MASARYKOVA UNIVERZITA

Přírodovědecká fakulta
Ústav botaniky a zoologie

Vegetace evropských dubohabřin

Disertační práce

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Brno 2020

MASARYK UNIVERSITY

Faculty of Science
Department of Botany and Zoology

Vegetation of European oak-hornbeam forests

Ph.D. Thesis

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Brno 2020

Bibliographical entry

Author:	Mgr. Pavel Novák
Title of Thesis:	Vegetation of European oak-hornbeam forests
Degree programme:	Ecological and Evolutionary Biology
Field of Study:	Botany
Supervisor:	prof. RNDr. Milan Chytrý, Ph.D.
Academic Year:	2019/2020
Number of pages:	45+151

Keywords: *Carpinetalia betuli*; *Carpino-Fagetea*; *Carpinus betulus*; Caucasus; central Europe; deciduous mesophilous forests; Euxinia; phytosociology; plant ecology; *Quercus*; relevé

Bibliografický záznam

Autor:	Mgr. Pavel Novák
Název práce:	Vegetace evropských dubohabřin
Studijní program:	Ekologická a evoluční biologie
Studijní obor:	Botanika
Školitel:	prof. RNDr. Milan Chytrý, Ph.D.
Akademický rok:	2019/2020
Počet stran:	45+151

Klíčová slova: *Carpinetalia betuli*; *Carpino-Fagetea*; *Carpinus betulus*; Kavkaz; střední Evropa; opadavé mezofilní lesy; Euxinie; fytocenologie; rostlinná ekologie; *Quercus*; fytocenologický snímek

Abstract

Oak-hornbeam forests are one of the most common forest vegetation types in Europe and the adjacent part of western Asia. They are deciduous forests with usually mixed tree layer, frequently dominated by common hornbeam (*Carpinus betulus*) and oaks (*Quercus* sp. div.). Forest mesophytes prevail in the understory. The knowledge of their variability differs from region to region. In some areas (e.g. western and central Europe), they have been studied by many authors and a large dataset of phytosociological relevés is available, however synthetic supranational studies overviewing their variability are mostly missing. In some areas mostly in the eastern part of their range (e.g. the Balkans, Caucasus, Euxinia), they still have not been sufficiently studied.

The thesis provides three regional studies dealing with the variability of oak-hornbeam forests in insufficiently explored regions. They are mostly based on analyses of original field data. In the paper from Transcarpathian Ukraine, we distinguished three associations of local oak-hornbeam forests (alliance *Carpinion*). They were Pannonian slightly hygrophilous types (association *Circaeo-Carpinetum*), Carpathian mesophilous types (*Carici pilosae-Carpinetum*) and thermophilous types (*Primulo veris-Carpinetum*, recognized as a new association for Ukraine). In the study dealing with unique Colchic forests of western Georgia, we distinguished two main types of the Euxinian oak-hornbeam forests (alliance *Castaneo-Carpinion*), one lacking an evergreen shrub layer (association *Digitali-Carpinetum*) and one with a thick evergreen shrub layer (*Rusco-Carpinetum*). The third study is focused on Caucasian oak-hornbeam forests in Georgia. We described one new association (*Clinopodio-Carpinetun*, alliance *Crataego-Carpinion*) and we also recorded to date little known vegetation types, Caucasian montane oak-hornbeam forests (*Astrantio-Carpinetum*, alliance *Astrantio-Carpinion*) and forests with a relict tree *Zelkova carpinifolia*.

For central European oak-hornbeam forests (alliances *Carpinion* and *Erythronio-Carpinion*), the thesis brings a synthetic study. We recognized thirteen main types of oak-hornbeam forests which we usually identified with previously described associations. Ordination analyses indicated biogeography and soil properties (mainly moisture and nutrient content) as the main source of variability in their species composition. Therefore, we organized the association into three informal ecological groups (hygrophilous, mesophilous, xerophilous) within which the associations were distinguished mainly biogeographically. We provided descriptions and formal definitions of the recognized associations as well as syntaxonomic revision which can serve as a baseline for further studies. Three traditionally used association names (*Galio sylvatici-Carpinetum*, *Lithospermo-Carpinetum*, *Stellario holostei-Carpinetum*) were proposed for conservation in the nomenclatural proposal as we found their older valid synonyms. The findings published in the synthesis were applied in the chapter dealing with oak-hornbeam forests in the Slovak vegetation survey. We distinguished four main associations for which we provided detailed descriptions. In the Carpathians, they are mesophilous association *Carici pilosae-Carpinetum* and thermophilous association *Primulo veris-Carpinetum*. In the Pannonian Basin, we recognized slightly hygrophilous association *Convallario-Carpinetum* and association *Polygonato-Carpinetum* which involves rare oak-hornbeam forests on loess bedrock.

Abstrakt

Dubohabrové lesy představují jeden z nejrozšířenějších typů lesní vegetace v Evropě a přilehlých částech západní Asie. Jsou to listnaté opadavé lesy s obvykle smíšeným stromovým patrem, ve kterém většinou dominuje habr obecný (*Carpinus betulus*) a duby (*Quercus* sp. div.). V podrostu převládají lesní mezofyty. Poznání jejich variability se liší podle regionu. V některých oblastech (např. západní a střední Evropa) byly intenzivně studovány a je k nim k dispozici velké množství fytocenologických snímků. Většinou však chybí syntetické nadnárodní studie, která by na základě analýz velkých datových souborů poskytly přehled variability těchto lesů. Na mnoha místech, zejména ve východní části svého areálu (např. Balkánský poloostrov, Euxinská oblast, Kavkaz), nebyly dubohabřiny dosud dostatečně vegetačně prozkoumány.

Dizertační práce obsahuje tři regionální studie zaměřené na variabilitu dubohabřin v dosud jen málo studovaných oblastech. Ty jsou založeny převážně na analýzách nově zaznamenaných fytocenologických snímků. Ve studii ze Zakarpatské Ukrajiny jsme rozlišili tři asociace dubohabřin (svaz *Carpinion*). Jde o panonské mírně vlhkomilné dubohabřiny (asociace *Circaeo-Carpinetum*), karpatské mezofilní dubohabřiny (asociace *Carici pilosae-Carpinetum*) a teplomilné dubohabřiny (asociace *Primulo veris-Carpinetum*, která dosud nebyla z Ukrajiny uváděna). Ve studii o unikátních kolchických lesích západní Gruzie jsme rozlišili dvě nové asociace euxinských dubohabřin (svaz *Castaneo-Carpinion*), jednu pro typ dubohabřin bez stálezeleného podrostu (*Digitali-Carpinetum*) a druhou pro dubohabřiny s hustým stálezeleným podrostem (*Rusco-Carpinetum*). Ve třetí studii jsme se zaměřili na kavkazské dubohabřiny v Gruzii. Vedle nově popsané asociace *Clinopodio-Carpinetum* (svaz *Crataego-Carpinion*) jsme zaznamenali dosud jen velmi málo známé vegetační typy, kavkazské vysokohorské dubohabřiny (asociace *Astrantio-Carpinetum*, svaz *Astrantio-Carpinion*) a lesy s reliktním stromem *Zelkova carpinifolia*.

Pro střední Evropu jsme připravili syntetickou práci zaměřenou na dubohabřiny (svazy *Carpinion* a *Erythronio-Carpinion*). Rozlišili jsme třináct hlavních typů dubohabřin, které byly zpravidla ztotožněny s dříve popsanými asociacemi. Ordinační analýzy ukázaly, že hlavním zdroje variability studovaných lesů jsou biogeografie a půdní podmínky (zejména půdních vlhkost a obsah živin). Podle toho jsme asociace uspořádali do tří neformálních ekologických skupin (vlhkomilné, mezofilní, suchomilné), uvnitř kterých jsou asociace odlišeny hlavně biogeograficky. Vedle charakteristiky jednotlivých asociací a jejich formálních definicí je k práci připojena i syntaxonomická revize, která může sloužit jako výchozí bod pro další výzkum variability středoevropských dubohabřin. Několik tradičně používaných jmen asociací (*Galio sylvatici-Carpinetum*, *Lithospermo-Carpinetum*, *Stellario holostei-Carpinetum*) bylo nutné navrhnout na konzervaci, neboť jsme našli jejich starší a platně publikovaná synonyma. Získané poznatky byly také uplatněny při zpracování kapitoly věnované dubohabřinám ve slovenském vegetačním přehledu. V něm byly rozlišeny a detailně popsány čtyři asociace. Z typů vázaných zejména na Karpaty šlo o mezofilní asociaci *Carici pilosae-Carpinetum* a teplomilnou asociaci *Primulo veris-Carpinetum*. V panonské části země jsme rozlišili mírně vlhkomilnou asociaci *Convallario-Carpinetum* a asociaci *Polygonato-Carpinetum*, která sdružuje vzácné dubohabřiny na spraších.

Poděkování / Acknowledgement

Na prvním místě děkuji svojí rodině za všestrannou podporu během studia. Zvláštní dík patří dvěma ústředním ženám mého života, mojí matce a mojí manželce.

Pro celou dizertační fázi mého života byl zásadní můj školitel Milan Chytrý. Jemu patří obrovský dík za jeho (abecedně) entusiasmus, humor, chuť vést nekonečné diskuze nad vegetací a její klasifikací, lidský přístup, nadhled, občasnou motivující náročnost, pragmatičnost a trpělivost.

I am grateful to Wolfgnag Willner, my external supervisor during my stay in Vienna. I spent there two sunny autumn months 2018, working on the Central European oak-hornbeam forest synthesis with his great assistance. He also helped me with many other vegetation issues.

Za myšlenkově podnětnou a téměř rodinnou atmosféru bych chtěl poděkovat všem obyvatelům našeho ústavu, těžko je tu všechny vyjmenovat a na nikoho nezapomenout. Z akademických záležitostí jde o Luboše a diskuze nad jeho potomkem Džusem, Gruliho a Danihela za pomoc při determinaci neurčitelných (a zpravidla obskurně sebraných a špatně vylisovaných) herbářových položek. Dále Dominikovi Z., Martinovi V., Patě S. a Verči K., jak za diskuze nad botanikou *sensu latissimo*, tak za účast na mnohých terénních výpadech. Všem našim knihovnicím za pomoc při dohledávání literatury. A Iloně za ochotné exporty dat z Evropského vegetačního archivu. Patě patří ještě poděkování za pečlivé pročtení subfinální verze dizertačky a mnohé užitečné poznámky k ní.

I am also indepted to many vegetation ecologists from various countries for inspirative discussions on forest vegetation and data providing as well as for their friendly assistance in the field. I would like to mention here Otar Abdaladze, Alla Aleksanyan, Idoa Biurrun, Gianmaria Bonari, Andraž Čarni, János Csiky, Mario Duchoň, Jörg Ewald, George Fayvush, Adrian Indreica, Ali Kavgacı, Jožo Kollár, Javier Loidi, Dejan Mandzhukovski, Viktor Onyshchenko, Jan Roleček, Vlado J. Stupar, Krzysztof Świerkosz, Milan Valachovič and Thomas Wohlgemuth.

Nerad bych zde zapomněl na své průvodce od nejrannějších fází studia na našem ústavu, Pavla Dř., Lucku H.-S. a Tomáše P., výpravy a diskuze s nimi byly veskrze obohacující. Také bych tu rád vzpomněl své dávné učitele na poli biologie, Lubora Urbánka, Filipa Jetmara a Pavla Lustyka, kteří mně k botanice kdysi pomohli najít cestu. V rodném kraji Litomyšlské pánve (62.) a Českomoravského mezihoří (63.) moje afinita k dubohabřinám i díky nim začala možná už v minulém tisíciletí.

Zvláštní poděkování patří všem dosavadním členům kavkazské výzkumné skupiny, že jich za ty roku už bylo! Jmenovitě Anničce, Dominikovi, Harasovi, Helče, Kamče, Kryštofovi, Kubovi, Ondrovi, Pavle, Verče a Vojtovi. And I would like to thank also native Caucasians for their existence. Field trips to the Caucasus would not be what they are without them. Díky/მადლობა/Շնորհակալություն!

Prohlášení

Prohlašuji, že jsem svou dizertační práci vypracoval samostatně pod vedením vedoucího práce s využitím informačních zdrojů, které jsou v práci citovány.

V Brně, 3. 9. 2020

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Pavel Novák

Don’t think that the quiet forest is empty,
there may be a leopard hiding there.

Caucasian proverb

List of the publications of the author related to the thesis and author contributions

Papers and book chapters

Paper 1 – Novák P., Zukal D., Večeřa M. & Píšťková K. (2017): Vegetation of oak-hornbeam, scree and ravine forests at lower altitudes in Transcarpathia, Western Ukraine. – Tuexenia 37: 47–63.

The field sampling was organized by PN and DZ and all the authors participated in it. PN led the writing and performed the analyses, DZ wrote the parts dealing with ravine forests, MV prepared the map and KP helped to measure soil pH. All the authors critically revised the manuscript.

Paper 2 – Novák P., Zukal D., Kalníková V., Chytrý K. & Kavgacı A. (2019): Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region). – Phytocoenologia 49: 231–248.

The field sampling was organized by PN and VK and conducted by PN, DZ, VK and KC. PN led the writing, designed the study and performed the statistical analyses. DZ wrote the texts on ravine forests. KC helped to prepare electronic appendices and other tables. AK provided digitized relevés from selected literature and contributed to the assessment of the communities. All the authors critically revised the manuscript.

Paper 3 – Novák P., Zukal D., Harásek M., Vlčková P., Abdaladze O. & Willner W.: Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia. – Folia Geobotanica, under revision.

PN and DZ designed the study. PN, DZ, MH and PV participated in the field sampling. PN led the writing and did the numerical analyses. DZ wrote the parts dealing with ravine forests. MH prepared the map. OA provided data on ecology of some species and assisted to select sampling sites. WW significantly helped with the parts dealing with phytosociological nomenclature. All the authors critically revised the manuscript.

Paper 4 – Novák P. (2019): Proposals (23–25): to conserve the names *Galio-Carpinetum* Oberdorfer 1957, *Lithospermo-Carpinetum* Oberdorfer 1957 and *Stellario-Carpinetum* Oberdorfer 1957. – Phytocoenologia 49: 409–411.

Paper 5 – Novák P., Willner W., Zukal D., Kollár J., Roleček J., Świerkosz K., Ewald J., Wohlgemuth T., Csiky J., Onyshchenko V. & Chytrý M. (2020): Oak-hornbeam forests of central Europe: A formalized classification and syntaxonomic revision. – Preslia 92: 1–34.

PN designed the study, led the writing and performed the statistical analyses. DZ helped to prepare the expert system to select oak-hornbeam forest relevés from the European Vegetation Archive. JR provided his unpublished relevés from Hungary. WW significantly contributed to the syntaxonomic part of the study and provided notes on associations occurring in Austria. JK made comments on associations in Slovakia. KS helped to syntaxonomically assign oak-hornbeam forests in Poland. JE and TW made notes on associations occurring in the western part of central Europe. JC and VO helped to assign relevés from Hungary or Ukraine, respectively. MC significantly helped to put *the study into a broader context of European vegetation research. All the authors critically revised the manuscript.*

Paper 6 – Kollár J. & Novák P. (2020): *Carpinetalia betuli* P. Fukarek 1968. – In: Kliment J., Valachovič M., Hegedüšová Vantarová K. (eds), Rastlinné spoločenstvá Slovenska 6, Lesná a krovinová vegetácia [Plant communities of Slovakia 6, Forest and shrub vegetation], Veda, Bratislava (*in press*). [in Slovak]

JK led the writing, performed the classification analyses and prepared the synoptic tables. PN contributed to biogeographical, ecological and syntaxonomic interpretations of the presented results.

Conference Abstracts

Novák P. (2016): Vegetation of European oak-hornbeam forests – an introduction to the project. – In: Chytrý M., Zelený D. & Hettenbergerová E. (eds) 58th Annual Symposium of the International Association for Vegetation Science: Understanding broad-scale vegetation patterns, 19–24 July 2015, Brno, Czech Republic, Abstracts, Masaryk University, Brno, p. 280. Poster.

Novák P. & project partners (2016): Formalized classification of oak-hornbeam forest vegetation in Central and Western Europe: the first insights. – In: Agrillo E., Attorre F., Spada F. & Casella L. (eds), 25th Meeting of European Vegetation Survey, Roma (Italy), 6–9 April 2016, Book of Abstracts, Posters, Sapienza Universitá di Roma, Rome, p. 78. Poster.

Novák P., Zukal D., Kalníková V., Chytrý K. & Kavgacı A. (2017): Vegetation of low-altitudinal mesophilous forests in south-western Georgia (Colchic Region). – In: Diversity patterns across communities in the frame of global change: conservation challenges / 26th Congress of the European Vegetation Survey, Bilbao, 13-16 September 2017, Abstracts, Universidad del País Vasco / Euskal Herriko Unibertsitatea, Bilbao, p. 81. Oral presentation.

Novák P. & data contributors (2018): Oak-hornbeam forests in Central Europe - New insights into old problems. – In: 27th Congress of the European Vegetation Survey, 23-26 May, 2018, Wrocław, Poland, Vegetation survey 90 years after the publication of Braun-Blanquet's textbook – new challenges and concepts, Book of Abstracts, University of Wrocław, Wrocław, p. 62. Oral presentation.

Novák P. & data contributors (2019): Oak-hornbeam forests from the European perspective – Currently recognized alliances, a faithful mirror of their floristic variability? – In: Gavilán R.G. & Gtiérrez-Girón A. (eds), Vegetation diversity and global change, 28th EVS meeting, 2-6 September 2019, Madrid, Spain, Abstract & Programme, Complutense University, Madrid, p. 38. Oral presentation.

Content

1. Introduction

1.1. Object of the Study – Oak-hornbeam Forests

1.1.1. General Description

Oak-hornbeam forests are deciduous forests usually with well-developed stratification of vegetation layers. They represent an important portion of European deciduous forest diversity (Neuhäusl 1977, Horvat et al. 1974, Neuhäusl 1977, 1995, Bohn et al. 2000–2003, Leuschner & Ellenberg 2017). The tree layer is dominated by broadleaved deciduous tree species. As the name indicates, the most frequent dominant trees, at least in central Europe, are common hornbeam (*Carpinus betulus*) and oaks (mostly *Quercus petraea* and *Q. robur*). *Acer campestre*, *A. platanoides*, *Fraxinus excelsior* or *Tilia cordata* are other common broadly distributed trees. Some others have a narrow distribution and thus only a regional importance, e.g. *Castanea sativa*, *Quercus macranthera* and *Tilia tomentosa*.

In the thesis, the term "oak-hornbeam forest" corresponds to the syntaxonomic orders *Carpinetalia betuli* and *Lathyro-Carpinetalia* (see Mucina et al. 2016 for details). It is a mesophilous broadleaved deciduous forest which mostly occupies zonal soils of lower elevations. Nevertheless, *Quercus* sp. div. and/or *Carpinus betulus* may be absent in some stands due to forest management (small geographical scales) or biogeography (large geographical scales) (Bohn et al. 2000–2003, Wallnöfer & Hotter 2008, Leuschner & Ellenberg 2017, Smirnova et al. 2018, Muñoz Sobrino et al. 2019).

Fig. 1. Oak-hornbeam forests (green-shaded) as potential natural vegetation in Europe and surroundings (excluding Turkey and Iran). Adopted from Bohn et al. (2000–2003).

The shrub layer predominantly contains mesophilous deciduous species. *Corylus avellana*, *Crataegus monogyna*, *Euonymus europaeus* and *Ligustrum vulgare* are among the most frequent ones (Neuhäusl 1977, Bohn et al. 2000–2003, Novák & data contributors 2019). The shrub layer with a higher cover of evergreen species is characteristic of limited parts of western Eurasia, especially stands in the Euxinian region lining the southern shore of the Black Sea (Quézel et al. 1980, Nakhutsrishvili 2013) and stands in the Hyrcanian region lining the southern shore of the Caspian Sea (Gholizadeh et al. 2020). In the Mediterranean Basin, chiefly in Italy, evergreen Mediterranean trees can also be admixed (Košir et al. 2012).

The herb layer is very diverse in species composition as this vegetation is developed under various edaphic, macroclimatic and biogeographic conditions. A few species accompany oak-hornbeam forests almost across their entire range. Of dicots, such species include e.g. *Galium odoratum*, *Polygonatum multiflorum* and *Viola reichenbachiana*. Of graminoids, they include e.g. *Brachypodium sylvaticum*, *Carex digitata* and *Poa nemoralis* (Neuhäusl 1977, Bohn et al. 2000–2003). Some genera or infrageneric species groups show a relatively high diversity within European mesophilous forests, including oak-hornbeam ones, since they contain numerous narrow-range species (e.g. Meusel 1969, Meusel & Jäger 1989, Willner et al. 2009). They are, for instance, *Cardamine* sect. *Dentaria* (Oberdorfer & Müller 1984), *Galium* ser. *Nemoralia* (Ehrendorfer 1975), *Helleborus* sp. div. (Oberdorfer & Müller 1984), *Pulmonaria* sp. div. (Puppi & Cristofolini 1996) and *Symphytum* sp. div. (Hacıoğlu & Erik 2011). In Europe, the number of nemoral narrow-range species is apparently increasing towards the south, reaching its maximum in the southern Alps, the Apennines and the western Balkans (e.g. Willner et al. 2009, Košir et al. 2012, Jiménez-Alfaro et al. 2018).

1.1.2. Distribution and Ecology

Oak-hornbeam forests are assumed to be potential natural vegetation across large parts of Europe and some neighbouring regions of western Asia. The potential distribution covers ~1 050 000 km^2, excluding Turkey and Iran (Fig. 1, 2). Their range stretches from Greece to southern Scandinavia and from Spain to northern Iran (Neuhäusl 1977, Bohn et al. 2000–2003, Mucina et al. 2016). In central Europe, oak-hornbeam forests represent the second most common type of potential natural vegetation, after beech forests, covering ~240 000 km^2 (i.e. ~a quarter of the region). They form zonal vegetation up to approximately 500 m a.s.l. (Neuhäusl 1977, Leuschner & Ellenberg 2017), occupying mesic sites on "average" soils, i.e. from slightly acidic to slightly basic, often deep and fresh.

Dominant tree species are diverse in their light demands (Le Due & Havill 1998, Vera 2000, Leuschner & Ellenberg 2017). They split into two groups; shade-tolerant and light-demanding ones, dependent on light requirements of their seedlings and young individuals that are crucial for forest regeneration. The former is represented by species which have the ability to cope with a relatively low light amount under a closed canopy (e.g. *Carpinus betulus*, *Acer campestre*, *A. platanoides*, *Tilia cordata*, *T. tomentosa*). The latter is represented mostly by oaks (e.g. *Quercus petraea*, *Q. robur*, *Q. castaneifolia*, *Q. macranthera*) and some thermophilous trees of the *Rosaceae* family including *Malus sylvestris*, *Prunus avium* and *Pyrus communis* (Vera 2000). In a closed oak-hornbeam forest, oaks are almost incapable to generatively regenerate. Oak seedlings are able to survive for an extended period of time due to a relatively high nutrient amount in their acorns, but when energy within the acorns runs out, they vanish. Thus, the present-day situation of the oak-hornbeam tree layer seems to be unstable, and we are witnessing oak decline. Presumably, the most accepted theory attributes the coexistence of oaks and shade-tolerant trees to former management (Fig. 3). This included coppicing, litter raking, tanbark management, forest pastures of domestic animals, mowing of forest-floor grasses and herbs and other ways of canopy opening and nutrient export (Vera 2000, Konvička et al. 2004, Sádlo et al. 2005). In ancient times, it was probably preceded by (or coupled with) natural disturbances such as forest fires and wild ungulates (Vera 2000, Roleček 2007). Over the last decades, anthropogenic depositions of nutrients could also accelerate the deletion of oaks and other light-demanding trees (Hofmeister et al. 2004). However, further research is needed to better understand these processes as some other causes (e.g. air pollutants, insect defoliation, pathogenic fungi) may play a role (Küster 1997, Kwiatowska et al. 1997, Thomas et al. 2002, Müllerová et al. 2015, Szabó et al. 2018).

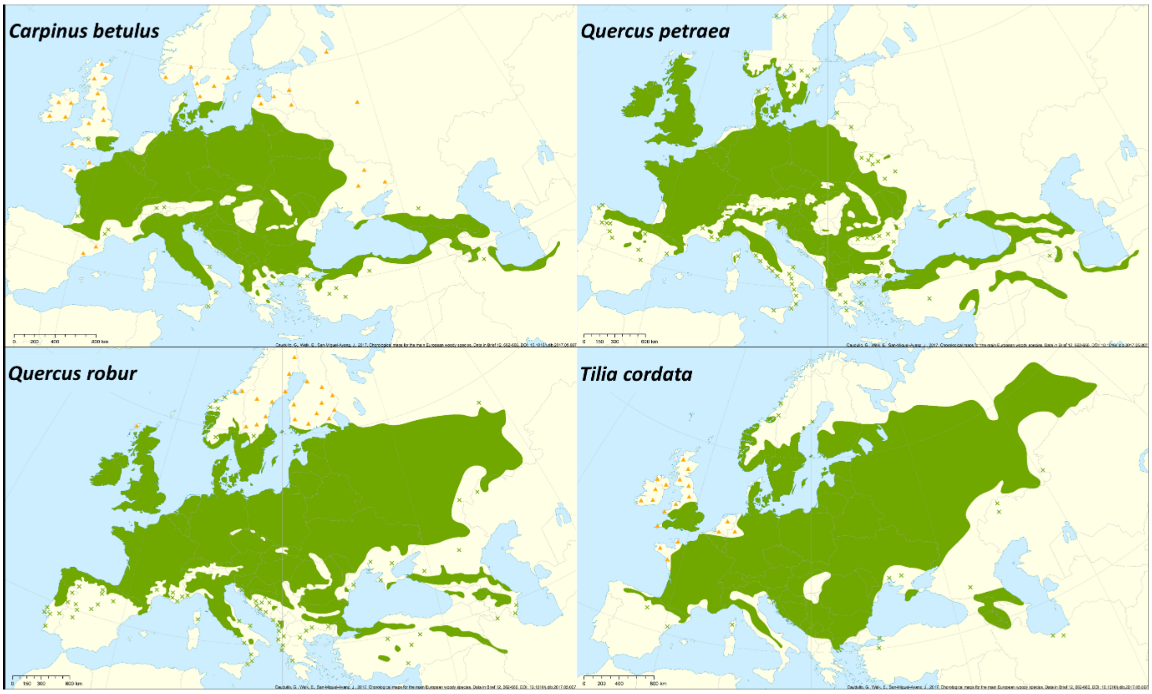

Fig. 2. Distribution of four key tree species of oak-hornbeam forests (adopted from Caudullo et al. 2017). Green shaded – native range, green cross – isolated population, orange triangle – synanthropic occurrence.

The oak-hornbeam forests prefer regions with subcontinental climate, i.e. with rather cold winters and low precipitation, summer drought periods and late spring frosts (Leuschner & Ellenberg 2017).

Since oak-hornbeam forests usually inhabit low elevations, they have been strongly affected by human activities including felling and transformation to arable land, settlements or even-aged plantations of various tree species, frequently alien ones (e.g. Neuhäuslová 2000, Borhidi et al. 2012, Chytrý 2013, Slabejová et al. 2019). Therefore nowadays we observe only a limited part of their variability (e.g. Leuschner 1997, Boublík et al. 2007).

Fig. 3. Traditional management practices of oak-hornbeam forests in Transcaucasia, still applied or only recently abandoned. a) A stand few years after coppicing (northern Armenia). b) A stand several decades after the last pollarding (central Georgia), c) Forest grazing of cows (northern Armenia). d) A pollarded tree used for hay storage at an edge of an oak-hornbeam forest (western Georgia). Photo P. Novák.

1.1.3. Importance, Threats and Protection

Forests are globally the most complex ecosystems. They provide a broad range of ecosystem services including oxygen production and carbon sequestration coupled with climate change mitigation, co-driving global water cycle and maintaining soil and air quality. They also produce raw materials for human food, fuel and shelter (Krieger 2001).

Oak-hornbeam forests represent an important diversity center of forest biota as they cover an extensive area of the continent. Especially in highly deforested and populated lowlands, they often represent the last refugia of forest species (Borhidi et al. 2012, Leuschner & Ellenberg 2017, Chytrý et al. 2019). In the Red List of the European Habitats (Janssen et al. 2016), oak-hornbeam forests are classified as near threatened for both the EU28 and the EU28+ countries. This rating is based on a fairly substantial reduction in their abiotic and biotic quality in the last fifty years. At the national level, oak-hornbeam forest habitats are also red-listed (e.g. Laiviņš 2014, Chytrý et al. 2019). They harbour many endangered vascular plant species, including several relict or endemic ones (e.g. *Hepatica transsilvanica*, *Waldsteinia ternata*), which are included in national or international red lists (e.g. Farkas 1999, Witkowski et al. 2003). The stands with canopy gaps, hollow trees and decaying wood are of special importance for invertebrates including many red-list species (e.g. Holecová et al. 2005, Konvička et al. 2004, Šebek et al. 2013). The most serious threats are broad-scale logging and transformation to alien tree or coniferous plantations (Neuhäuslová 2000, Rodwell & Dring 2001, Chytrý et al. 2019). On the other hand, successional changes mostly caused by a lack of traditional management are also among their threatening factors. It is especially the case for stands of semi-light-demanding species (Chytrý et al. 2020). In many regions, growing populations of wild ungulates (e.g. roe deer, fallow deer and wild board) negatively affect forests, including oak-hornbeam ones. This has been reported in game preserves as well as outside them (e.g. Fuller & Gill 2001, Hédl et al. 2010). Caucasian oak-hornbeam forests suffer from overgrazing by cattle and subsequent soil erosion and also from strong cutting pressure to obtain firewood (Akhalkatsi 2015). Stands rich in *Castanea sativa*, in the Caucasus, Euxinia or the Balkans for instance, are threatened by fungal ink disease and chestnut blight (Dolukhanov 2010, Akıllı et al. 2012).

Invasive alien species, regarded as a serious threat to European biota (Kalusová et al. 2015), are spreading in oak-hornbeam forests less compared to many other forest habitats such as riparian or swampy forests (Wagner et al. 2017). The relatively low level of alien plant invasions in European mesophilous deciduous forests was indicated in recent studies (e.g. Chytrý et al. 2009, Rejmánek et al. 2013, Kalusová et al. 2015, Wagner et al. 2017, Medvecká et al. 2018). The most frequent aliens (i.e. species non-native to Europe) are *Impatiens parviflora*, a dicot native to central and eastern Asia, and American tree *Robinia pseudoacacia*. Spreading of *Robinia pseudoacacia*, a nitrogen-fixing tree, may dramatically alter the herb layer, including a decline of many nemoral species and their substitution by nitrophytes and ruderal plants (Slabejová et al. 2019). Impact of the *Impatiens parviflora* invasion is lower as this annual preferentially colonizes gaps in the field layer (Diekmann et al. 2016). Only regionally occurring alien species include, for instance, *Acer negundo*, *Juglans nigra*, *Prunus serotina* or *Symphoricarpos albus*.

The spreading of evergreen broadleaved woody species ("laurophyllisation") is a specific problem of oak-hornbeam forests in some regions with mild winters where winter temperatures are gradually rising in the recent decades. Spreading of such species, both native (e.g. *Hedera helix*, *Ilex aquifolium*) and alien (e.g. *Cinnamomum glanduliferum*, *Trachycarpus fortunei*) to Europe, has been reported, for example, from in southernmost Switzerland (Walther 2000, Berger 2008).

1.2. Main Factors Driving Variability of Oak-hornbeam Forests

1.2.1. Abiotic Factors

Oak-hornbeam forests grow under diverse abiotic conditions, which mirror the ecological requirements of their dominant and diagnostic species. This chapter is focused chiefly on central European types which were subject to many ecological studies.

Oak-hornbeam forests prefer "average" soil conditions, i.e. mesic and deep soils, usually without rock particles, with average nutrient supply (Bohn et al. 2000–2003, Leuschner & Ellenberg 2017). Soil moisture seems to be highly important for their variability (Knollová & 2004, Leuschner & Ellenberg 2017). In paper 5, we distinguished three ecological groups of central European oak-hornbeam forests reflecting soil moisture gradient as the most important by numerical analyses. However, the general relation of oak-hornbeam forests to mesic soils does not apply in regions under different climatic regimes where they occur as extrazonal vegetation. It is the case for the oceanic parts of central and western Europe where beech is the most vigorous tree and often occupies mesic soils whereas oak-hornbeam forests were pushed to Stagnosols (Noirfalise 1968, Rodwell & Dring 2001).

Soil pH is a crucial ecological factor for European temperate vegetation (Ewald 2003). Oak-hornbeam forests reach their optimum on slightly acidic to slightly basic soils. However, they also occupy moderately acid and slightly podzolic soils and weakly alkaline humus carbonate soils (Bohn et al. 2000–2003). On strongly acidic soils, oak-hornbeam forests are largely substituted by acidophilous oak forests (Bohn et al. 2000–2003, Chytrý 2013, Leuschner & Ellenberg 2017). Though, some types of oak-hornbeam forests representing transitions to acidophilous oak forests were defined at the subassociation level of some *Carpinion* associations (e.g. Noirfalise 1968, Wraber 1969, Neuhäuslová 2000, Matuszkiewicz 2001).

Oak-hornbeam forests are widely distributed in the regions with subcontinental temperate climate (Bohn et al. 2000–2003, Leuschner & Ellenberg 2017). For the oak-hornbeam forest zone, annual precipitation between 500 and 600 mm and July mean temperature between 17 and 19 °C are characteristic (Neuhäusl 1977). Such climatic conditions are reported as less favourable for the fundamental competitor of the European broadleaved deciduous forests – beech (*Fagus sylvatica*, *F. orientalis*). Climatic conditions of oak-hornbeam forests were frequently studied in the relation to beech forests. Mölder et al. (2009) indicated that with decreasing oceanity, *Fagus sylvatica* is retreating while *Tilia cordata* is increasing as a co-dominant in German oak-hornbeam forests. On the other hand, beech tolerance to dry climate was presumably underestimated, as was pointed out by observation of beech forests in regions receiving only 450–500 mm annual precipitation. It is the case for rain shadow regions of central Germany or the northwestern Czech Republic which were traditionally regarded as "oak and oak-hornbeam" areas (e.g. Leuschner 1997, Boublík et al. 2007). Moreover, spreading of oak-hornbeam forests at the expense of beech forests has likely been promoted by traditional forest management suppressing beech (Neuhäusl 1977, Jahn 1984, Küster 1997, Sádlo & Pokorný 2003, Boublík et al. 2007, Chytrý 2013, Leuschner & Ellenberg 2017). The relationship between oak-hornbeam and beech forests appears highly complex as evident from a large body of literature addressing this issue (e.g. Klötzli 1968, Jahn 1984, Schmidt 2000, Leuschner & Ellenberg 2017).

1.2.2. Biogeographical Aspects

Biogeography has a prominent role in the species composition variability of European forest, due to their long and complicated history. During the Quaternary, former Neogene subtropical and tropical forest flora was gradually vanishing. Presumable Tertiary origin of some typical forest species (e.g. *Epimedium* sp. div., *Hedera colchica*, *Parrotia persica*, *Prunus laurocerasus*, *Zelkova carpinifolia*) is assumed chiefly for the Euxinian and Hyrcanian oak-hornbeam forests (Milne & Abbott 2002, Milne 2006). Each interglacial-glacial cycle meant a reduction and a re-expansion of forests. In the Last Glacial Maximum, mesophilous broad-leaved forests were restricted mainly to the southern part of the continent, presumably with some northern refugia in particular species (Milne & Abbott 2002, Svenning 2003, Milne 2006, Magri et al. 2017). We still do not have a precise picture of the European deciduous broad-leaved forest vegetation of the Last Glacial period, neither the tree layer nor the understory species. However, a combination of biogeographical, palaeoecological and phylogeographical findings provided valuable insights into this issue. It seems that *Carpinus betulus*, a key tree of oak-hornbeam forests, persisted the last glaciation in multiple refugia near the southern periphery of central Europe and in southern refugia (Grivet & Petit 2003, Coart et al. 2005, Postolache et al. 2017). For instance, Postolache et al. (2017) examined intra-population genetic patterns and revealed that its Holocene expansion across southeastern Europe originated from three refugia located in the Dinaric Alps, the eastern Balkans and the Strandzha Mts. However, microrefugia of *Carpinus betulus* could possibly exist in the southern half of central Europe (Willis et al. 2000). The analogical phylogeographical patterns were revealed for some other nemoral species (Palmé & Vendramin 2002, Tyler 2002). *Carpinus betulus* was a latercomer in the majority of central and northwestern Europe, where it was spreading mainly since the beginning of the Late Holocene (Godwin 1975, Dierschke 1985, Küster 1997, Pokorný & Kuneš 2005).

Concerning the late Quaternary history of oak-hornbeam forests, biogeographical patterns in nemoral herb species with narrow distribution provide some hints. A high concentration of such species in a certain type of mesophilous forests may imply their long-term survival, i.e. tracking mesophilous deciduous forest glacial refugia (e.g. Meusel 1969, Oberdorfer & Müller 1984, Meusel & Jäger 1989, Dierschke & Bohn 2004, Willner et al. 2009, Jiménez-Alfaro et al. 2018). This is possible due to the poor dispersal capacity of many nemoral species which are commonly spread by myrmecochory (Guitián et al. 2002, Svenning et al. 2008, Willner et al. 2009). Willner et al. (2009) reported that the number of narrow-range species in the European beech forests is negatively correlated with the distance from potential glacial refugia of beech. Since the investigated species are often common to beech and oak-hornbeam forests, one can expect similar mechanisms for the latter as well. Many narrow-range diagnostic species of the alliance *Erythronio-Carpinion* are a textbook example of this phenomenon (Horvat et al. 1974, Meusel & Jäger 1989, Biondi et al. 2002, Košir et al. 2012). They include monospecific genera (e.g. *Aremonia agrimonoides*, *Hacquetia epipactis*), geographically isolated members of subtropical genera (e.g. *Epimedium alpinum*, *Pseudostellaria europaea*) and a high number of endemic species belonging to the typical nemoral species groups (e.g. *Cardamine* sect. *Dentaria*, *Galium* ser. *Nemoralia* and *Pulmonaria* sp. div.).

The above-mentioned circumstances are projected to the present-day concept of the oak-hornbeam forest geographical alliances (Mucina et al. 2016, Gholizadeh et al. 2020). Oak-hornbeam forests of the southern half of Europe and adjacent areas in western Asia are usually well-defined by narrow-range species. It is the case of the alliances *Pulmonario-Quercion*, *Erythronio-Carpinion*, *Carpinion* (partly), *Castaneo-Carpinion*, *Paeonio-Quercion*, *Crataego-Carpinion*, *Astrantio-Carpinion* and *Parrotio-Carpinion*. Alliances of northern and eastern part of Europe, i.e. *Carpinion* (partly), *Scillo-Carpinion* and *Tilio-Carpinion*, are rather poor in narrow-distribution species and often negatively delimited against "southern" alliances. Towards the east, species typical of central Europe, including *Carpinus betulus* and *Quercus petraea*, are gradually vanishing and continental (e.g. *Acer tataricum*, *Scilla siberica*, *Tulipa biebersteiniana*) and/or boreal (e.g. *Dryopteris* spp., *Trientalis europaea*) species become more frequent. The Southern Ural alliance *Aconito-Tilion* represents a distinctive type of continental *Carpinetalia* forests with the Siberian floral element (e.g. *Anemone altaica*, *Cacalia hastata*, *Pleurospermum uralense*). This general biogeographical pattern in species composition of oak-hornbeam forests across Europe and surroundings was also detected by numerical analyses done on a large dataset of relevés of their entire range (Novák and data contributors 2019).

