giesecke et al. 2017, Giesecke & Brewer 2018).

There are several studies on CROLFs in central Europe, but most of them have a narrow, regional focus. Zólyomi (1936) described the association *Tilio-Fraxinetum excelsioris* in the Bükk Mts in northern Hungary, which subsequently was reported to occur in both the North Hungarian Mts (e.g. Zólyomi 1967, Csiky 2002) and the Apuseni Mts in Romania (Gergely 1962, Rațiu et al. 1966). In addition to the common constituents of CROLFs, it is characterized by the occurrence of species of the eastern part of the study area (e.g. *Galium intermedium*, *Sesleria heuflerana*, *Spiraea media*, *Waldsteinia geoides*). Later, Zólyomi and Jakucs reported *Tilio-Sorbetum* as an endemic association of the high altitudes in the Bükk Mts (Zólyomi 1967), which includes several mountain species (e.g. *Arabis alpina*, *Calamagrostis varia*, *Clematis alpina*). Šomšák & Háberová (1979) described another association, *Seslerio heufleranae-Quercetum petraeae*, from the Slovak Karst (Slovenský kras), which includes xero-mesophilous rock-outcrop forests dominated by *Quercus petraea* and *Tilia platyphyllos*, with some locally distinctive species (particularly *Poa stiriaca* and *Sesleria heuflerana*). Chytrý & Sádlo (1998) described *Seslerio albicantis-Tilietum cordatae* as a new association of calcicolous forests in the Czech Republic and adjacent areas in Austria. They compared relevés of this association with those of other calcicolous lime forests in central Europe reported in the literature by that time. Kliment et al. (2010) reported *Seslerio heufleranae-Quercetum petraeae* also from the Muránska planina, a mountain range near to the Slovak Karst. A rare occurrence of this association was recently reported by Hrivnák et al. (2019) from other limestone areas in Slovakia (Biele Karpaty Mts and Mičiná Karst). Other studies reported a few new localities of CROLFs, including the surroundings of lake Traunsee in northern Austria (Fischer 2000), Strážovské vrchy Mts in western Slovakia (Duchov 2013), limestone area near Štramperk in north-eastern Moravia (Zukal & Novák 2017), and river valleys in south-western (Rafajová 1999) and central Moravia (Novák & Zukal 2017).

Except for Chytrý & Sádlo (1998), whose study was based on a limited number of relevés, there are no comparisons of individual associations within CROLFs or descriptions of the differences between them. In addition, there is no clear consensus on the assignment of central European CROLFs to higher-level syntaxa. Therefore, our aims are to (i) assess the variability of CROLFs in the eastern part of central Europe by analyzing a representative dataset of phytosociological relevés, most of which were recorded by us in the field for this purpose, (ii) identify distinct types of these forests, describe their

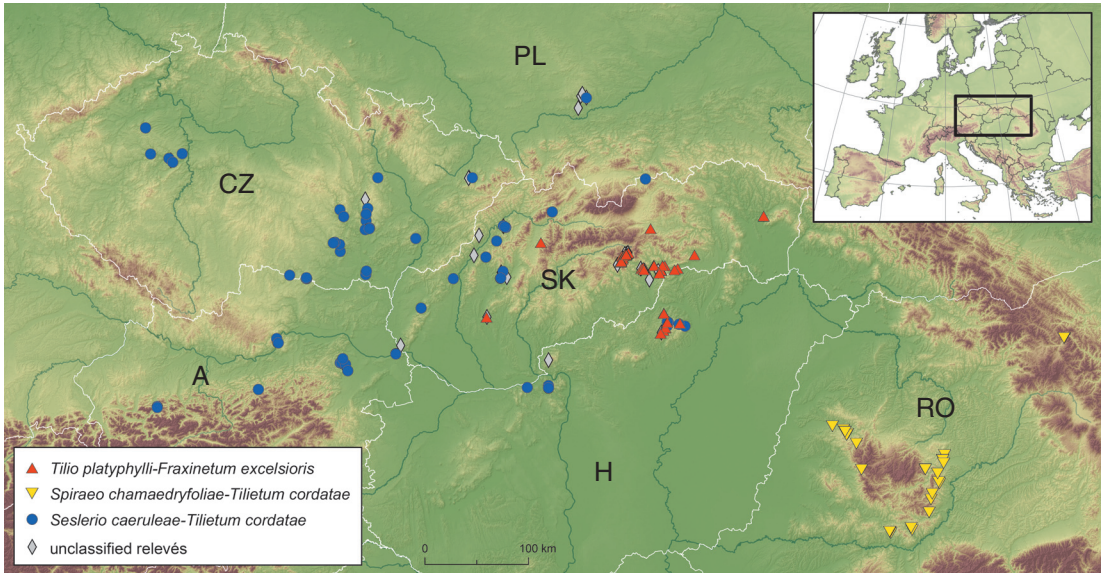


Fig. 1. – Map of study area showing the localities of the relevés.

floristic composition, ecology and the differences between them, (iii) prepare an expert system including formal definitions of the distinguished types, (iv) link these types with syntaxa, and (v) increase the awareness of CROLFs as an important relict community with great conservation importance.

## Material and methods

### *Study area*

The study area comprised the eastern part of central Europe, including north-eastern Austria, the Czech Republic, southern Poland, Slovakia, northern Hungary, Transcarpathian Ukraine and northern and western Romania (Fig. 1). Annual precipitation at the study sites ranges between 570–740 mm and mean annual temperature between 7.2–8.5 °C (Fick & Hijmans 2017).

As the studied vegetation occurs especially on limestone or other types of base-rich bedrock, our data originate especially from karst areas such as the Bohemian Karst (Český kras) and Moravian Karst (Moravský kras) in the Czech Republic, Slovak Karst (Slovenský kras) and Muránska planina Mts in Slovakia and Bükk Mts in Hungary.

### *Data collection*

To prepare a representative dataset of phytosociological relevés of CROLFs, we conducted field sampling in different parts of the study area during the years 2002–2019 (although most of the relevés were recorded in 2012–2019). Using geological maps, aerial

photographs and expert knowledge, we selected localities where CROLF presumably occurred based on the environmental conditions typical of already known localities. The selection focused on lowland to (sub)montane areas with limestone and steep rocky slopes with predominantly northern aspects. In total, we recorded 118 new relevés of CROLFs (see Electronic Appendix 1 for original relevés).

Relevés were usually sampled in areas of at least 100 m<sup>2</sup>, but smaller plots were also used in small CROLF stands. We estimated the percentage cover of the tree, shrub and herb layers, and the cover of each vascular plant species in each layer using a nine-degree cover-abundance scale (Westhoff & van der Maarel 1978). Numerous specimens collected in the field for subsequent identification were stored in the Herbarium of Masaryk University, Brno, Czech Republic (BRNU). For each plot, we recorded percentage cover of bryophytes, rocks and slope aspect and inclination. Geographical coordinates and altitude of the plots were recorded using a portable GPS device GPSmap 60CSx. Soil samples, each a mixture of four samples collected in relevé plots, were used to measure soil pH. Dried soil samples were separated from any particles larger than 2 mm using a sieve and mixed with distilled water in a ratio of 2:5. The pH of this suspension was determined using a GMH Greisinger pH meter. Climatic data (mean annual temperature and annual precipitation) were obtained from the WorldClim model version 2 (Fick & Hijmans 2017).

#### *Data selection*

Our relevés were digitized using the TURBOVEG 2.1 program (Hennekens & Schaminée 2001) and then exported to JUICE 7.0 (Tichý 2002). All relevés had to satisfy the selection criteria of the formal definition of CROLF (see Electronic Appendix 2) before they were included in the dataset. The formal definition was created to reflect the typical species composition of CROLFs based on both our original relevés and those from the above-mentioned studies on CROLFs. Besides our original relevés ( $n = 118$ ) and the published ones ( $n = 87$ ), we also used six unpublished relevés available in the European Vegetation Archive (EVA; Chytrý et al. 2016) that originated from the same area and had geographical coordinates. Relevés with plot sizes smaller than 25 m<sup>2</sup> were excluded. The final dataset (hereafter “dataset”) contained a total of 211 relevés.

Taxonomy and nomenclature of vascular plants recorded in all the relevés were unified according to the Euro+Med PlantBase (Euro+Med 2019). Nomenclature of higher syntaxa was unified based on EuroVegChecklist (Mucina et al. 2016). If we report syntaxa not accepted by EuroVegChecklist, we add author citations. Before analyzing the data, we deleted records of juvenile trees and shrubs occurring in the herb layer. Subsequently, we merged all the records of the same species occurring in different layers into a single layer. The taxa determined only to genus were excluded. We defined several species groups to include taxa recorded at different taxonomic levels (see Electronic Appendix 3 for the list of aggregates).

#### *Data analysis*

In order to detect the main vegetation types in our data, we tested several unsupervised classifications using JUICE and R software in the JUICE environment (R Core Team 2017), including modified TWINSpan (Roleček et al. 2009) and cluster analyses with

various settings. Different numbers of resulting clusters were also tested. Finally, we used flexible-beta clustering ( $\beta = -0.35$ ) with Bray-Curtis distance measure, transformed species cover values into pseudospecies using four cut levels (0–2–5–25%) and three resulting clusters, as this method yielded the best interpretable groups in terms of their ecology and biogeography.

As one of our aims was to define the final groups formally, we created an expert system that comprised formal definitions of the clusters distinguished by the unsupervised classification. The formal definitions were created to reflect the core of the variability of each cluster. Subsequently, we assessed the internal variability of each formally defined group and defined several subgroups (subassociations). Formal definitions of these subgroups were also created.

We selected diagnostic species of each formally defined group using the phi coefficient of association after virtually standardizing all the groups to the same size (Tichý & Chytrý 2006). After testing for non-randomness of species occurrences in groups using Fisher's exact test ( $P < 0.01$ ), species with a phi value greater than 0.25 were selected as diagnostic and species with a phi value greater than 0.50 as highly diagnostic for a given group of relevés. However, only the species with a constancy ratio (Dengler 2003) for a given group of at least  $1.5\times$  higher than that of other groups were selected.

Non-metric multidimensional scaling (NMDS) was computed using the package *vegan* 2.5-6 (Oksanen et al. 2019) in R software.

Most of the 211 relevés in the dataset (see Electronic Appendix 4 for the sources of relevés and their basic characteristics) originated from Slovakia (87 relevés), followed by the Czech Republic (42), Romania (31), Hungary (24), Austria (22) and Poland (5). Although the area of interest also included Transcarpathian Ukraine, no relevé satisfying the formal definition of CROLF was recorded there.

## Results and discussion

The dataset contained 546 vascular plant species (including species groups) with an average of 46 species per relevé. Since many species used here represent a group of two or more species, the true number of species is even greater, indicating a high species diversity. The following species were present in more than half of the relevés in the dataset: *Asplenium trichomanes* (occurring in 179 relevés), *Vincetoxicum hirundinaria* (171), *Hylotelephium maximum* (159), *Tilia platyphyllos* (156), *Campanula rapunculoides* (144), *Arabidopsis arenosa* (142), *Campanula persicifolia* (139), *Poa nemoralis* (130), *Carex digitata* (129), *Lactuca muralis* (125), *Galium mollugo* agg. (122), *Asplenium rutamuraria* (121), *Corylus avellana* (113), *Sorbus aria* agg. (110), *Pseudoturritis turrita* (109) and *Cornus mas* (107). Besides *Tilia platyphyllos* and *Sorbus aria* agg., the next most common tree species were *Fraxinus excelsior* (104), *Quercus petraea* agg. (103), *Tilia cordata* (96), *Carpinus betulus* (94), *Acer platanoides* (93) and *Fagus sylvatica* (69).

### Classification

The unsupervised classification revealed that the main floristic contrast within our dataset is connected with biogeography, as the relevé groups represent different regions within the study area (Fig. 1). First, the classification separated a group of relevés originating

in the Slovenské rudohorie Mts and adjacent areas (Group 1). They are characterized by the occurrence of species confined to the eastern part of the study area (e.g. *Galium intermedium*, *Spiraea media*, *Waldsteinia geoides*) and some characteristic species of the limestone areas in central Slovakia (especially *Calamagrostis varia* and *Poa stiriaca*) that are generally absent in relevés from the rest of the study area. The next division separated a group of northern and western Romanian CROLFs (Group 2) from the remaining relevés. This group is well distinguished by the occurrence of Eastern Carpathian endemic species (e.g. *Helictotrichon decorum*, *Melampyrum bihariense*, *Pulmonaria rubra*) and submediterranean species (e.g. *Asplenium ceterach*, *Fraxinus ornus*, *Tilia tomentosa*) typical of the easternmost part of the study area. The last and largest Group 3 comprises relevés originating from other parts of the study area: northern Austria, the Czech Republic, southern Poland, Slovakia (especially the western part of the country) and northern Hungary. This group is characterized by the occurrence of species typical of the western part of the study area (e.g. *Cyclamen purpurascens*, *Galium sylvaticum*) and species of rock-outcrop dry grasslands (e.g. *Erysimum odoratum*, *Sedum album*, *Seseli osseum*). We interpreted these three groups as the associations *Tilio platyphylli-Fraxinetum excelsioris*, *Spiraeo chamaedryfoliae-Tilietum cordatae* and *Seslerio caeruleae-Tilietum cordatae* (Fig. 2).

Of the 211 relevés forming the original dataset, 177 relevés (~84%) were classified, satisfying one of the formal definitions of associations or subassociations (see Electronic Appendix 2 for the formal definitions). Table 1 summarizes the main differences in species composition between the associations (see also the table in Electronic Appendix 5 for a comparison of species composition between subassociations). Differences in measured variables are compared using boxplots (Electronic Appendix 6). The communities are further described below.

*Tilio platyphylli-Fraxinetum excelsioris* Zólyomi 1936 (nomenclatural type: Kliment et al. 2010, Table 1, relevé 52, neotypus hoc loco)

The tree layer of this association usually consists of *Tilia platyphyllos*, *Quercus petraea* agg. and *Sorbus aria* agg., usually with an admixture of *Acer platanooides*, *Carpinus betulus*, *Fraxinus excelsior* and *Tilia cordata*. Compared to other types of CROLFs, the cover of shrub layer is usually not high. *Cornus mas* and *Corylus avellana* are the most frequent shrub species. The herb layer of this community is clearly different from that of the others: it is usually dominated by *Calamagrostis varia* or *Poa stiriaca*, species that are generally absent in other types of CROLFs. Other typical species include *Aconitum anthora*, *Cardamine bulbifera*, *Cephalanthera damasonium*, *Cruciata glabra* and also *Galium intermedium*, which is a diagnostic species even for the next community. Forest mesophytes (e.g. *Melica uniflora*, *Stellaria holostea*, *Waldsteinia geoides*) occur at slightly mesic sites, while the thermophilous species (e.g. *Bupleurum falcatum*, *Euphorbia epithymoides*, *Teucrium chamaedrys*) prevail at drier sites. Stands at the highest altitudes in the Bükk Mts are characterized by the occurrence of mountain species such as *Arabis alpina*, *Asplenium viride*, *Clematis alpina* and *Valeriana tripteris*.