1.3. Brief History of Oak-hornbeam Forest Vegetation Research

The research of European oak-hornbeam forests is a long tale reflecting the fundamental scheme of European vegetation research. They were investigated since the 1920s when the first Braun-Blanquetian associations of oak-hornbeam forests were described in local central European studies (e.g. Issler 1925, 1926, Domin 1928, Klika 1928). *Carpinion betuli* itself, as the first described alliance of oak-hornbeam forests, was introduced by Issler (1931). Later on, the first modern national oak-hornbeam forest vegetation overviews were published across most of the central European countries (e.g. Soó 1940, Klika 1948, Oberdorfer 1957, Traczyk 1962, Neuhäuslová-Novotná 1964). Passarge (1978) provided a list of syntaxa of central European oak-hornbeam forests described by then. Nowadays, the majority of the central European countries have their vegetation handbooks presenting the variability of oak-hornbeam forests (e.g. Matuszkiewicz 2001, Willner & Grabherr 2007, Borhidi et al. 2012, Chytrý 2013). However, classification approaches and delineation of syntaxonomic units may differ from country to country. A synthetic study dealing with central European *Carpinetalia* forests, focusing on their variability, ecology and syntaxonomy, has been provided recently (paper 5).

In other parts of Europe, the research of oak-hornbeam forest variability applying the Braun-Blanquet approach started in later decades of the 20th century. In western Europe, fundamental studies were led by Tansley (1935), Tüxen & Diemont (1936) and Noirfalise (1968, 1969) followed by many other authors (e.g. Rodwell 1991–2000, Catteau & Duhamel 2014). In southwestern Europe, Spanish oak-hornbeam forests were investigated since the 1960s (e.g. Vigo 1968). At the turn of millennia, *Carpinetalia* forests of the northern Iberian Peninsula and the Pyrenees were described as a separate alliance *Pulmonario longifoliae-Quercion roboris* (Rivas-Martínez et Izco in Rivas-Martínez et al. 2002).

In northern Europe, oak-hornbeam forests reach only its southern margin (Neuhäusl 1977, Bohn et al. 2000–2003) as it represents a fundamental biogeographical boundary for many nemoral species including hornbeam itself (Klötzli 1975, Diekmann 1994). Therefore, there are few studies dealing with their variability. Their comprehensive overview was published by Diekmann (1994), while syntaxa of Danish *Carpinion* vegetation were listed by Lawesson (2004).

Vegetation research of oak-hornbeam forests of northeastern and eastern Europe was essentially influenced by the dominant-based school of phytosociology broadly applied in the Soviet Union. The Braun-Blanquet studies were mostly published after 1990 (e.g. Laiviņš 1991). Nowadays, local oak-hornbeam forests are treated as a separate alliance *Querco robori-Tilion cordatae* (e.g. Onyshchenko 2009). However, the concept of the *Carpinetalia* alliances recognized in the eastern European lowlands is not stable in the national vegetation overviews (Onyshchenko 2009, Dubyna & Dziuba 2019). The eastern limit of *Carpinetalia* forests in eastern Europe is situated in the Southern Urals where these forests were studied mainly in the last decades and described as a separate alliance *Aconito septentrionalis-Tilion cordatae* (Schubert et al. 1979, Solomeshch 2016). The southern part of the Eastern European Plain is nowadays only sparsely forested. The oak-hornbeam forests of the steppe zone of southern Ukraine were described as an individual alliance *Scillo sibericae-Quercion roboris* (Onyshchenko

2009). An overview of oak-hornbeam forests of a major part of European Russia has been recently published by Smirnova et al. (2018).

Oak-hornbeam forests of the Crimean Peninsula (*Paeonio dauricae-Quercion petraeae*) were studied separately (Onyshchenko 2009). A related fundamental study applying the Braun-Blanquet approach was published by Didukh (1996). Passarge (1981) published a study on Caucasian oak-hornbeam forests. He distinguished two alliances: *Crataego-Carpinion* at lower elevations and *Astrantio-Carpinion* at higher elevations. Towards the east, oak-hornbeam forests extend to northern Iran where they reach the southeastern limit. Attempts to describe local types using the Braun-Blanquet procedures started in the 1960s (e.g. Noirfalise & Djazirei 1965). Recently, Gholizadeh et al. (2020) published a comprehensive overview of temperate forests of northern Iran using modern approaches. Local oak-hornbeam forests were presented under the newly established alliance *Parrotio persicae-Carpinion betuli*. Going from the Caucasus to the west, there is the Euxinian province lining the southern Black Sea coast where distinctive oak-hornbeam forests (*Castaneo sativae-Carpion orientalis* or *Trachystemono orientalis-Carpinion betuli*) are developed. The majority of studies dealing with these forests analysed solely data from northern Turkey, both local (e.g. Yurdakulol et al. 2002, Korkmaz et al. 2008) or covering the entire region (e.g. Quézel et al. 1980, Çoban & Willner 2019). So far, this vegetation has been rarely sampled outside Turkey.

In the Balkans, research of oak-hornbeam forests applying the Braun-Blanquet methods started in the late 1930s (e.g. Horvat 1938, Rudski 1949). *Carpinetalia* forests of the Italian Peninsula were investigated as well, mostly since the 1960s (e.g. Oberdorfer & Hofmann 1967, Oberdorfer 1968). An individual alliance *Erythronio-Carpinion* for the Apennine-Illyrian *Carpinetalia* forests was introduced later (Marinček in Wallnöfer et al. 1993). It was based on an older description by Horvat (1958) who proposed the alliance *Carpinion betuli illyrico-podolicum* encompassing oak-hornbeam forests between northern Croatia and eastern foothills of the Eastern Carpathians. A comprehensive survey summarizing variability of the western Balkanian and Italian *Carpinetalia* forests was prepared by Košir et al. (2012). The list of their syntaxa was also provided in national and regional vegetation overviews (e.g. Šilc & Čarni 2012, Trinajstić 2008, Biondi et al. 2002).

1.4. Classification Approaches and Schemes

In European oak-hornbeam forest vegetation research, syntaxonomic schemes mostly stressed two main sources of variability: ecology (mainly soil properties) and biogeography.

Published classification concepts differ in the spatial scale considered. At the local scale, authors mostly emphasized ecological differences among units, in most cases among associations or subassociations. When we zoom out to the national or supra-national scale, biogeography starts to play a prominent role in distinguishing oak-hornbeam units (Knollová & Chytrý 2006). Alliances were mostly biogeographically defined (e.g. Mucina et al. 2016 or Dierschke 2004 at the European scale; Borhidi et al. 2012 or Onyshchenko 2009 at national scales). An alternative approach identifying alliances based on ecological differences among them was applied rarely and over small geographical extents (Passarge & Hofmann 1968), thus their content resembled associations.

Biogeographical patterns represent relatively distinct criteria for alliance delineation. However, such an approach resulted in fuzzy boundaries among the alliances at biogeographic crossroads, i.e. in regions whose nemoral flora shows several contrasting biogeographic influences. Romanian oak-hornbeam forests can serve as an example of such a crossroad where such a situation was originally solved by designating an endemic Romanian alliance, *Lathyro hallersteinii-Carpinion* Boşcaiu 1974, into which all Romanian associations were traditionaly assigned. This concept persists in the national vegetation handbooks (Sanda et al. 2008, Coldea 2015) but it appears untenable at supra-national scales (Mucina et al. 2016). Indeed, Romanian associations could be relativelly well divided between the *Carpinion* and *Erythronio-Carpinion* alliances (Indreica et al. in prep.).

However, the relationship of biogeographical and ecological features in co-shaping plant communities appears highly complex. It fits into the general pattern of the changes of species composition of mesophilous forest vegetation across various spatial levels. At the local scale, it is more driven by site conditions while at the regional scale it is more driven by biogeography (e.g. Willner et al. 2009, Jiménez-Alfaro et al. 2018).

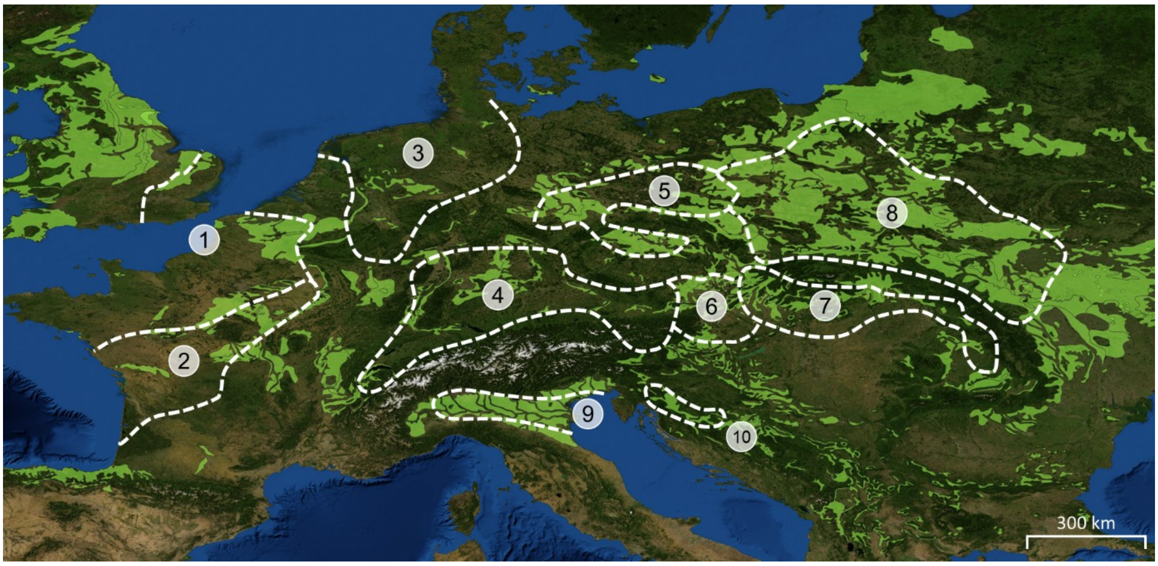

Fig. 4. Presumably the first overview of oak-hornbeam forest associations across Europe provided by Neuhäusl (1977). 1 – *Endymio-Carpinetum*, 2 – *Rusco-Carpinetum*, 3 – *Stellario-Carpinetum*, 4 – *Galio-Carpinetum*, 5 – *Melampyro-Carpinetum*, 6 – *Primulo veris-Carpinetum*, 7 – *Carici pilosae-Carpinetum*, 8 – *Tilio-Carpinetum*, 9 – *Physospermo-Quercetum*, 10 – *Querco petraeae-Carpinetum illyricum*. Areas of presumed natural oak-hornbeam forests according to Bohn et al. (2000–2003) are green-shaded.

At the scale of entire Europe, the very first coarse geographical classification scheme of oak-hornbeam forests was proposed by Neuhäusl (1977). He recognized ten fundamental associations across the continent (Fig. 4). An overview of the European oak-hornbeam forest alliances recognized at that time was provided by Dierschke (2004). The most recent list of European oak-hornbeam forests alliances was compiled in EuroVegChecklist (Mucina et al. 2016). They recognized ten alliances (Fig. 5). Novák and data contributors (2019) presented the first attempt to classify European oak-hornbeam forests based on the application of the alliance formal definitions. More supranational classification schemes were published for large parts of the continent like northern (Diekmann 1994) and southeastern (Košir et al. 2012) Europe.

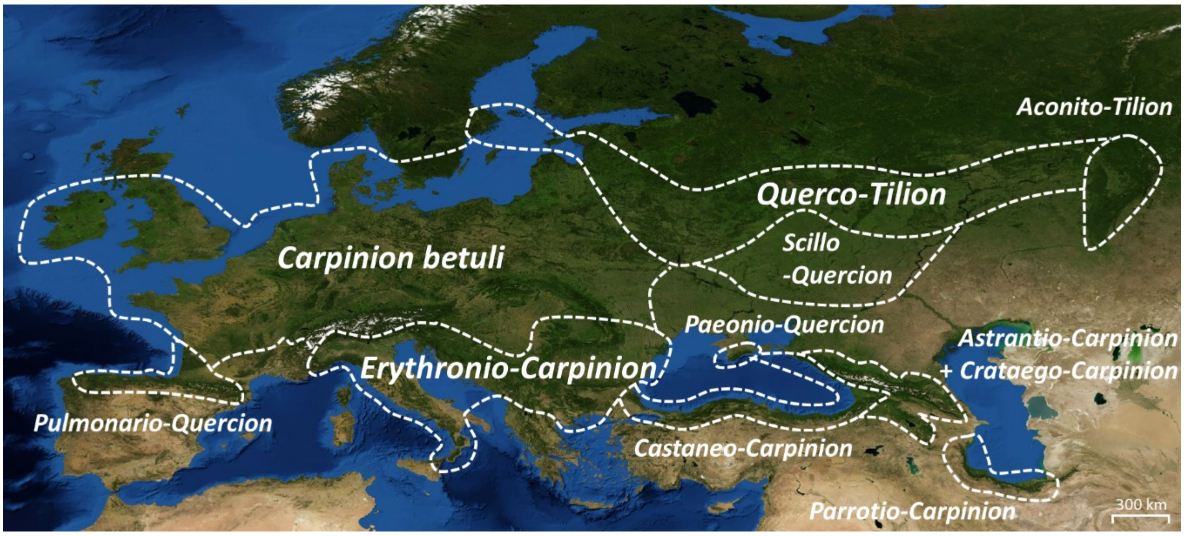

Fig. 5. Alliances of oak-hornbeam forests in Europe. According to Mucina et al. (2016), Novák and data contributors (2019) and Gholizadeh et al. (2020).

2. Main Aims of the Thesis

Vegetation surveys represent essential tools for basic ecological and biodiversity research, nature conservation and environmental monitoring (Chytrý et al. 2011, Rodwell et al. 2018). As shown in the previous chapter, the current stage of knowledge of oak-hornbeam forests needs improvement in several aspects. There are two aspects especially relevant for the thesis. In some regions (e.g. central and western Europe), their variability has been broadly examined and numerous studies have been published to date. However, classification systems used in particular countries usually exhibit limited compatibility without a broadly accepted supranational classification system. It seriously complicates international communication among vegetation scientists or nature conservationists. In some other regions where oak-hornbeam forests are frequent (e.g. Caucasus, Euxinia), even the lack of primary data and basic vegetation syntheses disable to better understand variability of local oak-hornbeam forest or to select among them types of special importance for nature conservation. To address the mentioned gaps, the main aims of the thesis are:

1) To explore variability of oak-hornbeam forests in understudied regions through sampling new phytosociological relevés and basic environmental data and to put new findings into a broader biogeographical, ecological and syntaxonomic context. **Papers 1, 2 and 3**.

2) To prepare a synthetic study of central European oak-hornbeam forest vegetation by performing numerical analyses of variability on a large dataset of oak-hornbeam forests

relevés recorded in the region. Afterwards to identify their principal types and drivers of variability. Finally to provide a formalised classification system supplemented by a syntaxonomic revision. **Papers 4 and 5**.

3) To implement new findings involved in the central European synthesis into national classification systems of oak-hornbeam forests. **Paper 6**.

3. Methods

Methods applied in the thesis are tightly linked to its explorative character. It is dealing with vegetation variability on various spatial scales, identifying basic vegetation units and drivers of their variability. Finally, vegetation units are organized into hierarchical systems. The presented studies are based on a quantitative investigation of vegetation diversity (details are provided below and in the particular papers).

3.1. Datasets

The papers presented in the thesis are based on vegetation plots (phytosociological relevés) recorded following the Braun-Blanquet methods (Dengler et al. 2008). Regional papers (papers 1, 2 and 3) were based particularly on original relevés yielded during field excursions. For the study dealing with Slovak oak-hornbeam forests (paper 6), relevés were chosen primarily according to *ad hoc* prepared formal definition from the Slovak vegetation database (Šibík 2012). Relevés for the central European synthesis (paper 5) were selected by the *ad hoc* designated formal definition of oak-hornbeam forests. It was based on application of GRIMP method (Tichý et al. 2019) to a large dataset of central European forest relevés mostly retrieved from the European Vegetation Archive (Chytrý et al. 2016).

Relevé area is a crucial variable in vegetation studies due to scale-dependence of vegetation attributes (Chytrý & Otýpková 2003). During the field sampling for the regional studies (papers 1, 2 and 3), we recorded square plots of 100 m^2. In the synthesis (paper 5), we omitted relevés with an area out of the range 50–1000 m^2. Relevés without area indicated were kept assuming that most of them were within the indicated range. In the synthesis (paper 5), we additionally deleted relevés without geographical coordinates as they were essential for further processing. Afterwards, we omitted relevés from oversampled regions in the following way. We stratified relevés geographically in a grid of 6'N × 10'E. Subsequently, we applied a heterogeneity-constrained resampling. Number of relevés to be kept in each grid-cell was 10–20, according to the beta-diversity within the cell measured by mean Bray-Curtis similarity between relevé pairs (Lengyel et al. 2011, Wiser & De Cáceres 2013).

Vascular plant nomenclature unification is another vital part of vegetation studies, especially those combining data from various sources (Jansen & Dengler 2010). The nomenclature was generally harmonized following the Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed) and supplemented by a small number of *ad hoc* defined aggregates whose content was described in the particular studies. For the Slovak vegetation survey (paper 6), we used the national vascular plant checklist as the taxonomic and nomenclature reference (Marhold & Hindák 1998). Bryophytes were omitted in the presented studies since they have not been recorded in the majority of analysed relevés. Moreover, they have only limited value for classification of the studied vegetation due to low cover and prevalence of forest generalists (Neuhäusl 1977, Košir et al. 2012, Chytrý 2013).

Environmental data were obtained from several sources. We mostly used species indicator values which represent an effective and robust tool for bioindication (Diekmann 2003). Unweighted means of indicator values provided rough estimations of site conditions of each relevé. In the synthetic study (paper 5), we used Ellenberg indicator values for light, moisture, nutrients, soil reaction and temperature (Ellenberg et al. 1992) supplemented by c-value for continentality (Berg et al. 2017). For the study from Transcarpathian Ukraine (paper 1), we applied analogous Borhidi indicator values (Borhidi 1995). For papers 2, 3 and 5, we extracted fundamental climatic data from the WorldClim Version2 (Fick & Hijmans 2017) or CHELSA (Karger et al. 2017) datasets. For original relevés used in the regional studies (paper 1, 2 and 3), measured soil pH values were also available.

3.2 Numerical Analyses

We applied a broad variety of analyses reflecting explorative character of the thesis. We mostly combined two aspects providing a complementary description of the vegetation studied. They were ordination analyses, working with vegetation continuum, and classification analyses, focused mainly on discontinuities in vegetation species composition (De Cáceres et al. 2015).

Ordination analyses were usually performed using the package vegan (more versions, e.g. Oksanen et al. 2013) in the R 3.6 environment (R core team 2017). Classification analyses were calculated using PC-ORD 5 (McCune & Mefford 1999) in Juice 7.0 (Tichý 2002) environment. Juice software was generally used for further data management and analyses. It included preparing and testing of expert systems, calculating of species-to-cluster fidelity or organizing synoptic table. Details of performed analyses are provided in the particular papers.

Classification analyses produced a certain number of clusters which we interpreted in sense of their species composition, ecology, distribution, physiognomy and syntaxonomy. We used hierarchical classification analyses as they better reflected the hierarchical structure of the studied vegetation. These analyses included mainly flexible beta clustering (Legendre & Legendre 1998), representing agglomerative techniques, and modified TWINSPAN (Roleček et al. 2009), representing divisive techniques. OptimClass procedure (Tichý et al. 2010) indicated the optimal number of final clusters.

We followed a common concept of three species groups essential for cluster descriptions (De Cáceres et al. 2015): diagnostic, constant and dominant species. Diagnostic species were usually determined by phi coefficient (Sokal & Rohlf 1995) assuming equal group sizes (Tichý & Chytrý 2006). Fisher’s exact test was additionally applied to omit rare species from lists of diagnostic species (Chytrý et al. 2002). It was supplemented by constancy ratio criterion (Dengler 2003) in papers 3 and 5. Constant species had to reach an arbitrary threshold of constancy in a cluster, e.g. to occur in 25% of its relevés. Species exceeding a cover of 25% in the given number of relevés of a cluster were mostly considered as dominant ones.

The synthesis (paper 5) provides formal definitions of each recognized association based on the Cocktail method. They enable unambiguous classification of each relevés, independent of the classified relevé dataset (Bruelheide 1995, 1997, 2000, Kočí et al. 2003). Defined sociological species groups were ecologically or geographically distinct. Number of species of a sociological group that needed to be present in a relevé to consider the group as being present was set empirically (Kočí et al. 2003). The sociological groups were connected by logical operators AND, OR, NOT in the association definitions (Bruelheide 1997).

In syntaxonomic parts of most of the presented papers, we applied rules of the 3rd edition of the International Code of the Phytosociological Nomenclature (Weber et al. 2000). Only in paper 3 dealing with Caucasian forests, we used the recently published 4th edition of the Code (Theurillat et al. 2020).

4. Main Results of the Thesis

1) Oak-hornbeam forests in insufficiently explored regions

We organized several field survey to study oak-hornbeam forests in insufficiently explored regions of Europe and its surroundings (Caucasus, Euxinia, Transcarpathian Ukraine). Afterwards, we prepared three papers based on the data yielded.

Paper 1 – Vegetation of oak-hornbeam, scree and ravine forests at lower altitudes in Transcarpathia, Western Ukraine

The study area encompassed the Eastern Carpathian foothills and adjacent parts of the Pannonian Basin (Transcarpathian Region, Ukraine). We recorded 54 relevés of local oak-hornbeam (alliance *Carpinion betuli*), ravine and scree (alliance *Tilio-Acerion*) forests in June 2016. They were supplemented by 22 relevés of oak-hornbeam forests from literature (Onyshchenko & Lukash 2005). The oak-hornbeam forest part of the dataset (n = 54) was divided into three clusters. Their classification reflected mainly soil moisture gradient (Fig. 6). We classified the recorded *Carpinion* forests into three associations commonly recognized in eastern part of central Europe: 1) *Circaeo-Carpinetum* for slightly hygrophilous oak-hornbeam forests of the northeastern part of the Pannonian Lowland, 2) *Carici pilosae-Carpinetum* for zonal oak-hornbeam forests of the Carpathian foothills and 3) *Primulo veris-Carpinetum* for rare and relatively thermophilous types growing on dry soils of volcanic intrusive hills scattered in the Carpathian foothills. It was the first record of this association for Ukraine (cf. Onyshchenko 2009).

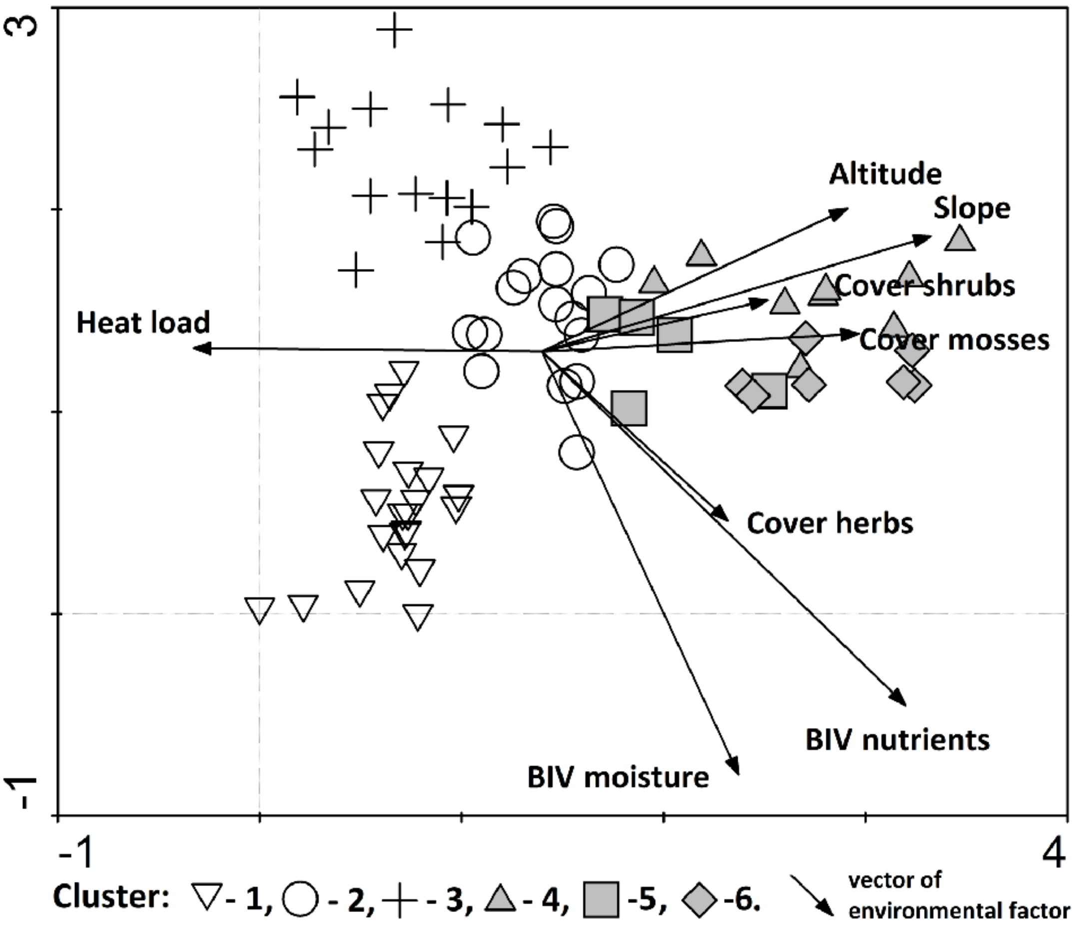

Fig. 6. Detrended correspondence analysis of Transcarpathian relevés (n = 76). The first DCA ordination axis explained 7.4% of the variance in species composition, the second 5.0%. Environmental variables correlated with at least one of the first two ordination axes ($p \leq 0.01$) were plotted onto the diagram. Relevés are distinguished by their cluster assignment. *Carpinion* clusters: 1 – *Circaeo-Carpinetum*, 2 – *Carici pilosae-Carpinetum*, 3 – *Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*; *Tilio-Acerion* clusters: 4 – *Phyllitido-Aceretum*, 5 – *Aceri-Tilietum* and its transitions to *Carici pilosae-Carpinetum*, 6 – *Arunco dioici-Aceretum pseudoplatani*. Abbreviations: "BIV" - Borhidi indicator values, "Heat load" – heat load index (McCune & Keon 2002).

Paper 2 – Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region)

Other understudied oak-hornbeam forests are reported from the eastern part of the Euxinian Province in western Georgia. Forest vegetation of this Caucasian country has been little studied by Braun-Blanquet methods to date (Bohn et al. 2000–2003, Nakhutsrishvili 2013). Paper 2 was focused on the Euxinian part of southwestern Georgia. We analysed a dataset of our original relevés (n = 53) of both oak-hornbeam (alliance *Castaneo-Carpinion*) and ravine (alliance *Alnion barbatae*) forests, yielded in July 2015 and 2016. Applying unsupervised classification analysis, we recognized two main types of oak-hornbeam forests (Fig. 7). Afterwards, we compiled a broader dataset of oak-hornbeam and ravine forest relevés from northern Turkey and appended it to our relevés. Their joint analysis indicated uniqueness of the Georgian relevés. Therefore, we described two new associations of oak-hornbeam forests in western Georgia. The association *Digitali schischkinii-Carpinetum betuli* (n = 16) comprised a relatively species-rich type with low cover of evergreen shrubs. The association *Rusco colchici-Castanetum sativae* (n = 18) was designated for forests with a thick evergreen shrub layer (e.g. *Prunus laurocerasus* and *Rhododendron ponticum*) and species-poor field layer. Our further observations (2017–2019) from western Georgia confirmed that these two types represent an important part of the local oak-hornbeam forest variability, at least on volcanic bedrock.

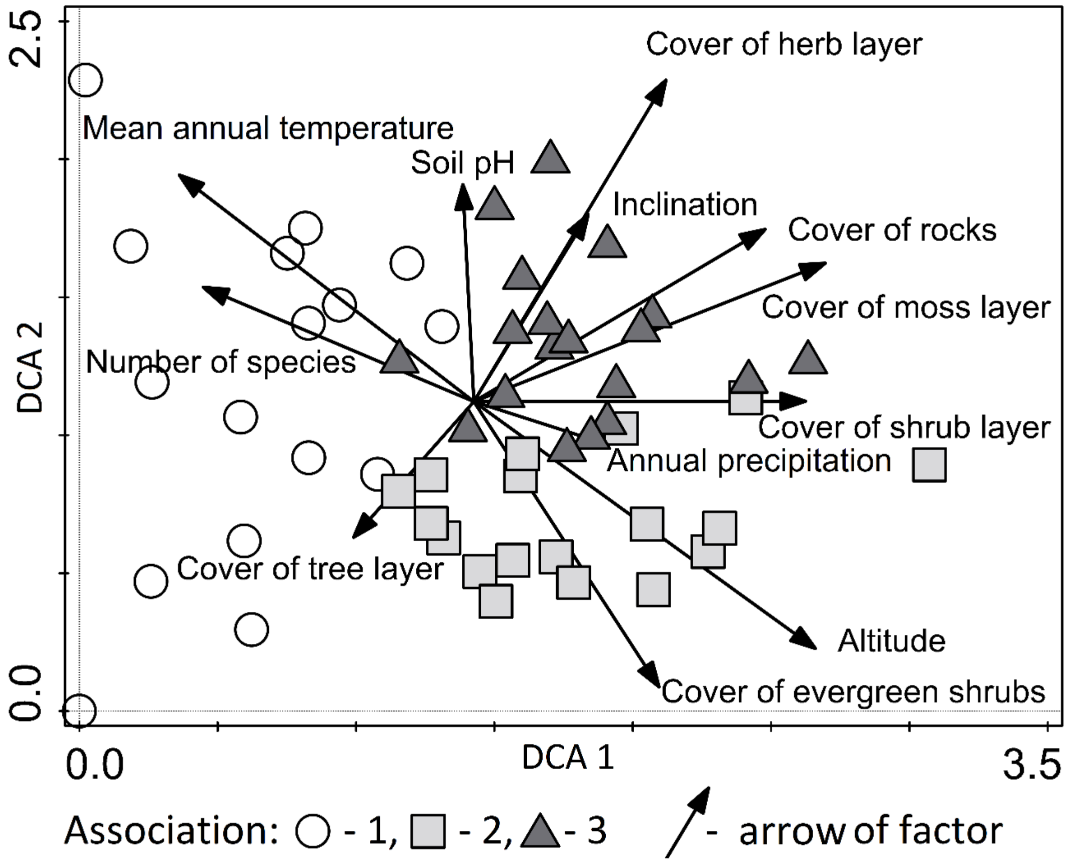

Fig. 7. Detrended correspondence analysis of relevés (n = 53) from Georgian Colchis. The first ordination axis explains 7.0% of the variance in species composition of relevés. The second axis explains 4.7% of the variance. Environmental, vegetation structure and species richness variables were passively plotted on the diagram. *Castaneo-Carpinion* associations: 1 – *Digitali-Carpinetum*, 2 – *Rusco-Castaneetum*; *Alnion barbatae* association: 3 – *Polysticho-Ulmetum*.

Paper 3 – Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia

The third regional study is dealing with Transcaucasian oak-hornbeam forests recorded in eastern Georgia, another understudied type among oak-hornbeam forests (Bohn et al. 2000–2003, Nakhutsrishvili 2013). Like in the above-mentioned studies, we analysed an original dataset of relevés comprising both oak-hornbeam and ravine forests (n = 110 relevés). The relevés were recorded mainly in August 2018. Concerning oak-hornbeam forests (n = 69), we recognized five vegetation types (Fig. 8) assigned to the alliances *Crataego-Carpinion* and *Astrantio-Carpinion*. One was described as a new association (*Clinopodio umbrosi-Carpinetum betuli*, alliance *Crataego-Carpinion*) comprising oak-hornbeam forests of the warm Eastern Greater Caucasian promontories in northeastern Georgia and it presumably occurring also in northern Azerbaijan. The other four types were identified with the associations described by Passarge (1981) or classified only at the alliance level. Additionally, the paper provides new data on the alliance *Astrantio-Carpinion*, which has been so far documented probably only by two Passarge's relevés. To put our results into a broader context of Georgian forest vegetation, we provide a joint classification of the original relevés and previously published deciduous broadleaved forest vegetation from Georgia. It highlighted the key role of biogeography in the Georgian forest vegetation variability, as forests from Colchis (western Georgia) and the Caucasus (central and eastern Georgia) were separated at the first level of the classification.

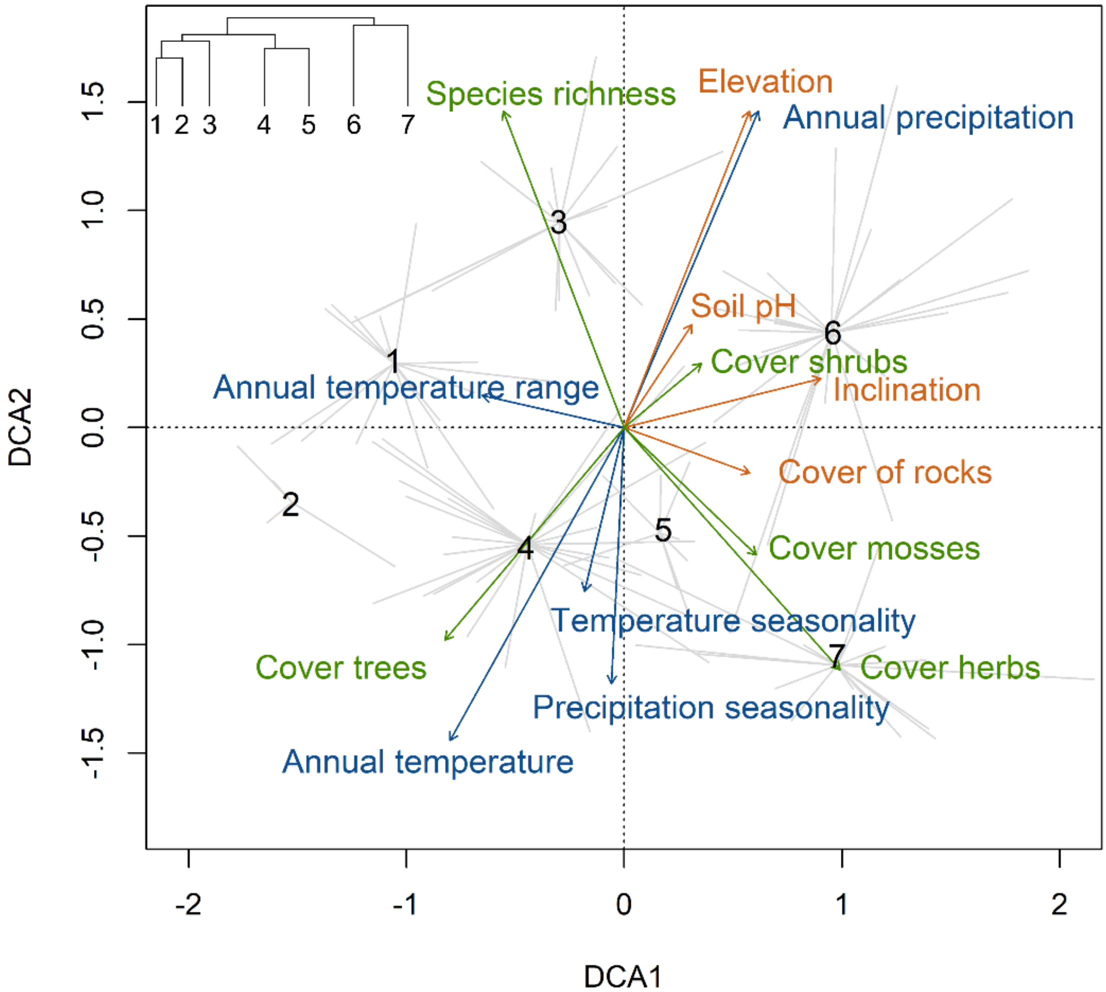

Fig. 8. DCA ordination of the dataset of original relevés (n = 110) from Georgia. The first two axes explain 6.0% and 4.9% of the variance in species composition of the dataset. Basic environmental and vegetation structure variables were passively plotted. Oak-hornbeam forest communities: 1 – *Cornus mas-Carpinus betulus*, 2 – *Zelkova carpinifolia-Carpinus betulus*, 3 – *Quercus macranthera-Carpinus betulus*, 4 –

Clinopodium umbrosum-Carpinus betulus, 5 – *Hedera pastuchovii-Carpinus betulus*; ravine forest communities: 6 – *Valeriana tiliifolia-Ulmus glabra*, 7 – *Hedera pastuchovii-Acer velutinum*.

2) Synthetic studies

Paper 4 – Proposals (23–25): to conserve the names Galio-Carpinetum *Oberdorfer 1957,* Lithospermo-Carpinetum *Oberdorfer 1957 and* Stellario-Carpinetum *Oberdorfer 1957*

A stable syntaxonomic nomenclature of plant communities is essential to find a common language among vegetation scientists from various countries or phytosociological schools. During the work on the syntaxonomic part of the synthetic central European paper, I revealed three association names, frequently used in central European vegetation handbooks, should be proposed for conservation since their older valid synonyms were discovered. They were *Galio sylvatici-Carpinetum betuli* Oberdorfer 1957 (vs. *Querco pedunculatae-Carpinetum betuli* Klika 1928), *Lithospermo-Carpinetum betuli* Oberdorfer 1957 (*Carpinetum betuli* Issler 1925) and *Stellario holosteae-Carpinetum betuli* (vs. *Alno glutinosae-Carpinetum betuli* Issler 1926). These proposals will be forwarded to the Committee for Changes and Conservation of Names of the Working Group for Phytosociological Nomenclature of the International Association for Vegetation Science for evaluation (see Willner et al. 2015 for details).

Paper 5 – Oak-hornbeam forests of central Europe: A formalized classification and syntaxonomic revision

The central European synthesis of oak-hornbeam forest vegetation represents the principal study of the thesis. For this study, we compiled relevés from the European Vegetation Archive (Chytrý et al. 2016) and several other sources, selected by *ad hoc* prepared formal definition of oak-hornbeam forests based on the GRIMP approach (Tichý et al. 2019). The initial dataset was afterwards stratified by combined geographical and heterogeneity constrained random resampling. The resampled dataset contained 6212 relevés. Ordination revealed the main drivers of the diversity of these forests, including the complex gradient of soil moisture and nutrient availability and biogeography (mainly latitudinal gradient). Of the climate variables, annual temperature amplitude and mean annual temperature were important. A series of unsupervised classification analyses revealed essential groups of relevés. We afterwards recognized 13 groups of relevés identified with previously described associations, nine of the alliance *Carpinion betuli* and four of the alliance *Erythronio-Carpinion* (Fig. 9, Fig. 10). They were organized into three informal ecological groups reflecting soil moisture gradient (i.e. hygrophytic, mesophytic and xerophytic one). To provide clear criteria for relevé assignment, each association was defined by its logical formula. An expert system based on these definitions classified 3413 relevés (ca 55%) of the dataset. To keep the presented *Carpinion betuli* association concepts more stable, we selected type relevés for associations which have been lacking typification so far. Additionally, two association names were validated (*Poo chaixii-Carpinetum*, *Pseudostellario-Carpinetum*).