This is a typical CROLF type of the southern part of central Slovakia, occurring mainly in the Slovak Karst and the Muránska planina Mts. Several relevés with similar species composition were also recorded in adjacent areas in Slovakia (Tribeč Mts, Veľká Fatra Mts, Slovenský raj Mts and Humenské vrchy Mts) and in the Bükk Mts in northern

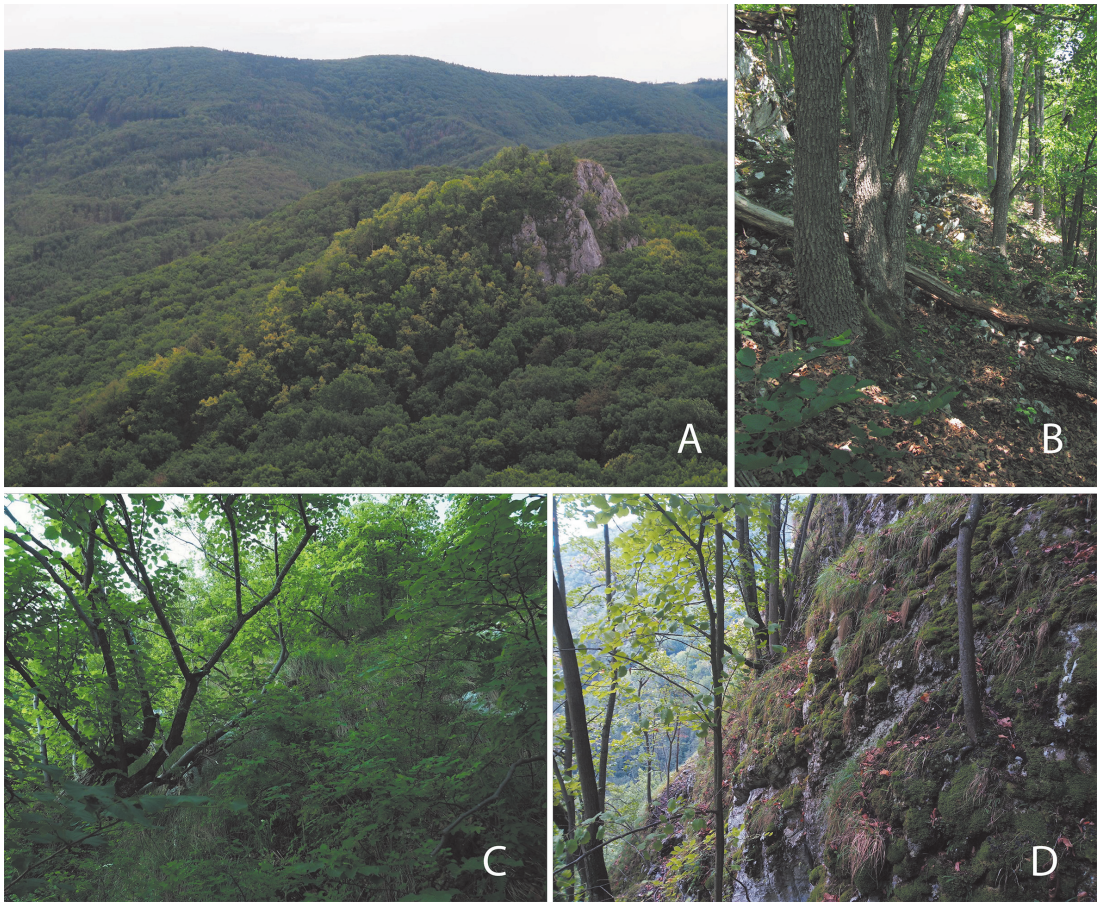


Fig. 2. – Photos of the studied CROLF types. (A) CROLF on the northern slopes of Dédesi-Kisvár peak (594 m), Bükk Mts, Hungary (photo M. Duchoň); (B) *Tilio platyphylli-Fraxinetum excelsioris*, south-eastern slopes of Cigánka (890 m), Muránska planina Mts, Slovakia (photo D. Blanár); (C) *Spiraeo chamaedryfoliae-Tilietum cordatae*, north-western slopes of Colții Trascăului peak (1113 m), Apuseni Mts, Romania (photo M. Duchoň); (D) *Seslerio caeruleae-Tilietum cordatae*, Manínska tiesňava gorge, Strážovské vrchy Mts, Slovakia (photo D. Zukal).

Hungary. Towards the west, this association is replaced by another type of CROLF characterized by the absence of some species typical of the Carpathians (e.g. *Galium intermedium*, *Sesleria heuflerana*).

Table 1. – Shortened synoptic table showing the percentage frequencies (constancies) of diagnostic species (shaded), *Tilia* species and other most frequent species of the distinguished associations. Diagnostic species are sorted by decreasing *phi* value and the others by decreasing frequency. Species with *phi* > 0.25 are considered as diagnostic, species with *phi* > 0.50 as highly diagnostic (in bold), but species with a constancy ratio lower than 1.5 or with non-significant Fisher's exact test ( $p > 0.01$ ) were excluded from the lists of diagnostic species. Abbreviations: TiF – *Tilio platyphylli-Fraxinetum excelsioris*, SpT – *Spiraeo chamaedryfoliae-Tilietum cordatae*, SeT – *Seslerio caeruleae-Tilietum cordatae*. ►



Association	TiF	SpT	SeT	Association	TiF	SpT	SeT
Number of relevés	67	31	79	Number of relevés	67	31	79
<b><i>Tilio platyphylli-Fraxinetum excelsioris</i></b>				<b><i>Seslerio caeruleae-Tilietum cordatae</i></b>			
<i>Poa stiriaca</i>	58	–	–	<i>Sesleria caerulea</i>	9	–	75
<i>Calamagrostis varia</i>	60	–	6	<i>Inula conyzae</i>	1	–	33
<i>Quercus petraea</i> agg.	84	13	39	<i>Cyclamen purpurascens</i>	–	–	23
<i>Convallaria majalis</i>	76	10	41	<i>Galium sylvaticum</i>	–	–	18
<i>Fragaria vesca</i>	73	35	22	<i>Anthericum ramosum</i>	39	10	58
<i>Melampyrum nemorosum</i>	39	–	15	<i>Allium lusitanicum</i>	6	–	23
<i>Campanula trachelium</i>	55	10	27	<i>Cornus sanguinea</i>	4	13	33
<i>Cardamine bulbifera</i>	25	3	1	<i>Erysimum odoratum</i>	7	–	23
<i>Laserpitium latifolium</i>	61	26	23	<i>Fourraea alpina</i>	–	–	13
<i>Alliaria petiolata</i>	48	16	13	<i>Aurinaria saxatilis</i>	–	–	11
<i>Heracleum sphondylium</i>	27	6	–	<i>Scabiosa ochroleuca</i>	3	–	15
<i>Veronica chamaedrys</i> agg.	57	29	27	<b>Species diagnostic for two associations</b>			
<i>Pseudoturritis turrita</i>	73	48	39	<i>Galium intermedium</i>	65	61	5
<i>Spiraea media</i>	22	10	–	<b>Tilia species</b>			
<i>Veronica austriaca</i>	12	–	1	<i>Tilia platyphyllos</i>	93	16	75
<b><i>Spiraeo chamaedryfoliae-Tilietum cordatae</i></b>				<i>Tilia cordata</i>	46	68	43
<i>Spiraea chamaedryfolia</i>	–	58	–	<i>Tilia tomentosa</i>	–	35	–
<i>Melampyrum bihariense</i>	–	55	–	<b>Other frequent species (f ≥ 33%)</b>			
<i>Hepatica nobilis</i>	–	77	29	<i>Asplenium trichomanes</i>	94	100	70
<i>Moehringia muscosa</i>	1	52	1	<i>Vincetoxicum hirundinaria</i>	82	84	81
<i>Valeriana stolonifera</i> subsp. <i>angustifolia</i>	27	81	11	<i>Hylotelephium maximum</i>	79	90	63
<i>Helictotrichon decorum</i>	–	29	–	<i>Campanula rapunculoides</i>	90	77	48
<i>Doronicum columnae</i>	–	26	–	<i>Campanula persicifolia</i>	79	74	57
<i>Potentilla chrysantha</i>	–	26	–	<i>Arabidopsis arenosa</i>	87	74	46
<i>Asarum europaeum</i>	15	45	5	<i>Carex digitata</i>	58	81	61
<i>Sesleria heuflerana</i> subsp. <i>heuflerana</i>	13	42	–	<i>Galium mollugo</i> agg.	67	58	51
<i>Calamagrostis arundinacea</i>	4	29	–	<i>Poa nemoralis</i>	64	77	44
<i>Fraxinus ornus</i>	–	26	4	<i>Lactuca muralis</i>	69	52	49
<i>Cirsium eristhales</i>	–	26	4	<i>Asplenium ruta-muraria</i>	57	65	52
<i>Seseli gracile</i>	–	19	–	<i>Cornus mas</i>	64	61	42
<i>Festuca valesiaca</i> agg.	–	19	–	<i>Corylus avellana</i>	39	71	59
<i>Lathyrus hallersteinii</i>	–	19	–	<i>Sorbus aria</i> agg.	76	10	52
<i>Crataegus monogyna</i>	18	45	9	<i>Digitalis grandiflora</i>	76	55	25
<i>Rhamnus saxatilis</i>	–	19	1	<i>Fraxinus excelsior</i>	57	32	47
<i>Selaginella helvetica</i>	1	19	–	<i>Polygonatum odoratum</i>	55	32	48
<i>Quercus cerris</i>	1	23	3	<i>Carpinus betulus</i>	39	61	47
<i>Peucedanum austriacum</i>	–	16	–	<i>Polypodium vulgare</i> agg.	54	77	28
<i>Pulmonaria rubra</i>	–	16	–	<i>Euonymus verrucosus</i>	36	58	49
<i>Saxifraga cuneifolia</i>	–	16	–	<i>Hieracium murorum</i>	54	3	53
<i>Sesleria rigida</i>	–	16	–	<i>Mercurialis perennis</i>	58	39	35
<i>Trifolium medium</i>	–	16	–	<i>Acer platanoides</i>	61	13	42
<i>Asplenium ceterach</i>	–	16	1	<i>Geranium robertianum</i>	57	55	28
<i>Melica picta</i>	1	16	–	<i>Lathyrus vernus</i>	60	58	24
<i>Viola jooi</i>	–	13	–	<i>Tanacetum corymbosum</i>	57	29	33
<i>Primula acaulis</i>	–	13	1	<i>Dactylis glomerata</i>	54	42	28
<i>Veronica urticifolia</i>	–	13	1	<i>Bupleurum falcatum</i>	42	–	54
<i>Prunus avium</i>	–	16	4	<i>Melittis melissophyllum</i>	54	45	27
<i>Erysimum crepidifolium</i>	–	10	–	<i>Primula veris</i>	37	45	35
<i>Helleborus purpurascens</i>	–	10	–	<i>Securigera varia</i>	45	35	33
<i>Sedum hispanicum</i>	–	10	–	<i>Melica nutans</i>	45	32	33
<i>Lamium maculatum</i>	7	26	8	<i>Teucrium chamaedrys</i>	42	23	39

Most of the relevés from Slovakia were classified in the association *Seslerio heufleranae-Quercetum petraeae* Šomšák et Háberová 1979 by their authors (Šomšák & Háberová 1979, Kliment et al. 2010, Hrivnák et al. 2019). However, as several relevés of this vegetation type from the Bükk Mts correspond to *Tilio platyphylli-Fraxinetum excelsioris* Zólyomi 1936, we identify this group of CROLFs with this association. Four relevés of this community type were originally classified as *Tilio-Sorbetum* Zólyomi et Jakucs in Zólyomi 1967. As the original diagnosis of *Tilio-Sorbetum* (Zólyomi 1967: 30–31) includes a shortened synoptic table that does not contain all the species with a constancy above 20%, we consider this association name as invalid (Art. 7 of ICPN, Theurillat et al. 2020). One relevé recorded in the Veľká Fatra Mts (Uhlířová et al. 1999), at the north-western distribution limit of this community type, was originally classified in the association *Vincetoxico-Tilietum* Winterhoff 1963, which was described to include scree forests on south- or west-facing slopes in central Germany. However, according to the original publication (Winterhoff 1963), *Vincetoxico-Tilietum* includes few thermophilous species, no rock-outcrop specialists and is species-poor. Thus we do not classify our Slovak relevés in this association, which we do not consider to be a CROLF.

Analysis of the internal variability of this association suggested three subassociations:

***Tilio platyphylli-Fraxinetum excelsioris typicum* subass. nova hoc loco** (nomenclatural type: identical with the nomenclatural type of the association, holotypus hoc loco)

This subassociation represents mesophytic stands of the association. It is characterized by a frequent occurrence of *Carpinus betulus* in the tree layer and numerous nemoral species in the herb layer (e.g. *Glechoma hirsuta*, *Melica uniflora*, *Stellaria holostea*, *Waldsteinia geoides*). Compared to the following association, this one occurs on west- or north-facing slopes in the Slovak Karst and the northern part of the Bükk Mts, while it is less common in the Muránska planina Mts. One relevé was also recorded in the Tribeč Mts in western Slovakia, which is the westernmost distribution limit of this association. Relevés with the original description of *Seslerio-Quercetum* are very similar to this subassociation, as they include numerous mesophilous forest species (Šomšák & Háberová 1979), therefore we consider *Seslerio-Quercetum* as a synonym of *T. p.-F. e. typicum*. The *Seslerio-Quercetum* variant with *Galium odoratum* proposed by Kliment et al. (2010) also corresponds to this subassociation.

***Tilio platyphylli-Fraxinetum excelsioris euphorbietosum epithymoidis* subass. nova hoc loco** (nomenclatural type: Kliment et al. 2010, Table 1, relevé 57, holotypus hoc loco)

This subassociation includes relevés with a high proportion of drought-adapted, thermophilous species of open forests, their edges and dry grasslands (e.g. *Achillea distans*, *Carex humilis*, *Euphorbia epithymoides*, *Origanum vulgare*, *Teucrium chamaedrys*, *Thalictrum minus*, *Veronica austriaca*). Unlike the previous subassociation, the relevés are usually from south- or south-east-facing slopes and contain drought-tolerant species. A high concentration of such species indicates that *T. p.-F. e. euphorbietosum epithymoidis* is a transitional subassociation to thermophilous oak forests. This subassociation was recorded mainly in the Muránska planina Mts, with single occurrences in the Veľká Fatra Mts, Slovenský raj Mts, Humenské vrchy Mts and the Bükk Mts. The *Seslerio-Quercetum* variant with *Rhamnus catharticus* described in the Muránska planina Mts by Kliment et al. (2010) can be included in this subassociation.

***Tilio platyphylli-Fraxinetum excelsioris arabidetosum alpinae* subass. nova hoc loco** (nomenclatural type: this paper, relevé TR1, see also Electronic Appendix 1, relevé 51, holotypus hoc loco)

This subassociation comprises several relevés recorded at the highest altitudes in the Bükk Mts in northern Hungary (630–820 m). Although it shares diagnostic species with other subassociations (e.g. *Calamagrostis varia*, *Galium intermedium*), it also contains several species typical of mountain forests (especially *Arabis alpina*, *Asplenium viride*, *Clematis alpina*, *Sesleria heuflerana* subsp. *hungarica* and *Valeriana tripteris*), which are among the most endangered species in Hungary and are only found at a few localities in that country (Farkas 1999). Stands with a higher proportion of such species may possibly be found also at high altitudes in central Slovakia. Relevés of this subassociation were originally classified within the association *Tilio-Sorbetum* Zólyomi et Jakucs in Zólyomi 1967 described from the Bükk Mts; however, this association was not described validly (see above). Based on the species composition and geographical proximity, we propose to establish a new subassociation within *Tilio-Fraxinetum* to include the above-mentioned relevés.