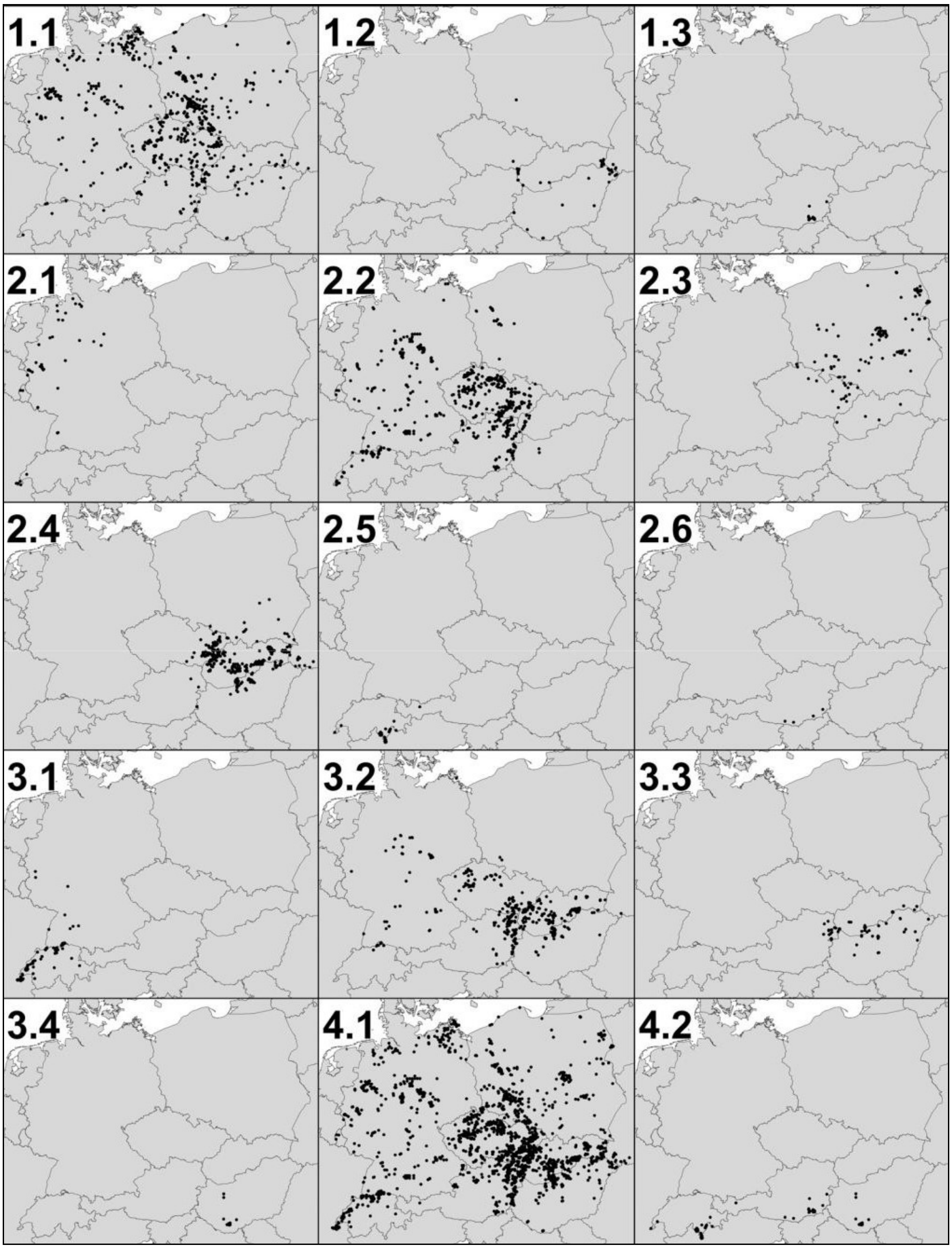

Fig 9. Distribution of relevés classified in the particular associations of oak-hornbeam forests in central Europe (n = 3413). Hygrophytic group of associations: 1.1. *Stellario-Carpinetum*, 1.2. *Convallario-Carpinetum*, 1.3. *Pseudostellario-Carpinetum*. Mesophytic group of associations: 2.1. *Poo-Carpinetum*, 2.2. *Galio-Carpinetum*, 2.3. *Tilio-Carpinetum*, 2.4. *Carici-Carpinetum*, 2.5. *Cruciato-Quercetum*, 2.6. *Epimedio-Carpinetum*. Xerophytic group of associations: 3.1. *Lithospermo-Carpinetum*, 3.2. *Primulo-Carpinetum*, 3.3. *Polygonato-Carpinetum*, 3.4. *Helleboro-Carpinetum*, 4.1. all relevés assigned to the *Carpinion betuli* associations, 4.2. all relevés assigned to the *Erythronio-Carpinion* associations.

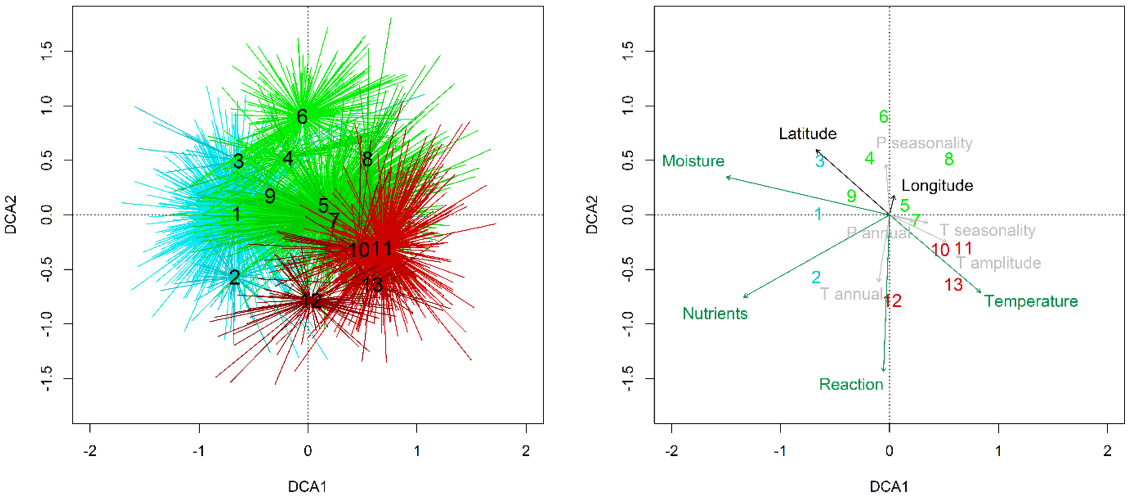

Fig. 10. Detrended correspondence analysis of the dataset of central European oak-hornbeam forest relevés classified by formal definitions. Spider plots with association centroids are plotted. The three colours are representing hygrophytic (blue), mesophytic (green) and xerophytic (red) associations. The second diagram shows the same ordination with vectors of geographical positions (black), Ellenberg indicator values (green) and climate variables (grey) plotted together with the association centroids. All the plotted variables were significantly ($p < 0.05$) correlated with at least one of the two first ordination axes. The first axis explained 1.28% and the second 0.97% of the variability of the dataset. Association numbers: 1 – *Stellario-Carpinetum*, 2 – *Convallario-Carpinetum*, 3 – *Pseudostellario-Carpinetum*, 4 – *Poo-Carpinetum*, 5 – *Galio-Carpinetum*, 6 – *Tilio-Carpinetum*, 7 – *Carici-Carpinetum*, 8 – *Cruciato-Quercetum*, 9 – *Epimedio-Carpinetum*, 10 – *Lithospermo-Carpinetum*, 11 – *Primulo-Carpinetum*, 12 – *Polygonato-Carpinetum*, 13 – *Helleboro-Carpinetum*.

3) Central European national vegetation surveys

Paper 6 – chapter "Carpinetalia betuli P. Fukarek 1968" in the book "Plant communities of Slovakia 6, Forest and shrub vegetation

The findings gained during the preparation of the central European synthesis also contributed to a manuscript of the chapter dealing with *Carpinion betuli* forests which will be included in the 6th volume of the Slovak vegetation survey. The presented book chapter provides the first detailed overview of oak-hornbeam forests in Slovakia, including a syntaxonomic revision. The study is based on analyses of a large relevé dataset (n = 1180 relevés) covering the entire range of oak-hornbeam forests in Slovakia. In the previous list of Slovak vegetation units, 14 associations were recognized (Jarolímek et al. 2008). The majority of them were difficult to distinguish from others since they lacked a sufficient number of good diagnostic species or had diagnostic species with only local validity. Applying numerical analyses, we revealed 4 main vegetation units which were identified as associations. Afterwards, we summarized data on their distribution, dynamics, ecology, phenology, physiognomy and species composition in Slovakia. Their main division reflected basic biogeographical units of Slovakia (Carpathians and Pannonian Basin). The associations *Carici pilosae-*

Carpinetum unifies zonal mesophilous oak-hornbeam forests of the Carpathian foothills (n = 950). As this association has a relatively high inner variability, we subsequently recognized three subassociations reflecting mainly various soil nutrient availability (poor, intermediate and rich). The association *Primulo veris-Carpinetum* (n = 185) represents slightly thermophilous types of oak-hornbeam forests of the warmer Western Carpathian foothills. The association *Polygonato latifoliae-Carpinetum* (n = 11) involves rare oak-hornbeam forests of loess hills and plateaus in the Pannonian Basin. The association *Convallario-Carpinetum* (n = 34) includes slightly wet oak-hornbeam forests of the Pannonian Basin. The proposed syntaxonomic classification system should become a baseline for a revised Slovak habitat classification system.

5. Conclusions

Vegetation of oak-hornbeam forests was studied at various geographical scales, regional (Transcarpathian region of Ukraine, southwestern and northeastern Georgia), national (Slovakia) and international (central Europe). The gap-oriented regional studies contributed to the knowledge of forest vegetation in western Eurasia. They provided descriptions of variability and insights into the ecology of the studied vegetation in the investigated areas. Moreover, yielded vegetation plots could be used in future vegetation and ecological research.

The central European synthesis of oak-hornbeam forests indicated biogeographical patterns and soil parameters as the main drivers of their variability. The biogeographical patterns represent a highly complex driver encompassing vegetation history and related processes such as population migrations, survivals and extinctions as species responded to environmental changes during the Quaternary climatic oscillations. Moisture and nutrient amount were identified as the most important current environmental parameters. Syntaxonomic revisions included in the synthesis can serve as a baseline for further studies and can be implement into the emerging national classification systems. The use of unified names of the main oak-hornbeam types across the whole of central Europe should facilitate communication among vegetation scientists themselves and between vegetation scientists and nature conservation authorities. The results of the synthesis were broadly applied in the chapter dealing with oak-hornbeam forests in the Slovak vegetation survey.

In the near future, a revised classification system of the oak-hornbeam forest alliances of western Eurasia should be prepared.

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7. Papers

The thesis includes four first-author papers already published in journals with Impact Factor, one paper submitted to an Impact Factor journal and one accepted book chapter. For the manuscript in Slovak, English summary is appended. Selected electronic supplements of the presented papers are also provided.

7.1. Paper 1

Novák P., Zukal D., Večeřa M. & Píšťková K. (2017): Vegetation of oak-hornbeam, scree and ravine forests at lower altitudes in Transcarpathia, Western Ukraine. – Tuexenia 37: 47–63.

Tuexenia 37: 47–63. Göttingen 2017.
doi: 10.14471/2017.37.021, available online at www.tuexenia.de

Vegetation of oak-hornbeam, scree and ravine forests at lower altitudes in Transcarpathia, Western Ukraine

Vegetation der Eichen-Hainbuchen- sowie Hangschutt- und Schluchtwälder der unteren Lagen Transkarpatiens, West-Ukraine

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Abstract

Transitional between the Pannonian Basin and the Eastern Carpathians the Transcarpathian Ukraine (Transcarpathia) has a diverse geology including Quaternary sediments, volcanites, limestones and flysch, and its climate at low altitudes is relatively warm and humid. We conducted a field survey in June 2016 focusing on mesophilous forest vegetation along a transect covering almost the whole low-altitudinal part of Transcarpathia. We recorded 54 relevés in the field and further digitized 22 relevés from literature. Using classification analysis, we distinguished three clusters of oak-hornbeam forests (alliance *Carpinion betuli*; 1–3) and three clusters of scree and ravine forests (alliance *Tilio platyphylli-Acerion*; 4–6): (1) Slightly wet Pannonian oak-hornbeam forests occurring in the lowland part of the region (*Circaeo-Carpinetum*); (2) Mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*); (3) Xero-mesophilous oak-hornbeam forests (a drier subtype of the *Carici pilosae-Carpinetum* and the association *Primulo veris-Carpinetum*); (4) Mesophilous scree forests (*Phyllitido-Aceretum*); (5) Forests of steep slopes (*Aceri-Tilietum*) and transitions to mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*); (6) Cool and wet scree and ravine forests (*Arunco dioici-Aceretum pseudoplatani*). Using indirect ordination analysis, three environmental variables (altitude, heat load index and slope) were identified as factors of significant influence on the species composition. These factors well distinguish oak-hornbeam forests from scree and ravine forests.

Keywords: *Carpinion betuli*, Eastern Carpathians, forest vegetation, Pannonian Basin, phytosociology, syntaxonomy, *Tilio platyphylli-Acerion*

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Mesophilous forests are considered natural vegetation with a wide potential distribution across Central Europe (BOHN et al. 2000–2003). Due to deforestation of lowland regions and the occurrence of endangered biota, some types of these forests have been recorded on the European Red List of Habitats (JANSSEN et al. 2016).

The Carpathians and their foothills are regarded as one of the centres of diversity of deciduous forest vegetation in Europe (OSZLÁNYI et al. 2004, WILLNER et al. 2009). Many regional and national phytosociological studies considering Carpathian forests have been conducted in all the Carpathian countries including Ukraine (e.g., ONYSHCHENKO 2007,

Manuscript received 29 March 2017, accepted 22 July 2017
Co-ordinating Editor: Erwin Bergmeier

ŠEBESTA et al. 2011). Yet relatively little attention has been paid to oak-hornbeam, scree and ravine forests, which typically occur below the beech forest belt (ONYSHCHENKO 2009). Therefore, our aim was to fill this gap and describe the diversity of forest vegetation at the lower altitudes of Transcarpathia, a region in Western Ukraine comprising the southwestern slopes of the Ukrainian Carpathians and the adjacent part of the Pannonian Basin.

Local oak-hornbeam forests have been surveyed near the towns of Uzhhorod and Mukacheve, though no attention has been paid to scree and ravine forests in the studies published so far (KRAMARETS et al. 1992, ONYSHCHENKO & LUKASH 2005, VOROBYOV et al. 2008, ONYSHCHENKO 2009). In contrast, the forest vegetation in adjacent areas of the Pannonian-Carpathian transitional zone in neighbouring countries has been investigated fairly intensively in eastern Slovakia (e.g., HADAČ & TERRAY 1989) and north-western Romania (e.g., RAŢIU & GERGELY 1979, MARIAN 2008).

The main goals of our study are: (1) to survey the studied vegetation based on numerical analyses and to compare it with syntaxa previously described in Ukraine and adjacent countries; (2) to provide clearer understanding of the environmental factors that drive the floristic composition of the studied vegetation types in Transcarpathia.

2. Study area

The study area comprises the flat margins of the Pannonian Basin filled by Quaternary sediments and the Carpathian foothills. The Carpathian foothills are formed of three geologically distinct zones (from lowland to upland parts) starting with the Vihorlat–Gutâi Belt composed of volcanic hills and ridges with prevailing andesite, basalt and dacite. Towards the north-east, this belt is followed by a large region of Carpathian flysch comprising the highest peaks of the Ukrainian Carpathians. Between these two zones, the Pieniny Klippen Belt composed of Mesozoic limestone appears locally at the surface (ANDÓ 1999). Relevés were recorded at sites of various types of bedrock with the exception of flysch.

The region is situated in a climatically transitional zone between the continental Pannonian Basin with dry and hot summers and the mountain climate of the Carpathians with lower mean temperatures and higher precipitation (800–1,000 mm). The mean annual temperature ranges between 7 and 9.5 °C, the mean July temperature between 17 and 20 °C and the mean January temperature between -4 and -2 °C (ANDÓ 1999).

Transcarpathia is one of the most forested regions of Ukraine, though the Pannonian part has been strongly deforested in the past and current forest cover is predominantly restricted to patches in the agricultural landscape. Alluvial hardwood and willow-poplar forests in the flat lowlands and oak-hornbeam forests in the lower parts of the Carpathian foothills are regarded as natural vegetation. Beech forests prevail at higher altitudes (BOHN et al. 2000–2003, DIDUKH & SHELYAG-SOSONKO 2008). Thermophilous oak forests are locally developed on the steep and sunny slopes of volcanic hills (FODOR 1958, STOYKO 2009). Relevés were recorded along the whole altitudinal gradient of oak-hornbeam forests and in the lower part (120–625 m a.s.l.) of the altitudinal range of scree and ravine forests.

Flora and vegetation of the Transcarpathian lowlands differ significantly from the rest of Ukraine due to strong influences from neighbouring Pannonian and Carpathian regions (e.g., FODOR 1958, 1974, KRICSFALUSY 1999, ONYSHCHENKO 2009). This is reflected in the geobotanical zonation of Ukraine, where the lower altitudes of Transcarpathia belong to the distinctive Pannonian Province, which is part of the Eurasian Steppe Region (DIDUKH & SHELYAG-SOSONKO 2008).

3. Methods

3.1 Vegetation sampling

In June 2016, we conducted an extensive field survey in a transect 80 km long and 30 km wide between the cities of Mukacheve and Bushtyno (48°03'–48°35' N, 22°36'–23°37' E) and the study area (approximately 2,400 km^2) thus comprises a major part of the low-altitudinal areas of Transcarpathia. The survey focused on the vegetation of oak-hornbeam (alliance *Carpinion betuli*) and scree and ravine forests (*Tilio platyphylli-Acerion*). These forests have a tree layer dominated by *Carpinus betulus*, *Quercus petraea*, *Q. robur* or noble hardwood trees such as *Acer* spp., *Fraxinus excelsior*, *Tilia* spp. and *Ulmus glabra*.

Vegetation was sampled following the Braun-Blanquet approach (DENGLER et al. 2008). Each relevé (n = 54) had a uniform area size of 100 m^2. First, the percentage cover of each vegetation layer was estimated. Subsequently, the cover of each species was estimated using the extended nine-degree Braun-Blanquet cover-abundance scale (DENGLER et al. 2008). Cryptogams were not determined. Basic environmental variables (aspect and inclination of slope, percentage of rocks) were recorded for all relevés, as well as coordinates (WGS–84) taken using a GPS receiver. Furthermore, we took a mixed soil sample within each relevé (from the uppermost 15 cm at four places within the site). Subsequently, the pH of dried soil samples was measured in a water suspension (2:5) by portable instruments (GMH Greisinger). The heat load index (HLI) indicating the potential heat load of a given site based on its slope and aspect was calculated for each relevé using *Equation 3* in MCCUNE & KEON (2002). Relevés from our field work were saved in TURBOVEG 2.0 (HENNEKENS & SCHAMINÉE 2001) and further analysed, primarily with the use of JUICE 7.0 (TICHÝ 2002). To obtain a more representative dataset, we included and digitized relevés of oak-hornbeam or scree and ravine forests (n = 22) from the study area published by ONYSHCHENKO & LUKASH (2005). Although the area size of these relevés (150–1,600 m^2) differed from ours, their species richness was similar. Sampled twice – in spring and summer – relevés from ONYSHCHENKO & LUKASH (2005) contain several vernal species that we missed during our field work carried out in June. Therefore we excluded vernal species (VYMAZALOVÁ et al. 2016) from relevés originating from the given study in order to make the two datasets comparable.

We did not include relevés of oak-hornbeam forests from Transcarpathia published by VOROBYOV et al. (2008) due to the lack of any site information other than species covers.

The final dataset used for numerical analyses contained 76 relevés of oak-hornbeam, scree and ravine forest vegetation from Transcarpathia. Tree and shrub species recorded in the herb layer were deleted from all the relevés and subsequently all layers were merged into a single layer prior to analyses. The nomenclature of taxa follows the Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/; accessed 2017–01–12) and supplemented by The Plant List (http://www.theplantlist.org; accessed 2017–01–12) for those families not yet covered in Euro+Med PlantBase.

3.2. Data analyses

3.2.1. Classification analyses

For classification, we first computed TWINSPAN with pseudospecies cut levels set at 0, 1, 5 and 25% cover (HILL & ŠMILAUER 2005) to distinguish the two main vegetation types the study is concerned with – oak-hornbeam forests (*Carpinion betuli*) and scree and ravine forests (*Tilio platyphylli-Acerion*). Due to the different levels of heterogeneity within each of those two main clusters, we classified each of them separately.

We tried several approaches with various classification algorithms, intersample distance measures and cover-abundance transformations. All methods used produced relatively similar results. Finally, we followed the formalized OptimClass 1 method (TICHÝ et al. 2010). Subsequently, we selected the final number of subclusters being relatively homogeneous from both the ecological and geographical point of view. Within each of the two main clusters, the optimal classification was achieved using a different classification method. For classification of oak-hornbeam forests, we used the beta-flexible algorithm (beta = -0.25) and Bray-Curtis index as a measure of distance between relevés, with logarithmically transformed cover values. The classification was performed using PC-ORD (MCCUNE & MEFFORD 1999) incorporated in JUICE. For the classification of scree and ravine forests, we applied modified TWINSPAN (ROLEČEK et al. 2009) with the same cut levels as in the first case. The final number of subclusters within each of the main clusters was three.

The interpretation of the species composition and structure of subclusters was based on diagnostic, constant and dominant species. The *phi* coefficient (SOKAL & ROHLF 1995) was calculated for the identification of diagnostic species. Species with a *phi* coefficient higher than 0.5 were accepted as being highly diagnostic and species with a *phi* coefficient higher than 0.2 were considered diagnostic. Fisher's exact test (alpha = 0.01) was used to exclude rarely occurring species from the lists of diagnostic species. As the identification of diagnostic species depends on the size of the given subcluster, the sizes of all subclusters were virtually standardized so as to be equal (TICHÝ & CHYTRÝ 2006). The diagnostic species of the two main clusters were identified in the same way.

Differences in Borhidi indicator values (BIVs; BORHIDI 1995), the covers of each layer, environmental variables and species richness among distinguished subclusters were tested using Kruskal-Wallis ANOVA in the software Statistica (STATSOFT 2006). As BIVs are connected with species composition, ANOVA results were checked using a permutation approach (ZELENÝ & SCHAFFERS 2011; $p_{modif} \leq 0.05$). Subsequently, multiple comparison tests of mean ranks were calculated to distinguish groups of homogenous subclusters for variables with significant differences among subclusters (alpha = 0.05). Boxplots of selected variables with the most significant differences within subclusters are shown.

The results were syntaxonomically interpreted using the Ukrainian phytosociological literature (mainly ONYSHCHENKO 2009) and selected studies from nearby countries (e.g., HADAČ & TERRAY 1989, OBERDORFER 1992, MATUSZKIEWICZ 2001, JAROLÍMEK & ŠIBÍK 2008, WILLNER & GRABHERR 2007, BORHIDI et al. 2012, CHYTRÝ 2013, COLDEA et al. 2015).

3.2.2 Ordination analysis

We performed Detrended Correspondence Analysis (DCA) in CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002) to facilitate the ecological interpretation of subclusters. Species cover values were logarithmically transformed before the analysis. The length of the first DCA axis was 3.469 which suggested that ordination methods assuming the unimodal response of species to the environmental gradient were appropriate. Both the environmental variables (only those available for all relevés – altitude, heat load index and slope) and covers of all vegetation layers that were significantly correlated (Spearman's correlation, r_s, alpha = 0.01) with at least one of the first two axes were passively projected onto the ordination space. Borhidi indicator values for continentality, light, moisture, nutrients, soil reaction and temperature were used. BIVs were proposed for the flora of Hungary which is highly similar to the low-altitudinal parts of Transcarpathia, which is why we preferred these values over the Didukh indicator values (DIDUKH 2011) calibrated for the territory of Ukraine. We worked with unweighted means of BIVs for each relevé. The significance of the correlations of BIVs with the two first DCA axes was checked using the permutation approach (ZELENÝ & SCHAFFERS 2011).

4. Results and discussion

4.1 Overview of species composition and forest types

In total, the dataset contained 210 species. The most frequent species were: *Carpinus betulus* (71 records), *Rubus* subgen. *Rubus* (58), *Lamium galeobdolon* (53), *Anemone nemorosa* (49), *Cardamine bulbifera* (43), *Galium odoratum* (41), *Polygonatum multiflorum* (40), *Fagus sylvatica* (38), *Dryopteris filix-mas* (37), *Carex pilosa* (35), *Viola reichenbachiana* (34), *Corylus avellana* (32), *Hedera helix* (31) and *Stellaria holostea* (31).

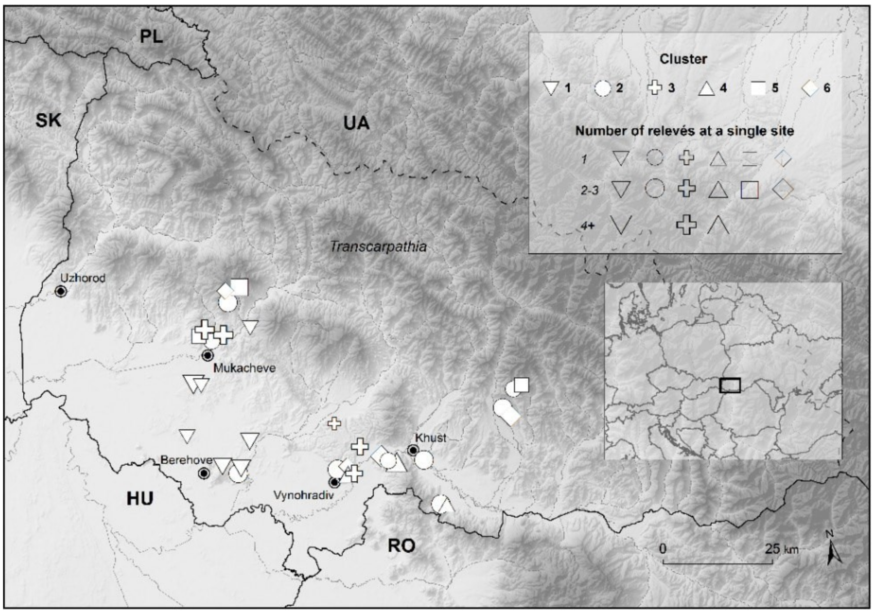

Fig. 1. Distribution map of relevés of subclusters 1–6 (for corresponding associations see text) based on analysed dataset (*n* = 76).

Abb. 1. Verbreitungskarte der klassifizierten Vegetationsaufnahmen (*n* = 76) der Teilgruppen 1–6 (korrespondierende Assoziationen siehe Text).

Forest mesophytes obviously highly prevailed. Besides common species, several species of the Red List of the Ukrainian flora (DIDUKH 2009) were recorded (*Asplenium adiantum-nigrum*, *Cepha- lanthera longifolia*, *Drymochloa drymeja*, *Lathyrus transsilvanicus*, *Lunaria rediviva*, *Sco- polia carniolica*). *Geranium lucidum* was discovered as a new species for Transcarpathian Ukraine (cf. FODOR 1974).

Using TWINSPAN, we distinguished two main clusters that corresponded well to phyto- sociological alliances: the first cluster of 54 relevés to *Carpinion betuli*, the second cluster of 22 relevés to *Tilio platyphylli-Acerion*. Three subclusters were identified in each of these two clusters and further interpreted at association level. A list of the diagnostic species of each cluster and subcluster as well as frequent species of the dataset are shown in Supplement S1. For relevés recorded in 2016 see Supplements E1–E3. The distribution of all vegetation types is summarized in Figure 1. The ecological interpretation of subclusters follows measured environmental variables and BIVs (Fig. 2 and Supplement E4). Photos of all vegetation types are provided in Figure 3.

4.1.1 Main cluster 1 – Oak-hornbeam forests

Subcluster 1 – Eutrophic slightly wet oak-hornbeam forests (*Circaeo-Carpinetum*)

This subcluster represents oak-hornbeam forests of the lowland part of Transcarpathia. They occur on relatively fertile and deep soils with high moisture, probably due to temporar- ily high groundwater level, which are developed on lowland alluvial sediments. Their mean pH value is 5.1.

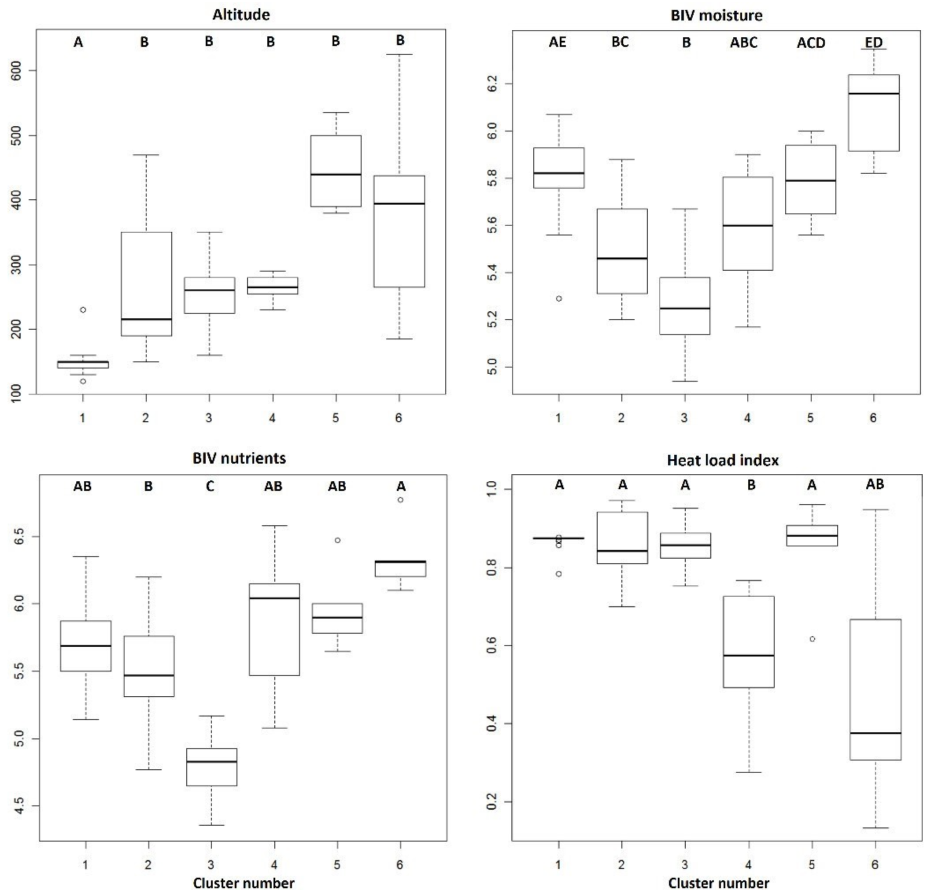

Fig. 2. Comparison of selected environmental variables and BIVs among subclusters. Mean, quartiles, standard deviation and outliers are plotted. Homogenous groups are signed with the same letters. 1 – *Circaeo-Carpinetum*, 2 – *Carici pilosae-Carpinetum*, 3 – *Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*, 4 – *Phyllitido-Aceretum*, 5 – *Aceri-Tilietum* and transitions to *Carici pilosae-Carpinetum*, 6 – *Arunco dioici-Aceretum pseudoplatani*.

Abb. 2. Ausgewählte Umweltvariablen und Zeigerwerte nach Borhidi im Vergleich der Teilgruppen 1–6 (Assoziationen). Die Boxplot-Diagramme zeigen Mittelwerte, Quartile, Standardabweichungen und statistische Ausreißer. Gleiche Buchstaben weisen auf nichtsignifikante Unterschiede zwischen Gruppen.

The tree layer is composed mainly of *Carpinus betulus* and *Quercus robur*. The shrub layer (cover usually below 25%) contains common shade-tolerating species (e.g., *Cornus sanguinea* and *Corylus avellana*). The herb layer is relatively dense and is dominated by forest mesophytes. In addition to these, there are also numerous moisture- and nutrient-demanding species (e.g., *Aegopodium podagraria*, *Carex brizoides* and *Circaea lutetiana*). Several subcontinental species (e.g., *Acer tataricum*, *Oenanthe banatica*) also occur in this community. The moss layer has predominantly very low cover.

We assign these relevés to the *Circaeo-Carpinetum* reported in the Pannonian Basin in Hungary including Transcarpathian borderlands (BORHIDI et al. 2012). ONYSHCHENKO (2009) describes forests of this association as zonal vegetation on the flatlands of the Pannonian Basin in Transcarpathia, and this is in agreement with our results.

Subcluster 2 – Mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*)

This community is characteristic for the Carpathian foothills in the studied area (up to 470 m). It occurs on mesic sites, often on mild slopes. The bedrock is volcanic or limestone, the soils are rather deep and usually strongly acidic (mean soil pH 5.2).

The canopy of these forests is relatively closed, dominated mainly by *Carpinus betulus*, although the admixture of *Fagus sylvatica* and *Quercus petraea* is frequent. Common occurrence of beech could indicate the origin of some growth from beech forests under strong human pressure. The shrub layer is often well developed (mean cover approximately 10%) and mainly contains species of the tree layer and *Corylus avellana*. Concerning the herb layer (cover ranging from 15 to 70%), in addition to common forest mesophytes, there is also notable co-occurrence of subcontinental (*Carex pilosa*, *Galium intermedium*) and submediterranean (e.g., *Euphorbia amygdaloides*, *Primula vulgaris*) mesophilous forest species. The moss layer is usually developed, though only with low cover.

The species composition of these forests corresponds to the *Carici pilosae-Carpinetum* which is characteristic of the western part of the Carpathian arc. It has been reported in the area between the Czech Republic and Ukraine (ONYSHCHENKO 2009, CHYTRÝ 2013).

Subcluster 3 – Xero-mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*)

This community comprises xero-mesophilous oak-hornbeam forests on volcanic hills above the Pannonian lowland around the towns of Mukacheve and Vynohradiv. It grows mainly on warm mild slopes with strongly acidic soils (pH ranging from 4.7 to 5.3).

The tree layer is relatively open, reaching a mean cover of approximately 70%. It is predominantly composed of *Carpinus betulus* and *Quercus petraea*, with the latter even prevailing in some relevés. The shrub layer (cover mainly up to 5%) contains various species, including thermophilous ones (e.g., *Cornus mas* and *Ligustrum vulgare*). The herb layer of these forests is dominated by forest mesophytes as in Subcluster 2. In addition, there is a notable presence of xero-mesophilous acidotolerant (e.g., Hieracium laevigatum, Pteridium aquilinum) as well as slightly thermophilous species (e.g., Lathyrus niger and Melittis melissophyllum).

The majority of relevés can be assigned to a xerophilous subtype of the Carici pilosae-Carpinetum. In addition, some relevés (nos. 31 and 33) containing more thermophilous species are similar to the thermophilous oak-hornbeam forests of the Primulo veris-Carpinetum described in the volcanic hills of south-central Slovakia (NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ 1964), comprising thermophilous oak-hornbeam forests of Central Europe with a distribution centre on the northern edge of the Pannonian Basin. It is recognized mainly in the Czech Republic and Slovakia, including the eastern part of the country (HADAČ & TERRAY 1989), and, according to some studies, also in Austria (CHYTRÝ 2013). Several similar associations are also recognized in Hungary (BORHIDI et al. 2012). It has not yet been distinguished in Ukraine (cf. ONYSHCHENKO 2009) and is, therefore, the first record based on original field data.

Fig. 3. Photos of forest vegetation of particular subclusters distinguished in Transcarpathian Ukraine **a)** Lowland slightly wet oak-hornbeam forests of the association *Circaeo-Carpinetum* (Subcluster 1) near the village of Pavshino in the Mukacheve District; **b)** Mesophilous oak-hornbeam forests of the association *Carici pilosae-Carpinetum* (Subcluster 2) on the western slope of the Chorna hora Mt. above the town of Vynohradiv; **c)** Xero-mesophilous oak-hornbeam forest of the association *Carici pilosae-Carpinetum* (Subcluster 3) on the upper terrace of the Tisa River at the village of Velyka Kopanya in the Vynohradiv District; **d)** Scree forest of the association *Phyllitido-Aceretum* (Subcluster 4) on slope above of the Tisa River near the village of Kryva in the Khust District; **e)** Slope forest from the Subcluster 5 in Matekova River valley near the village of Syniak in the Mukacheve District and **f)** Edge of a scree forest with *Aruncus dioicus* of the association *Arunco-Aceretum* (Subcluster 6) developed on the slope above the Tisa River near the village of Kryva in the Khust District (All photos: P. Novák, June 2016).

4.1.2 Main cluster 2 – Scree and ravine forests

Subcluster 4 – Mesophilous scree forests (*Phyllitido-Aceretum*)

This group comprises scree forests of lower volcanic hills in the deep Tisa River valley between the towns of Khust and Vynohradiv. Relevés of this group were recorded predominantly on slopes of inclinations from 10 to 45° with strongly acidic soil (pH ranging from 4.4 to 7.2).

The canopy cover of these forests varies among sites, ranging from 55 to 95%. They are dominated by *Acer pseudoplatanus* and *Carpinus betulus* with *Fagus sylvatica* or *Ulmus glabra* being frequent admixtures. The shrub layer is often well developed, containing mainly *Corylus avellana* and young trees. The cover of the herb layer varies greatly among the studied sites (15–70%), depending on the occurrence and size of boulders and blocks of rock. The presence of scree favours chasmophytes, both herbs (e.g., *Arabidopsis arenosa* and *Hylotelephium maximum*) and ferns (e.g., *Asplenium scolopendrium*, *Cystopteris fragilis* and *Polypodium vulgare*). In addition to chasmophytes, nutrient-demanding species (e.g., *Geranium robertianum* and *Scopolia carniolica*) are also frequent. The moss layer is developed and its cover varies from 3 to 55% in the sites of our relevés.

Scree forests with frequent occurrence of the ferns *Asplenium scolopendrium*, *Polypodium vulgare* and *Polystichum aculeatum* have been classified as *Phyllitido-Aceretum* Moor 1945 (MATUSZKIEWICZ 2001, WILLNER & GRABHERR 2007, ONYSHCHENKO 2009). This

association comprises scree forests of narrow ravines mainly on limestone. It includes mois- ture-demanding species among others. Our relevés lack most of these species, though they are characterized by the frequent occurrence of several diagnostic species of this association (mainly the above-mentioned fern species). The relatively warm climate of the sampled sites could be the reason for the lower frequency of species with higher moisture requirements. We therefore consider most of the relevés of this subcluster as being on the margin of the variation range of the *Phyllitido-Aceretum*.