***Spiraeo chamaedryfoliae-Tilietum cordatae* ass. nova hoc loco** (nomenclatural type: this paper, relevé TR2, see also Electronic Appendix 1, relevé 61, holotypus hoc loco)

Relevés of this community type are usually dominated by *Tilia cordata*, often with an admixture of *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior* and *F. ornus*. In warmer areas, *Tilia cordata* is replaced by *T. tomentosa*. Unlike in the other CROLF types, *Tilia platyphyllos* is rare. The shrub layer is usually well-developed and includes both the species shared with other CROLF types (e.g. *Cornus mas*, *Corylus avellana*, *Crataegus monogyna*, *Euonymus verrucosus*) and some diagnostic species for this association, especially *Rhamnus saxatilis* and *Spiraea chamaedryfolia*. In addition to the other common species of CROLFs, there are numerous species characteristic of this vegetation in north-western Romania that are generally missing in the other types of the studied CROLFs, including species of the Eastern Carpathian zonal forests (e.g. *Lathyrus hallersteinii*, *Melampyrum bihariense*, *Pulmonaria rubra*), rock-outcrop specialists (*Moehringia muscosa*, *Saxifraga cuneifolia*, *Seseli gracile*, *Viola jooi*) and the Romanian endemic species *Cephalaria radiata* and *Helictotrichon decorum*. *Sesleria heuflerana* subsp. *heuflerana* or *S. rigida* may prevail in some stands, although most of the relevés lack a single dominant species in the herb layer.

This association was recorded exclusively in the northern and western parts of Romania. Most of the relevés originate from limestone canyons in the Apuseni Mts in the north-western part of the country. However, two relevés of this association were recorded on calcareous rocky slopes of the Bistrița river in the Eastern Carpathians near Vatra Dornei. Most likely, similar stands occur in other parts in the Eastern and possibly also Southern Carpathians.

There are several vegetation studies reporting *Tilia*-dominated forests in northern and western Romania. Täuber (1986) established two new associations (*Carpino-Tilietum platyphylli*, *Staphyleo-Tilietum platyphylli*) occurring along the lower section of the river Mureș in western Romania. Both of them clearly differ in having a small proportion of rock-outcrop specialists and by the occurrence or even dominance of numerous other species, often confined to oak-hornbeam or beech forests (e.g. *Acer tataricum*, *Carex*

*pilosa*, *C. sylvatica*, *Drymochloa drymeja*, *Ruscus aculeatus*). Close to the localities of this community in the Bistrița river valley in the Eastern Carpathians, Oprea (2007) reported two relevés of *Tilia*- and *Corylus*-dominated forests from slopes on the Rarău Massif under the name *Spiraeo ulmifoliae-Coryletum* Ujvárosi 1944; however, it differs in the occurrence of several hygrophilous species (e.g. *Impatiens noli-tangere*, *Scirpus sylvaticus*) and absence of rock-outcrop specialists. Mardari (2009) reported *Poo nemoralis-Tilietum cordatae* Firbas et Sigmond 1928 occurring also in the Bistrița valley. Like other studies reporting this association, the relevés of Mardari (2009) differ in the absence of calcicolous species and rock-outcrop specialists. Although described from the Bükk Mts in Hungary, *Tilio-Fraxinetum excelsioris* Zólyomi 1936 was reported also from the Apuseni Mts in Romania (Gergely 1962, Rațiu et al. 1966). However, as the name *Tilio-Fraxinetum* is used for the previous association, respecting its original description, we propose to establish a new association *Spiraeo chamaedryfoliae-Tilietum cordatae* to include CROLFs in northern and western Romania.

***Spiraeo chamaedryfoliae-Tilietum cordatae typicum* subass. nova hoc loco** (nomenclatural type: identical with the type of the association, holotypus hoc loco)

The typical subassociation comprises mesophytic stands dominated by *Tilia cordata*, rarely by *T. platyphyllos*. Several mesophilous tree species are often present (especially *Fagus sylvatica* and *Fraxinus excelsior*). The shrub layer is usually formed of two sublayers, with *Corylus avellana* dominating the upper and *Spiraea chamaedryfolia* the lower. Differential species can also be found in the herb layer, including common species of mesophilous forests (e.g. *Asarum europaeum*, *Calamagrostis arundinacea*, *Dryopteris filix-mas*) and mountain species (e.g. *Cirsium erisithales*, *Clematis alpina*, *Selaginella helvetica*). Some rare species of higher altitudes were also recorded (e.g. *Noccaea kovatsii*, *Pedicularis comosa*). In addition to limestones, stands of this subassociation were recorded on different types of bedrock, including dolomitic marble (Alba Region) and calcareous andesitic metatuffite (Suceava Region). It is characteristic of the eastern periphery of the Apuseni Mts (e.g. Cheile Ampoștei, Cheile Turzii and Piatra Cetii protected areas), but it has also been recorded in the Suceava Region in the Eastern Carpathians. It occurs at higher altitudes than the other subassociation (mean altitude 602 m).

***Spiraeo chamaedryfoliae-Tilietum cordatae tilietosum tomentosae* subass. nova hoc loco** (nomenclatural type: this paper, relevé TR3, see also Electronic Appendix 1, relevé 79, holotypus hoc loco)

This subassociation includes forests in warm areas dominated exclusively by *Tilia tomentosa*, while *T. cordata* is usually absent. Other characteristic species of this subassociation include both woody (e.g. *Cornus mas*, *Ligustrum vulgare*, *Sorbus torminalis*) and herbaceous species (e.g. *Lathyrus niger*, *Melica uniflora*, *Potentilla chrysantha*). Remarkable is the occurrence of submediterranean species (e.g. *Asplenium ceterach*, *Fraxinus ornus*, *Quercus cerris*). Compared to the previous subassociation, *Spiraea chamaedryfolia* is often absent. The subassociation was recorded at lower altitudes (mean altitude 436 m) in two different regions on the periphery of the Apuseni Mts: in the north-westernmost part at the transition to the Pannonian Basin (including the Crișul Repede valley) and in the canyons incised in the southernmost part of the Apuseni Mts north of the city of Deva. It is possible that this community type might be better considered

as a separate association rather than a subassociation within *Spiraeo-Tilietum*. However, as we have only a limited number of relevés from a small area, we do not propose this.

*Seslerio caeruleae-Tilietum cordatae* Chytrý et Sádlo 1998 nom. corr. (synonym: *Seslerio albicantis-Tilietum cordatae* Chytrý et Sádlo 1998 nom. inept.; the association name is corrected by replacing the incorrect name-giving species name *Sesleria albicans* Schult. by the correct name *Sesleria caerulea* (L.) Ard.; nomenclatural type: Chytrý & Sádlo 1998, Table 1, relevé 21, holotypus)

This group comprises relevés dominated by *Tilia cordata* or *T. platyphyllos*. Other common tree species include *Acer platanoides*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus petraea* agg. and *Sorbus aria* agg. The shrub layer is usually developed, with *Berberis vulgaris*, *Cornus mas*, *C. sanguinea*, *Corylus avellana* and *Euonymus verrucosus* being among the most frequent shrubs. *Sesleria caerulea* is a typical dominant species present in most of the relevés, and the most faithful diagnostic species. Other diagnostic species in the herb layer include several light-demanding species characteristic of rock outcrops in dry areas (e.g. *Allium lusitanicum*, *Aurinia saxatilis*, *Erysimum odoratum*, *Seseli osseum*) and species occurring almost exclusively in the western part of the study area: the Bohemian Massif and the Eastern Alps (especially *Cyclamen purpurascens*, *Fourraea alpina* and *Galium sylvaticum*).