Previous page (vorherige Seite):

Abb. 3. Fotos der Waldvegetation bestimmter in der transkarpatischen Ukraine unterschiedener Untercluster **a)** Feuchter Eichen-Hainbuchenwald des Tieflands des *Circaeo-Carpinetum* (Subcluster 1) beim Dorf Pashino im Distrikt Mukacheve; **b)** Mesophiler Eichen-Hainbuchenwald des *Carici pilosae-Carpinetum* (Subcluster 2) am Westabhang der Chomabergs oberhalb der Stadt Vynohradiv; **c)** Xeromesophiler Eichen-Hainbuchenwald des *Carici pilosae-Carpinetum* (Subcluster 3) auf der oberen Terasse des Tisa-Flusses beim Dorf Velyka Kopanya im Distrikt Vynohradiv; **d)** Blockschuttwald des *Phyllitido-Aceretum* (Subcluster 4) auf einem Hang über dem Tisa-Fluss beim Dorf Kryva im Distrikt Khust; **e)** Hangwald im Subcluster 5 im Matekova-Flusstal beim Dorf Syniak im Distrikt Mukacheve und **f)** Saum eines zum *Arunco-Aceretum* gehörenden Blockschuttwaldes mit *Aruncus dioicus* (Subcluster 6) auf derm Hang über dem Tisa-Fluss beim Dorf Kryva im Distrikt Khust (Alle Fotos: P. Novák, Juni 2016).

Subcluster 5 – Slope forests (*Aceri-Tilietum*) and transitions to mesophilous oak-hornbeam forests (*Carici pilosae-Carpinetum*)

This group includes several relevés of forests on slopes of moderate inclination (15–25°) and of relatively flat places at the foot of slopes with skeletal soil. The community was recorded in the Krychovo and Mukacheve surroundings. The bedrock of this vegetation is volcanic or limestone, though the soils tend to be rather acidic (mean pH approximately 4.9).

The canopy of this group is relatively closed (75–95%), dominated by *Carpinus betulus*, with *Acer pseudoplatanus* or *Fagus sylvatica* usually admixed. The shrub layer has a mean cover of approximately 10%, containing predominantly younger individuals of the tree species and *Corylus avellana*. The herb layer is usually dense, with a cover above 60% – the highest of all the subclusters. It is composed mainly of oak-hornbeam forest elements (e.g., *Anemone nemorosa*, *Cardamine bulbifera* and *Carex pilosa*) with a notable presence of species with higher nutrient requirements (e.g., *Aegopodium podagraria*, *Mercurialis perennis* and *Pulmonaria obscura*). Ferns (mainly *Dryopteris filix-mas*) are also common. Mosses cover up to 5%.

Central European slope forests of lower altitudes with a high proportion of Carpinus betulus, noble hardwood tree species, oak-hornbeam forest species and nitrophytes are usually assigned to the Aceri-Tilietum Faber 1936. This association is recognized in Germany (OBERDORFER 1992), Austria (WILLNER & GRABHERR 2007), the Czech Republic (CHYTRÝ
2013), Poland (MATUSZKIEWICZ 2001) and, under the name *Aceri-Carpinetum* Klika 1941, Slovakia (JAROLÍMEK & ŠIBÍK 2008). However, if we examine the data in more detail, only relevé no. 45 with noble hardwoods prevailing can be clearly assigned to the *Aceri-Tilietum*, while the other four relevés of this group are dominated by *Carpinus betulus*. Moreover, one of these four relevés is dominated by *Festuca drymeja* and another two relevés are co-dominated by *Carex pilosa*, indicating that they should rather be classified into the alliance *Carpinion betuli*. On the other hand, these relevés contain species typical for scree and ravine forests (e.g., *Lunaria rediviva*, *Polystichum aculeatum* and *Symphytum cordatum*), in addition to other nutrient-demanding species and ferns. We assume, therefore, that relevé no. 45 belongs to the *Aceri-Tilietum*, while the other relevés of this subcluster are transitional between *Aceri-Tilietum* and oak-hornbeam forests of the *Carici pilosae-Carpinetum*.

Subcluster 6 – Cool and wet scree and ravine forests (*Arunco dioici-Aceretum pseudoplatani*)

This community comprises scree and ravine forests recorded on the slopes of the Tisa River valley and in narrow ravines above streams. It is developed on rather steep slopes (usually between 30 and 50°) on sites where beech is probably suppressed by solifluction. Mean soil pH of the sites is approximately 5.9, the highest among studied communities.

The tree layer of this group has variable cover (40–95%) and is composed mainly of *Acer pseudoplatanus* and *Fagus sylvatica*, while other tree species are less frequent (e.g., *Carpinus betulus*, *Fraxinus excelsior* and *Ulmus glabra*). The shrub layer is usually well-developed, composed of *Corylus avellana*, *Sambucus nigra* and young tree. The herb layer is also typically dense (50–75%), and is comprised of moisture- and nutrient-demanding species (e.g., *Aruncus dioicus*, *Impatiens noli-tangere* and *Lunaria rediviva*), typical herbs of the Carpathian beech forests (*Cardamine glanduligera*, *Symphytum cordatum*) and ferns (*Athyrium filix-femina*, *Dryopteris filix-mas*, *Polystichum aculeatum*). The cover of the moss layer varies among our relevés.

Two possible associations correspond to the relevés in this subcluster: *Arunco dioici-Aceretum pseudoplatani* Moor 1952 and *Lunario-Aceretum* Schlüter in Grüneberg et Schlüter 1957. However, some authors consider them synonyms (e.g., ONYSHCHENKO 2009, CHYTRÝ 2013) or the latter as a subtype of the former (WILLNER & GRABHERR 2007). Since both associations occur on similar sites and their species composition is very similar (as also documented by the assignment of our relevés with *Aruncus dioicus* to the same subcluster as those with *Lunaria rediviva*), we agree that the *Lunario-Aceretum* should be considered a synonym of the *Arunco dioici-Aceretum pseudoplatani*.

4.1.3 Syntaxonomical system

The syntaxonomical interpretations of clusters, on which the syntaxonomical system stated below is based, were adopted from syntaxa recognized in the Western Carpathians and surrounding regions (e.g., ONYSHCHENKO 2009, BORHIDI et al. 2012, CHYTRÝ 2013). Com- paring the studied vegetation in Transcarpathia with analogous vegetation in adjacent areas in Romania (COLDEA et al. 2015), it was obvious that relevés in Romania are richer in Eastern Carpathian and Balkan elements (e.g., *Galium pseudaristatum*, *Melampyrum bihariense*, *Lathyrus hallersteinii*), for what reason we worked mainly with syntaxa distinguished in the western part of the Carpathians. Above association level, the system follows MUCINA et al. (2016).

Class *Carpino-Fagetea* Jakucs ex Passarge 1968
- Order 1. *Carpinetalia betuli* P. Fukarek 1968
  - Alliance 1.1. *Carpinion betuli* Issler 1931
    - Association 1.1.1. *Circaeo-Carpinetum* Borhidi 2003
    - Association 1.1.2. *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964
    - Association 1.1.3. *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964
- Order 2. *Aceretalia pseudoplatani* Moor 1976
  - Alliance 2.2. *Tilio platyphylli-Acerion* Klika 1955
    - Association 2.2.1. *Phyllitido-Aceretum* Moor 1945
    - Association 2.2.2. *Aceri-Tilietum* Faber 1936
    - Association 2.2.3. *Arunco dioici-Aceretum pseudoplatani* Moor 1952

4.2 The relationship between vegetation and measured environmental factors

The first DCA ordination axis explained 7.4% of the variance in the species composition of relevés (Fig. 4). The second axis explained 5.0% of variance, and the first four axes together explained 18.3% of variance. The first ordination axis was positively correlated ($p \leq 0.01$) with the cover of the moss layer ($r_s = 0.73$), slope (0.71), altitude (0.62), cover of shrub layer (0.42) and the indicator value for nutrients (0.51). A negative correlation ($p \leq 0.01$) was shown for the heat load index (-0.44). The first axis is interpreted to visualize a complex environmental gradient specifying the local distribution of oak-hornbeam and scree and ravine forests in the landscape of Transcarpathia (zonal habitats vs. shady rocky slopes, respectively).

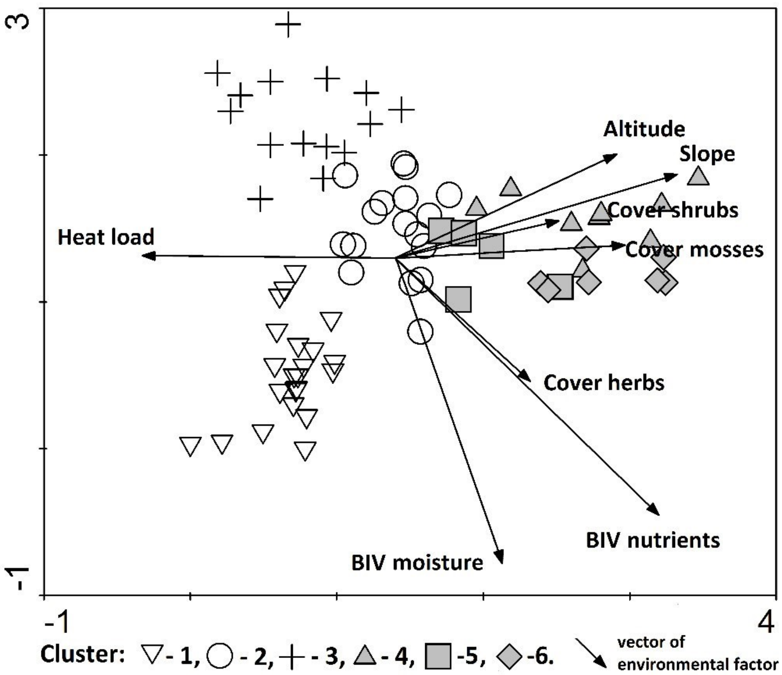

Fig. 4. Detrended Correspondence Analysis (DCA) of relevés from the final dataset. Environmental variables correlated with at least one of the first two ordination axes ($p \leq 0.01$) were plotted into the diagram. Subcluster numbers as in Figure 2.

Abb. 4. Detrended Correspondence Analysis (DCA) der Vegetationsaufnahmen. Umweltvariablen, die mit wenigstens einer der beiden Ordinationsachsen korreliert sind, wurden nachträglich im Diagramm aufgetragen. Nummern der Teilgruppen wie in Abbildung 2.

The second axis was positively correlated with altitude (0.51) and slope (0.49) and negatively with indicator values for moisture (-0.79), nutrients (-0.60) and the cover of the herb layer (-0.39). The second) axis can be interpreted to represent a complex gradient combining soil moisture and nutrient availability.

The main clusters are fairly well distinguished by their position along the first ordination axis. Oak-hornbeam forests, situated on the left side of the plot, prefer flat terrain or mild slopes and sites with higher heat load. On the other hand, scree and ravine forests, situated on the right side of the plot, are confined mainly to steep and shady slopes, often with rock outcrops as is indicated by higher moss cover.

The DCA results corresponded well with our classification of oak-hornbeam forests in which associations were distinguished mainly by soil moisture and nutrients. Relevés of the wetter type (Subcluster 1) were situated in the lower part of the diagram, those of the mesophilous type (Subcluster 2) in the central part, and those of the drier type (Subcluster 3) in the upper part.

Scree and ravine forests represented a rather homogeneous group within our dataset. They were distributed mainly along the first axis. Relevés of Subcluster 5 were distributed mainly between oak-hornbeam forests and the rest of scree and ravine forests, indicating their transitional character between the two alliances. The results of indirect gradient analysis were in agreement with the results of classification.

4.2 Previously reported associations in Transcarpathia – a comparison with the proposed classification system

As we performed numerical classification of our relevés with previously published data from the Mukacheve surroundings (ONYSHCHENKO & LUKASH 2005), relevés from both sources were clustered together and their syntaxonomical interpretation was similar.

In recent decades, several phytosociological studies considering the forest vegetation of Transcarpathia have been carried out. Within the *Carpinion betuli*, the previously mentioned central position of mesophilous oak-hornbeam forests of the *Carici pilosae-Carpinetum* in Transcarpathia (KRICSFALUSY 1999, ONYSHCHENKO & LUKASH 2005, ONYSHCHENKO 2009) was confirmed by our study. This vegetation has also been reported under the synonym *Brachypodio sylvatici-Quercetum petraeae* (KRAMARETS et al. 1992, VOROBYOV et al. 2008). It is also a leading type of oak-hornbeam forests in the adjacent part of Eastern Slovakia (HADAČ & TERRAY 1989). In addition to *Carici pilosae-Carpinetum*, KRICSFALUSY (1999) mentioned the *Melampyro nemorosi-Carpinetum* Passarge 1962, which is currently believed to be a synonym of the association *Galio sylvatici-Carpinetum*, including the oak-hornbeam forests of the western part of Central Europe (CHYTRÝ 2013). They contain species characteristic of western Central Europe (e.g., *Galium sylvaticum* or *Potentilla sterilis*) which are rare or missing in the flora of Transcarpathia (cf. FODOR 1974). We conclude that the *Galio sylvatici-Carpinetum* does not occur in the study area.

Lowland slightly wet oak-hornbeam forests have been reported in Transcarpathia as *Fraxino pannonicae-Carpinetum* Soó & Borhidi 1962 in some studies (ONYSHCHENKO & LUKASH 2005, OMELCHUK 2016). This association was described in the Illyrian part of Hungary and comprises slightly wet oak-hornbeam forests with a higher frequency of submediterranean elements (BORHIDI et al. 2012) which do not occur in the study area (cf. FODOR 1974). The more suitable name *Circaeo-Carpinetum* was used for these forests in the synopsis of mesophilous forest vegetation in Ukraine (ONYSHCHENKO 2009).

Some xero-mesophilous oak-hornbeam forests are close to the *Primulo veris-Carpinetum*; this association has not yet been mentioned on the basis of Ukrainian field data (ONYSHCHENKO 2009). There is a single mention in a study by OMELCHUK (2016), accompanied only by a list of diagnostic species. According to these species and the indicated ecology (river banks), it seems to be similar to the *Circaeo-Carpinetum*.

Concerning the alliance *Tilio-Acerion*, ONYSHCHENKO (2009) reported four associations of the alliance *Tilio platyphylli-Acerion* occurring in Ukraine, though only two of these can be expected to occur in the Carpathians: *Arunco-Aceretum* and *Phyllitido-Aceretum*. Although his work lacks relevés from the study area, we can confirm that these associations occur in this area. In addition, there is a single report of the association *Aceri-Carpinetum* in Transcarpathia (KRICSFALUSY 1999), though without relevés. Our results confirm that this association, believed to be a synonym of the *Aceri-Tilietum*, occurs in this area.

Erweiterte deutsche Zusammenfassung

Einleitung – Mesophile Wälder Transkarpatiens (Karpaten-Ukraine) sind bisher kaum untersucht worden, obwohl sie ausgedehnt und recht gut erhalten sind. Wir haben daher im Juni 2016 die Eichen-Hainbuchen-Wälder, Hangschutt- und Schluchtwälder untersucht.

Untersuchungsgebiet – Wir untersuchten die niederen Lagen Transkarpatiens zwischen 120 und 625 m ü.M. Das Gebiet umfasst die weitgehend entwaldete Quartärebene des Pannonischen Beckens und das bewaldete Karpatenvorland. Die Aufnahmen aus dem Karpatenvorland stammen von Standorten über Vulkangestein und mesozoischem Kalk. Das Klima zeichnet sich durch heiße Sommer und relativ milde Winter aus. Das Temperatur-Jahresmittel liegt bei 7 bis 9,5 °C; die Jahresniederschläge (800–1000 mm) sind selbst in den tieferen Lagen relativ hoch.

Methoden: Der Datensatz wurde aus eigenen Vegetationsaufnahmen von 2016 (54 Probeflächen; jeweils 100 m²; mit pH-Messungen) und Aufnahmen aus einer Untersuchung von ONYSHCHENKO & LUKASH (2005; 22 Flächen) zusammengestellt. Ungewichtete mittlere Zeigerwerte nach Borhidi (1995) wurden berechnet. Eichen-Hainbuchen-Wälder wurden mit einem agglomerativ-hierarchischen Verfahren (*beta-flexible algorithm*) klassifiziert, Hangschutt- und Schluchtwälder mit TWINSPAN (modifiziert nach ROLEČEK et al. 2009). Beziehungen zwischen Artenzusammensetzung und Umweltfaktoren wurden mittels der indirekten Gradientenanalyse DCA dargestellt.

Ergebnisse – Der Datensatz enthält 210 Gefäßpflanzenarten. Sechs Teilgruppen wurden klassifiziert (Fig. 1, Anhang S1), nämlich drei Gruppen von Eichen-Hainbuchen-Wäldern und drei Gruppen Hangschutt- und Schluchtwälder. Erstere umfassen folgende Gruppen: a) Schwach feuchte eutrophe Ei-Hb-Wälder des pannonischen Beckens mit *Carpinus betulus* und *Quercus robur* (*Circaeo-Carpinetum*), b) Mesophile Ei-Hb-Wälder mit Buchen-Beimischung auf Kalk und Vulkanit im Karpatenvorland (*Carici pilosae-Carpinetum*) und c) Xero-mesophile Ei-Hb-Wälder an warmen Vulkangesteinshängen des Karpatenvorlandes mit thermophilen Arten in der Krautschicht und *Quercus petraea* als kodominanter Baumart (*Carici pilosae-Carpinetum* und *Primulo veris-Carpinetum*).

Die azonalen Hangschutt- und Schluchtwälder, gekennzeichnet durch Edellaubbäume, nährstoffanspruchsvolle Arten sowie Farne, umfassen folgende Gruppen: a) Mesophile Blockhangwälder mit Felsspaltenpflanzen (*Phyllitido-Aceretum*) und b) Schluchtwälder im Übergang von mesophilen Ei-Hb-Wäldern (*Carici pilosae-Carpinetum, Carpinion betuli*) und *Aceri-Tilietum* (*Tilio platyphylli-Acerion*) - Steilhangwälder oberhalb von Wasserläufen mit Feuchtezeigern und Arten der karpatischen Buchenwälder (*Arunco dioici-Aceretum pseudoplatani*).

Eine indirekte Gradientenanalyse (DCA) zeigte, dass Ei-Hb-Wälder vor allem entlang der zweiten Ordinationsachse angeordnet sind, welche einen Feuchte- und Nährstoffgradienten nachzeichnet. Hangschutt- und Schluchtwälder verteilen sich vor allem entlang der ersten Ordinationsachse. Diese Achse lässt sich als Gradient der Verteilung in der Landschaft deuten, da diese Wälder kühlere Lagen und felsige Steilhänge in höheren Lagen bevorzugen.

Diskussion – Die unterschiedenen Gruppen ließen sich im Kontext zentraleuropäischer Syntaxa interpretieren, wie sie in den nationalen Übersichten von WILLNER & GRABHERR (2007), BORHIDI et al. (2012) und CHYTRÝ (2013) publiziert wurden. Zwei Assoziationen – *Primulo veris-Carpinetum* (thermophile Ei-Hb-Wälder) and *Aceri-Tilietum* (Schluchtwälder des Tieflandes) – wurden erstmals für die Ukraine mit Aufnahmen belegt (cf. ONYSHCHENKO 2009). Mittels Gradientenanalyse (DCA) wurden Höhe ü.M., *heat load* und Hangneigung als für die Artenzusammensetzung wichtige Umweltfaktoren erkannt. Diese Faktoren trennen die beiden Hauptgruppen deutlich – Ei-Hb-Wälder sowie Hangschutt- und Schluchtwälder, und sie bestimmen ihre weitere Verbreitung in den tieferen Lagen des südlichen Zentraleuropas.

Acknowledgement

We thank Milan Chytrý, Jan Divíšek and Veronika Kalníková for valuable comments on a previous version of the manuscript; Mário Duchoň for help with plant determination, Kryštof Chytrý for taking care of the herbarium in the field and digitizing relevés from the literature; László Demeter for information about sites of lowland forests in Transcarpathia; and Adrian Indreica, Monica Marian and Iveta Škodová for providing regional botanical literature. The study was supported by the Czech Science Foundation (project 14-36079G).

Supplements

Supplement S1. Synoptic table of subclusters (associations) and main clusters (alliances).

Beilage S1. Synoptische Tabelle der klassifizierten Teilgruppen (Assoziationen) und Hauptgruppen (Verbände).

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Table of relevés recorded in 2016 and classification of relevés published in ONYSHCHENKO & LUKASH (2005) which were used in analyses.

Anhang E1. Tabelle der 2016 angefertigten Vegetationsaufnahmen und in ONYSHCHENKO & LUKASH (2005) publizierte Klassifikation der Aufnahmen, die für die Analysen verwendet wurden .

Supplement E2. Localities of relevés recorded in 2016.

Anhang E2. Lokalitäten der 2016 angefertigten Vegetationsaufnahmen.

Supplement E3. Additional information about altitude, slope, aspect, soil pH, cover of each layer and number of species for relevés recorded in 2016.

Anhang E3. Zusätzliche Informationen über Höhenlage, Inklination, Exposition, Boden-pH, Wärmebelastungsindex, Deckungsgrad der Schichten und Artenzahl für die 2016 angefertigten Vegetationsaufnahmen.

Supplement E4. Comparison of BIVs, cover of all vegetation layers, environmental variables and number of species amongst clusters.

Anhang E4. Vergleich der Zeigerwerte nach Borhidi (BIVs), Deckungsgrad aller Vegetationsschichten, Umweltvariablen und Artenzahlen zwischen den Clustern.

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Supplement S1. Synoptic table of subclusters (associations) and main clusters (alliances). The left table shows species percentage frequencies and the right table the fidelity values represented by the *phi* coefficient multiplied by 100. Highly diagnostic species (*phi* ≥ 0.5; in bold) and diagnostic species (*phi* ≥ 0.2) are listed. Tree species recorded in more than one relevé and other frequent shrub and herb species recorded in more than 25% of relevés are listed as well. Species in subclusters are sorted by decreasing *phi* coefficient values. Indices (1, 2) indicate diagnostic species of the alliances (main clusters) *Carpinion betuli* and *Tilio platyphylli-Acerion*, respectively. Abbreviations: CC – *Circaeo-Carpinetum*; CpC – *Carici pilosae-Carpinetum*; CpC+PC – *Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*; PA – *Phyllitido-Aceretum*; AT – *Aceri-Tilietum* and transitions to *Carici pilosae-Carpinetum*; AA – *Arunco-Aceretum*.

Anhang S1. Synoptische Tabelle der klassifizierten Teilgruppen (Assoziationen) und Hauptgruppen (Verbände). Die Tabelle links zeigt Stetigkeitswerte in Prozent, die Tabelle rechts Treuewerte gemäß *phi* -Koeffizient multipliziert mit 100. Hochdiagnostische Arten (*phi* ≥ 0,5; fett) und diagnostische Arten (*phi* ≥ 0,2) sind aufgeführt. Arten in Teilgruppen sind nach abnehmendem *phi* angeordnet. In mehr als einer Aufnahme vorkommende Baumarten sowie in mehr als 25% der Aufnahmen vorkommende strauchige und krautige Arten sind ebenfalls aufgeführt. Arten in den Unterclustern sind nach abnehmendem *phi* -Koeffizient sortiert.
Exponenten (1, 2) kennzeichnen diagnostische Arten der Verbände *Carpinion betuli* bzw. *Tilio platyphylli-Acerion*. Abkürzungen der Assoziationen siehe oben.

	Frequency (%)						Fidelity (phi * 100)					
Subcluster	1	2	3	4	5	6	1	2	3	4	5	6
Association	CC	CpC	CpC +PC	PA	AT	AA	CC	CpC	CpC +PC	PA	AT	AA
Number of relevés	22	17	15	10	5	7	22	17	15	10	5	7
Subcluster 1 – *Circaeo-Carpinetum*												
Quercus robur[1]	86	–	–	–	–	–	91.7	–	–	–	–	–
Geum urbanum[1]	50	24	–	–	–	–	51.1	–	–	–	–	–
Ficaria verna[1]	50	–	27	–	–	–	49.9	–	–	–	–	–
Viola reichenbachiana[1]	86	47	33	–	40	–	48.8	–	–	–	–	–
Oenanthe banatica	27	–	–	–	–	–	48.8	–	–	–	–	–
Rubus caesius	27	–	–	–	–	–	48.8	–	–	–	–	–
Ranunculus auricomus	32	6	–	–	–	–	47.1	–	–	–	–	–
Carex brizoides	41	18	–	–	–	–	46.9	–	–	–	–	–
Acer tataricum	32	–	7	–	–	–	46.4	–	–	–	–	–
Milium effusum	64	24	7	–	40	–	44.4	–	–	–	–	–
Lysimachia nummularia	23	–	–	–	–	–	44.4	–	–	–	–	–
Anemone nemorosa[1]	100	65	67	10	100	–	38.9	–	–	–	–	–
Galium aparine	50	29	20	10	–	–	36.8	–	–	–	–	–
Ajuga reptans[1]	68	47	33	–	20	14	36.6	–	–	–	–	–
Maianthemum bifolium	36	6	13	20	–	–	32	–	–	–	–	–
Glechoma hederacea	23	–		–	–	14	30.8	–	–	–	–	–
Polygonatum multiflorum	77	35	53	50	60	14	25.9	–	–	–	–	–
Circaea lutetiana	41	12	–	10	–	57	23.4	–	–	–	–	–
Subcluster 2 – *Carici pilosae-Carpinetum*												
Primula vulgaris	–	29	–	–	–	–	–	50.8	–	–	–	–
Luzula luzuloides	–	47	40	10	–	14	–	32.8	–	–	–	–
Fagus sylvatica[2]	–	88	33	70	100	86	–	23.5	–	–	–	–
Subcluster 3 – *Carici pilosae-Carpinetum* + *Primulo veris-Carpinetum*												
Quercus petraea[1]	–	35	100	10	20	–	–	–	72.5	–	–	–
Prunus avium[1]	23	18	80	–	–	14	–	–	61.7	–	–	–
Symphytum tuberosum[1]	14	41	80	–	20	–	–	–	55.4	–	–	–
Hieracium laevigatum	–	–	33	–	–	–	–	–	54.2	–	–	–

	Frequency (%)						Fidelity (phi * 100)					
Subcluster	1	2	3	4	5	6	1	2	3	4	5	6
Number of relevés	22	17	15	10	5	7	22	17	15	10	5	7
Dactylis glomerata	14	18	53	–	–	–	–	–	50.4	–	–	–
Pteridium aquilinum	–	–	27	–	–	–	–	–	48.2	–	–	–
Crataegus sp.[1]	36	–	53	–	–	–	–	–	48.1	–	–	–
Lathyrus niger	–	–	20	–	–	–	–	–	41.5	–	–	–
Frangula alnus	–	–	20	–	–	–	–	–	41.5	–	–	–
Ligustrum vulgare	–	–	27	10	–	–	–	–	38.4	–	–	–
Subcluster 4 – *Phyllitido-Aceretum*												
Polypodium vulgare	6	–	–	80	–	14	–	–	–	75.9	–	–
Asplenium scolopendrium[2]	–	–	–	70	–	17	–	–	–	72	–	–
Chelidonium majus[2]	–	6	–	60	–	–	–	–	–	70.1	–	–
Hylotelephium maximum[2]	–	–	–	40	–	–	–	–	–	59.8	–	–
Scopolia carniolica[2]	–	–	–	40	–	14	–	–	–	48.3	–	–
Fallopia convolvulus	–	6	13	40	–	–	–	–	–	45.2	–	–
Subcluster 5 – *Aceri-Tilietum* + transitions to *Carici pilosae-Carpinetum*												
Mercurialis perennis[2]	–	6	–	20	100	29	–	–	–	–	76	–
Ulmus glabra[2]	–	18	–	20	80	43	–	–	–	–	53.8	–
Subcluster 6 – *Arunco dioici-Aceretum pseudoplatani*												
Chrysosplenium alternifolium[2]	–	–	–	–	–	57	–	–	–	–	–	72.5
Impatiens noli-tangere	14	12	13	20	–	86	–	–	–	–	–	64.5
Stellaria nemorum	–	–	–	–	–	43	–	–	–	–	–	62
Aruncus dioicus[2]	–	–	–	–	20	57	–	–	–	–	–	59.2
Angelica sylvestris	5	–	–	–	–	43	–	–	–	–	–	58
Sambucus nigra	14	6	–	10	20	71	–	–	–	–	–	57.2
Polystichum aculeatum[2]	–	–	7	40	40	86	–	–	–	–	–	56.3
Petasites albus[2]	–	–	–	–	20	43	–	–	–	–	–	47.3
Lunaria rediviva[2]	–	–	–	10	40	43	–	–	–	–	–	33.9
Species diagnostic for two subclusters												
Acer pseudoplatanus[2]	–	6	–	100	80	100	–	–	–	46.9	–	46.9
Carex pilosa[1]	9	88	87	10	80	–	–	38.2	36.8	–	–	–
Other diagnostic species for the Main cluster 1 – *Carpinion betuli*												
Hedera helix	55	35	67	30	–	–	–	–	–	–	–	–
Stellaria holostea	64	35	53	10	20	14	–	–	–	–	–	–
Carpinus betulus	100	100	100	90	100	43	–	–	–	–	–	–
Other diagnostic species for the Main cluster 2 – *Tilio platyphylli-Acerion*												
Dryopteris filix-mas	27	41	33	80	100	86	–	–	–	–	–	–
Symphytum cordatum	–	12	–	30	60	57	–	–	–	–	–	–
Salvia glutinosa	–	18	13	50	40	57	–	–	–	–	–	–
Urtica dioica	23	18	–	60	20	71	–	–	–	–	–	–
Geranium robertianum	9	41	20	70	20	71	–	–	–	–	–	–
Cardamine bulbifera	23	82	40	90	80	71	–	–	–	–	–	–
Cardamine glanduligera	–	6	–	10	40	43	–	–	–	–	–	–
Lactuca muralis	14	24	13	60	–	71	–	–	–	–	–	–
Fraxinus excelsior	23	–	–	20	40	57	–	–	–	–	–	–

	Frequency (%)						Fidelity (phi * 100)					
Subcluster	1	2	3	4	5	6	1	2	3	4	5	6
Number of relevés	22	17	15	10	5	7	22	17	15	10	5	7
Other frequent tree species												
Carpinus betulus	100	100	100	90	100	43	–	–	–	–	–	–
Tilia cordata	36	41	7	10	–	14	–	–	–	–	–	–
Acer campestre	23	29	20	30	20	–	–	–	–	–	–	–
Fraxinus excelsior	23	–	–	20	40	57	–	–	–	–	–	–
Acer platanoides	–	18	–	–	40	43	–	–	–	–	–	–
Tilia tomentosa	–	12	–	10	–	–	–	–	–	–	–	–
Alnus glutinosa	5	6	–	–	–	–	–	–	–	–	–	–
Robinia pseudacacia	–	6	7	–	–	–	–	–	–	–	–	–
Sorbus torminalis	–	–	13	–	–	–	–	–	–	–	–	–
Tilia platyphyllos	–	–	–	10	–	14	–	–	–	–	–	–
Other frequent shrub and herb species												
Rubus subgen. *Rubus*	55	71	93	80	100	100	–	–	–	–	–	–
Lamium galeobdolon	73	88	40	90	60	57	–	–	–	–	–	–
Galium odoratum	68	59	13	70	60	57	–	–	–	–	–	–
Corylus avellana	41	29	33	60	40	71	–	–	–	–	–	–
Carex sylvatica	59	47	13	–	60	29	–	–	–	–	–	–
Pulmonaria obscura	36	41	27	30	60	29	–	–	–	–	–	–
Moehringia trinervia	23	41	20	60	–	14	–	–	–	–	–	–
Asarum europaeum	45	24	7	50	20	–	–	–	–	–	–	–
Aegopodium podagraria	45	24	–	–	80	43	–	–	–	–	–	–
Poa nemoralis	18	41	47	20	–	–	–	–	–	–	–	–

7.2. Paper 2

Novák P., Zukal D., Kalníková V., Chytrý K. & Kavgacı A. (2019): Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region). – Phytocoenologia 49: 231–248.

Phytocoenologia Vol. 49 (2019), Issue 3, 231–248
Research Paper

Ecology and syntaxonomy of Colchic forests in south-western Georgia (Caucasus region)

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Abstract
Aim: The aim of the paper is to describe species composition, ecology and syntaxonomy of unique mesophilous forests in Georgian Colchis in the context of the Euxinian forests. **Location:** SW Georgia, western part of the Caucasus Region, slopes of the Lesser Caucasus (80–990 m). **Methods:** Forest vegetation was sampled following the Braun-Blanquet approach and basic environmental characteristics were recorded for each relevé (n = 53). The dataset was clustered using modified TWINSPAN and diagnostic species for each cluster were defined by phi fidelity index. Links between the species composition of vegetation and environmental factors were analysed by detrended correspondence analysis. Numerical comparison of the distinguished clusters with previously published associations from northern Turkey was carried out (expanded dataset, n = 173). **Results**: Among the new relevés, we distinguished three vegetation types subsequently described as new associations: (i) *Digitali schischkinii-Carpinetum betuli*, chestnut-hornbeam forests of slightly dry sites, with low cover of evergreen shrubs, (ii) *Rusco colchici-Castaneetum sativae*, chestnut-hornbeam forests with a dense evergreen shrub layer, and (iii) *Polysticho woronowii-Ulmetum glabrae*, ravine forests with noble hardwood trees and ravine forest specialists. These associations were classified to the alliances of Euxinian forests, the first two to *Castaneo-Carpinion* and the third to *Alnion barbatae*. Major turnover in species composition within the dataset followed gradients of rockiness, slope inclination, altitude and mean annual temperature. The analysis of the expanded dataset revealed a decreasing occurrence of Mediterranean species and an increasing number of fern species along an easterly gradient. This change in species composition is likely to be driven by macroclimatic gradients. **Conclusions:** This paper presents the first numerical comparison of chestnut-hornbeam and ravine forests across central and eastern parts of the Euxinian Province. Our results have highlighted the uniqueness of Georgian Colchic forests, described as new associations, in the context of Euxinian forest vegetation.

Keywords: *Alnion barbatae*; *Castaneo-Carpinion*; Caucasus; Colchis; chestnut-hornbeam forest; environmental factor; Euxinian Province; Georgia; phytosociology; ravine forest; relict; *Rhododendro-Fagetalia*.

Taxonomic references: Euro+Med (2017), except The Plant List (2013) for *Ranunculaceae* and Gagnidze (2005) for *Celastraceae.*
Syntaxonomic reference: Quézel et al. (1980).
Abbreviations: DCA = Detrended Correspondence Analysis.

Submitted: 8 Nov 2017; first decision: 31 Jan 2018; accepted: 13 Nov 2018; co-ordinating Editor: Idoia Biurrun

Introduction

Georgia is a country with an extraordinarily diverse flora that is concentrated within a relatively small area (69,700 km^2). It is situated in the Caucasus Region, which is included amongst the 25 most threatened biodiversity hotspots worldwide (Mittermeier et al. 2004). The flora of Georgia, containing approximately 4100 species, is species rich when compared to comparable areas at similar latitudes within the northern hemisphere (Barthlott et al. 2005; Gagnidze 2005; Nakhutsrishvili 2013). However, Georgian plant diversity is considered to be strongly endangered by land-use and future climate changes (Giam et al. 2010).

The Caucasus Region contains two important Pleistocene refugia for forest biota – the Colchic refugium (hereafter "Colchis") in the west and the Hyrcanian refugium (hereafter "Hyrcania") in the southeast. Colchis is located in western Georgia and adjacent regions of north-eastern Turkey (Davis et al. 1971; Nakhutsrishvili et al. 2015). In Georgia, it is composed of the Colchic Lowland, along the Black Sea coast, and surrounding Caucasian slopes. From the phytogeographical point of view, Colchis is an eastern extension of the Euxinian Province. This province comprises the hilly southern coastline of the Black Sea from south-eastern Bulgaria through northern Turkey and western Georgia to the south-western slopes of the Caucasus in Russia (Takhtajan 1986).

Deciduous forests are supposed to be the dominant natural vegetation of Colchis (Bohn et al. 2000–2003). They are unique in the sense of their long history, extremely floristically rich, and include numerous relict and endemic species. For these reasons they are a priority for nature conservation. As the Colchic Lowland was strongly deforested in ancient times, the largest woodland areas are preserved on the surrounding Caucasian slopes. Illegal wood cutting, human-induced fires and overgrazing by domestic ungulates, followed by soil erosion and the spread of alien species and tree diseases, represent serious threats to a large part of the remaining forests. To conserve well-preserved areas of these forests, national parks and nature reserves have been established (Nakhutsrishvili 2013; Akhalkatsi 2015).

There are numerous overviews of vegetation formations and their altitudinal zonation in western Georgia and adjacent areas brought e.g. by Flahault (1900), Kolakovskii (1961), Zohary (1973) and Walter (1974). In Colchis, four main altitudinal belts are often recognized and several forest communities have been described along this altitudinal zonation (Quézel et al. 1980; Ketenoglu et al. 2010a, 2010b; Kavgacı et al. 2012; Nakhutsrishvili 2013). All these forests belong to the class *Querco-Fagetea* according to the syntaxonomical scheme proposed by Quézel et al. (1980; see discussion). Hygrophilous forests of the order *Populetalia albae* with *Alnus glutinosa* subsp. *barbata*, *Fraxinus excelsior*, *Populus alba*, *Pterocarya fraxinifolia* and *Quercus robur* occupy moist soils of the lowland areas along the Black Sea coast. Mesophilous deciduous forests of the order *Rhododendro pontici-Fagetalia orientalis* (alliance *Castaneo sativae-Carpinion orientalis*) with dominance of *Carpinus betulus*, *C. orientalis*, *Castanea sativa* and *Quercus petraea* subsp. *iberica* occur up to 1000 m a.s.l.. Beech forests of *Fagus orientalis* are distributed in the montane altitudinal belt. They are classified in various alliances of the orders *Fagetalia sylvaticae* and *Rhododendro pontici-Fagetalia*. Coniferous forests of the order *Pino sylvestris-Piceetalia orientalis* with *Abies nordmanniana*, *Picea orientalis* and *Pinus sylvestris* prevail within the altitudes of 1500 and 2000 m a.s.l. where they meet the subalpine belt. However, in hyperhumid parts of Colchis, *Fagus orientalis* locally forms the timberline. Azonal forest vegetation in Colchis is represented by alluvial and ravine forests (alliance *Alnion barbatae*) scattered within almost the whole altitudinal gradient of deciduous forest vegetation.

For the majority of these forest types, the presence of a well-developed shrub layer (the so-called "Colchic understorey" sensu Nakhutsrishvili 2013) is a characteristic feature. It is composed of both evergreen (e.g. *Ilex colchica*, *Prunus laurocerasus* and *Rhododendron ponticum*) and deciduous (e.g. *Corylus avellana*, *Euonymus leiophloea* and *Vaccinium arctostaphylos*) species, some of which are relict or endemic. Lianas are frequently represented by evergreen elements (e.g. *Hedera colchica* and *Smilax excelsa*). Besides numerous forest mesophytes of broader distribution (e.g. *Drymochloa drymeja*, *Salvia glutinosa* and *Viola alba*), the presence of species limited to the Euxinian Province and surrounding area (e.g. *Omphalodes cappadocica*, *Polystichum woronowii*, *Ruscus colchicus* and *Trachystemon orientalis*) are typically found within the herb layer (Kolakovskii 1961; Dolukhanov 1980; Nakhutsrishvili 2013; Nakhutsrishvili et al. 2015).

Whereas forest vegetation is one of the most studied vegetation types within Europe, only a few studies of Georgian forests that utilise the Braun-Blanquet approach have been published. Moreover, these were mainly performed outside the Colchic part of the country (e.g. Passarge 1981a, 1981b; Korotkov 1995; Denk 1998). One exception is the study by Filibeck et al. (2004), but the focus of this study was the physiognomy and phytogeography of deciduous forest vegetation of Georgian Colchis. Also phytosociological studies that apply the Braun-Blanquet approach to similar forest vegetation types have been published for northern Turkey (e.g. Quézel et al. 1980; Ketenoglu et al. 2010a; Çoban & Willner 2019). There are also numerous descriptive studies following the dominant-based phytosociological school, which classified Georgian forest vegetation based on the main woody species (e.g. Dolukhanov 1980; Nakhutsrishvili 2013). Our paper presents the first survey of low-altitudinal mesophilous forests of south-western Georgia based on the Braun-Blanquet approach. Additionaly, a comprehensive analysis of the field data collected from Georgia and previously published data from adjacent areas of Turkey is presented.