Relevés classified within this community were recorded mainly in the western part of the study area. Most of them originate from the Czech Republic and northern Austria, with several relevés also recorded in northern Hungary, north-western Slovakia and the Wyżyna Krakowsko-Częstochowska upland in southern Poland. The occurrence of CROLF in Poland has so far not been reported (cf. Matuszkiewicz 2001, 2007). However, in the Wyżyna Krakowsko-Częstochowska upland, where we recorded CROLFs, Medwecka-Kornaś (1952) mentioned the association *Peucedano cervariae-Coryletum* as a typical community on rocky limestone slopes. This shrub vegetation resembles a CROLF in the co-occurrence of forest mesophytes and thermophilous species, but it lacks most of the rock-outcrop specialists.

We identify this community with the association *Seslerio caeruleae-Tilietum cordatae* Chytrý et Sádlo 1998 described from calcareous areas in the Czech Republic. Most of the relevés classified within this community originate either from the original publication describing the association (Chytrý & Sádlo 1998) or from our fieldwork. A few other relevés published before the description of *Seslerio-Tilietum*, originally classified within other vegetation types (e.g. *Fagion sylvaticae*, *Quercion pubescenti-petraeae*), were also included in this association because they were dominated by *Tilia* spp. with many characteristic species of CROLFs including rock-outcrop specialists.

Following Chytrý & Sádlo (1998), we distinguished two subassociations:

*Seslerio caeruleae-Tilietum cordatae typicum* (synonym: *Seslerio albicantis-Tilietum cordatae euphorbietosum cyparissiae* Chytrý et Sádlo 1998; nomenclatural type identical with the type of the association, holotypus)

This subassociation occurs at warmer sites, as indicated by higher annual mean temperature and occurrence of numerous thermophilous species (e.g. *Allium flavum*, *A. lusitanicum*, *Melica ciliata*, *Prunus mahaleb*, *Seseli osseum*). Compared to the next subassociation, it usually occurs on steeper slopes (mean inclination 50°). As the mean

cover of the tree layer (66%) is rather low there, most of its differential species are light-demanding. Cover of rocks is usually high (mean 58%), and several rock-outcrop specialists (e.g. *Asplenium ruta-muraria*, *Hylotelephium maximum*, *Jovibarba globifera*, *Sedum album*) occur in the herb layer. Relevés of this subassociation have been recorded in various parts of the study area. Most of them are confined to the transitional areas between the Pannonian Basin and adjacent mountain ranges: the Alps, the Bohemian Massif and the Western Carpathians. There are also single relevés matching the formal definition of this subassociation from the Štramberk Karst in north-eastern Moravia and southern Poland. This subassociation was originally described to include stands from warm and dry southern Moravia (Chytrý & Sádlo 1998); however, our study based on a large dataset shows that it also occurs with a very similar species composition in neighbouring areas.

*Seslerio caeruleae-Tilietum cordatae campanuletosum rapunculoidis* Chytrý et Sádlo 1998 (nomenclatural type: Chytrý & Sádlo 1998, Table 1, relevé 18, holotypus)

This subassociation comprises more mesophytic stands of the association, which are differentiated by mesophilous forest species (e.g. *Cyclamen purpurascens*, *Galium sylvaticum*, *Hepatica nobilis*, *Melica nutans*) in the herb layer. As this subassociation represents a (south)-westernmost type of CROLF occurring in the Bohemian Massif and north-eastern periphery of the Alps, it includes several species characteristic of this part of the study area (e.g. *Amelanchier ovalis*, *Buphthalmum salicifolium*, *Fourraea alpina*, *Polygala chamaebuxus*).

#### *Biogeography and specific features of CROLFs*

As biogeography is the main factor underlying the gradient of floristic composition within our dataset, the distinguished associations represent vicariant communities within central European CROLFs. It is well reflected in NMDS (Fig. 3), as *Spiraeo-Tilietum* and *Seslerio-Tilietum* are located on the left and right periphery of the diagram, respectively, while *Tilio-Fraxinetum* occupies the central area of the ordination space. Differences within individual associations are mainly connected with moisture/temperature.

The studied CROLFs are notable for their high diversity in terms of both species richness and numerous rare species unique to individual regions. Some of the published relevés of CROLFs from the Slovenský raj and Muránska planina National Parks are among the most species-rich forest relevés ever recorded in the Czech Republic and Slovakia (Chytrý et al. 2015) with 105 and 94 vascular plant species in an area of 400 m<sup>2</sup>, respectively. High species richness results from high environmental heterogeneity in a small area. Therefore species with various ecological requirements can grow together in CROLF stands. However, direct comparisons of the mean species numbers between individual associations are biased, since the majority of the relevés from the Slovak Karst and the Muránska planina Mts (i.e. most of the *Tilio-Fraxinetum* relevés) are from plots of 300–400 m<sup>2</sup>, while the plot area of most of the other relevés in the dataset is 100–200 m<sup>2</sup>.

Species composition of CROLFs is also influenced by adjacent vegetation types. CROLF stands surrounded by beech and oak-hornbeam forests are generally characterized by a more frequent occurrence of mesophilous forest species (e.g. *Tilio-Fraxinetum typicum*). In contrast, stands bordering on thermophilous oak forests and dry grasslands are

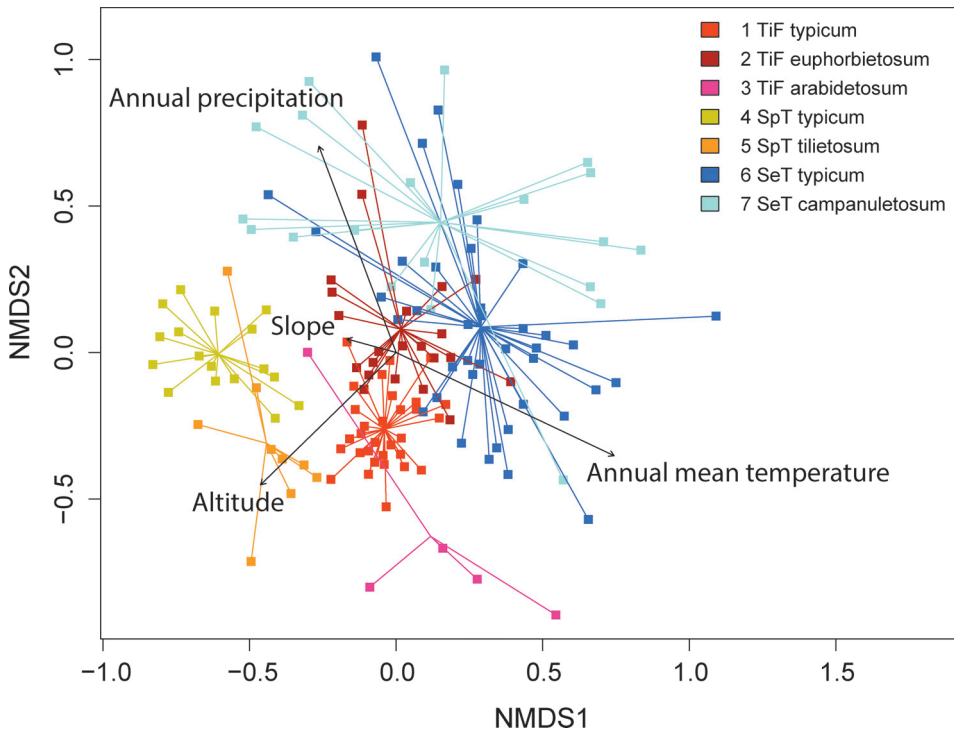


Fig. 3. – NMDS diagram of the CROLF relevés classified to subassociations. Selected environmental variables were superimposed on the ordination plot. The stress of the analysis is 0.26. Abbreviations: TiF – *Tilio platyphylli-Fraxinetum excelsioris*, SpT – *Spiraeo chamaedryfoliae-Tilietum cordatae*, SeT – *Seslerio caeruleae-Tilietum cordatae*.

characterized by a higher proportion of species typical of these habitats. CROLF communities occurring in extensive rocky areas with patches of dealpine grasslands host higher number of relict and endemic species (e.g. *Spiraeo-Tilietum typicum* in the canyons of the Apuseni Mts). The CROLF stands at high altitudes surrounded by beech forests (e.g. *Tilio-Fraxinetum arabidetosum* in the Bükk Mts) are also less thermophilous and with a more frequent occurrence of dealpine species.