The aims of this paper are: i) To describe the variability of low-altitudinal mesophilous forests in south-western Georgia based on the numerical analyses of original phytosociological relevés and propose their syntaxonomical classification to alliance level; ii) To analyse environmental factors influencing the variability of this vegetation; iii) To place the vegetation recorded in Georgia in the broader context of mesophilous forests of the Euxinian Province.

Study area

The study area is situated in south-western Georgia (41°30'–41°54' N, 41°43'–42°08' E), approximately within a rectangle of 20 km × 50 km between the cities of Batumi, Ozurgeti and Kobuleti (Fig. 1). Relevés were recorded at six localities (Table 1), all of which were deep and narrow river valleys in the Meskheti Range of the Lesser Caucasus (80–990 m a.s.l.). Localities were selected that were environmentally variable and would support the development of diverse forest vegetation. Currently human settlement within these poorly accessible valleys is rare. Therefore they support large areas of relatively well-preserved forest vegetation compared to more accessible places, i.e. seaside lowlands and adjacent low hills or plateaus, where mesophilous woodlands were intensively cut to obtain more space for human settlement and crop or alien tree plantations (Nakhutsrishvili 2013; Akhalkatsi 2015).

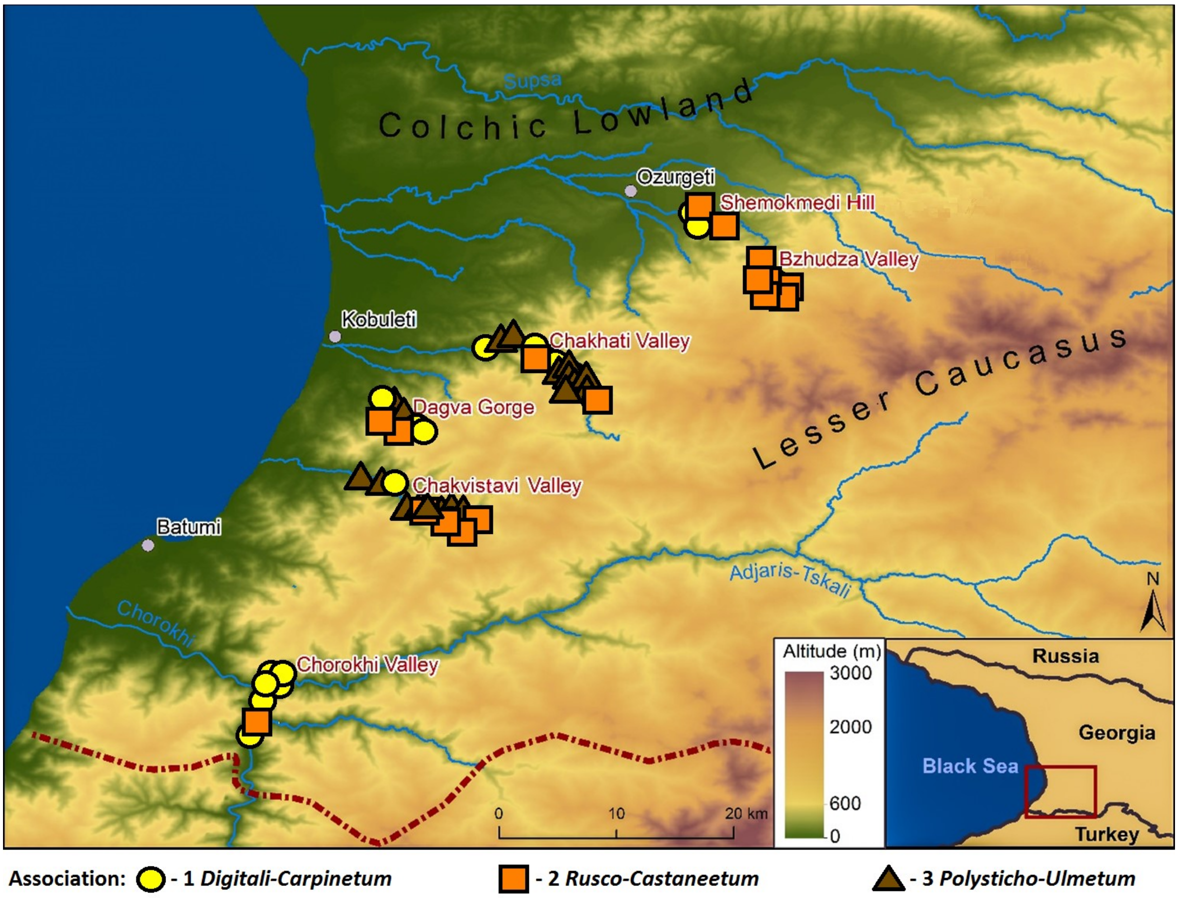

Fig. 1. Map of south-western Georgia with locations of relevés (symbols) and localities (red titles).

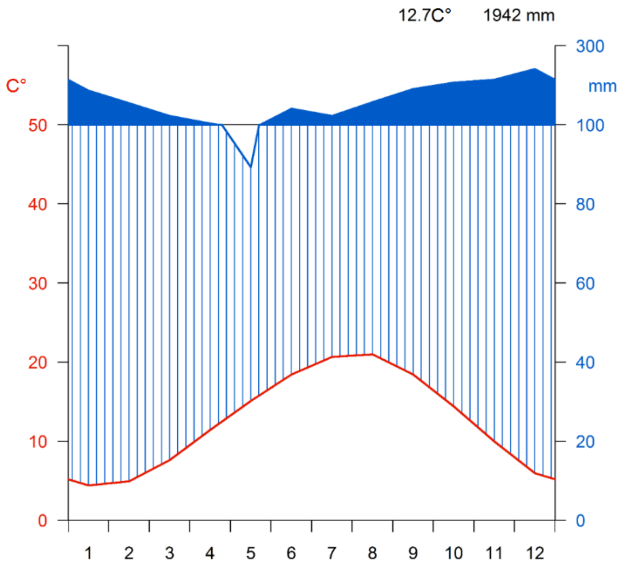

Fig. 2. Average Walter-type climate diagram of the studied region based on data from WorldClim version 2 (1970–2000, http://www.worldclim.org). The upper curve represents precipitation, the lower curve represents temperature.

Table 1. List of localities of relevés, their basic characteristics and number of relevés (n).

Locality (region)	Altitude (m a.s.l.)	Bedrock	Geographical coordinates (N, E)	n
1 - Chorokhi Valley (Adjara)	140–240	volcanic	41°30’–41°33’, 41°43’–41°44’	8
2 - Chakvistavi Valley (Adjara)	100–250	volcanic, plutonic	41°40’–41°42’, 41°48’–41°53’	13
3 - Dagva Gorge (Adjara)	150–290	volcanic	41°45’, 41°49’–41°50’	7
4 - Chakhati Valley (Adjara)	80–440	volcanic	41°47’–41°49’, 41°54’–41°58’	15
5 - Shemokmedi Hill (Guria)	160–230	volcanic	41°54’, 42°04’ E	4
6 - Bzhuzha Valley (Guria)	490–990	volcanic, plutonic	41°50’–41°52’, 42°06’–42°08’	6

Eocene volcanic rocks (basaltic, basalt-andesitic and dacitic types) and their tuff sediments represent the prevailing bedrock type within the study area. Furthermore, there are isolated patches of plutonic rocks (e.g. monzonite, syenite; Adamia 2010). Acrisols, cambisols and nitisols that are poor in bases are the main soil types (Urushadze & Ghambashidze 2013). The climate of the region is unique within western Eurasia being hyperhumid and warm-temperate (Fig. 2). Precipitation is relatively evenly distributed throughout the year and increases within more mountainous areas. At Batumi, that is almost at sea level, precipitation is approximately 2400 mm per year, while on the adjacent slopes of the Meskheti Range it exceeds 4000 mm (Walter & Lieth 1967; Dolukhanov 1989; Denk et al. 2001). Climatic data based on WorldClim version 2 (Fick & Hijmans 2017) showed that annual precipitation varied between 1809 and 2164 mm for the studied localities. The study region is situated on windward slopes and therefore affected by frequent fogs caused by moist air masses coming from the Black Sea. Mean annual temperature varies between 10 and 14 °C, the mean temperature for July is between 18 and 22.5 °C and for January it is between 1 and 6 °C. Despite the relatively mild winters, there is regular snow cover, especially at altitudes above 300 m, which helps to protect the frost-sensitive evergreen understorey from the impact of low temperatures (Dolukhanov 1980, 1989; Denk et al. 2001; Filibeck et al. 2004).

Methods

Data collection

The field research was carried out in July 2015 and July 2016.We sampled 53 relevés of square area of 100 m^2 in six localities (Table 1). Within each relevé the percentage cover of the tree, shrub, herb and moss layers was estimated and the cover of particular species in each layer, except moss layer since non-vascular cryptogams were not identified, was assessed using the nine-degree Braun-Blanquet cover-abundance scale (Dengler et al. 2008). Specimens collected in the plots were stored in the Herbarium of Masaryk University, Brno, Czech Republic (BRNU). Geographical coordinates (WGS 84) and the altitude of relevés were recorded using a portable GPS device GPSmap 60CSx. The following environmental characteristics were recorded for each relevé: aspect, inclination of slope and percentage cover of rocks (hereafter “E_R”). A mixed soil sample consisting of four individual soil samples from each relevé was used for measuring soil pH. Determination of pH was done on the dried mixed sample in a suspension of distilled water (2:5) using a GMH Greisinger pH meter.

In order to compare the species composition of the Georgian relevés with previously described associations from northern Turkey, we prepared an expanded dataset (n = 173) containing both our relevés and relevés published in the original descriptions of analogous syntaxa. For the alliance *Castaneo-Carpinion* the data from seven associations were analysed: *Campanulo alliariifoliae-Castaneetum sativae*, *Erico arboreae-Carpinetum orientalis*, *Epimedio colchici-Pinetum lazicae* (all three from Quézel et al. 1980), *Smilaco-Castaneetum sativae* (Ketenoglu et al. 2010a), *Hedero-Castaneetum sativae* (Yurdakulol et al. 2002), *Rubo caucasici-Quercetum hartwissianae* and *Carpino betuli-Populetum tremulae* (both from Korkmaz et al. 2008). For the alliance *Alnion barbatae* the data from two associations were analysed: *Thelypterido limbospermae-Alnetum barbatae* (Quézel et al. 1980) and *Diospyro loti-Alnetum barbatae* (Korkmaz et al. 2008) (Fig. 3). The nomenclature for the taxa within the expanded dataset was unified. Several pairs of species were merged together to avoid possible bias in the results due to the different taxonomical approaches of authors. Geographic coordinates for non-georeferenced relevés from the literature were assigned based on the published sites descriptions. Climatic data (mean annual temperature and annual precipitation) were obtained from the model WorldClim version 2 (Fick & Hijmans 2017).

Data analysis

All relevés were digitized using the software TURBOVEG (version 2.1, Hennekens & Schaminée 2001) and exported to the JUICE software (version 7.0, Tichý 2002) for classification analyses and subsequent species-to-cluster fidelity calculations.

Prior to the analyses, the number of species in each relevé was calculated. Records of tree and shrub species in the herb layer were deleted due to the fact that they had not been recorded in the relevés from Turkey that were used in later comparisons. Records of plants determined only to the genus level were also omitted. For each relevé, the total cover of evergreen shrubs (E_{EG}) was calculated. All records of a single species were merged into one layer. The latter two steps were done applying a procedure designated by Fischer (2015). Due to determination difficulties, the taxa *Polypodium cambricum*, *P. interjectum* and *P. vulgare* were grouped together under the name *Polypodium vulgare* s.l. and *Rubus* species were recognized only on the subgenus level as *Rubus* subgen. *Rubus* (Sochor & Trávníček 2016).

For the classification of the Georgian relevés a modified TWINSPAN algorithm with Whittaker's beta as a measure of inner heterogeneity of clusters (Roleček et al. 2009) was used. Cover data in a nine-degree scale were converted into percentage scale, using the average value of each degree, and subsequently transformed with three cut levels for pseudospecies (0, 5, 25%). The final number of clusters was checked using the formal method OptimClass (Tichý et al. 2010). To identify diagnostic species for each cluster, phi coefficient applied to species presence-absence was calculated as a measure of fidelity (Sokal & Rohlf 1995). Fisher's exact test ($p \leq 0.05$) was performed to omit rare species from the lists of diagnostic species. As the identification of diagnostic species depends on the size of the given cluster, the sizes of all clusters were virtually standardized to be equal (Tichý & Chytrý 2006). Species with phi > 0.25 were considered to be diagnostic for a certain cluster and species with phi > 0.50 were considered as highly diagnostic. Diagnostic species for groups of relevés in the expanded dataset were identified in the same way. Species that occurred in more than 50% of relevés from a cluster were considered as frequent and species with a cover higher than 25% in at least one relevé from a cluster were considered as dominant. For naming new associations we applied the rules of the International Code of Phytosociological Nomenclature (Weber et al. 2000).

To analyse relationships between species composition, vegetation structure and environmental factors in the Georgian relevés, Dentrended Correspondence Analysis

(DCA, length of the first DCA axis = 3.07) was computed in the R software (version 3.4.1, R Core Team) using the package vegan (version 2.4-4, Oksanen et al. 2013). Percentage cover values for species were log-transformed before the analysis. Structural and environmental variables were passively plotted in an ordination diagram. For the expanded dataset, another DCA (length of the first DCA axis = 4.46) was computed in the same way. Three variables available for all relevés (altitude, annual precipitation and mean annual temperature) were utilised.

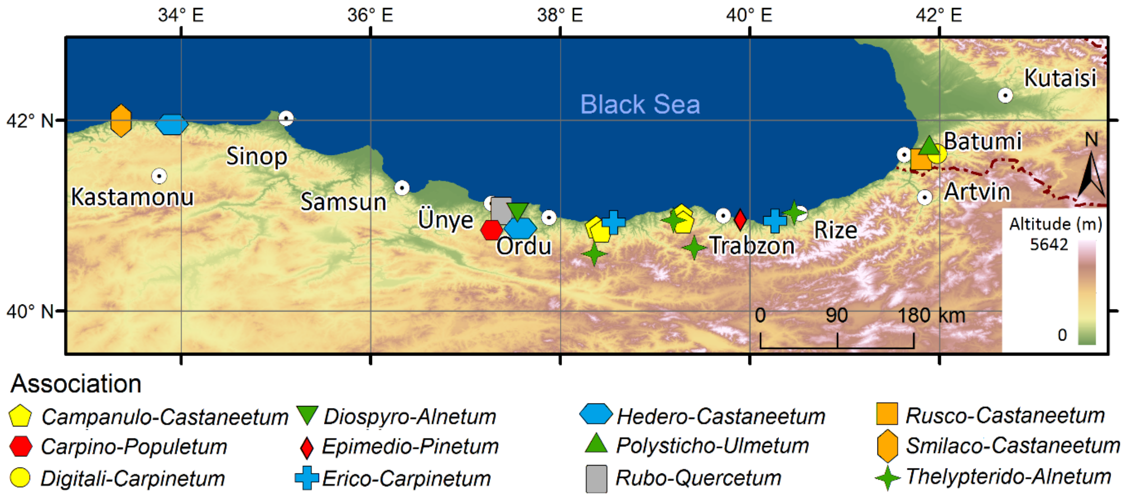

Fig. 3. Distribution map of relevés of associations of the alliances *Castaneo-Carpinion* and *Alnion barbatae* published from Turkey and associations from Georgia published in the current study.

Results

Overview of floristic composition

In total, the dataset of 53 Georgian relevés (Supplement S1) contained 164 taxa of vascular plants. The most frequent taxa were *Rubus* subgen. *Rubus* (occurring in 46 relevés), *Hedera colchica* (44), *Oplismenus hirtellus* subsp. *undulatifolius* (39), *Carpinus betulus* (37), *Dryopteris borreri* (37), *Castanea sativa* (34), *Rhododendron ponticum* (34), *Luzula forsteri* (33), *Potentilla micrantha* (33), *Smilax excelsa* (33) and *Pteris cretica* (32). Alien species (sensu Kikodze et al. 2009) were relatively frequent in the relevés. *Oplismenus hirtellus* subsp. *undulatifolius* (39), *Lysimachia japonica* (11), *Potentilla indica* (8), *Crassocephalum crepidioides* (6), *Erigeron annuus* (5) and *Phytolacca americana* (5) were the most common ones.

Relict species characteristic for Colchis (sensu Kolakovskii 1961; Nakhutsrishvili 2013) were well-represented in the dataset, both shrubs (e.g. *Daphne pontica*, *Diospyros lotus*, *Ilex colchica*, *Prunus laurocerasus*, *Rhododendron ponticum*, *Vaccinium arctostaphylos* and *Viburnum orientale*) and herbs (e.g. *Ruscus colchicus* and *Trachystemon orientalis*).

Classification and ecological characterization of the original dataset

The Georgian relevés were classified into three clusters according to species composition (Table 1 in Supplement S1). Table 2 presents means and standard deviations of the environmental and structural variables of the three clusters. Boxplots showing the differences of these variables among the three clusters are in Supplement S2. Photographs of representative stands of each cluster are also provided (Fig. 4). Each cluster is described in terms of its distribution within the study area, ecology, physiognomy and species composition.

Table 2. Means and standard deviations of selected variables among distinguished clusters. Altitude, inclination of slope, cover of tree (E_3), shrub (E_2), herb (E_1) and moss (E_0) layers, cover of evergreen shrubs (E_{EG}), species richness, cover of rocks (E_R), soil pH, annual precipitation (P) and mean annual temperature (T) were involved.

Cluster		Altitude (m a.s.l.)	Inclination (°)	E_3 (%)	E_2 (%)	E_1 (%)	E_0 (%)	E_{EG} (%)	No. of species	E_R (%)	Soil pH	P (mm)	T (°C)
1	m	169.1	42.5	75.9	30.3	36.3	4.6	25.8	30.9	1.4	5.4	1974.2	13.3
	SD	*57.6*	*13.7*	*13.4*	*24.5*	*22.0*	*2.9*	*24.6*	*6.1*	*2.6*	*0.4*	*97.3*	*0.3*
2	m	421.1	33.2	78.6	46.6	30.3	7.8	50.1	20.2	7.8	5.0	1861.3	12.0
	SD	*288.1*	*20.1*	*13.1*	*25.9*	*21.2*	*14.3*	*26.8*	*9.2*	*14.9*	*0.9*	*142.8*	*1.3*
3	m	216.6	49.7	73.2	45.5	43.4	19.3	30.5	31.8	23.4	5.7	1990.1	12.8
	SD	*67.2*	*16.8*	*15.5*	*19.0*	*19.6*	*17.7*	*26.9*	*6.5*	*26.7*	*0.7*	*97.0*	*0.5*

Cluster 1 – *Digitalis ferruginea* subsp. *schischkinii-Carpinus betulus* community

Diagnostic species: *Asplenium adiantum-nigrum*, *Brachypodium sylvaticum*, *Campanula rapunculoides*, *Carex muricata*, *Carpinus betulus*, *Cornus sanguinea*, *Corylus avellana*, *Digitalis ferruginea* subsp. *schischkinii*, *Drymochloa drymeja*, *Euonymus latifolia*, *Hedera helix*, *Lapsana communis*, *Leontodon hispidus*, *Potentilla micrantha*, *Silene italica*, *Polypodium vulgare* s.l., *Prunella vulgaris*, *Pteridium aquilinum*, *Smilax excelsa*, *Vinca major*, *Viola alba*.

Constant species: *Asplenium adiantum-nigrum*, *Brachypodium sylvaticum*, *Campanula rapunculoides*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Drymochloa drymeja*, *Hedera colchica*, *Luzula forsteri*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Potentilla micrantha*, *Pteridium aquilinum*, *Pteris cretica*, *Rubus* subgen. *Rubus*, *Smilax excelsa*, *Trachystemon orientalis*, *Viola alba.*

Dominant species: *Carpinus betulus*, *Corylus avellana*, *Drymochloa drymeja*, *Rhododendron ponticum*.

This community represents the vegetation of warmer sites and this is reflected by the highest mean annual temperatures amongst the Georgian clusters. It inhabits low altitudes of the studied region, predominantly up to 300 m. It is typical for the Chorokhi River Valley with a warmer and drier climate compared to the other localities. Nevertheless, this vegetation was recorded in all localities, except the Bzhuzha Valley, as it favours the lowest parts of the valleys where opened to the lowland.

The tree layer is generally well-developed (mean cover approx. 75%). It is composed mainly of *Carpinus betulus* and *Castanea sativa*. The shrub layer is often present, but the cover of evergreen species is lower than in the second cluster and deciduous ones, mainly *Corylus avellana*, prevail. Admixture of the spiny evergreen liana *Smilax excelsa* is also typical. The herb layer varies in cover (5–70%) and the rhizomatous xeromesophilous grass *Drymochloa drymeja* frequently dominates. Besides widespread forest mesophytes, species of slightly dry soils (e.g. *Asplenium adiantum-nigrum*, *Digitalis ferruginea* subsp. *schischkinii* and *Luzula forsteri*) show a strong association with this community. Non-forest species indicating cattle grazing (e.g.

Leontodon hispidus and *Prunella vulgaris*) occur locally. The moss layer is low in cover or almost absent.

Cluster 2 – *Ruscus colchicus-Castanea sativa* community

Diagnostic species: *Athyrium filix-femina*, *Dryopteris borreri*, *D. dilatata*, *Prunus laurocerasus*, *Rhododendron ponticum*, *Ruscus colchicus*.
Constant species: *Athyrium filix-femina*, *Carpinus betulus*, *Castanea sativa*, *Dryopteris borreri*, *Hedera colchica*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Prunus laurocerasus*, *Rhododendron ponticum*, *Rubus* subgen. *Rubus*.
Dominant species: *Carpinus betulus*, *Castanea sativa*, *Fagus orientalis*, *Prunus laurocerasus*, *Rhododendron ponticum*, *Rubus* subgen. *Rubus*, *Staphylea pinnata*.

These forests are most frequently found in deep valleys and on mountain slopes, most likely due to their preference for shady places with a higher air humidity, the result of high rainfall and fogs. Compared to the forests included in the third cluster, they prefer slopes without rock outcrops. Soils are strongly acidic since they have developed on a base-poor bedrock. Bases are additionally leached from the soil profile by the high rainfall. This community represents the main forest vegetation type of the studied region and it was recorded along the whole altitudinal gradient. Of the studied localities it is common everywhere except in the Chorokhi River Valley, where it is usually substituted by the previous community.

The tree layer is composed mainly of *Carpinus betulus* and *Castanea sativa* (mean cover approx. 80%). The shrub layer is well-developed (cover usually ranging from 20 to 70%). It is characterized by a high proportion of evergreen species, mainly *Prunus laurocerasus* and *Rhododendron ponticum*, generally reaching up to 4 m in height. The development of the herb layer, including tree regeneration, is usually suppressed by the thick evergreen shrub layer or by the dominance of clonal stands of *Rubus* subgen. *Rubus*. Common forest ferns (e.g. *Athyrium filix-femina* and *Dryopteris borreri*) and evergreen species (*Hedera colchica* and *Ruscus colchicus*) are frequent probably due to their ability to tolerate heavy shading (Page 2002; Nakhutsrishvili 2013). The moss layer is usually sparse or even absent. With an average of 20 species per relevé it is the most species-poor of the vegetation types.

Cluster 3 - *Polystichum woronowii-Ulmus glabra* community

Diagnostic species: *Alnus glutinosa* subsp. *barbata*, *Aruncus dioicus*, *Asplenium scolopendrium*, *A. trichomanes*, *Calystegia silvatica*, *Carex pendula*, *Circaea lutetiana*, *Clinopodium umbrosum*, *Crassocephalum crepidioides*, *Cystopteris fragilis*, *Dryopteris borreri*, *Fragaria moschata*, *Ilex colchica*, *Lamium galeobdolon*, *Lysimachia japonica*, *Moehringia trinervia*, *Oxalis acetosella*, *Polystichum woronowii*, *Potentilla indica*, *Pteris cretica*, *Sambucus nigra*, *Saxifraga cymbalaria*, *Staphylea pinnata*, *Symphytum grandiflorum*, *Ulmus glabra*, *Urtica dioica*.
Constant species: *Alnus glutinosa* subsp. *barbata*, *Asplenium scolopendrium*, *A. trichomanes*, *Athyrium filix-femina*, *Calystegia silvatica*, *Carex pendula*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Dryopteris borreri*, *Hedera colchica*, *Lamium galeobdolon*, *Luzula forsteri*, *Moehringia trinervia*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Polystichum woronowii*, *Potentilla micrantha*, *Pteris cretica*, *Rhododendron ponticum*, *Rubus* subgen. *Rubus*, *Ulmus glabra*.
Dominant species: *Alnus glutinosa* subsp. *barbata*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Fagus orientalis*, *Hedera colchica*, *Rhododendron ponticum*, *Rubus* subgen. *Rubus*, *Tilia begoniifolia*, *Ulmus glabra*.

This community usually occurs on shady steep slopes with rock outcrops and in narrow ravines with a cooler topoclimate compared to the surroundings. Soil pH is often higher compared to the previous clusters since high microbial activity, weathering of rocks, and calcium from the leaf litter of noble hardwood trees enrich the soil in bases and nutrients. It was recorded mainly at low altitudes (mostly between 170–230 m a.s.l.), especially in the Chakhati and Chakvistavi valleys.

The tree layer is dominated by *Alnus glutinosa* subsp. *barbata* and *Castanea sativa* with *Carpinus betulus* and *Ulmus glabra* usually in admixture. In most cases, cover of the tree layer exceeds 70%. However, in stands where rocks cover most of the ground, it can have a sparse canopy (40–55% cover). The shrub layer is usually well-developed (mean cover approximately 45%) and is composed of both deciduous (*Corylus avellana*, *Sambucus nigra* and *Staphylea pinnata*) and evergreen species (*Ilex colchica*, *Prunus laurocerasus* and *Rhododendron ponticum*). Evergreen lianas (mainly *Hedera colchica*) climbing the trees and shrubs are conspicuous. Fern species (e.g. *Asplenium scolopendrium*, *A. trichomanes*, *Dryopteris borreri*, *Polystichum woronowii* and *Pteris cretica*) are abundant within the rock crevices of the ravines. Due to the higher air humidity in the ravines, some of them use epiphytic growth. The occurrence of numerous nutrient-demanding herbs (e.g. *Aruncus dioicus*, *Lamium galeobdolon* and *Urtica dioica*) is also typical. The cover of the moss layer is significantly higher than in the other two groups (usually 10–30%) partly due to their ability to cover the rocky surface.

Fig. 4. Photographs of the mesophilous forest communities in the studied area. a) *Digitali-Carpinetum* (Confluence of Chorokhi and Adjariskali Rivers). b) *Rusco-Castaneetum* (Bzhudza Valley). c) *Polysticho-Ulmetum* (Chakvistavi Valley).

DCA performed with the Georgian relevés showed that the chestnut-hornbeam forests (Clusters 1 and 2) differ from the ravine forests (Cluster 3) in environmental conditions (Fig. 5). The former develop on zonal sites, thus on gentler slopes with rather deep and strongly acidic soils. The latter are confined to rocky, rather cool, and shady slopes of river valleys and ravines. They are characteristic of the lower parts of valley slopes and have often developed near streams. The sub-division for chestnut-hornbeam forests is linked mainly to climatic differences. Vegetation of the *Digitalis-Carpinus* community is characteristic for relatively warm places at lower altitudes. Conversely, vegetation of the *Ruscus-Castanea* community with a well-developed evergreen shrub layer, occurs more commonly at higher altitudes with lower mean annual temperatures and frequent fogs. These results do not appear to be consistent with the data shown in Table 2 and Supplement 2, which show that the former community occurs in slightly more humid conditions compared to the latter one. However, these differences are only minor and precipitation models may be biased in regions with complicated orography (Fick & Hijmans 2017).

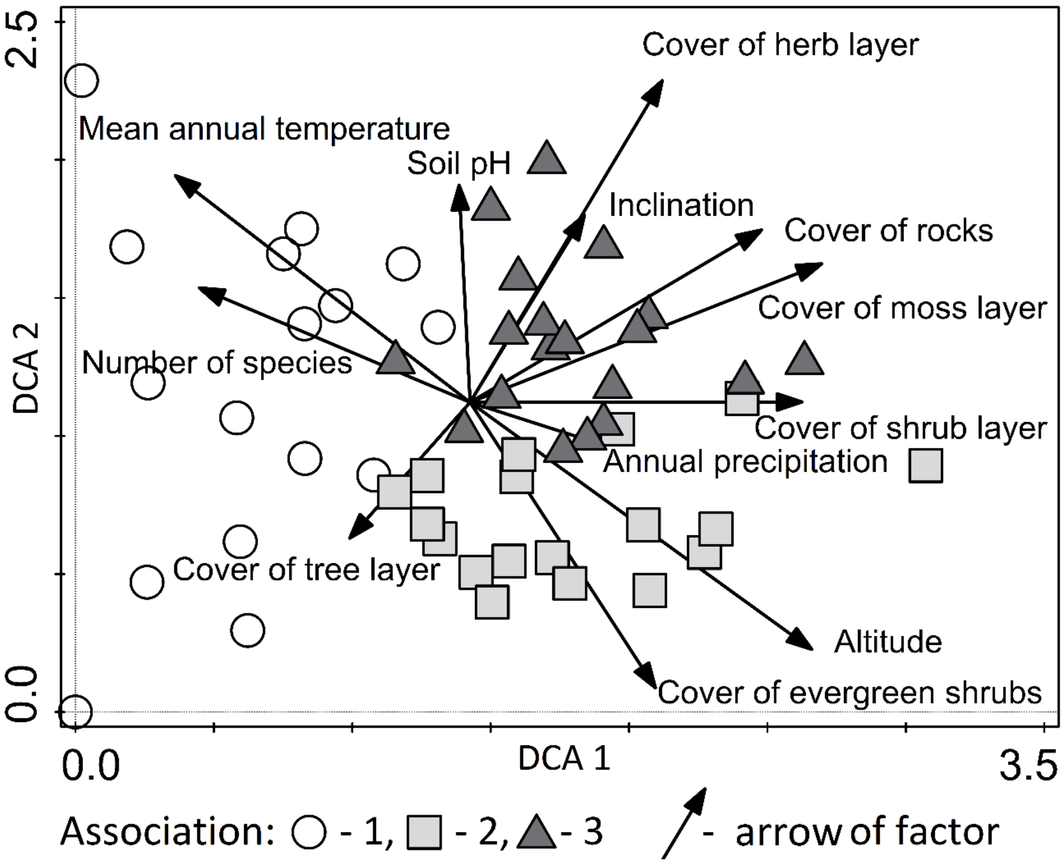

Fig. 5. DCA ordination of relevés from Georgian Colchis. The first ordination axis explains 7.03% of variance in species composition of relevés. The second axis explains 4.68% of variance. Environmental, vegetation structure and species richness variables were passively plotted in the diagram. Associations: 1 – *Digitali-Carpinetum*, 2 – *Rusco-Castaneetum*, 3 – *Polysticho-Ulmetum*.

Floristic and climatic gradients in the expanded dataset

The results of the DCA performed with the expanded dataset are shown in Fig. 6. Relevés from hyperhumid Georgian Colchis are located on the bottom left side of the ordination diagram and relevés from the *Erico arboreae-Carpinetum orientalis* association are located on the extreme right side. The *Erico arboreae-Carpinetum orientalis* association comprises forests and macchia-like vegetation both with *Carpinus* *orientalis* and evergreen Mediterranean shrubs (e.g. *Arbutus unedo* and *Erica arborea*) which are rare or missing in south-western Georgia and the adjacent parts of the Euxinian Province in Turkey. Indicators of dry basic soils (e.g. *Ruscus aculeatus*) are common in its herb layer. Associations in the central part of the diagram do not usually contain Mediterranean elements. However, besides forest mesophytes, both evergreen (e.g. *Daphne pontica*) and deciduous (e.g. *Rhododendron luteum* and *Vaccinium arctostaphylos*) shrub species with the capability to grow in regions with lower annual precipitation compared to *Prunus laurocerasus* and *Rhododendron ponticum* (Dolukhanov 1980; Nakhutsrishvili 2013) are characteristic components of these forest associations. Georgian relevés are well-distinguished from the rest of the dataset by including species typical for areas with a stable humid climate and mild winters, e.g. *Asplenium scolopendrium*, *Dryopteris borreri* and *Prunus laurocerasus*.

The diagnostic species for the associations within the expanded dataset are provided in Table 3 and Table 1 in Supplement S3. Table 2 in Supplement S3 highlights the diagnostic species of the alliances *Castaneo-Carpinion* and *Alnion barbatae*. The diagnostic species for *Castaneo-Carpinion* (11 species) are species of dry and often nutrient-poor soils. Of the woody species, *Castanea sativa* and deciduous shrubs have a high diagnostic value. Diagnostic species for the alliance *Alnion barbatae* (32 species) are represented by numerous nutrient- and moisture-demanding species, including noble hardwood trees, together with species of rock crevices.

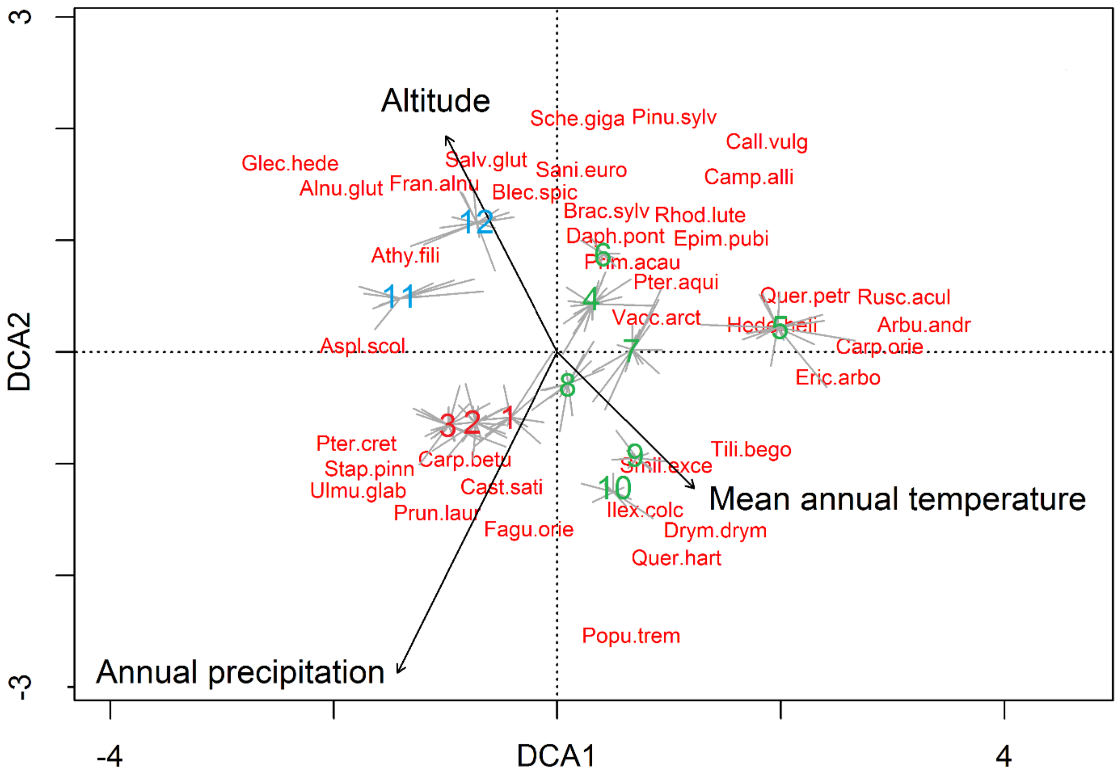

Fig. 6. DCA ordination of the expanded dataset with relevés from south-western Georgia (red) and northern Turkey (*Castaneo-Carpinion,* green, and *Alnion barbatae,* blue). Groups of relevés from Georgia: 1 – *Digitali-Carpinetum*, 2 – *Rusco-Castaneetum*, 3 – *Polysticho-Ulmetum*. Groups of relevés from literature (Turkey): 4 – *Campanulo -Castaneetum*, 5 – *Erico-Carpinetum*, 6 – *Epimedio-Pinetum*, 7 – *Smilaco-Castaneetum*, 8 – *Hedero-Castaneetum*, 9 – *Rubo-Quercetum*, 10 – *Carpino-Populetum*, 11 – *Thelypterido-Alnetum* and 12 - *Diospyro-Alnetum*. The first ordination axis explains 4.68% of variance in species composition of relevés. The second axis explains 3.36% of variance. Mean annual temperature, annual precipitation and altitude were passively plotted. Only species with the highest weight in the analysis are shown.
Abbreviations: Alnu.glut – *Alnus glutinosa* subsp. *barbata*, Arbu.andr – *Arbutus andrachne*, Aspl.scol – *Asplenium scolopendrium*, Athy.fili – *Athyrium filix-femina*, Blec.spic – *Blechnum spicant*, Brac.sylv – *Brachypodium sylvaticum*, Call.vulg – *Calluna vulgaris*, Camp.alli – *Campanula alliariifolia*, Carp.betu – *Carpinus betulus*, Carp.orie – *Carpinus orientalis*, Cast.sati – *Castanea sativa*, Daph.pont – *Daphne pontica*, Drym.drym – *Drymochloa drymeja*, Epim.pubi – *Epimedium pubigerum*, Eric.arbo – *Erica arborea*, Fagu.orie – *Fagus orientalis*, Fran.alnu – *Frangula alnus*, Glec.hede – *Glechoma hederacea*, Hede.heli – *Hedera helix*, Ilex.colc – *Ilex colchica*, Pinu.sylv – *Pinus sylvestris*, Popu.trem – *Populus tremula*, Prim.acau – *Primula acaulis*, Prun.laur – *Prunus laurocerasus*, Pter.aquil – *Pteridium aquilinum*, Pter.cret – *Pteris cretica*, Quer.hart – *Quercus hartwissiana*, Quer.petr – *Quercus petraea* subsp. *iberica*, Rhod.lute – *Rhododendron luteum*, Rusc.acul – *Ruscus aculeatus*, Salv.glut – *Salvia glutinosa*, Sani.euro – *Sanicula europaea*, Sche.giga – *Schenodorus giganteus*, Smil.exce – *Smilax excelsa*, Stap.pinn – *Staphylea pinnata*, Tili.bego – *Tilia begoniifolia*, Ulmu.glab – *Ulmus glabra*, Vacc.arct – *Vaccinium arctostaphylos*.

Discussion

Vegetation classification and comparison with the previously described syntaxa

Macroclimatic gradients seem to be important in determining the species composition of the oak-hornbeam and ravine forests of the central and eastern parts of the Euxinian Province. The analysis of mesophilous forests from Georgian Colchis and adjacent areas in northern Turkey has revealed a change in species composition along an easterly gradient, characterized by a decreasing number of Mediterranean species. Simultaneously, there is an increase in the number of characteristic Euxinian species, often evergreen shrubs (Quézel et al. 1980), and in fern species that prefer a higher humidity and a relatively stable and warm climate (Page 2002). A similar pattern was reported by Kavgacı et al. (2012) in the case of Euxinian *Fagus orientalis* forests in Bulgaria and Turkey where communities with a high proportion of Mediterranean species occur chiefly in the western part of the Euxinian Province and communities with high proportion of Euro-Siberian species are typical for the central and eastern parts of the province. The occurrence of western Euxinian forest types with Mediterranean elements has also recently been reported from Turkey (Çoban & Willner 2019). This geographical differentiation is probably linked to the increasing annual precipitation as you move eastwards, reaching its maximum in Colchis. Moreover, the summer arid period typical for the central and western parts of the province is missing in the eastern part (Walter & Lieth 1967; Davis et al. 1971).

The analyses (Fig. 6, Table 3, Supplement S3) demonstrated that hornbeam-chestnut forests from Georgia have many common features with zonal Euxinian hornbeam-chestnut forests unified in the alliance *Castaneo-Carpinion*. They are all characterized by *Carpinus betulus* and *Castanea sativa* in the tree layer and evergreen species in the shrub layer. There are also many common herb and liana species (e.g. *Drymochloa drymeja* and *Smilax excelsa*). However, we can see some differences as well. Species with the centre of their distribution in the central and western parts of the Euxinian Province (e.g. *Hypericum calycinum* and *Salvia forsskaolei*), mountain species (e.g. *Gentiana asclepiadea* and *Lactuca bourgaei*) as well as Mediterranean species (e.g. *Erica arborea*) are diagnostic for the relevés from Turkey while they are rare or missing in the relevés from Georgia. Simultaneously, relevés from Georgia contain more ferns and some endemic species of the Euxinian Province, mainly *Ruscus colchicus*.

While *Digitalis-Carpinus* and *Ruscus-Castanea* communities are classified to the alliance *Castaneo-Carpinion*, we propose to assign the last one (*Polystichum woronowii-Ulmus glabra* community) to the alliance *Alnion barbatae*, described by Quézel et al. (1980). This alliance comprises Euxinian ravine and alluvial forests frequently dominated by *Alnus glutinosa* subsp. *barbata*. The diagnostic species for this alliance (Quézel et al. 1980) *Aruncus dioicus*, *Cardamine wiedemanniana*, *Carex pendula*, *Chrysosplenium dubium*, *Circaea lutetiana* and *Salvia glutinosa* are frequently distributed in ravine forests in the Georgian part of Colchis. Additionally, the shrubs *Corylus avellana*, *Ilex colchica*, *Prunus laurocerasus, Rhododendron ponticum, Sambucus nigra* and *Staphylea pinnata* as well as the evergreen liana *Hedera colchica*, all typical elements of *Alnion barbatae*, grow densely in the ravine forests surveyd during this study. Due to the hyperhumid climate, *Alnus glutinosa* subsp. *barbata* is widespread within the studied valleys in southwestern Georgia since it is not limited to places influenced by underground water (Denk 1998).

The alliance *Alnion barbatae* contains only two validly described associations from northern Turkey, *Diospyro loti-Alnetum barbatae* and *Thelypterido limbospermae-Alnetum barbatae* (Quézel et al. 1980; Korkmaz et al. 2008; Ketenoglu et al. 2010b). The former differs from the *Polystichum-Ulmus* community by the occurrence of species from central and western parts of the Euxinian Province (e.g. *Chaerophyllum byzantinum* and *Geranium subcaulescens*) while the latter differs mainly by the higher frequency of mountain (e.g. *Gentiana asclepiadea* and *Rhynchocorys elephas*) and hygrophilous species (e.g. *Lycopus europaeus* and *Petasites hybridus*). Moreover, relevés from the *Polystichum-Ulmus* community contain species of rock outcrops (e.g. *Asplenium scolopendrium*, *A. trichomanes* and *Saxifraga cymbalaria*) usually accompanied by the typical Euxinian-Hyrcanian ferns *Polystichum woronowii* and *Pteris cretica*. Based on these differences, we conclude that the *Polystichum-Ulmus* community represents a different community than the previously described associations *Diospyro loti-Alnetum barbatae* and *Thelypterido limbospermae-Alnetum barbatae*.

Table 3. Shortened synoptic table of Central and Eastern Euxinian associations of the alliances *Castaneo-Carpinion* and *Alnion barbatae*. The percentage occurrences of species are shown. For associations diagnostic species are shaded and sorted by decreasing fidelity (phi > 0.25 for diagnostic species, phi > 0.50 for highly diagnostic species, in bold). Only species reaching a constancy of 30% in at least one association are shown. For the full version of the table see Table 1 in Supplement S3.
Association abbreviations: DsC – *Digitali schischkinii-Carpinetum*, RcC – *Rusco colchici-Castaneetum*, PwU – *Polysticho woronowii-Ulmetum*, CaC – *Campanulo alliariifoliae-Castaneetum*, EaC – *Erico arboreae-Carpinetum*, EcP – *Epimedio colchici-Pinetum*, SeC – *Smilaco excelsi-Castaneetum*, HcC – *Hedero colchicae-Castaneetum*, RcQ – *Rubo caucasici-Quercetum*, CbP – *Carpino betuli-Populetum*, TlA – *Thelypterido limbospermae-Alnetum*, DlA – *Diospyro loti-Alnetum*.

Association	DsC	RcC	PwU	CaC	EaC	EcP	SeC	HcC	RcQ	CbP	TlA	DlA
Group	1	2	3	4	5	6	7	8	9	10	11	12
Number of plots	16	18	19	19	16	7	20	13	10	10	15	10
Digitali-Carpinetum												
Campanula rapunculoides	63	6	16	37	.	14	.	.	.	.	.	.
Carex muricata	38	11	5	.	.	.	.	.	.	.	.	.
Silene italica	31	6	5	.	.	.	.	.	.	.	.	.
Vinca major+minor	44	.	16	16	13	.	.	.	.	.	7	.
Rusco-Castaneetum												
Ruscus colchicus	13	50	32	37	.	.	10	.	.	.	7	.
Polysticho-Ulmetum												
Lamium galeobdolon	19	22	**74**	.	.	.	.	.	.	.	.	.
Polystichum woronowii	6	6	**53**	.	.	.	.	.	.	.	.	.
Lysimachia japonica	6	6	**47**	.	.	.	.	.	.	.	.	.
Clinopodium umbrosum	6	11	**42**	.	.	.	.	.	.	.	.	.
Asplenium scolopendrium	44	22	**89**	16	.	14	.	.	.	.	40	30
Calystegia silvatica+sepium	31	6	63	11	.	.	.	.	.	.	27	.
Symphytum grandiflorum	6	.	32	.	.	.	.	.	.	.	.	.
Ulmus glabra	19	6	53	16	.	.	.	.	.	.	7	.
Potentilla indica	.	11	32	.	.	.	.	.	.	.	.	.
Saxifraga cymbalaria	.	6	32	.	.	.	.	.	.	.	.	20
Viola reichenbachiana	19	17	32	.	.	.	.	.	.	.	.	.
Staphylea pinnata	6	22	42	.	6	.	.	15	.	.	20	.
Campanulo-Castaneetum												
Galium rotundifolium	.	.	.	**32**	.	.	.	.	.	.	.	.
Lactuca bourgaei	.	.	.	42	.	14	.	.	.	.	27	.
Lathyrus hirsutus	.	.	.	32	19	.	.	.	.	.	.	.
Acer cappadocicum	13	.	16	53	19	14	.	.	.	.	20	.
Hypericum xylosteifolium	13	.	16	42	25	.	.	.	.	.	.	.
Helleborus orientalis	.	.	.	37	25	.	20	.	.	.	.	.
Rhamnus imeretina	.	.	.	26	19	.	.	.	.	.	20	.
Erico-Carpinetum												
Carpinus orientalis	.	.	.	5	**88**	.	.	.	.	.	.	.
Ruscus aculeatus	.	.	.	16	**94**	.	.	.	.	.	.	.

Table 3. cont.

Association	DsC	RcC	PwU	CaC	EaC	EcP	SeC	HcC	RcQ	CbP	TlA	DlA
Group	1	2	3	4	5	6	7	8	9	10	11	12
Number of plots	16	18	19	19	16	7	20	13	10	10	15	10
Brachypodium pinnatum	.	.	.	.	**63**	.	.	.	.	.	.	.
Cistus creticus	.	.	.	.	**63**	.	.	.	.	.	.	.
Vitis vinifera	6	.	.	.	**50**	.	.	.	.	.	.	.
Arbutus andrachne	.	.	.	.	**44**	.	.	.	.	.	.	.
Table 3. cont.												
Erica arborea	.	.	.	.	**100**	43	.	.	40	40	.	.
Laurus nobilis	.	.	.	.	**38**	.	.	.	.	.	.	.
Cistus salvifolius	.	.	.	.	**38**	.	.	.	.	.	.	.
Bituminaria bituminosa	.	.	.	.	**31**	.	.	.	.	.	.	.
Ligustrum vulgare	.	.	.	.	**31**	.	5	.	.	.	.	.
Geum urbanum	.	.	.	5	**31**	.	.	.	.	.	.	.
Quercus petraea subsp. *iberica*	19	6	5	11	63	29	5	.	.	.	.	.
Crataegus germanica	6	6	.	11	50	.	.	8	20	.	.	.
Hypericum calycinum	.	.	.	21	31	.	10	.	.	.	.	.
Asperula cimulosa	.	.	.	21	31	.	.	.	.	.	20	.
Tilia begoniifolia	13	.	16	26	31	.	.	.	.	.	.	.
Epimedio-Pinetum												
Pinus sylvestris	.	.	.	.	.	**100**	.	.	.	.	.	.
Potentilla erecta	.	.	.	11	.	**100**	.	.	.	.	.	.
Schenodorus giganteus	.	.	.	.	.	**86**	.	.	.	.	.	.
Calluna vulgaris	.	.	.	11	6	**86**	.	.	.	.	.	.
Picea orientalis	.	.	.	.	.	**71**	.	.	.	.	13	.
Lycopodium tristachyum	.	.	.	.	.	**57**	.	.	.	.	.	.
Berberis integerrina	.	.	.	.	.	**43**	.	.	.	.	.	.
Hyalopoa pontica	.	.	.	.	.	**43**	.	.	.	.	.	.
Blechnum spicant	6	33	21	37	.	**100**	.	.	.	.	27	.
Osmunda regalis	.	.	.	16	.	**57**	.	.	.	.	27	.
Primula acaulis+veris	19	.	5	42	13	71	30	23	.	.	13	.
Daphne pontica	31	11	11	68	31	86	15	54	20	.	40	30
Sanicula europaea	13	6	16	53	13	57	25	31	.	.	47	.
Smilaco-Castaneetum												
Euphorbia amygdaloides	.	.	.	.	.	.	**30**	.	.	.	.	.
Hedero-Castaneetum												
Cardamine bulbifera	.	.	.	.	.	.	.	**31**	.	.	.	.
Viola odorata	.	.	.	.	.	.	.	46	30	.	.	30
Carex sylvatica	13	6	11	11	6	29	.	46	.	.	27	.
Cirsium hypoleucum	.	.	.	26	25	.	.	31	.	.	7	.
Rubo-Quercetum												
Quercus hartwissiana	.	.	.	16	.	29	.	.	**100**	.	7	.
Pyrus communis	.	.	.	.	13	.	.	.	**60**	.	.	.
Dictamnus albus	.	.	.	.	.	.	.	.	**40**	.	.	.
Crataegus microphylla	.	.	.	.	.	.	.	.	**40**	.	.	.

Table 3. cont.

Association	DsC	RcC	PwU	CaC	EaC	EcP	SeC	HcC	RcQ	CbP	TlA	DlA
Group	1	2	3	4	5	6	7	8	9	10	11	12
Number of plots	16	18	19	19	16	7	20	13	10	10	15	10
Epipactis helleborine	.	.	.	5	.	.	.	.	30	.	.	.
Prunus avium	13	6	.	.	.	.	.	.	30	.	.	.
Dioscorea communis	31	28	16	42	31	.	25	.	80	.	40	30
Populo-Carpinetum												
Populus tremula	.	.	.	5	.	.	.	23	.	**100**	.	.
Thelypterido-Alnetum												
Thelypteris limbosperma	.	6	.	.	.	.	.	.	.	.	**100**	.
Lactuca macrophylla	.	.	.	.	.	.	.	.	.	.	**60**	.
Sorbus aucuparia	.	.	.	5	.	.	.	.	.	.	**40**	.
Rhynchocorys elephas	.	.	.	11	.	.	.	.	.	.	**60**	30
Sambucus ebulus	.	.	5	5	.	14	.	.	.	.	**47**	.
Viburnum orientale	.	6	.	.	.	.	.	.	.	.	**33**	.
Cardamine wiedemanniana	13	22	21	.	.	.	.	.	.	.	40	.
Sedum stoloniferum	13	.	5	26	.	.	.	.	.	.	33	.
Diospyto-Alnetum												
Diospyros lotus	6	6	5	.	.	.	.	.	.	.	.	**100**
Urtica dioica	.	.	37	.	.	.	.	.	.	.	.	**100**
Polygonum bistorta subsp. *carneum*	.	.	.	.	.	.	.	.	.	.	.	**60**
Prunella vulgaris	31	6	5	.	.	.	.	8	.	.	.	**90**
Geranium subcaulescens	.	.	.	.	.	.	.	.	.	.	.	**50**
Chaerophyllum byzantium	.	.	.	.	.	.	.	.	.	.	.	**50**
Clematis vitalba	.	.	.	26	19	.	.	.	.	20	.	**90**
Potentilla crantzii	.	.	.	.	.	.	.	.	.	.	.	**40**
Impatiens noli-tangere	.	.	5	.	.	.	.	.	.	.	20	**50**
Myosoton aquaticum	.	.	.	.	.	.	.	.	.	.	.	**30**
Salvia forsskaolei	.	.	.	53	31	.	.	15	30	.	33	**90**
Clinopodium vulgare	.	.	.	.	6	.	5	.	.	.	.	**30**
Lycopus europaeus	.	.	.	.	.	.	.	.	.	.	20	30
Phytolacca americana	.	17	11	.	.	.	.	.	.	.	13	30
Species diagnostic for two and more associations												
Asplenium adiantum-nigrum	**100**	6	26	26	63	.	10	.	.	.	.	.
Luzula forsteri	**81**	39	68	.	.	.	5	.	.	.	.	.
Viola alba+siehiana	81	11	32	32	13	86	.	.	.	.	33	.
Corylus avellana	75	17	68	21	13	43	10	31	.	.	20	.
Carpinus betulus	94	67	53	63	.	.	5	46	.	100	47	.
Oplismenus hirtellus s. *undulatif.*	81	56	84	63	13	57	.	.	.	.	27	40
Pteris cretica	56	33	**89**	47	.	.	.	.	.	.	20	.
Polypodium vulgare s.l.	50	22	16	.	.	.	.	.	30	10	.	60
Brachypodium sylvaticum	56	11	16	53	31	29	.	.	.	.	60	.
Asplenium trichomanes	38	11	**84**	.	.	.	.	.	.	.	.	.
Dryopteris borreri	25	89	89	47	.	57	.	.	.	.	.	.
Moehringia trinervia	13	39	58	5	.	.	.	8	.	.	.	.

Table 3. cont.

Association	DsC	RcC	PwU	CaC	EaC	EcP	SeC	HcC	RcQ	CbP	TlA	DlA
Group	1	2	3	4	5	6	7	8	9	10	11	12
Number of plots	16	18	19	19	16	7	20	13	10	10	15	10
Sambucus nigra	.	17	47	.	.	.	.	.	.	.	.	30
Iris lazica	.	.	5	58	44	29	.	.	.	.	.	.
Campanula alliariifolia	.	.	.	68	50	29	.	.	.	.	40	.
Gentiana asclepiadea	.	.	.	47	.	.	.	.	.	.	53	.
Hypericum androsaemum	.	.	.	68	.	14	.	15	.	60	53	40
Cyclamen coum	.	.	.	26	.	.	.	.	30	.	.	.
Salvia glutinosa	19	17	37	58	13	.	.	.	.	.	67	50
Aruncus dioicus	.	.	32	42	.	29	.	.	.	.	60	.
Hedera helix	38	6	.	.	81	.	45	15	.	.	.	60
Tanacetum parthenium	.	.	.	5	25	.	.	.	.	.	.	30
Rhododendron luteum	13	6	.	63	25	100	50	77	30	.	40	.
Milium effusum	.	.	.	5	.	29	.	.	.	.	33	.
Pteridium aquilinum	69	33	42	63	63	100	65	46	.	100	60	.
Prunus laurocerasus	25	67	32	.	.	.	15	85	30	.	13	.
Circaea lutetiana	.	11	26	.	13	.	.	46	.	.	60	.
Eragrostis collina	.	.	.	.	.	.	.	.	**100**	**90**	.	.
Fagus orientalis	13	17	21	5	.	.	15	62	**100**	.	7	.
Drymochloa drymeja	69	17	16	37	56	14	.	15	90	100	.	.
Hedera colchica	69	83	95	74	.	71	20	69	100	100	40	.
Ruscus hypoglossum	.	.	.	.	6	.	.	.	40	**100**	.	.
Rubus sanctus	.	.	.	.	.	.	.	.	.	30	.	40
Alnus glutinosa subsp. *barbata*	38	22	58	21	6	14	.	.	.	.	100	100
Epimedium pubigerum	19	6	.	63	25	100	.	23	90	.	13	.
Vaccinium arctostaphylos	13	11	16	58	44	100	45	69	100	80	27	.
Sorbus umbellata	.	.	.	.	.	.	.	.	**100**	70	.	.
Ilex colchica	6	22	42	26	31	.	55	54	100	100	20	.
Potentilla micrantha	88	33	68	32	19	14	.	.	.	.	67	.
Athyrium filix-femina	13	72	63	37	.	.	.	.	.	.	60	.
Carex pendula	19	22	63	.	.	.	.	8	.	70	20	**100**

Syntaxonomical outline

As almost the whole Euxinian Province, including Georgia, is outside the scope of the EuroVeg Checklist (Mucina et al. 2016) we prefer to use the syntaxonomical scheme proposed by Quézel et al. (1980; syntaxa validated in Quézel et al. 1992). It is also important to mention that there is still insufficient knowledge of forest vegetation within the Euxinian Province (Kavgacı et al. 2012). A recently published paper dealing with the variability and syntaxonomy of the forest vegetation of NW Turkey (Çoban & Willner 2019) also suggests that further research of Euxinian forest vegetation is necessary.

As we have already stated, our communities from south-western Georgia differ from the associations recorded in northern Turkey and we propose new associations corresponding to the three clusters of the Georgian relevés.

Querco-Fagetea Br.-Bl. et Vlieger in Vlieger 1937

Rhododendro pontici-Fagetalia orientalis Quézel et al. 1992

Castaneo sativae-Carpinion orientalis Quézel et al. 1992

1. *Digitali schischkinii-Carpinetum betuli* Novák et al. 2019

2. *Rusco colchici-Castaneetum sativae* Novák et al. 2019

Alnion barbatae Quézel et al. 1992

3. *Polysticho woronowii-Ulmetum glabrae* Zukal in Novák et al. 2019

Typification of newly described associations:

Digitali schischkinii-Carpinetum betuli ass. nova hoc loco (rel. 9 in Table 1, Supplement S1, holotypus hoc loco; name giving taxon: *Digitalis ferruginea* subsp. *schischkinii*); Cluster 1 in this study.
Holotypus (hoc loco) of the association: Georgia, Adjara region, Kveda Dagva, a slope above the Kveda Gorge, 1 km ESE from the village Kveda Dagva, 290 m a.s.l. Coordinates: 41°44'59.7" N, 41°49'59.3" E. Habitat: upper part of the valley slope. Relevé area: 100 m^2; Aspect: 170°; Slope: 35°; Cover of rocks: 0%. Cover of tree layer: 80%; Cover of shrub layer: 25%; Cover of herb layer: 40%; Cover of moss layer: 4%. Recorded on July 15, 2016. Author of the relevé: Pavel Novák.
Tree layer: *Carpinus betulus* 5, *Castanea sativa* 1, *Vitis vinifera* 1;
Shrub layer: *Corylus avellana* 2b, *Carpinus betulus* 1, *Castanea sativa* 1, *Camellia sinensis* +, *Elaeagnus commutata* +, *Prunus domestica* +, *Smilax excelsa* +;
Herb layer: *Drymochloa drymeja* 2a, *Oplismenus hirtellus* subsp. *undulatifolius* 2a, *Pteridium aquilinum* 2a, *Camellia sinensis* 1, *Hedera colchica* 1, *Hypericum xylosteifolium* 1, *Smilax excelsa* 1, *Asplenium adiantum-nigrum* +, *Calystegia silvatica* +, *Cardamine impatiens* +, *Carex muricata* +, *Carpinus betulus* +, *Digitalis ferruginea* subsp. *schischkinii* +, *Diospyros lotus* +, *Fragaria vesca* +, *Frangula alnus* +, *Hieracium* sp. +, *Hypericum androsaemum* +, *Hypochaeris radicata* +, *Lapsana communis* +, *Leontodon hispidus* +, *Potentilla micrantha* +, *Prunus domestica* +, *Trachystemon orientalis* +, *Viola alba* +, *Castanea sativa* r, *Erigeron canadensis* r, *Ficus carica* r.

Rusco colchici-Castaneetum sativae ass. nova hoc loco (rel. 31 in Table 1, Supplement S1, holotypus hoc loco); Cluster 2 in this study.
Holotypus (hoc loco) of the association: Georgia, Guria region, Gomi, Gomi near Ozurgeti: a forest on a slope 5.2 km S from the village, near a road to Gomismta Resort, 990 m a.s.l. Coordinates: 41°51'12.6" N, 42°7'34.5" E. Habitat: slope of the mountain. Relevé area: 100 m^2; Aspect: 50°; Slope: 50°; Cover of rocks: 0%. Cover of tree layer: 85%; Cover of shrub layer: 20%; Cover of herb layer: 60%; Cover of moss layer: 1%. Recorded on July 18, 2016. Author of the relevé: Pavel Novák.
Tree layer: *Castanea sativa* 5, *Carpinus betulus* 1;
Shrub layer: *Rhododendron ponticum* 2a, *Vaccinium arctostaphylos* 2a, *Castanea sativa* 1, *Ilex colchica* +, *Prunus laurocerasus* +, *Carpinus betulus* +;
Herb layer: *Rubus* subgen. *Rubus* 4, *Athyrium filix-femina* 1, *Ruscus colchicus* 1, *Acer pseudoplatanus* +, *Carpinus betulus* +, *Castanea sativa* +, *Dryopteris borreri* +, *Hedera colchica* +, *Ilex colchica* +, *Prunus laurocerasus* +, *Rhododendron ponticum* +, *Sambucus nigra* +, *Hypericum xylosteifolium* r, *Juncus effusus* r.

Polysticho woronowii-Ulmetum glabrae Zukal ass. nova hoc loco (rel. 47 in Table 1, Supplement S1, holotypus hoc loco); Cluster 3 in this study.
Holotypus (hoc loco) of the association: Georgia, Adjara region, Chakvistavi, side valley of the Chakvistavi river, ca 5 km SE from the village Khala, 255 m a.s.l. Coordinates: 41°40'50.2" N, 41°50'12.8" E. Habitat: the base of slope. Relevé area: 100 m^2; Aspect: 315°; Slope: 30°; Cover of rocks: 2%. Cover of tree layer: 45%; Cover of shrub layer: 55%; Cover of herb layer: 75%; Cover of moss layer: 30%. Recorded on July 17, 2016. Author of the relevé: Dominik Zukal.
Tree layer: *Acer cappadocicum* 2b, *Alnus glutinosa* subsp. *barbata* 2a, *Castanea sativa* 2a;
Shrub layer: *Sambucus nigra* 3, *Ulmus glabra* 2m, *Acer cappadocicum* 1, *Euonymus* sp. 1, *Staphylea pinnata* 1, *Hedera colchica* +, *Ilex colchica* +;
Herb layer: *Rubus* subgen. *Rubus* 3, *Dryopteris borreri* 2b, *Athyrium filix-femina* 2a, *Asplenium scolopendrium* 1, *Clinopodium umbrosum* 1, *Lamium galeobdolon* 1, *Trachystemon orientalis* 1,

Asplenium trichomanes +, *Carex pendula* +, *Circaea lutetiana* +, *Impatiens noli-tangere* +, *Onoclea struthiopteris* +, *Paris incompleta* +, *Polystichum woronowii* +, *Sambucus nigra* +, *Saxifraga cymbalaria* +, *Symphytum grandiflorum* +, *Aruncus dioicus* r, *Cardamine impatiens* r.

Species composition, species richness and human influence

South-western Georgia has a long history of significant human influence on the forest vegetation lasting at least 4000 years (Nikolaishvili et al. 2015). It includes cutting, coppicing, and forest grazing. In the last century, local forests have also been damaged by intensive farming practices including cutting forests to obtain land for bamboo, citrus, tea and tung tree plantations, as well as firewood. Numerous alien species, originating mainly in Eastern Asia, have been brought to the region with the new crops. In addition, new infrastructure, such as paths and roads, have been constructed within the region (Nakhutsrishvili 2013; Akhalkatsi 2015). These activities, coupled with the humid mild climate, have resulted in the frequent occurrence of alien species in the contemporary flora (Kikodze et al. 2009). We recorded various alien plant species during our field survey, mainly species that had escaped from crop plantations (e.g. *Camellia sinensis* and *Juglans ailanthifolia*) and gardens (e.g. *Miscanthus sinensis* and *Citrus trifoliata*), or annual weeds spreading along forest paths (e.g. *Crassocephalum crepidioides* and *Erigeron annuus*).

Of the studied vegetation types, forests of gorges and ravines of the association *Polysticho-Ulmetum* have been impacted the least by human activities. This is probably due to their occurrence within poorly accessible rocky places. Numerous endemic and relict species are also confined to this community. Chestnut-hornbeam forests (alliance *Castaneo-Carpinion*) are more significantly influenced by human activities as they are generally found in more accessible places (Nakhutsrishvili 2013). Due to human disturbance it can be difficult to distinguish how much of the variability in their species composition is driven by environmental conditions and how much by human disturbance. Forests with a sparse tree layer and dense evergreen shrub layer are typical for the association *Rusco-Castaneetum*. In areas with deep soils they are thought to represent the remnants of former dense forests that have been significantly impacted by human activities. Opening of the canopy of these forests, through felling and forest fires, may have led to the expansion of evergreen shrubs which can propagate themselves vegetatively and suppress tree regeneration. However, they are also assumed to be the natural vegetation for areas with shallow soils unsuitable for closed forests, e.g. the rocky tops of valley ridges (Golitsyn 1948; Kolakovskii 1961). The association *Digitali-Carpinetum* includes forests with a rather poorly-developed shrub layer. They were probably often used as forest pastures for cattle and they are still occasionally managed in this way, as is reflected by the relatively frequent occurrence of pasture weeds.

Concerning species richness, the associations *Digitali-Carpinetum* and *Polysticho-Ulmetum* are relatively similar. The lowest mean number of species per relevé was recorded for the association *Rusco-Castaneetum*. The low species richness within this association is the result of several factors including the dense evergreen shrub layer reducing the light available to the herb layer and the fact *Rhododendron ponticum* has a negative allelopathic effect on associated species, including the majority of tree and shrub seedlings (Eşen et al. 2006). Under this dense shrub layer ferns are at an advantage due to their ability to withstand very low amounts of light (Page 2002), as are shrubs capable of clonal spreading. A similar pattern of species richness was described in Western Caucasian coniferous forests, where communities with a dense evergreen shrub layer are the most species poor (Korotkov 1995).

Comparison of Colchic and Hyrcanian mesophilous forest flora

Hyrcania forms a narrow strip between the Caspian Sea and the Alborz mountain range (N Iran, SE Azerbaijan) and, similar to Colchis, represents the south-eastern distribution limit of numerous woody species (e.g. *Carpinus betulus*, *Fagus orientalis* and *Ulmus glabra*) characteristic for European mesophilous forest vegetation (Noirfalise & Djazirei 1965). A detailed comparison of the woody species composition of the forest vegetation within these two refugia has recently been provided by Nakhutsrishvili et al. (2015), therefore we focus here only on a comparison of their herb layer. These refugia both share many species with a broad distribution range (e.g. *Cardamine bulbifera*, *Dioscorea communis*, *Drymochloa drymeja* and *Viola alba*) as well as Euxine-Hyrcanian elements (e.g. *Cyclamen coum*, *Polystichum woronowii* and *Vincetoxicum scandens*). However, Colchic forests seem to have a higher number of endemic or subendemic species (e.g. *Epigaea gaultherioides*, *Epimedium pinnatum* subsp. *colchicum*, *Paris incompleta, Ruscus colchicus* and *Trachystemon orientalis*) compared to Hyrcania (e.g. *Campanula odontosepala* and *Danae racemosa*; Moradi et al. 2016). Additionally, some species characteristic for European mesophilous forests that also occur in Colchis have not been reported from Hyrcania (e.g. *Hedera helix*, *Impatiens noli-tangere* and *Scopolia carniolica*).

Floristic differences between Hyrcanian and Colchic forests are believed to be caused by both historical (development of flora and vegetation in the past) and environmental causes. Compared to Colchis, the recent climate of Hyrcania is more Mediterranean-like, usually with an arid season in the summer and lower annual precipitation (Nakhutsrishvili et al. 2015).

Conclusions

The present survey provides new vegetation data for the relict Colchic forests in western Georgia and their ecological characteristics. We have distinguished two new associations of chestnut-hornbeam forests (*Castaneo-Carpinion* alliance): *Digitali schischkinii-Carpinetum betuli*, a type with species of slightly dry soils and a low cover of evergreen shrubs, and *Rusco colchici-Castaneetum sativae*, a type with a well-developed evergreen shrub layer and sparse herb layer. For ravine forests (*Alnion barbatae* alliance), the new association *Polysticho woronowii-Ulmetum glabrae* was distinguished, characterized by noble hardwood trees and ravine forest specialists. Among the analysed environmental variables, altitude, inclination of slope, mean annual temperature and rockiness of site are among the most important factors for the species composition of the recognized forest communities in Georgia. Numerical analysis of available data from analogous forests from the central and eastern parts of the Euxinian Province has revealed a change in species composition as you move east. The number of Mediterranean species, and drought-tolerant species in general, decreased and the occurrence of ferns and other species preferring humid regions increased from west to east. This shift seems to be driven by macroclimatic gradients.

The studied forests are important from a nature conservation perspective as they harbour many relict and endemic species characteristic of the Euxinian Province (e.g. *Hedera colchica*, *Ruscus colchicus* and *Trachystemon orientalis*). However, illegal felling, forest fires and overgrazing by domestic ungulates continue to negatively impact large areas of Georgian Colchic forests. This study has provided new valuable knowledge on the forest vegetation diversity of Colchis. Nevertheless, further studies are still required to investigate the forest vegetation diversity of this unique refugial region.

Author contributions

P.N. led the writing, designed the study and performed the statistical analyses. Field sampling was organized by P.N. and V.K. D.Z. wrote the text on ravine forests. K.C. helped to prepare electronic appendices and other tables. The field sampling was conducted by all four above-mentioned persons. A.K. provided digitalized relevés from selected literature and contributed to the assessment of the communities. All authors critically revised the manuscript.

Acknowledgements

We thank Idoia Biurrun, Milan Chytrý and three anonymous reviewers for valuable remarks on the previous versions of the manuscript. For help with the fieldwork, we thank Kamila Čížková, Anna Hlaváčková, Helena Prokešová, Jakub Salaš and Ondřej Škeřík. Jiří Danihelka, Libor Ekrt, Vít Grulich and David Kikodze kindly helped with the plant determination. Hamid Gholizadeh provided valuable notes on the Hyrcanian forest flora and Mariya Sydoruk prepared the map. The study was supported by the Czech Science Foundation (Center of Excellence Pladias, 14-36079G).

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Electronic Supplements

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Supplement S1. Ordered relevé table of the original data.
Supplement S2. Comparison of environmental variables, cover of vegetation layers and species richness among clusters of Georgian relevés.
Supplement S3. Supplementary data for the expanded dataset: full version of synoptic table at association and alliance levels.

7.3. Paper 3

Novák P., Zukal D., Harásek M., Vlčková P., Abdaladze O. & Willner W.: Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia. – Folia Geobotanica, under revision.

Ecology and vegetation types of oak-hornbeam and ravine forests of the Eastern Greater Caucasus, Georgia

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Abstract
The Caucasus harbours unique forest vegetation only little studied using the Braun-Blanquet approach so far. The study is mostly based on a dataset (n = 110) of the original phytosociological relevés of oak-hornbeam and ravine forests from the Eastern Greater Caucasus, Georgia. Their unsupervised classification produced seven communities. Five belong to oak-hornbeam forests (order *Lathyro-Carpinetalia caucasicae*). Of the zonal Caucasian alliance *Crataego-Carpinion*, association *Corno-Carpinetum* inhabits valleys of the Greater Caucasus and *Clinopodio umbrosi-Carpinetum* is confined to the warm Eastern Greater Caucasus promontories. Association *Astrantio maximae-Carpinetum* of the alliance *Astrantio-Carpinion* represents distinctive Caucasian mountain oak-hornbeam forests. The other two communities documented by a few relevés were described at the community level only. Within ravine forests of the order *Aceretalia pseudoplatani*, we introduce a new Caucasian alliance *Pachyphragmo macrophyllae-Tilion begoniifoliae* with two associations. *Valeriano-Ulmetum glabrae* comprises Caucasian montane ravine forests, while *Hedero pastuchowii-Aceretum velutini* inhabits the Eastern Greater Caucasian foothills. To provide a broader context of the recognized communities, an expanded dataset (n = 231) of the original relevés and previously published relevés of Georgian deciduous forests was analysed. It indicates a major turnover in species composition following biogeographical pattern presumably driven by macroclimate and vegetation history.

Keywords: biogeography; *Carpino-Fagetea*; Caucasus; classification; phytosociology; syntaxonomy

1. Introduction

The Caucasus is a rugged landscape of high mountain ridges forming the boundary between Europe and Asia. It is an approximately 1200 km long west-east mountain chain stretching between the Black and Caspian Sea and exceeding the elevation of 5000 m. The region is ranked among 34 world terrestrial biodiversity hotspots due to its species-rich biota with a high level of endemism (Mittermeier et al. 2004; Barthlott et al. 2005; Zazanashvili and Mallon 2009). Its unique biota is related to high variability of environmental conditions and a distinctive history during the Pleistocene climatic oscillations, as the region harbours numerous Tertiary relicts (Denk et al. 2001; Shatilova et al. 2011) including several nowadays dominant trees (e.g. *Picea orientalis*, *Quercus macranthera*) or shrubs (e.g. *Prunus laurocerasus*, *Rhododendron ponticum*). Georgia

(~69 700 km^2) is situated in Transcaucasia, i.e. between the main ridges of the Greater and the Lesser Caucasus. Vast areas of the country (~43%) are forested, of which 80% are deciduous forests representing a high proportion of the overall variability of the Caucasian forests (Gulisashvili et al. 1975; Krever et al. 2001; Akhalkatsi 2015).

The Caucasus is an area of developing vegetation survey based on the Braun-Blanquet approach. Numerous local descriptive studies were published (e.g. Kolakovskii 1961; Ketskhoveli et al. 1975; Gulisashvili et al. 1975; Dolukhanov 2010; Nakhutsrishvili 2013), although they presented dominant-based classification systems. Only several pioneering Braun-Blanquetian studies were issued over the last decades. They were dealing with the Western Greater Caucasian subalpine birch (Onipchenko 2002), coniferous (Korotkov 1995) and xerophilous (Litvinskaya and Postarnak 2002) forests as well as mesophilous deciduous forests of Central Georgia (Passarge 1981a, 1981b) and Colchis (Novák et al. 2019).

Our study focuses on the oak-hornbeam and ravine forests of the Eastern Greater Caucasus in Georgia, i.e. mesophilous forests dominated by *Acer campestre*, *Carpinus betulus*, *Quercus macranthera*, *Q. petraea* subsp. *iberica* and *Zelkova carpinifolia* or *Acer laetum*, *A. velutinum*, *Tilia begoniifolia* and *Ulmus glabra*, respectively. Therefore, the study by Passarge (1981a) is particularly relevant as it contains the description of two alliances of oak-hornbeam forests of the southern macroslope of the Greater Caucasus in Georgia. In contrast, ravine forests have hardly been investigated so far. Besides the recently established association *Polysticho woronowii-Ulmetum glabrae* describing Colchic ravine forests in western Georgia (Zukal in Novák et al. 2019), no syntaxonomic attention has been paid to this vegetation type so far. This is likely due to their intrazonal character and polydominant tree layer that can be hardly described by a dominant-based approach (Dolukhanov 2010). Some authors (e.g. Gulisashvili et al. 1975; Nakhutsrishvili 2013) presented part of their variability under beech forest formations. Kolakovskii (1961) distinguished an individual forest type growing in ravines that likely corresponds to *Aceretalia* forests.

The environmental conditions, structure and species composition of Caucasian oak-hornbeam forests have been co-shaped by human activities (e.g. coppicing, pollarding, forest pasturing of livestock), similarly as in other parts of their broad distribution range (Bohn et al. 2000–2003; Leuschner and Ellenberg 2017). Signs of such treatments are often apparent. Locally, they are even still practised (e.g. Hübl et al. 2010, Bussmann 2017) allowing genuine opportunities to study traditional forest management, abandoned in the majority of Europe and its surroundings (e.g. Sebek et al. 2013). Nevertheless, the last decades also brought forest overexploitation to obtain firewood in places. In addition, forest grazing of domestic ungulates may be intensive at the local scale, reducing the herb layer, preventing tree rejuvenation and promoting soil erosion and invasion of alien species (Dolukhanov 2010; Akhalkatsi 2015). Compared to oak-hornbeam forests, Caucasian ravine forests are less influenced by human activities as they mostly inhabit poorly accessible sites (e.g. Kolakovskii 1961; Dolukhanov 2010; Novák et al. 2019).

Of the studied vegetation, ravine and *Zelkova carpinifolia* forests are considered as sensitive habitats of Georgia (Akhalkatsi 2015). In the European context (Janssen et al. 2016), oak-hornbeam forests are treated as near threatened habitat (EU 28, EU 28+), similarly as ravine forests (EU 28). A better understanding of their variability should lead to classification systems that can be implemented into national or international habitat classification and thus be important for nature protection, protected areas management planning or environmental monitoring (Rodwell et al. 2018).

The aims of our study are as follows: 1) To describe the variability of oak-hornbeam and ravine forests of the study area. 2) To analyse variables driving their species composition. 3) To compare the recognized vegetation types with the previously described associations in Georgia. 4) To present a new revised syntaxonomic system of the studied vegetation.

2. Material and methods

Study region

The study region (Figure 1) stretches over the southern macroslope of the Eastern Greater Caucasus, including mountain valleys of the north-central Georgia and slopes above the Alazani River valley in the Kakheti region. It spans from the piedmont (455 m a.s.l.) nearly to the timberline (1690 m a.s.l.). The geological bedrock is rather uniform, composed mainly of Mesozoic sediments (marls, slates, turbidites), locally calcareous. They often form steep erosion-prone slopes with deeply incised river valleys separated by sharp ridges. Bodies of volcanic rocks are limited to the northwestern part of the region (Adamia 2010). Climate of the region is relatively diverse, with the annual mean temperature of the sampled sites varying between 2.7 and 12.1 °C (mean 8.5 °C) and the annual precipitation between 710 and 1190 mm (mean 821 mm) with noticeable seasonality (Fick and Hijmans 2017).