As this vegetation type occurs on isolated rock outcrops, within calcareous mountain ranges that are also isolated, each locality is unique to some extent, with a different history and often very local occurrence of relict and endemic species. Two major ecological groups can be recognized among the relict light-demanding species in CROLFs. The first group is represented by rock-outcrop specialists that also inhabit rocky habitats in the surroundings of CROLFs. Some of them are of dealpine origin (e.g. *Primula auricula*, *Saxifraga paniculata*, *Sesleria* spp.; Skalický 1990). This group also includes some species with a narrow distribution (e.g. *Campanula carpatica*, *Viola jooi*). The second group comprises mesophilous species (e.g. *Bupleurum longifolium*, *Carex brevicollis*, *Laserpitium latifolium*, *Tephrosieris integrifolia*, *Veratrum nigrum*) inhabiting patches of relatively deep soil in CROLFs. Due to their specific ecology, they are usually very rare in the surrounding landscape, preferring other presumably relict types of vegetation, e.g. ancient

grasslands (Roleček et al. 2014). Co-occurrence of the mentioned species indicates the probable relict character of CROLF vegetation.

CROLF localities are predictably distributed in limestone areas in low mountain ranges (usually not exceeding 1000 m in central Europe) and their foothills. Although most of these stands are of very limited extent, they may cover larger areas in regions with extensive rocky habitats (e.g. edges of karst plateaus in the Slovak Karst, canyons in the Apuseni Mts). In contrast to limestone, CROLF vegetation is rarely recorded on dolomite. Cooler north-facing slopes in some areas (e.g. Malá Fatra Mts, Strážovské vrchy Mts) are often occupied by beech forests or relict pine forests. Slightly similar yet different type of rock-outcrop forest vegetation can also be found on other base-rich bedrocks (e.g. basalt, spilite). However, as they are usually not calcareous, they are generally poor in basiphilous rock-outcrop specialists, and they do not satisfy the formal definition of CROLFs. Relationship of such vegetation to CROLFs requires further study. Although frequently occurring in mosaics, lime can be completely replaced by *Corylus avellana* shrubs. At a few limestone localities in the Apuseni Mts, typical CROLF habitats are occupied by patches of *Betula pendula*- and *Populus tremula*-dominated open forest. What determines the occurrence of either *Tilia*- or *Betula/Populus*-dominated vegetation requires further study.

Although we aimed at covering the study area by relevés representatively, no relevé from Transcarpathian Ukraine matched the formal definition of CROLFs. This is probably due to the fact that there are very few limestone areas there, and they occur mainly in the precipitation-rich areas covered by extensive beech forests. Onyshchenko (2007) published one relevé dominated by *Tilia platyphyllos* together with several rock-outcrop species under a provisional name *Seselio libanotidis-Fagetum* from the limestone rocky slopes in the Uholka-Shyrokyi Luh protected area. However, the relevé is co-dominated by *Fagus sylvatica* and contains species typical of acidophilous montane forests (e.g. *Maianthemum bifolium*, *Orthilia secunda*, *Vaccinium myrtillus*), therefore it does not satisfy the formal definition of CROLFs.

#### *Assignment of CROLFs to higher-level syntaxa*

As the species composition of the studied vegetation is rather diverse, the individual CROLF associations were originally assigned to various higher-level syntaxa, including subcontinental oak forests (*Aceri tatarici-Quercion* Zólyomi 1957) and calcicolous beech forests (*Cephalanthero-Fagenion* Tüxen in Tüxen et Oberdorfer 1958). However, the majority of the recent studies classify CROLFs within thermophilous lime forests (*Melico-Tilion platyphylli*, often under the suballiance name *Tilienion platyphylli* (Moor 1975) Müller in Oberdorfer 1992) or mesophilous scree forests (*Tilio-Acerion*), both within the order *Aceretalia pseudoplatani*, class *Carpino-Fagetea* (Mucina et al. 2016). Although the stands with a high proportion of species of *Quercetea pubescentis* suggest affinity to thermophilous oak forests, the prominent contribution of lime, the prevalence of species of *Carpino-Fagetea* and the occurrence of rock-outcrop specialists together with the azonal nature of the sites imply a close relation of CROLFs with the order *Aceretalia pseudoplatani* and alliance *Melico-Tilion platyphylli*. The alliance *Melico-Tilion* represents thermophilous lime forests at low altitudes in the southern regions of central Europe. Compared to *Tilio-Acerion*, it is characterized by the occurrence of



species with high temperature and light requirements (e.g. *Hylotelephium maximum*, *Quercus petraea*, *Tilia* spp., *Vincetoxicum hirundinaria*) together with nemoral species (e.g. *Campanula persicifolia*, *Hepatica nobilis*, *Lathyrus vernus*). Analogous types of CROLFs are also likely to occur in south-eastern Europe. They would be classified in the submediterranean alliance *Ostrya carpinifoliae-Tilion platyphylli*, which is characterized by species with a southern and south-eastern distribution (e.g. *Dioscorea communis*, *Helleborus odoratus*, *Ostrya carpinifolia*, *Ruscus hypoglossum*) that are rare or absent in central Europe.

We propose the following syntaxonomical outline, which is compatible with EuroVegChecklist (Mucina et al. 2016):

Class: *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968

Order: *Aceretalia pseudoplatani* Moor 1976

Alliance: *Melico-Tilion platyphylli* Passarge et G. Hofmann 1968

Association: *Tilio platyphylli-Fraxinetum excelisioris* Zólyomi 1936

Subassociation: *T. p.-F. e. typicum*

Subassociation: *T. p.-F. e. euphorbietosum epithymoidis* Zukal et al. 2020

Subassociation: *T. p.-F. e. arabidetosum alpinae* Zukal et al. 2020

Association: *Spiraeo chamaedryfoliae-Tilietum cordatae* Zukal et al. 2020

Subassociation: *S. c.-T. c. typicum*

Subassociation: *S. c.-T. c. tilietosum tomentosae* Zukal et al. 2020

Association: *Seslerio caeruleae-Tilietum cordatae* Chytrý et Sádlo 1998 nom. corr.

Subassociation: *S. a.-T. c. typicum*

Subassociation: *S. a.-T. c. campanuletosum rapunculoidis* Chytrý et Sádlo 1998

See [www.preslia.cz](http://www.preslia.cz) for Electronic Appendices 1-6

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## Souhrn

V této práci jsme studovali variabilitu vzácné vegetace vápnomilných skalních lipin (s převládající lípou srdčitou, velkolistou a stříbrnou) v severním Rakousku, České republice, jižním Polsku, na Slovensku, v severním Maďarsku a severozápadním Rumunsku. Tato vegetace zahrnuje druhově bohaté lesy, ve kterých se mísí druhy mezofilních a teplomilných lesů s druhy suchých trávníků a skalních výchozů. Vápnomilné skalní lipiny se obvykle vyskytují na horních hranách prudkých skalnatých svahů s mělkou půdou na vápenci nebo jiných bazických horninách. Jelikož jsou tyto podmínky nepříznivé pro výskyt zonálních lesů se zapojeným stromovým patrem, přežívají zde mnohé světlo milné reliktní druhy, např. *Dianthus praecox*, *D. spiculifolius*, *Primula auricula*, *Sesleria caerulea*, *S. heuflerana*, *Tephrosia integrifolia*, *Viola jooi* a další. Na základě výsledků neřízené klasifikace datového souboru 118 originálních, 87 publikovaných a 6 nepublikovaných fytoecologických snímků uložených v Evropském vegetačním archívu (celkem 211 snímků) jsme rozlišili tři asociace vápnomilných skalních lipin: (i) *Tilio platyphylli-Fraxinetum excelisioris* vyskytující se na středním Slovensku

a v severním Maďarsku, (ii) *Spiraeo chamaedryfoliae-Tilietum cordatae*, nová asociace zaznamenaná v severním a západním Rumunsku, a (iii) *Seslerio caeruleae-Tilietum cordatae* vyskytující se v České republice, severním Rakousku, severním Maďarsku, na západním Slovensku a také v jižním Polsku, kde vápnomilné skalní lipiny nebyly doposud zaznamenány. Vytvořili jsme expertní systém formálních definic tří asociací a sedmi subasociací, který klasifikoval 84 % souboru fytoocenologických snímků. Všechny tři asociace řadíme do svazu *Melico-Tilion platyphylli* řádu *Aceretalia pseudoplatani* (třída *Carpino-Fagetea*).