Oak-hornbeam and oriental beech forests are supposed to be the prevailing natural forest vegetation of the region, with open woodlands of *Acer trautvetteri*, *Betula litwinowii* and *Quercus macranthera* mostly forming the timberline (Bohn et al. 2000–2003). The forest flora in Kakheti is enriched by several species of the Hyrcanian floral element coming from southeast (e.g. *Acer velutinum*, *Hedera pastuchovii*), including relict species shared by the Colchic and Hyrcanian refugia, for instance *Diospyros lotus* and *Prunus laurocerasus* (Denk et al. 2001; Nakhutsrishvili 2013; Nakhutsrishvili et al. 2015).

Fig 1 Map of the study region with locations of relevés and their classification

Data collecting

We conducted field surveys in 2015–2018. The majority of the dataset was yielded in August 2018. The aim of the sampling was to cover a broad variability of the oak-hornbeam and ravine forests. We sampled vegetation-plot records (hereafter "relevés"). For each relevé (100 m^2), we estimated percentage covers of tree, shrub, herb and moss layers . Species cover values in each layer were assessed in the extended nine-degree Braun-Blanquet cover-abundance scale (Dengler et al. 2008), except for bryophytes, as the latter were not identified. Inclination, slope aspect and percentage cover of rocks were assessed as well. Geographical coordinates (WGS84)and elevation were measured by the GPSMAP 60CSx receiver. Climatic data were extracted from WorldClim 2 (Fick and Hijmans 2017). In each relevé, we took a soil sample of the uppermost 15 cm of soil and measured its pH in a distilled water suspension (2:5) by a portable instrument GMH Greisinger.

Dataset and data processing

The taxonomy and nomenclature of vascular plants follow the Euro+Med PlantBase (Euro+Med 2006-). We defined several *ad hoc* aggregates: *Arum maculatum* aggr. (*Arum maculatum*, *A. megobrebi*, *A. orientale*), *Carex muricata* aggr. (*Carex divulsa*, *C. muricata*, *C. spicata*), *Crataegus monogyna* aggr. (*Crataegus microphylla*, *C. monogyna*, *C. pentagyna*, *C. pseudoheterophylla*, *C. rhipidophylla*) and *Rosa canina* aggr. (*Rosa canina*, *R. corymbifera*, *R. iberica*, *R. irysthonica*, *R. marschalliana*, *R. oxyodon*). An expanded dataset (n = 231 relevés) was compiled to compare our dataset with relevés of the class *Carpino-Fagetea* previously recorded in Georgia (Passarge 1981a, n = 18; Passarge 1981b, n = 50; Novák et al. 2019, n = 53). Relevés from Passarge's studies were georeferenced based on the published data on sample sites, with a maximal bias of 5 minutes. Relevés were stored in Turboveg 2.1 (Hennekens and Schaminée 2001) and processed mostly in Juice 7.0 (Tichý 2002). Ordination analyses were done in the R 3.6.0 environment (R Core Team 2018), using the package vegan 2.5-6 (Oksanen et al. 2019). Occurrences of the same taxon in different layers were merged prior to the analyses applying the procedure by Fischer (2015). Vernal ephemeroids were deleted before the analyses as they were recorded only in few spring relevés.

Classification analyses were performed in PC-ORD 5 (McCune and Mefford 1999). We applied various classification strategies (Flexible Beta, modified TWINSPAN, Ward's method) and numbers of clusters. Optimal partition was indicated by the OptimClass 1 method (Tichý et al. 2010). Diagnostic value of species was determined by the *phi* coefficient (Sokal and Rohlf 1995). Prior to its calculation, number of plots in clusters were virtually standardized to be equal (Tichý and Chytrý 2006). We used Fisher's exact test ($p \leq 0.05$) to omit species with non-significant fidelity from the diagnostic species lists. Species with $phi \geq 0.35$ were regarded as diagnostic and with $phi \geq 0.5$ as highly diagnostic (in bold). In addition, we applied a constancy ratio criterion (Dengler 2003), i.e., the constancy of a diagnostic species must be at least 1.3× higher than in the cluster where it reaches the second highest constancy. Species with frequency ≥ 50% were listed as constant species in a cluster. Species with cover ≥ 25% in at least 40% of relevés of a cluster were considered as dominant. In the syntaxonomic part of the study, we applied the rules of phytosociological nomenclature published in the 4rd edition of the Code (Theurillat et al. 2020). The nomenclature of the higher syntaxa follows the EuroVegChecklist (Mucina et al. 2016).

3. Results

Classification

During the field surveys, we recorded 110 phytosociological relevés (stored in GIVD AS-00-005 - Transcaucasian Vegetation Database, see https://www.givd.info/ID/AS-00-005) which contained 304 species in total. Based on the results of the Flexible Beta clustering (β = -0.4, square-root transformed species cover data), we recognized seven vegetation types, all of the class *Carpino-Fagetea*, orders *Lathyro-Carpinetalia* (communities 1–5) and *Aceretalia* (communities 6 and 7). A synoptic table of the recognized communities is provided in Table 1. Their overview is also provided by DCA results (Figure 2) and boxplots (Figure 3). Photographs of the communities are in Figure S6 in Electronic supplementary material. The major division of the dataset at the level of two clusters reflected well differences between oak-hornbeam and ravine forests.

Community 1:* Cornus mas-Carpinus betulus *(16 relevés)

Diagnostic species: *Aegonychon purpurocaeruleum*, *Astragalus glycyphyllos*, *Berberis vulgaris*, *Carex digitata*, ***Cornus mas***, *Euonymus latifolius*, ***Euonymus verrucosus***, *Helleborus orientalis*, *Juglans regia*, *Lonicera caucasica*, ***Physospermum cornubiense***, *Polygonatum glaberrimum*, *Quercus petraea* subsp. *iberica*, *Securigera varia*, *Sorbus torminalis*, ***Vincetoxicum hirundinaria***.

Constant species: *Acer campestre*, *Acer cappadocicum*, *Campanula rapunculoides*, *Carex digitata*, *Carpinus betulus*, *Carpinus orientalis*, *Corylus avellana*, *Cornus mas*, *Cornus sanguinea*, *Crataegus germanica*, *Euonymus latifolius*, *Fagus orientalis*, *Fraxinus excelsior*, *Galium odoratum*, *Ligustrum vulgare*, *Prunus avium*, *Quercus petraea* subsp. *iberica*, *Sorbus torminalis*, *Tilia begoniifolia*, *Vincetoxicum hirundinaria*, *Viola alba*.

Dominant species: *Carpinus betulus*

This community involves zonal oak-hornbeam forests of the Greater Caucasus southern forehills (750–1210 m) in the western half of the study region, mainly in the lower parts of the Aragvi river valley. They occur on slopes of various inclination and orientation, generally without rock outcrops or scree. They preferentially grow on neutral soils (mean soil pH 6.8) usually covering calcareous turbidites. The climate is moderate (mean annual temperature 8.9 °C, mean annual precipitation 780 mm).

Carpinus betulus dominates the tree layer, often accompanied by *Acer cappadocicum*, *Fagus orientalis* and *Carpinus orientalis*. Both hornbeam species used to be locally pollarded. The shrub layer is mostly well-developed (mean cover 28%) and dominated by the thermophilous shrub *Cornus mas* and species of the tree layer. Evergreen lianas are almost absent, likely due to cold winters. The herb layer reaches the lowest cover among the recognized communities (mean cover 18%), usually lacking a distinctive dominant. Along forest mesophytes (e.g. *Galium odoratum*, *Veronica peduncularis*), these forests harbour thermophilous species including both species with broad distribution ranges in the submediterranean zone of western Eurasia (e.g. *Lonicera caprifolium*, *Physospermum cornubiense*) and Caucasian endemics (e.g. *Peucedanum caucasicum*, *Polygonatum glaberrimum*). The poisonous rhizomatous herb *Helleborus orientalis* may expand in patches frequently grazed by cattle. The moss layer is low in cover or missing.

This cluster corresponds to the association *Corno-Carpinetum* described from the same region by Passarge (1981a).

Community 2:* Zelkova carpinifolia-Carpinus betulus *(4 relevés)
Diagnostic species: *Brachypodium sylvaticum*, *Carex flacca*, *Carex michelii*, *Carex sylvatica*, *Drymochloa drymeja*, ***Klasea quinquefolia***, ***Lathyrus laxiflorus***, ***Ligustrum vulgare***, ***Lonicera caprifolium***, *Melica uniflora*, ***Piptatherum virescens***, ***Quercus petraea* subsp. *iberica***, ***Zelkova carpinifolia***.
Constant species: *Ajuga reptans*, Brachypodium *sylvaticum*, *Campanula rapunculoides*, *Carex michelii*, *Carex muricata* aggr., *Carex sylvatica*, *Carpinus betulus*, *Carpinus orientalis*, *Cornus sanguinea*, *Drymochloa drymeja*, *Fraxinus excelsior*, *Klasea quinquefolia*, *Lathyrus laxiflorus*, *Ligustrum vulgare*, *Lonicera caprifolium*, *Melica uniflora*, *Piptatherum virescens*, *Prunus avium*, *Quercus petraea* subsp. *iberica*, *Smilax excelsa*, *Viola alba*, *Viola reichenbachiana*, *Zelkova carpinifolia*.
Dominant species: *Carpinus betulus*.

This community comprises xeromesophilous forests with *Zelkova carpinifolia*, a relict species of the Tertiary flora. It was recorded exclusively in the Babaneuri Reserve in Kakheti, established to protect *Zelkova* forests. They grow on neutral soils (mean pH 6.7) with various content of gravel developed on sedimentary carbonate parent rock. They occupy sunny slopes and their site represents one of the warmest and driest parts of the study area (mean annual temperature 11.5 °C, annual precipitation 735 mm). In the driest places, such as tops of south-facing slopes, they are substituted by scrubs of *Carpinus orientalis* and *Paliurus spina-christi*. Our relevés represent the only known forests with *Zelkova carpinifolia* in eastern Georgia and likely in the whole Eastern Greater Caucasus. The rest of its Georgian sites are in Colchis in the western part of the country (Maharramova et al. 2015).

Carpinus betulus, *C. orientalis*, *Quercus petraea* subsp. *iberica* and *Zelkova carpinifolia* prevail in the tree layer. The shrub layer is usually sparse, having the lowest mean cover among the distinguished communities (6%) and composed mainly of the tree rejuvenation and the thermophilous semi-deciduous species *Ligustrum vulgare*. In the field layer, xeromesophilous graminoids (e.g. *Drymochloa drymeja*, *Piptatherum virescens*) and dicots (e.g. *Klasea quinquefolia*, *Lonicera caprifolium*) play a prominent role. The diversity of forest mesophytes is rather low. The moss layer is mostly poorly developed.

We provisionally classify this community under the order *Lathyro-Carpinetalia*. However, further phytosociological research on the Transcaucasian *Zelkova carpinifolia* forests is needed.

Community 3:* Quercus macranthera-Carpinus betulus *(16 relevés)
Diagnostic species: *Campanula alliariifolia*, *Carex humilis*, *Clinopodium vulgare*, ***Fragaria vesca***, *Hieracium lachenalii*, *Lactuca racemosa*, *Pimpinella rhodantha*, *Platanthera chlorantha*, ***Poa nemoralis***, ***Quercus macranthera***, *Rosa canina* aggr., *Solidago virgaurea*, *Sorbus aucuparia*, *Stellaria holostea*.
Constant species: *Acer cappadocicum*, *Brachypodium sylvaticum*, *Campanula alliariifolia*, *Campanula rapunculoides*, *Carpinus betulus*, *Corylus avellana*, *Fagus orientalis*, *Fragaria vesca*, *Galium odoratum*, *Lapsana communis*, *Poa nemoralis*, *Polygonatum multiflorum*, *Prunus avium*, *Rosa canina* aggr., *Salvia glutinosa*, *Sedum stoloniferum*, *Solidago virgaurea*, *Valeriana tiliifolia*, *Veronica peduncularis*, *Viola alba*.
Dominant species: *Carpinus betulus*.

This community includes the Greater Caucasian montane oak-hornbeam forests. They were recorded at the highest elevations in the study region (mean elevation 1416 m), which is also expressed by the lowest annual temperature (mean 6.3 °C) and high annual precipitations (mean 928 mm). In some mountain valleys, they may even reach the timberline. They grow on slopes of various orientation, usually slightly rocky (mean cover of rocks 5%). The bedrock is formed by diverse turbidites and rarely also by basaltic lavas (Gudauri environs).

Carpinus betulus dominates the tree layer. *Quercus macranthera* and *Fagus orientalis* are its frequent canopy companions. However, *Fagus* is likely supressed by harsh climate and therefore it does not reach high covers. The shrub layer is rather well-developed (mean cover 13%). Besides mesophilous species typical of the Caucasian forests (e.g. *Euonymus latifolius*, *Lonicera caucasica*) also species forming the local treeline (*Betula litwinowii*, *Rhododendron luteum*) may be admixed. Besides forest mesophytes, tall forbs (e.g. *Valeriana tiliifolia*) and other species of the upper montane and subalpine belt (e.g. *Lactuca racemosa*, *Pimpinella rhodantha*) are characteristic for the herb layer. A boreal floral element is represented by species characteristic of the Caucasian coniferous forests (e.g. *Orthilia secunda*, *Rubus saxatilis*). On shallow soils of convex relief shapes, drought-tolerant *Carex humilis* occurs. Rock crevices of small rock outcrops harbour mesophilous chasmophytes (e.g. *Asplenium trichomanes*, *Sedum stoloniferum*). The moss layer is usually well-developed, preferentially covering rocks. A striking difference against other recorded oak-hornbeam forests is the rare occurrence or absence of thermophilous species (e.g. *Cornus mas*, *Hedera* spp., *Sorbus torminalis*).
Concerning syntaxonomy, this community probably corresponds to montane types of the Caucasian oak-hornbeam forests described by Passarge (1981a) under the names *Astrantio-Carpinetum*, *Clinopodio-Carpinetum* and *Rhododendro-Carpinetum*.

Community 4:* Clinopodium umbrosum-Carpinus betulus *(25 relevés)
Diagnostic species: ***Calystegia silvatica***, *Carex sylvatica*, *Castanea sativa*, *Clematis vitalba*, *Clinopodium umbrosum*, ***Diospyros lotus***, *Euphorbia stricta*, *Glechoma hederacea*, *Hedera helix*, *Luzula forsteri*, ***Oplismenus hirtellus* subsp. *undulatifolius***, ***Prunella vulgaris***, *Pterocarya fraxinifolia*, *Schedonorus giganteus*, *Torilis japonica*.
Constant species: *Brachypodium sylvaticum*, *Calystegia silvatica*, *Carex muricata* aggr., *Carex sylvatica*, *Carpinus betulus*, *Clinopodium umbrosum*, *Corylus avellana*, *Dioscorea communis*, *Diospyros lotus*, *Dryopteris filix-mas*, *Fagus orientalis*, *Geranium robertianum*, *Lapsana communis*, *Moehringia trinervia*, *Oplismenus hirtellus* subsp. *undulatifolius*, *Prunus avium*, *Salvia glutinosa*, *Sanicula europaea*, *Tilia begoniifolia*, *Viola alba*.
Dominant species: *Carpinus betulus*.

This community represents zonal vegetation of the Greater Caucasian promontories in Kakheti (455–1330 m). It occurs on slopes of various inclination and orientation. It was mostly recorded on slightly acidic soils (mean soil pH 6.2) developed on black slates and turbidites. With 35 species per relevé in average, it is the species richest community. The climate is relatively warm (mean temperature 10.8 °C).

The tree layer is dominated by *Carpinus betulus*, with some other rather mesophilous species (e.g. *Acer cappadocicum*, *Fagus orientalis*, *Ulmus glabra*) in admixture. The shrub layer is mostly well developed (mean cover 18%) with prevailing thermophilous (e.g. *Cornus mas*, *Crataegus germanica*) and mesophilous (e.g. *Cornus sanguinea*, *Corylus avellana*) shrubs. The common relict shrub *Diospyros lotus* prefers canopy gaps

which it can rapidly colonize via endozoochory. Evergreen lianas, both mesophilous (*Hedera helix*, *H. pastuchovii*) and xeromesophilous (*Smilax excelsa*), climb the shrubs and trees as they favour rather mild winters characteristic for the region (mean temperature of the coldest quarter the year 0.8 °C, mean precipitations 97 mm). The herb layer is often dominated by stoloniferous grasses, *Drymochloa drymeja* on drier soils, whereas the alien *Oplismenus hirtellus* subsp. *undulatifolius* on mesic soils. Forest mesophytes (e.g. *Dryopteris filix-mas*, *Salvia glutinosa*) and shade-tolerant nitrophytes (e.g. *Geum urbanum*, *Lapsana communis*) are frequent. Thermophilous drought-tolerant species (e.g. *Asplenium adiantum-nigrum*, *Luzula forsteri*) are admixed mostly on shallow soils. Near settlements, these woodlands occasionally serve as intermittent cow pastures, which has resulted in spreading of pasture weeds (e.g. *Euphorbia stricta*, *Pteridium aquilinum*). The moss layer varies in cover (mean 7%).
We classify this community under the alliance *Crataego-Carpinion* and describe it as a new association (see below).

Community 5: **Hedera pastuchovii-Carpinus betulus** ***(8 relevés)***
Diagnostic species: *Hedera pastuchovii*, ***Rubus*** **subgen.** ***Rubus***.
Constant species: *Acer cappadocicum*, *Carpinus betulus*, *Clinopodium umbrosum*, *Crataegus germanica*, *Corylus avellana*, *Drymochloa drymeja*, *Dryopteris filix-mas*, *Fagus orientalis*, *Fraxinus excelsior*, *Galium odoratum*, *Hedera pastuchovii*, *Pachyphragma macrophylla*, *Rubus* subgen. *Rubus*, *Tilia begoniifolia*, *Ulmus glabra*, *Viola alba*, *Viola reichenbachiana*.
Dominant species: *Carpinus betulus*.

These forests are typical for fertile soils in the valleys of the Greater Caucasus in Kakheti. It preferentially grows on slightly wet and nutrient rich soils (mean pH 6.1) covering higher river terraces and slope bases. Nevertheless, the cover of rocks is very limited. Black slates and other turbidites prevail in the bedrock.
The tree layer is dominated by *Carpinus betulus*, with *Acer cappadocicum* and *Fagus orientalis* as common co-dominants. The shrub layer is often constituted by *Acer cappadocicum*, *Corylus avellana* and *Crataegus germanica*. The herb layer is frequently predominated by species forming dense grows such as *Drymochloa drymeja*, *Hedera pastuchovii* and *Rubus* sect. *Rubus*. Stony soils and vicinity of ravine forests support the local occurrence of ravine forest species, mainly *Pachyphragma macrophylla*. Therefore, this community represents a transition between *Lathyro-Carpinetalia* and *Aceretalia* forests. As it was grouped together with the other oak-hornbeam forests in the unsupervised classification, we keep this assignment.

Community 6: **Valeriana tiliifolia-Ulmus glabra** ***(25 relevés)***
Diagnostic species: *Acer platanoides*, *Actaea spicata*, *Arum maculatum* aggr., ***Aruncus dioicus***, *Asplenium trichomanes*, ***Cystopteris fragilis***, *Dipsacus pilosus*, *Geranium robertianum*, *Impatiens noli-tangere*, *Paris incompleta*, *Petasites albus*, *Pimpinella tripartita*, ***Polygonatum multiflorum***, *Salvia glutinosa*, *Sambucus nigra*, *Scutellaria altissima*, *Symphytum asperum*, *Telekia speciosa*, *Urtica dioica*.
Constant species: *Acer cappadocicum*, *Aruncus dioicus*, *Asplenium scolopendrium*, *Asplenium trichomanes*, *Carpinus betulus*, *Corylus avellana*, *Cystopteris fragilis*, *Dryopteris filix-mas*, *Fraxinus excelsior*, *Galium odoratum*, *Geranium robertianum*, *Polygonatum multiflorum*, *Polypodium vulgare*, *Salvia glutinosa*, *Sambucus nigra*, *Ulmus glabra*.

Dominant species: *Ulmus glabra*.

This community comprises mountain ravine forests of Caucasian valleys in the western part of the study area. Although relevés of this community were documented over a broad elevation range (495–1690 m), all but two relevés were recorded higher than 1000 m a.s.l. Stands from the highest altitudes can be transitional to subalpine scrub and elfin forests. They inhabit steep (mean inclination 45°) and usually north- or west-facing slopes that can be either loamy or with scree accumulations (mean cover of rocks 13%) formed mostly of turbidites, locally also carbonates, with basic soils (mean pH 7.2). With respect to the broad elevation range of study localities, the climatic data are diverse, with the mean annual temperature between 2.7–12.1 °C (mean 6.6 °C) and annual precipitations between 725–1190 mm (mean 924 mm). Compared to the following community, it is colder during the whole year. This community is also richer in species, with 32 species per relevé in average.

The tree layer is dominated by noble hardwood tree species (*Acer platanoides*, *Fraxinus excelsior*, *Ulmus glabra*) including the Caucasian subendemics *Acer cappadocicum* and *Tilia begoniifolia*. Zonal species (*Carpinus betulus*, *Fagus orientalis*) are locally admixed. The tree canopy can be rather open (mean cover 74%). However, the shrub layer is usually well-developed (mean cover 24%), species-rich and contains mesophilous shrubs (e.g. *Corylus avellana*, *Euonymus europeaus*, *Sambucus nigra*) as well as tree rejuvenation. The occurrence of typical ravine forest species (*Aruncus dioicus*, *Impatiens noli-tangere*, *Pachyphragma macrophylla*) and other stolon-forming species (e.g. *Lamium album*, *Scutellaria altissima*) indicating occasionally moving substrate are diagnostic for the herb layer. Specialists of rock crevices are mainly represented by mesophilous species (e.g. *Asplenium scolopendrium*, *A. trichomanes*, *Cystopteris fragilis*). Forest ferns are common (e.g. *Dryopteris filix-mas*, *Polystichum braunii*) and in comparison to the following community, also the species spectrum of forest mesophytes is much broader (e.g. *Galium odoratum*, *Polygonatum multiflorum*), including Caucasian subendemics (e.g. *Paris incompleta*, *Pimpinella tripartita*) and montane tall forbs (e.g. *Telekia speciosa*, *Valeriana tiliifolia*). Mean cover of the moss layer is the highest among all communities (9%), even though it can vary markedly from place to place.

Community 7: **Hedera pastuchovii-Acer velutinum** ***(16 relevés)***
Diagnostic species: *Acer velutinum*, ***Asplenium scolopendrium***, *Carex pendula*, *Dryopteris borreri*, *Hedera pastuchovii*, *Pachyphragma macrophylla*, ***Philadelphus coronarius***, ***Polystichum aculeatum***, *Polystichum braunii*, Rubus subgen. *Rubus*.
Constant species: *Acer velutinum*, *Asplenium scolopendrium*, *Asplenium trichomanes*, *Carpinus betulus*, *Corylus avellana*, *Hedera pastuchovii*, *Pachyphragma macrophylla*, *Philadelphus coronarius*, *Polypodium vulgare*, *Polystichum aculeatum*, *Polystichum braunii*, *Rubus* subgen. *Rubus*, *Tilia begoniifolia*.
Dominant species: *Hedera pastuchovii*, *Tilia begoniifolia*.

This community represents ravine forests confined to the deeply incised valleys in the Greater Caucasian foothills in Kakheti (594–979 m). They occur on slopes of various orientations usually covered by scree, mainly on immobilized scree accumulations on slope bases. The parent rock is mostly formed of black slates with basalt or carbonate admixture (mean pH 6.7). The climate is warmer compared to the previous community (mean annual temperature 8.7 °C). Annual precipitations (mean 749 mm) are lower, however, as this community is confined to deeply incised valleys, air humidity is relatively high thanks to shading of valley slopes and adjacent rivers. Cover of rocks is the highest compared to other communities (mean cover 22%). Among the recognized communities, this one has the lowest mean number of species per relevé (18 species). On the moving screes, this forest community rapidly transits to open tall-herb vegetation with *Datisca cannabina*.

The tree layer is mostly dominated by noble hardwood tree species, mainly by typical species of the warm parts of Eastern Transcaucasia (*Acer velutinum*, *Tilia begoniifolia*). Other noble hardwood tree species commonly occurring in the previous community are less common or even absent (*Acer platanoides*). The shrub layer is formed by mesophilous species, *Corylus avellana* and *Sambucus nigra* reach the highest cover. *Philadelphus coronarius*, frequently colonizing shaded scree slopes, is highly diagnostic for this community. Numerous fern species occur in the herb layer (e.g. *Asplenium scolopendrium*, *Polystichum aculeatum*, *P. braunii*) including species of rock crevices (*Asplenium trichomanes*, *Polypodium vulgare* aggr.). Compared to the previous community, *Dryopteris filix-mas* is often substituted by *D. borreri* indicating warmer and more humid climate. The evergreen liana *Hedera pastuchovii*, often also climbing the trees, or stoloniferous *Rubus* subgen. *Rubus* form dense growths, presumably due to the mild climate. Other ravine forest species are mostly represented by *Pachyphragma macrophylla*. The diversity of forest mesophytes of phanerogams is usually low, *Salvia glutinosa* and *Viola alba* are among the most frequent. The moss layer is developed, although usually does not reach high cover.

Table 1 A synoptic table of the recognized communities in the dataset (n = 110). Values are percentage frequency. Diagnostic species of the orders are in the upper part of the table and sorted by decreasing fidelity. Diagnostic species of communities are shaded and also sorted by decreasing fidelity. Only species reaching a frequency ≥ 30% in at least one community are show. Diagnostic (*phi* ≥ 0.35) and highly diagnostic (*phi* ≥ 0.5, in bold) species are shown. Other frequent species (f ≥ 30% at least in one community and recorded at least in 4 communities) are provided at the bottom of the table, sorted by decreasing frequency. Communities: 1 – *Cornus mas-Carpinus betulus*, 2 – *Zelkova carpinifolia-Carpinus betulus*, 3 – *Quercus macranthera-Carpinus betulus*, 4 – *Clinopodium umbrosum-Carpinus betulus*, 5 – *Hedera pastuchovii-Carpinus betulus*, 6 – *Valeriana tiliifolia-Ulmus glabra*, 7 – *Hedera pastuchovii-Acer velutinum*.

Community	1	2	3	4	5	6	7
Number of relevés	16	4	16	25	8	25	16
Lathyro-Carpinetalia betuli							
Viola alba	75	100	50	92	75	20	38
Quercus petraea s. *iberica*	81	100	38	40	.	.	13
Crataegus germanica	56	.	6	48	50	.	.
Prunus avium	63	50	69	56	38	16	13
Acer campestre	69	25	38	40	38	8	6
Carex sylvatica	13	75	.	72	13	.	6
Oplismenus hirtellus s. *undulatifolius*	.	.	.	**76**	13	.	.
Carpinus betulus	100	100	94	92	100	52	88
Sanicula europaea	44	.	38	56	.	8	6
Geum urbanum	6	25	25	40	13	.	.

Table 1 (continued)

Community	1	2	3	4	5	6	7
Number of relevés	16	4	16	25	8	25	16
Clinopodium umbrosum	31	.	13	72	50	.	25
Pyrus communis	38	.	31	20	.	.	.
Campanula rapunculoides	75	75	75	48	25	40	.
Aceretalia pseudoplatani							
Asplenium scolopendrium	6	.	.	44	13	68	**100**
Polystichum braunii	.	.	.	12	.	48	63
Polystichum aculeatum	.	.	.	32	25	48	**88**
Asplenium trichomanes	19	.	25	36	25	84	56
Aruncus dioicus	.	.	6	.	13	**64**	6
Polygonatum multiflorum	6	.	56	4	25	**96**	13
Cystopteris fragilis	6	.	25	.	.	**72**	6
Corylus avellana	50	.	56	64	100	100	81
Sambucus nigra	.	.	.	32	13	56	38
Onoclea struthiopteris	.	.	.	.	.	24	25
Pachyphragma macrophylla	.	.	.	12	50	24	69
1. *Cornus mas-Carpinus betulus* community							
Cornus mas	**81**	.	6	32	.	4	13
Euonymus verrucosus	**44**	.	6	.	.	.	.
Physospermum cornubiense	**31**	.	.	.	.	.	.
Vincetoxicum hirundinaria	**50**	.	13	12	.	.	.
Sorbus torminalis	50	25	.	8	.	.	.
Helleborus orientalis	31	.	.	8	.	.	.
Polygonatum glaberrimum	44	.	19	4	.	.	6
Securigera varia	38	.	19	4	.	.	.
Euonymus latifolius	63	.	44	12	13	20	6
Carex digitata	69	.	38	12	25	44	.
Lonicera caucasica	44	.	31	8	.	8	.
2. *Zelkova carpinifolia-Carpinus betulus* community							
Piptatherum virescens	.	**75**	.	.	.	.	.
Zelkova carpinifolia	.	**75**	.	.	.	.	.
Ligustrum vulgare	50	**100**	.	8	.	.	.
Klasea quinquefolia	19	**75**	.	8	.	.	.
Lathyrus laxiflorus	19	**75**	13	8	.	.	.
Lonicera caprifolium	44	**100**	25	24	13	28	.
Brachypodium sylvaticum	19	100	56	64	25	28	.
Carex michelii	31	50	.	8	.	.	.
Drymochloa drymeja	31	100	44	44	63	24	13
Melica uniflora	6	50	13	8	13	8	6
3. *Quercus macranthera-Carpinus betulus* community							
Quercus macranthera	.	.	**44**	.	.	.	.
Fragaria vesca	19	.	**75**	24	.	8	.
Poa nemoralis	6	.	**75**	20	.	44	.
Carex humilis	6	.	31	.	.	.	.

Table 1 (continued)

Community	1	2	3	4	5	6	7
Number of relevés	16	4	16	25	8	25	16
Rosa canina aggr.	13	.	56	32	.	4	6
Sorbus aucuparia	6	.	38	.	.	12	.
Solidago virgaurea	6	.	56	16	.	36	.
Campanula alliariifolia	38	.	50	.	.	8	.
Clinopodium vulgare	19	.	38	.	.	4	.
4. *Clinopodium umbrosum-Carpinus betulus* community							
Diospyros lotus	6	.	.	**64**	.	4	6
Calystegia silvatica	6	.	.	**56**	13	12	.
Prunella vulgaris	.	.	13	**40**	.	.	.
Luzula forsteri	.	.	.	32	.	.	6
Torilis japonica	.	.	13	36	.	4	.
Castanea sativa	.	.	.	40	25	4	13
6. *Valeriana tiliifolia-Ulmus glabra* community							
Geranium robertianum	13	.	38	56	13	84	19
Impatiens noli-tangere	.	.	6	8	.	40	6
Paris incompleta	.	.	25	8	.	44	.
Salvia glutinosa	25	.	69	52	38	96	38
Urtica dioica	.	.	13	16	.	48	19
Acer platanoides	.	.	13	4	.	32	.
Scutellaria altissima	6	.	13	.	.	32	.
Arum maculatum aggr.	.	.	6	24	.	40	6
Pimpinella tripartita	13	.	19	.	.	36	.
7. *Hedera pastuchovii-Acer velutinum* community							
Philadelphus coronarius	.	.	.	.	.	.	**50**
Acer velutinum	.	.	.	4	38	.	50
Dryopteris borreri	.	.	.	8	.	4	31
Species diagnostic for two communities							
Rubus subgen. *Rubus*	.	.	6	36	100	24	81
Hedera pastuchovii	25	25	.	48	88	12	100
Other common species (f ≥ 30% in any community, recorded in ≥ 4 communites)							
Acer cappadocicum	94	25	50	44	75	56	31
Galium odoratum	50	.	69	40	50	88	25
Fagus orientalis	81	.	75	56	75	44	13
Tilia begoniifolia	50	25	.	52	75	36	81
Fraxinus excelsior	75	75	38	20	63	64	19
Ulmus glabra	13	.	13	36	63	76	13
Polypodium vulgare	19	.	25	24	38	52	56
Dryopteris filix-mas	.	.	25	56	50	56	13
Dioscorea communis	38	.	38	56	13	36	.
Cornus sanguinea	75	50	19	36	38	12	13
Lapsana communis	31	.	50	52	13	20	6
Circaea lutetiana	6	.	.	40	13	44	44
Moehringia trinervia	.	.	38	56	38	16	19

Viola reichenbachiana	13	75	13	44	50	16	19
Sedum stoloniferum	13	.	50	40	.	32	.
Carex muricata aggr.	6	50	.	64	38	4	6
Veronica peduncularis	44	.	50	8	.	24	.
Lactuca muralis	13	.	31	20	.	40	6
Potentilla micrantha	6	.	19	44	25	20	6
Primula veris s. *macrocalyx*	19	.	38	12	.	32	6
Euonymus europaeus	13	.	.	16	13	36	25
Crataegus monogyna aggr.	44	25	13	32	.	4	.
Smilax excelsa	6	50	.	48	.	8	13
Primula acaulis	31	.	19	28	.	8	6
Asplenium adiantum-nigrum	19	25	.	32	25	.	19
Carpinus orientalis	50	50	.	8	.	4	.

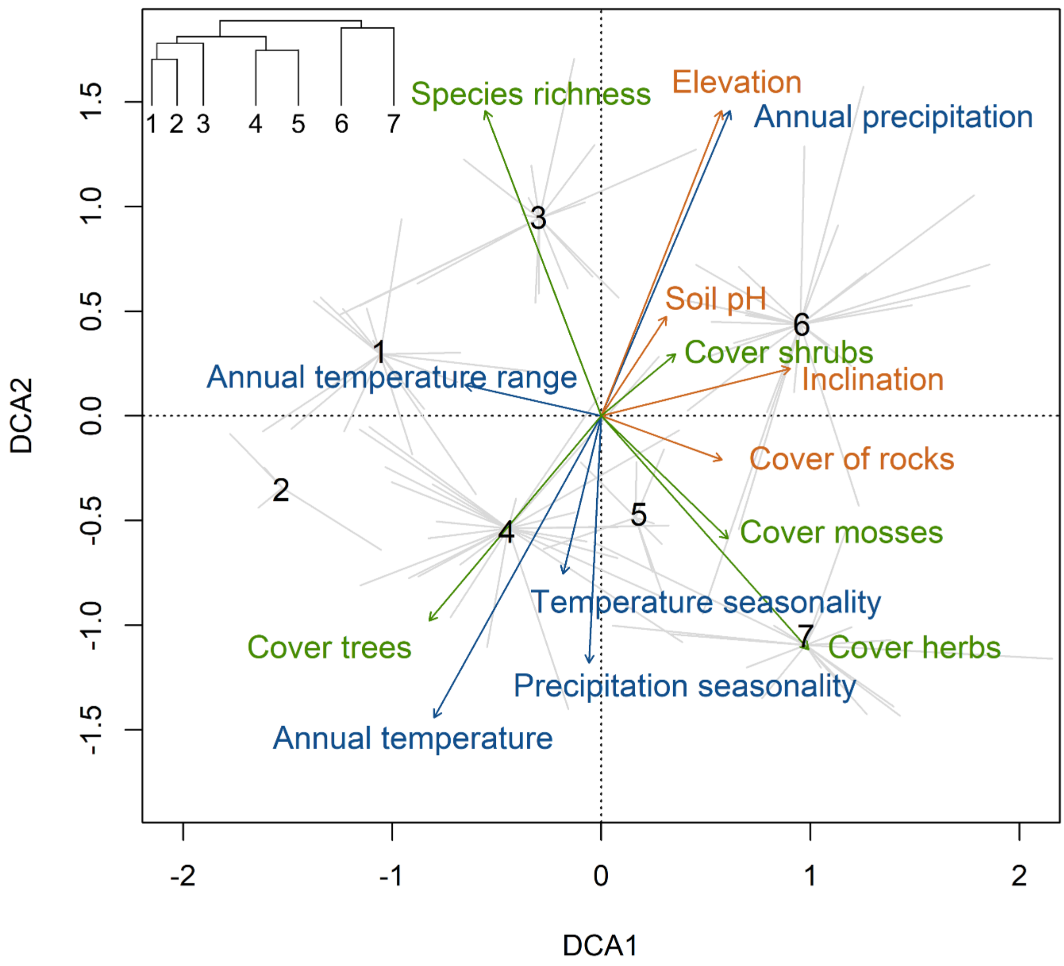

Fig 2 DCA ordination of the dataset of original relevés (n = 110). The first two ordination axes are shown. The first axis explains 5.98%, the second one 4.90% of the variance in species composition of the dataset. Basic environmental and vegetation structure variable vectors were passively plotted. Communities: 1 – *Cornus mas-Carpinus betulus*, 2 – *Zelkova carpinifolia-Carpinus betulus*, 3 – *Quercus macranthera-Carpinus betulus*, 4 – *Clinopodium umbrosum-Carpinus betulus*, 5 – *Hedera pastuchovii-Carpinus betulus*, 6 – *Valeriana tiliifolia-Ulmus glabra*, 7 – *Hedera pastuchovii-Acer velutinum*

Ordination

Similarly to the unsupervised classification, DCA revealed a clear pattern distinguishing between *Lathyro-Carpinetalia* and *Aceretalia* forests along the first ordination axis. It shows that *Aceretalia* forests favour steeper slopes with a higher cover of rocks. The second ordination axis represents a complex gradient of elevation and related increasing annual precipitation and decreasing annual temperature together with precipitation and temperature seasonality. Montane communities (1,3) are therefore situated in the upper part of the diagram and communities of lower elevations in the lower part.

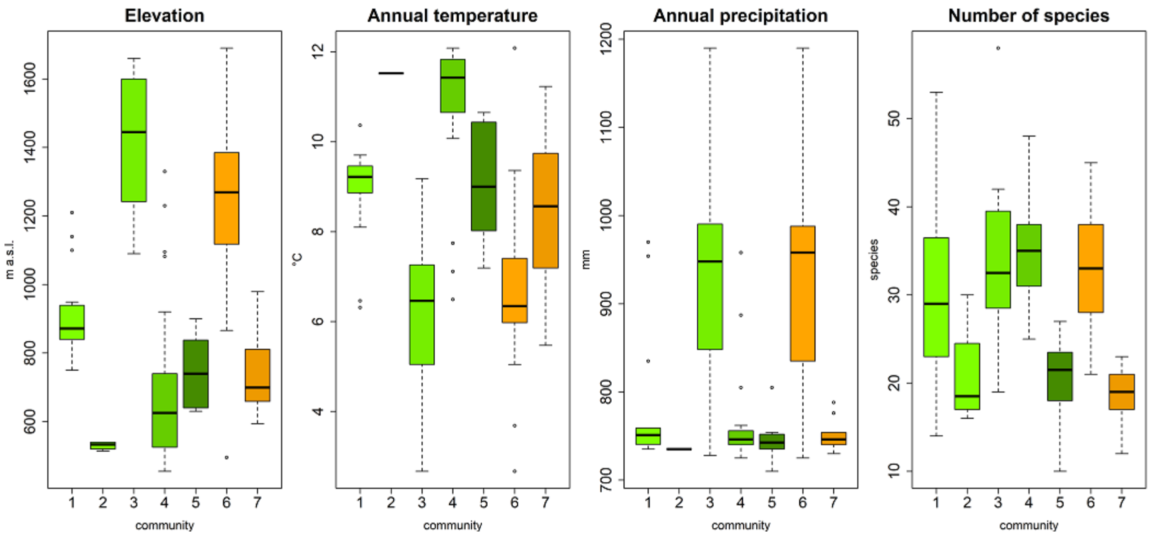

Fig 3 Comparison of the selected of selected environmental variables and number of species among the communities in the original dataset. Boxes indicate 25–75% interquartile range with their median (bold line), whiskers show the range of values, outliers are also provided. Communities: 1 – *Cornus mas-Carpinus betulus*, 2 – *Zelkova carpinifolia-Carpinus betulus*, 3 – *Quercus macranthera-Carpinus betulus*, 4 – *Clinopodium umbrosum-Carpinus betulus*, 5 – *Hedera pastuchovii-Carpinus betulus*, 6 – *Valeriana tiliifolia-Ulmus glabra*, 7 – *Hedera pastuchovii-Acer velutinum*

The expanded dataset

In order to evaluate the position of the studied vegetation in a context of mesophilous deciduous vegetation of Transcaucasia, we analysed an expanded dataset containing both our original relevés and relevés from the literature (221 relevés in total). The classification analysis setting was the same as for the original dataset. We recognized eleven clusters. The results are summarized in an ordination diagram (Figure 4).