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## Appendix 1. – Typification of syntaxa.

TR1: *Tilio platyphylli-Fraxinetum excelsioris arabidetosum alpinae* Zukal et al. 2020, holotypus (also included in Electronic Appendix 1, relevé 51). Hungary, Northern Hungary Region, Szilvássvár: forest on a steep rocky slope, 0.15 km N from the peak Holló-kő (823 m), 790 m a.s.l. Coordinates: 48.08616° N, 20.44163° E; Relevé area: 100 m<sup>2</sup> (10 m × 10 m); Aspect: 360°; Slope: 70°; Covers: tree layer 75%, shrub layer 20%, herb layer 10%, moss layer 5%; Cover of rocks: 90%; Soil pH: 7.6. Recorded by D. Zukal & P. Novák on July 24, 2018. – Tree layer: *Tilia cordata* 3, *T. platyphyllos* 2b. – Shrub layer: *Euonymus verrucosus* 2a, *Sorbus aria* agg. 2a, *S. aucuparia* 1, *Lonicera xylostium* +, *Viscum album* subsp. *album* +. – Herb layer: *Asplenium trichomanes* 1, *Campanula rapunculoides* 1, *Valeriana tripteris* 1, *Arabidopsis arenosa* +, *Arabis alpina* +, *Asplenium ruta-muraria* +, *A. viride* +, *Carex digitata* +, *Clematis alpina* +, *Cystopteris fragilis* +, *Digitalis grandiflora* +, *Festuca pallens* +, *Galium mollugo* agg. +, *Genista pilosa* +, *Hieracium murorum* +, *Hylotelephium maximum* +, *Lactuca muralis* +, *Mercurialis perennis* +, *Pimpinella major* +, *Poa nemoralis* +, *Polypodium vulgare* agg. +, *Primula veris* +, *Pseudoturritis turrita* +, *Saxifraga paniculata* +, *Scabiosa lucida* +, *Sesleria heuflerana* subsp. *hungarica* +, *Silene nutans* +, *Calamagrostis varia* r, *Campanula persicifolia* r, *Galium intermedium* r, *Lathyrus vernus* r, *Lilium martagon* r, *Moehringia trinervia* r, *Senecio sylvaticus* r, *Silene nemoralis* r, *Solidago virgaurea* r, *Acer platanoides* r, *Fagus sylvatica* r.

TR2: *Spiraeo chamaedryfoliae-Tilietum cordatae* Zukal et al. 2020, holotypus (also included in Electronic Appendix 1, relevé 61). Romania, Alba Region, Valea Mănăstirii: forest on a rocky slope above right bank of the river Râmeț, 0.7 km NE from the peak Piatra Cheii (1189 m), 560 m a.s.l. Coordinates: 46.29250° N, 23.47247° E; Relevé area: 100 m<sup>2</sup> (10 m × 10 m); Aspect: 340°; Slope: 45°; Covers: tree layer 85%, shrub layer 40%, herb layer 40%, moss layer 30%; Cover of rocks: 40%; Soil pH: 6.7. Recorded by P. Novák on June 7, 2018. – Tree layer: *Tilia cordata* 5, *Fagus sylvatica* 1, *Fraxinus excelsior* 1. – Shrub layer: *Corylus avellana* 2b, *Spiraea chamaedryfolia* 2b, *Euonymus verrucosus* 1, *Berberis vulgaris* +, *Viburnum lantana* +. – Herb layer: *Sesleria heuflerana* subsp. *heuflerana* 2b, *Asarum europaeum* 1, *Calamagrostis arundinacea* 1, *Dryopteris filix-mas* 1, *Polypodium vulgare* agg. 1, *Scopolia carniolica* 1, *Valeriana stolonifera* subsp. *angustifolia* 1, *Aconitum anthora* +, *Asplenium scolopendrium* +, *A. trichomanes* +, *A. viride* +, *Campanula rapunculoides* +, *Carex digitata* +, *Clematis alpina* +, *Cystopteris fragilis* +, *Festuca pseudodalmatica* +, *Galium intermedium* +, *G. odoratum* +, *Hepatica nobilis* +, *Hylotelephium maximum* +, *Melampyrum bihariense* +, *Melica nutans* +, *Moehringia muscosa* +, *Poa nemoralis* +, *Salvia glutinosa* +, *Saxifraga cuneifolia* +, *S. paniculata* +, *Corydalis capnoides* r, *Vincetoxicum hircundinaria* r, *Fraxinus ornus* +, *Acer pseudoplatanus* r, *Fagus sylvatica* r.

TR3: *Spiraeo chamaedryfoliae-Tilietum cordatae tilietosum tomentosae* Zukal et al. 2020, holotypus (also included in Electronic Appendix 1, relevé 79). Romania, Bihor Region, Bălnaca-Groși: open forest on a rocky slope, 2.8 km ENE from the peak Vf. Runcului (822 m), 485 m a.s.l. Coordinates: 46.92319° N, 22.53431° E; Relevé area: 150 m<sup>2</sup> (15 m × 10 m); Aspect: 360°; Slope: 45°; Covers: tree layer 55%, shrub layer 30%, herb layer 40%, moss layer 50%; Cover of rocks: 35%; Soil pH: 7.2. Recorded by D. Zukal, P. Novák & M. Duchoň on June 4, 2018. – Tree layer: *Tilia tomentosa* 3, *Carpinus betulus* 2a, *Quercus cerris* 2a. – Shrub layer: *Tilia tomentosa* 3, *Cornus mas* 1, *Rhamnus saxatilis* 1, *Carpinus betulus* +, *Corylus avellana* +, *Crataegus monogyna* +, *Pyrus communis* +, *Rosa* sp. +, *Sorbus aria* agg. +. – Herb layer: *Sesleria heuflerana* subsp. *heuflerana* 3, *Asplenium trichomanes* 1, *Brachypodium pinnatum* 1, *Galium mollugo* agg. 1, *Vincetoxicum hircundinaria* 1, *Achillea distans* +, *Arabidopsis arenosa* +, *Arabis hirsuta* +, *Asplenium ceterach* +, *A. ruta-muraria* +, *Campanula persicifolia* +, *Carex digitata* +, *C. montana* +, *Chamaecytisus hirsutus* +, *Clematis vitalba* +, *Clinopodium vulgare* +, *Cruciata glabra* +, *Dactylis glomerata* +, *Dianthus carthusianorum* agg. +, *Euphorbia cyparissias* +, *Hedera helix* +, *Hepatica nobilis* +, *Melica nutans* +, *Moehringia muscosa* +, *Peucedanum oreoselinum* +, *Poa nemoralis* +, *Primula veris* +, *Securigera varia* +, *Sempervivum marmoratum* +, *Tanacetum corymbosum* +, *Teucrium chamaedrys* +, *Thymus praecox* +, *Viola hirta* +, *Edraianthus graminifolius* r, *Hylotelephium maximum* r, *Potentilla chrysantha* r, *Viola riviniana* r, *Sorbus torminalis* +.