The first ordination axis mainly represents a biogeographical gradient connected with macroclimate and vegetation history.The Caucasian forests are situated to the right side, while forests recorded in Kakheti, a Caucasian region enriched by the Colchic-Hyrcanian floral element, are situated to the center. Colchic forests are grouped to the left side. The second axis likely corresponds to a gradient of productivity as it is strongly correlated with cover of herb layer. Forests with nutrient- and moisture-demanding forbs and shade-tolerant nitrophytes are grouped to the upper part of the diagram while forests of drier soils are at the bottom.

These results revealed a clear difference between Colchic types (clusters 7, 8 and 9) and Caucasian types (other clusters) of forest vegetation, at least in the context of the analysis. Within the Caucasian vegetation, there is a clear separation of beech forests (clusters 10 and 11), ravine (clusters 1, 3) and oak-hornbeam (clusters 2, 4, 5, 6) forests.

The majority of communities described in our dataset were well-reproduced by the unsupervised classification of the broader dataset. Regarding oak-hornbeam forests, the Kakhetian communities (*Clinopodium umbrosum-Carpinus betulus*, *Hedera pastuchovii-Carpinus betulus*) formed own cluster 2. The montane *Quercus macranthera-Carpinus betulus* community was grouped with Passarge's associations recorded at high elevations (*Astrantio-Carpinetum*, *Clinopodio-Carpinetum*, *Rhododendro-Carpinetum*) in cluster 4. The *Cornus mas-Carpinus betulus* community and the *Zelkova carpinifolia-Carpinus betulus* community were included in cluster 6, with one of Passarge's relevés of the association *Corno-Carpinetum*. The rest of its relevés were unified in cluster 5. The Caucasian ravine forests (clusters 1, 3) formed two sharp clusters identical to the communities distinguished in the original dataset. Colchic forests are rather separated (clusters 7, 8, 9).

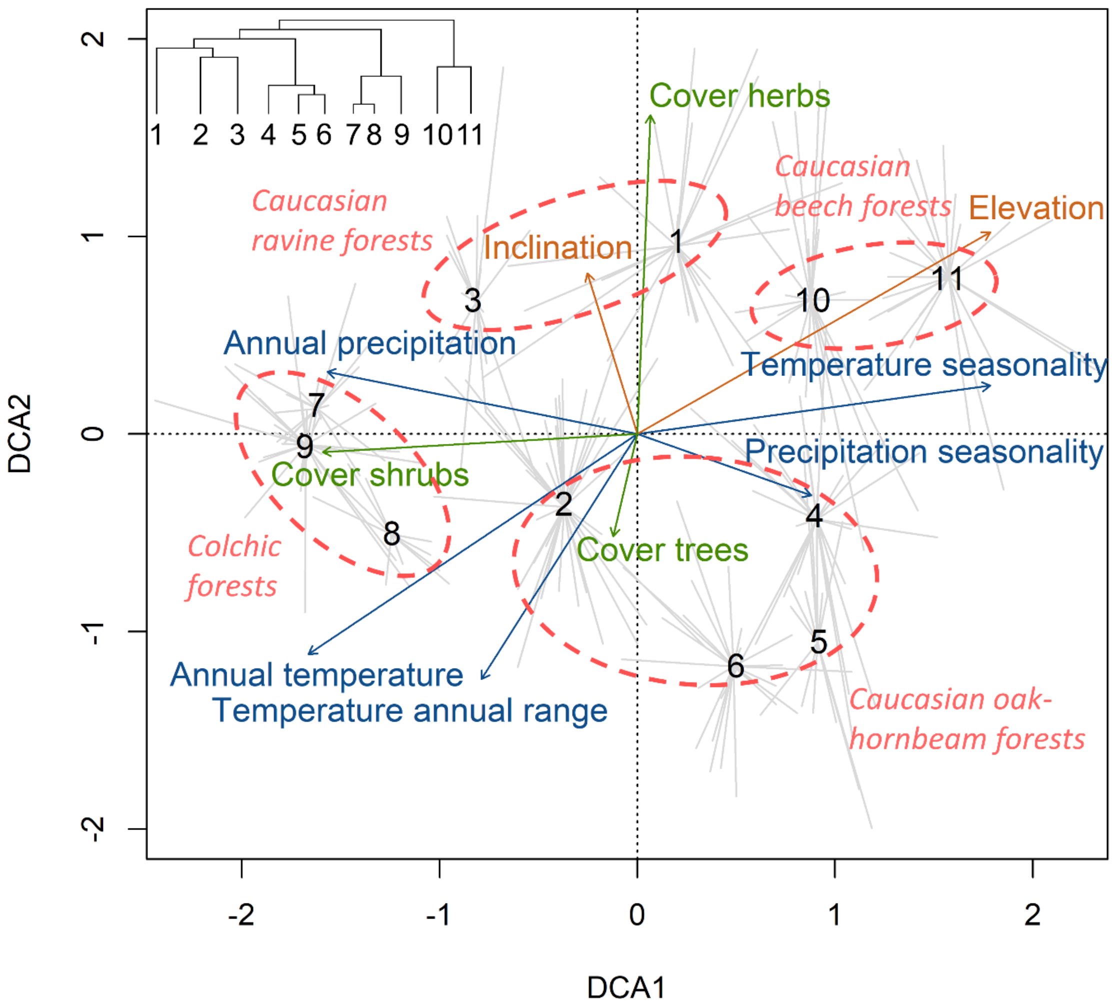

Fig 4 DCA ordination of the broader dataset (n = 231). The first two ordination axes are shown. The first axis explained 4.96%, the second one 4.08% of the variance in species composition of the dataset. Basic environmental and vegetation structure variable vectors were passively plotted. Principal groups of the clusters are indicated by the dashed lines

4. Discussion

Species composition and species richness

Most of the studied communities have a mean species richness exceeding 30 species per plot. The lowest species richness was recorded within the communities from Kakheti. Local ravine and nutrient-rich oak-hornbeam forests, with the mean number of species per relevé 18.3, resp. 20.4 were apparently species-poor. A climate with hot summers and mild winters resulted in the dominance of species with high ability of clonal spreading (*Hedera pastuchovii*, *Rubus* subgen. *Rubus*), especially observed in sheltered valleys with higher air humidity as reported also by Dolukhanov (2010). It is partly analogical to the situation in some Colchic forests where the thick evergreen shrub layer suppresses the development of the herb layer (Korotkov 1995; Novák et al. 2019). Lack of patches with developed soils may also play a role. The *Zelkova carpinifolia-Carpinus betulus* community was also species-poor (20.8). It is probably due to summer drought periods which are strengthened on the sunny slopes where this community was recorded. Compared to the thermophilous oak forests, *Carpinus* spp. and *Zelkova carpinifolia* often form dense canopy reducing light in the herb layer. A combination of such stress factors may lead to the low species richness, at least in summer aspect.
Alien species (sensu Kikodze et al. 2009) are much less frequent in the studied forests compared to the Colchic ones (Novák, Zukal et al. 2019). This is presumably due to the fact that the study region was much less affected by the introduction of subtropical crops (e.g. bamboos, citruses, tea) with which numerous aliens were unintentionally brought to Colchis (Nakhutsrishvili 2013; Akhalkatsi 2015). The shallowly rooted perennial grass *Oplismenus hirtellus* subsp. *undulatifolius* is the only frequent alien taxon recorded in the sampled vegetation. It can intensively invade forests via stolons. Spreading over large distances is provided by epizoochory (Beauchamp and Koontz 2013). However, it was recorded only in the Kakhetian mesophilous oak-hornbeam forests (reported also by Dolukhanov 2010) where it is still apparently less frequent than in Colchis (cf. Novák et al. 2019).

Syntaxonomy of oak-hornbeam forests

For the Caucasian oak-hornbeam forests, Passarge (1981a) described a separate order *Lathyro-Carpinetalia*. His concept was accepted in the EuroVegChecklist (Mucina et al. 2016) where *Lathyro-Carpinetalia* stands next to the order *Carpinetalia betuli* unifying oak-hornbeam forests of the rest of Europe. However, *Lathyro-Carpinetalia* is an invalid name (Art. 3g). Çoban and Willner (2019) proposed to merge these two orders since Caucasian oak-hornbeam forests lack their own dominant tree species. Its key species *Carpinus caucasica* is mostly supposed to be conspecific with *C. betulus* (Holstein and Weigend 2017). Recent numerical analyses of the variability of oak-hornbeam forests across the whole of Europe and surroundings (Novák and data contributors 2019) also supported the unification of these two orders.

At the level of alliance, both units described by Passarge, the zonal alliance *Crataego-Carpinion* and the high-elevation alliance *Astrantio-Carpinion*, were adopted in the EuroVegChecklist. The former contains only one validly described association *Corno-Carpinetum* while the other two (*Clinopodio-Carpinetum*, *Rhododendro-Carpinetum*) are invalid (§ 3b). These two associations were mentioned together with *Astrantio-Carpinetum* (*Astrantio-Carpinion*) as oak-hornbeam forests of the higher elevations, although classified within the *Crataego-Carpinion*. In our paper, we provisionally keep the concept of two Caucasian alliances since these forests are still very undersampled, especially the high-elevation types which are supposed to be natural vegetation across waste regions of the Caucasus (Bohn et al. 2000–2003; Dolukhanov 2010; Nakhutsrishvili 2013). Moreover, high-elevation oak-hornbeam forests are a rather unique feature of the Caucasus. Probably the only analogy reported so far are mixed forests of *Carpinus betulus* and *Quercus macranthera* described from the mountains of northern Iran (Gholizadeh et al. 2020).

The correct name of the *Crataegus* species in the alliance *Crataego-Carpinion* needs further investigation. In its type association, the *Corno-Carpinetum*, Passarge (1981a) recorded a single *Crataegus* species, "*Crataegus* cf. *kyrtostyla*". Passarge cited the compendium Flora of the Caucasus (Fedorov 1952) as the nomenclature source, and in this publication, *C. kyrtostyla* is the (probably misapplied; Euro+Med 2006-) name for *C. rhipidophylla*. Therefore, if we accept Passarge's determination as correct, since *C. rhipidophylla* is a common member of the Transcaucasian forests (Fedorov 1952), the full alliance name must be corrected to *Crataego rhipidophyllae-Carpinion caucasicae* nom. corr. (Art. 44).

Oak-hornbeam and ravine forests recorded in Kakheti (comm. 2, 4, 5, 7) show a significant level of Hyrcanian floristic influence. However, they lack numerous diagnostic species of the Hyrcanian forests, including both woody (e.g. *Alnus subcordata*, *Parottia persica*, *Quercus castaneifolia*) and herb (e.g. *Danae racemosa*, *Ruscus hyrcanus*) species (Gholizadeh et al. 2020). Therefore, we assign them into the Caucasian higher syntaxa rather than Hyrcanian ones.

The analysis of the broader dataset confirmed that the Caucasian oak-hornbeam forests (clusters 2, 4, 5, 6) differ from the Colchic ones (clusters 8, 9) growing along the southern coast of the Black Sea, unified under the alliance *Castaneo-Carpinion* (or *Trachystemono orientalis-Carpinion*, see Çoban and Willner 2019). The most important feature of the Colchic forests, relict evergreen shrubs (e.g. *Ilex colchica*, *Osmanthus decorus*, *Rhododendron ponticum*, *Rh. ungernii*), are almost absent in the Caucasian types. In Eastern Transcaucasia, the evergreen Colchic liana *Hedera colchica* is substituted by closely related *Hedera pastuchovii* (Nakhutsrishvili 2013). *Castanea sativa*, a very frequent companion of *Carpinus betulus* in the Colchic oak-hornbeam forests, is rather scarce in the Caucasian ones (Dolukhanov 2010). However, there are some common species in the herb layer (e.g. *Clinopodium umbrosum*, *Oplismenus hirtellus* subsp. *undulatifolius*). Accordingly, we classify the newly recorded communities within the Caucasian alliances of oak-hornbeam forests (see syntaxonomic scheme below). The *Clinopodium umbrosum-Carpinus betulus* community is described as a new association due to its genuine species composition combining typical species of the Caucasian mesophilous forests with species of Colchic-Hyrcanian or Hyrcanian-Eastern Caucasian distribution. The other two communities (1, 3) are identified with previously described associations by Passarge (1981a). The *Hedera pastuchovii-Carpinus betulus* community represents rather a transition between oak-hornbeam and ravine forests. The *Zelkova carpinifolia-Carpinus betulus* community contains xeromesophilous forests with *Zelkova carpinifolia*. Since it is geographically very limited and documented by only four relevés, we do not formally describe this unit as a new syntaxon and classify it directly under the order *Lathyro-Carpinetalia*.

Syntaxonomy of ravine forests

Caucasian ravine forests have not been phytosociologically studied so far. In Europe and surroundings, they are classified within the order *Aceretalia pseudoplatani*, comprising scree and ravine maple-lime forests of the nemoral zone of temperate Europe (Mucina et al. 2016). As Caucasian ravine forests are dominated by noble hardwood trees (even though frequently by different species of the same genera, including *Acer cappadocicum*, *A*. *velutinum* and *Tilia begoniifolia*) and many of characteristic species of ravine forests of the order *Aceretalia* occur in the undergrowth (e.g. *Aruncus dioicus*, *Asplenium scolopendrium*, *Dryopteris filix-mas*), we also classify them into this order.

Until now, only the association *Polysticho woronowii-Ulmetum glabrae* has been recognized in Georgia, describing Colchic ravine forests of the southwesternmost part of the country (Zukal in Novák et al. 2019). As *Alnus glutinosa* subsp. *barbata* and *Castanea sativa* are common tree dominants, it has been classified within the alliance *Alnion barbatae* including both Colchic ravine and riverine forests. Comparing Caucasian ravine forests with *Polysticho-Ulmetum*, they share several characteristics (e.g. similar site conditions, occurrence of noble hardwood trees and some other typical ravine forest species). On the other hand, there are also numerous differences: *Alnus glutinosa* subsp. *barbata* is much rarer in the Caucasian ravine forests, most probably due to drier climate (in Colchis, it occurs extensively on slopes even without springs, while in the Caucasus it is confined to the foot of slopes and the vicinity of rivers). Conversely, dominance of the endemic and subendemic Caucasian trees *Acer cappadocicum*, *A*. *velutinum* and *Tilia begoniifolia* is characteristic. Another striking differential feature of *Polysticho-Ulmetum* is the occurrence of evergreen shrubs that are missing in the Central Greater Caucasus. Clear differences can also be found in the herb layer, as there are numerous relict or endemic species that are rare or missing in Georgia outside Colchis (e.g. *Polystichum woronowii*, *Pteris cretica*, *Ruscus colchicus*, *Trachystemon orientalis*). Vice versa, the Caucasian types are richer in species of higher elevations (e.g. *Gentiana asclepiadea*, *Primula veris* subsp. *macrocalyx*, *Valeriana tiliifolia*) and in forest mesophytes of broad distribution ranges (e.g. *Galium odoratum*, *Polygonatum multiflorum*). Considering these differences, we describe ravine forests of the Caucasus as a new alliance with two associations.

5. Syntaxonomic outline

Syntaxonomic scheme

Carpino-Fagetea Jakucs ex Passarge 1968
Lathyro-Carpinetalia caucasicae Passarge 1981 *Crataego rhipidophyllae-Carpinion caucasicae* Passarge 1981 *nom. corr. hoc loco*
Corno australis-Carpinetum caucasicae Passarge 1981 (comm. 1)
Clinopodio umbrosi-Carpinetum betuli Novák *ass. nova hoc loco* (comm. 4)
Astrantio maximae-Carpinion caucasicae Passarge 1981
Astrantio maximae-Carpinetum caucasicae Passarge 1981 (comm. 3)
Aceretalia pseduoplatani Moor 1976
Pachyphragmo macrophyllae-Tilion begoniifoliae Zukal *all. nova hoc loco*.
Valeriano tiliifoliae-Ulmetum glabrae Zukal *ass. nova hoc loco* (comm. 6)
Hedero pastuchowii-Aceretum velutini Zukal *ass. nova hoc loco* (comm. 7)

Typification of the new syntaxa

***Crataego-Carpinion* Passarge 1981**
***Clinopodio umbrosi-Carpinetum betuli* Novák ass. nova hoc loco**; Community 4 in this study. Holotypus (hoc loco) of the association: Georgia, Lagodekhi district, Khizabavra: a slope above the N edge of the village, 630 m a.s.l. 41.8738889° N, 46.2391667° E. Relevé area: 10 m × 10 m; Aspect: 150°; Slope: 7°;

Soil pH: 5.84; Cover of rocks: 0%. Covers: tree layer 85%, shrub layer 15%, herb layer 30%, moss layer 2%. Recorded on August 3, 2018. Author: Pavel Novák.
Tree layer: *Carpinus betulus* 5, *Tilia begoniifolia* 2a;
Shrub layer: *Cornus sanguinea* 2a, *Pyrus communis* 1, *Prunus domestica* 1, *Castanea sativa* +, *Carpinus betulus* +, *Crataegus germanica* +, *Diospyros lotus* +, *Hedera pastuchovii* +, *Ulmus minor* +;
Herb layer: *Oplismenus hirtellus* subsp. *undulatifolius* 2a, *Hedera pastuchovii* 2m, *Carex muricata* aggr. 1, *C. sylvatica* 1, *Rubus* subgen. *Rubus* 1, *Viola alba* 1, *Brachypodium sylvaticum* +, *Clinopodium umbrosum* +, *Dryopteris filix-mas* +, *Glechoma hederacea* +, *Poa angustifolia* +, *Polystichum aculeatum* +, *Potentilla micrantha* +, *Schedonorus giganteus* +, *Smilax excelsa* +, *Cephalanthera longifolia* r, *Sanicula europaea* r; *Carpinus betulus* +, *Cornus sanguinea* +, *Crataegus germanica* +, *Diospyros lotus* +, *Prunus avium* +, *P. domestica* +, *Tilia begoniifolia* +.

***Pachyphragmo macrophyllae-Tilion begoniifoliae* Zukal all. nova hoc loco**.
Nomenclature type: *Hedero pastuchovii-Aceretum velutini* Zukal ass. nova (see below) (holotypus). Noble hardwood forests on steep slopes, in ravines and narrow valleys of the Greater Caucasus.

***Valeriano tiliifoliae-Ulmetum glabrae* Zukal ass. nova hoc loco**; Community 6 in this study. Holotypus (hoc loco) of the association: Georgia, Dusheti district, Vashlobi: forest on a slope above the left bank of the stream, 0.65 km NNW from centre of the village, 1268 m a.s.l. 42.2966667° N, 44.7286111° E. Relevé area: 12.5 m × 8 m; Aspect: 345°; Slope: 35°; Soil pH: 7.46; Cover of rocks: 20%. Covers: tree layer 85%, shrub layer 6%, herb layer 27%, moss layer 3%. Recorded on August 10, 2018. Author: Dominik Zukal.
Tree layer: *Carpinus betulus* 3, *Tilia begoniifolia* 2b, *Acer campestre* 2a, *Fagus orientalis* 2a, *Ulmus glabra* 2a;
Shrub layer: *Carpinus betulus* 1, *Corylus avellana* 1, *Sambucus nigra* 1, *Acer cappadocicum* +, *Euonymus latifolius* +, *Fraxinus excelsior* r;
Herb layer: *Pimpinella tripartita* 1, *Polystichum aculeatum* 1, *Primula veris* subsp. *macrocalyx* 1, *Salvia glutinosa* 1, *Viola odorata* 1, *Actaea spicata* +, *Aruncus dioicus* +, *Asplenium scolopendrium* +, *A. trichomanes* +, *Brunnera macrophylla* +, *Campanula rapunculoides* +, *Carex digitata* +, *Circaea lutetiana* +, *Dioscorea communis* +, *Galium odoratum* +, *Geranium robertianum* +, *Heracleum* sp. +, *Hordelymus europaeus* +, *Lactuca muralis* +, *Melica nutans* +, *Poa nemoralis* +, *Polygonatum multiflorum* +, *Sanicula europaea* +, *Scutellaria altissima* +, *Solidago virgaurea* +, *Valeriana tiliifolia* +, *Arum maculatum* agg. r, *Dipsacus pilosus* r, *Paris incompleta* r, *Polypodium vulgare* r, *Corylus avellana* +, *Fraxinus excelsior* r, *Sambucus nigra* r.

***Hedero pastuchovii-Aceretum velutini* Zukal ass. nova hoc loco**; Community 7 in this study. Holotypus (hoc loco) of the association: Georgia, Lagodekhi district, Khizabavra: a forest above the left bank of a brook, 2.7 km SW from Ninoskhevi waterfall, 646 m a.s.l. 41.8805556° N, 46.2447222° E. Relevé area: 10 m × 10 m); Aspect: 300°; Slope 40°; Soil pH: 6.08; Cover of rocks: 30°. Covers: tree layer 85%, shrub layer 6%, herb layer 75%, moss layer 10%. Recorded on August 3, 2018. Author: Dominik Zukal.
Tree layer: *Acer velutinum* 5, *Tilia begoniifolia* 1, *Carpinus betulus* +, *Hedera pastuchovii* +;
Shrub layer: *Euonymus latifolius* 1, *Philadelphus coronarius* 1, *Sambucus nigra* +;
Herb layer: *Hedera pastuchovii* 3, *Rubus* subgen. *Rubus* 2b, *Pachyphragma macrophylla* 2a, *Polystichum aculeatum* 2m, *Asplenium scolopendrium* 1, *Galium odoratum* 1, *Polystichum kadyrovii* 1, *Dryopteris borreri* +, *Geranium robertianum* +, *Onoclea struthiopteris* +, *Polystichum braunii* +, *Viola alba* +, *V. odorata* +; *Carpinus betulus* r.

Acknowledgement

For help with the fieldwork, we thank Kryštof Chytrý, Kamila Čížková, Anna Hlaváčková, Veronika Kalníková, Helena Prokešová, Vojtěch Sedláček and Ondřej Škeřík. Renata Piwowarczyk kindly determined herbarium specimens of the genus *Orobanche* and Naiba Mehdiyeva of the genus *Polystichum*. Hamid Gholizadeh provided notes on ecology of some species. This work was supported by the Czech Science Foundation under Grant EXPRO (GX19-28491X).

Author contribution

PN and DZ designed the study. PN, DZ, MH and PV participated in the field sampling. PN led the writing and did the numerical analyses. DZ wrote the parts dealing with ravine forests. MH prepared the map. OA provided data on ecology of some species and assisted to select sampling sites. WW significantly helped with the parts dealing with phytosociological nomenclature. All the authors critically revised the manuscript.

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7.4. Paper 4

Novák P. (2019): Proposals (23–25): to conserve the names *Galio-Carpinetum* Oberdorfer 1957, *Lithospermo-Carpinetum* Oberdorfer 1957 and *Stellario-Carpinetum* Oberdorfer 1957. – Phytocoenologia 49: 409–411.

Phytocoenologia Vol. 49 (2019), Issue 4, 419–421
Nomenclatural Proposal

Proposals (23–25): to conserve the names *Galio-Carpinetum* Oberdorfer 1957, *Lithospermo-Carpinetum* Oberdorfer 1957 and *Stellario-Carpinetum* Oberdorfer 1957

Pavel Novák

Submitted: 21 April 2019; first decision: 07 May 2019, accepted: 20 June 2019
Co-ordinating Editor: Wolfgang Willner

(23) *Galio sylvatici-Carpinetum betuli* Oberdorfer 1957: 424–435.
Typus: Oberdorfer (1952), Table 2, rel. 86a (lectotypus Willner & Grabherr 2007: 232).
(=) *Querco pedunculatae-Carpinetum betuli* Klika 1928: 34–37.
Typus: Klika (1928), Table on pp. 35–37, rel. 1 (lectotypus hoc loco).

(24) *Lithospermo-Carpinetum betuli* Oberdorfer 1957: 440–442. Typus: Issler (1926), Table 3, rel. 2 (typus cons. propos.).
(=) *Carpinetum betuli* Issler 1925: 276–279.
Typus: Issler (1925), rel. on pp. 278–279 (lectotypus hoc loco).

(25) *Stellario holostei-Carpinetum betuli* Oberdorfer 1957: 419–424.
Typus: see below.
(=) *Alno glutinosae-Carpinetum betuli* Issler 1926: 18–20, 22–25.
Typus: Issler 1926, Table 2, rel. 6 (lectotypus hoc loco).

I propose to conserve the names of three associations of the *Carpinion* alliance, all published in the influential monograph of the vegetation of southern Germany by Oberdorfer (1957). These proposals are based on an emerging study dealing with variability and syntaxonomy of Central European oak-hornbeam forests (e.g. Novák et al. 2018). The taxonomic nomenclature used follows The Plant List (2019).

(23) *Galio-Carpinetum* Oberdorfer 1957

The first proposal is dealing with mesophytic oak-hornbeam forests of the western and central parts of Central Europe, traditionally unified under the name *Galio-Carpinetum* Oberdorfer 1957 (e.g. Willner & Grabherr 2007, Chytrý 2013). They are rich in forest mesophytes including species with a distribution centre in Central Europe (e.g. *Galium sylvaticum* and *Hepatica nobilis*). At the same time, they are characterized by the absence, or rare occurrence, of the diagnostic species of the other Central European *Carpinion* associations. As indicated by Moravec et al. (1982), "*Querceto pedunculatae-Carpinetum*" [recte: *Querco pedunculatae-Carpinetum*] Klika 1928 is the oldest valid name for such forests, since Klika (1928) published this name for the mesophytic oak-hornbeam forests of the Bohemian Karst in Central Bohemia (Czech Republic). However, this name was rarely used in the sense of Klika's concept (e.g. Husová 1968). *Quercus pedunculata* Hoffm. is a later synonym of *Q. robur* L., and many authors, mostly from Hungary and Slovakia (e.g. Soó 1962, Berta 1970), applied the name *Querco roboris-Carpinetum* for hygrophytic oak-hornbeam forests. Chytrý (2013) proposed to conserve the name *Galio-Carpinetum* Oberdorfer 1957 against *Querco* *pedunculatae-Carpinetum* Klika 1928. However, to date the proposal has not been submitted to the Working Group for Phytosociological Nomenclature for evaluation.

(24) *Lithospermo-Carpinetum* Oberdorfer 1957

This proposal concerns thermophytic oak-hornbeam forests of southwestern Central Europe and the adjacent parts of France. Their tree layer is dominated by *Carpinus betulus* and *Quercus petraea* with *Acer campestre*, *Fagus sylvatica*, *Fraxinus excelsior* and *Sorbus aria* in admixture. They often have an extraordinarily species-rich shrub layer, containing both mesophytes and some thermophilous species indicating submediterranean influences (e.g. *Hippocrepis emerus*). Their herb layer is characterised by a co-occurrence of submediterranean (e.g. *Helleborus foetidus*) and suboceanic (e.g. *Potentilla sterilis*) species. Such forests were first described by Issler (1924, 1925, 1926) in his pioneering studies from the Upper Rhine Valley (France–Germany border). However, apart from Issler's later study (Issler 1931), this name has never been applied in its original sense. For instance, Domin (1928) used a heterotypic homonym for mesophytic hornbeam forests of Central Bohemia. Later on, the forest type reported by Issler was described by Oberdorfer (1957) as a new association *Lithospermo-Carpinetum*, while "*Carpinetum betuli* Issl. 24" was cited in brackets below the name of this new association. In the bibliography Oberdorfer gave the three parts of Issler's study, published between 1924 and 1926, as a single reference. In the first part, Issler (1924) provided only a species list with the range of cover values of this association ("Association à *Carpinus betulus*"). A sufficient diagnosis, including a relevé table, was provided in the third part (Issler 1926). However, Issler published the name with a sufficient original diagnosis in another study (Issler 1925). Therefore, the *Carpinetum betuli* Issler 1926 is a homotypic younger homonym. The two names of Issler are homotypic because the type relevé of the *Carpinetum betuli* Issler 1925 is part of the table published in Issler (1926). Oberdorfer included only five of Issler's relevés (from Issler 1926) in the synoptic table, together with two unpublished relevés that he recorded. However, it is clear from the synoptic table that the type relevé of the *Carpinetum betuli* Issler 1925 was included by Oberdorfer. Moreover, the *Carpinetum betuli* Issler is cited as a synonym. Therefore, Oberdorfer's *Lithospermo-Carpinetum* is a nomen superfluum, and therefore automatically typified by Issler's earlier name (Art. 18b). Unfortunately, unlike the other relevés of Issler's table, the relevé published by Issler in 1925 (identical to rel. 4 in Issler 1926) does not contain *Lithospermum purpurocaeruleum* (= *Buglossoides purpurocaerulea*), which obviously was intended by Oberdorfer as the name-giving species of the *Lithospermo-Carpinetum* (he mentions it as a character species of the association), but instead *Lithospermum officinale* was recorded. Therefore, I propose a different type for the *Lithospermo-Carpinetum* Oberdorfer 1957 and at the same time I ask for a binding decision to clarify the name-giving *Lithospermum* species in Oberdorfer's association name.

The *Lithospermo-Carpinetum* was not adopted in later German vegetation overviews (e.g. Schubert et al. 2001), either because it was not considered to be present in Germany or because it was included in the *Galio sylvatici-Carpinetum*. However, these forests were reported under the name *Lithospermo-Carpinetum* in works from northeastern France (e.g. Boeuf et al. 2014). Since the re-introduction of the oldest valid name for these forests, *Carpinetum betuli* Issler 1925, would contradict the intention of the Code to promote nomenclatural stability, I propose to conserve the name *Lithospermo-Carpinetum* Oberdorfer 1957.

(25) *Stellario-Carpinetum* Oberdorfer 1957

The last proposal is focused on Central European hygrophytic oak-hornbeam forests. They are usually dominated by *Carpinus betulus* and *Quercus robur*. Besides mesophytes, their shrub and herb layers contain many nutrient- and moisture-demanding species (e.g. *Euonymus europaeus*, *Ficaria verna*, *Glechoma hederacea* and *Sambucus nigra*). They are distributed in the northwestern part of Central Europe since they prefer flat landscapes with rather moist, often poorly-drained soils (plateaus, upper river terraces etc.). They were first described by Issler (1926) as "association à *Alnus glutinosa* et à *Carpinus betulus*" [recte: *Alno glutinosae-Carpinetum betuli*]. However, similarly to his *Carpinetum betuli* discussed above, it was later used only by himself (e.g. Issler 1931) in this sense. Afterwards, homonyms were introduced (e.g. Hargitai 1942) for different vegetation types. Oberdorfer (1957) described similar forests as a new association *Stellario-Carpinetum*, describing them as a subatlantic oak-hornbeam forest. However, in the published synoptic tables, there are nearly no subatlantic species, except *Arum maculatum* and *Potentilla sterilis*, while broadly distributed nemoral species, including nutrient- and moisture-demanding ones, prevail. The name was adopted for hygrophytic oak-hornbeam forests across most Central European countries (e.g. Willner & Grabherr 2007, Chytrý 2013). Therefore, I propose to conserve it against the older, but hardly ever used name *Alno-Carpinetum* Issler 1926.
Oberdorfer (1957) based his synoptic tables on his own relevés, which have never been published and which are currently not available (they might still exist in the archive of the State Museum of Natural History Karlsruhe; Jörg Ewald, pers. comm.). However, Oberdorfer also made a reference to the manuscript of Knapp (1946), where 16 relevés of this association were presented under the name "*Querceto-Carpinetum mogontiacense*". Since this manuscript is not effectively published (Art. 1), I present here one of the Knapp's relevés as neotypus:

Stellario-Carpinetum Oberdorfer 1957, neotypus hoc loco:
Knapp (1946), Table 7, rel. 13, Mönchbruch (Germany, distr. Gross-Gerau), 90 m a.s.l., 1000 m^2; Tree layer (90%): *Carpinus betulus* 5, *Quercus robur* 2; Herb layer (70%): *Melica uniflora* 3, *Brachypodium sylvaticum* 2, *Dactylis glomerata* v. *pendula* [= *Dactylis glomerata* subsp. *lobata*] 1, *Deschampsia cespitosa* 1, *Glechoma hederacea* 1, *Maianthemum bifolium* 1, *Milium effusum* 1, *Oxalis acetosella* 1, *Vicia sepium* 1, *Viola silvatica* [= *V. reichenbachiana*] 1, *Ajuga reptans* +, *Alliaria officinalis* [= *Alliaria petiolata*] +, *Anemone nemorosa* +, *Campanula trachelium* +, *Carex remota* +, *Carex sylvatica* +, *Carpinus betulus* +, *Cicerbita muralis* [= *Lactuca muralis*] +, *Fagus sylvatica* +, *Fraxinus excelsior* +, *Geranium Robertianum* +, *Hedera helix* +, *Lysimachia nummularia* +, *Moehringia trinervia* +, *Myosotis sylvatica* +, *Poa nemoralis* +, *Quercus robur* +, *Stellaria holostea* +, *Veronica chamaedrys* +, *Viola riviniana* +, *Athyrium filix femina* [= *Athyrium filix-femina*] r, *Cardamine impatiens* r, *Circaea lutetiana* r, *Crataegus oxyacantha* [= *Crataegus laevigata*] r, *Dryopteris filix mas* [= *Dryopteris filix-mas*] r, *Geum urbanum* r, *Urtica dioica* r. Moss layer (2%): *Mnium undulatum* [= *Plagiomnium undulatum*] 1, *Catharinea undulata* +, *Eurhynchium* spec. +, *Mnium* spec. +.

Acknowledgement
I thank Milan Chytrý and Wolfgang Willner for valuable comments on a previous version of the proposal and Jörg Ewald for providing information concerning Oberdorfer's unpublished relevés. The study was supported by the Czech Science Foundation (project GX19-28491X).

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7.5. Paper 5

Novák P., Willner W., Zukal D., Kollár J., Roleček J., Świerkosz K., Ewald J., Wohlgemuth T., Csiky J., Onyshchenko V. & Chytrý M. (2020): Oak-hornbeam forests of central Europe: A formalized classification and syntaxonomic revision. – Preslia 92: 1–34.

Oak-hornbeam forests of central Europe: a formalized classification and syntaxonomic revision

Dubohabřiny střední Evropy: formalizovaná klasifikace a syntaxonomická revize

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Oak-hornbeam forests (order *Carpinetalia*) are a widespread vegetation type in central Europe. As vegetation ecologists focused on them since the pioneering times of vegetation research, many syntaxonomic units are described. However, classification systems used in various central-Euro-pean countries suffer from inconsistencies and overlaps of the concepts of particular associations. Currently there is no consistent syntaxonomic system based on numerical analysis of vegetation plots that would be valid for the whole of central Europe. Therefore, the main goal of this study is to provide a revised syntaxonomic system of oak-hornbeam forests across central Europe, develop formal definitions of the associations and include these definitions in a classification expert sys-tem. We recognized 13 associations, 9 from the alliance *Carpinion betuli* (central-European oak-hornbeam forests) and four from the alliance *Erythronio-Carpinion* (Illyrian and northern Italian oak-hornbeam forests). We prepared an expert system that classified 55% of the relevés in a cen-tral-European oak-hornbeam forest dataset (n = 6212) at the association level. To stabilize the *Carpinion betuli* association names, we selected nomenclatural type relevés for associations that have not been typified so far. In addition, two association names (*Poo chaixii-Carpinetum* and *Pseudostellario-Carpinetum*) were validated. Ordination revealed the main drivers of species

doi: 10.23855/preslia.2020.001

diversity in these forests, including a complex gradient of soil moisture, nutrient availability and geographical position (mainly latitude). Among the climate variables, annual temperature amplitude and mean annual temperature were most closely correlated with species composition.

K e y w o r d s: *Carpinetalia betuli*, *Carpinion betuli,* classification expert system, *Erythronio-Carpinion*, formalized vegetation classification, syntaxonomy, temperate broad-leaved deciduous forests

Introduction

Vegetation surveys are important instruments for basic ecological and biodiversity research, nature conservation and environmental monitoring. Several comprehensive national classification systems of forest vegetation have been published in central Europe recently (e.g. Willner & Grabherr 2007, Jarolímek et al. 2008, Niemeyer et al. 2010, Borhidi et al. 2012, Chytrý 2013). However, there is an increasing need for international classification schemes and surveys spanning large regions, which could be implemented into habitat classifications used in the European Union and beyond (Rodwell et al. 2018). Development of vegetation databases and related ecoinformatic tools make it possible to base such analyses on large sets of vegetation plots. Several studies systematically describing the variability of certain vegetation types across large areas were published over the last decade (e.g. Košir et al. 2013, Douda et al. 2016, Peterka et al. 2017, Willner et al. 2017, 2019, Marcenň et al. 2018, 2019). Although the EuroVegChecklist (Mucina et al. 2016) provides a coherent classification of European vegetation to the level of classes, orders and alliances, many unresolved issues still remain. Moreover, association-level classifications across broad geographical scales are still lacking for most vegetation types, including oak-hornbeam forests.

Oak-hornbeam forests are traditionally recognized as mesophytic mixed forests in which oaks (*Quercus petraea* agg., *Q. robur*) and common hornbeam (*Carpinus betulus*) play a prominent role. The co-occurrence of light-demanding oaks and shade-tolerant tree species such as hornbeam is usually ascribed to former management practices including coppicing with standards, livestock grazing and litter raking (e.g. Jakubowska-Gabara 1996, Vera 2000, Chytrý 2013, Müllerová et al. 2015). Other trees, e.g. *Acer campestre*, *A. platanoides*, *Prunus avium*, *Tilia cordata* and *Ulmus minor*, are frequently admixed or even dominate in some types. Forest mesophytes (also called nemoral species) are characteristic of the shrub and herb layers (Neuhäusl 1977, Leuschner & Ellenberg 2017).

The estimated potential distribution of oak-hornbeam forests in central Europe is ~240,000 km^2 (i.e. about a quarter of the region), the second largest after beech forests (Bohn et al. 2000–2003). Also in current vegetation, they are one of the most frequent for-est types. They occur mainly at low altitudes up to 500 m, growing on a broad range of soil types, from basic to acidic, usually mesotrophic or eutrophic. They are more common in areas with a subcontinental climate, i.e. low annual precipitation, summer droughts, early or late frosts and other climatic features to which hornbeam is better adapted than the competitively superior but sensitive beech (Leuschner & Ellenberg 2017). Traditional forest management has presumably favoured an expansion of oak-hornbeam forests at the expense of beech forests since hornbeam and some associated tree species have a higher stump-sprouting ability than beech (Neuhäusl 1977, Vera 2000, Leuschner & Ellenberg 2017). Oak-hornbeam forests (EUNIS habitat T1E) are a Near Threatened habitat according to the European Red List of Habitats (Janssen et al. 2016). Some types of these forests are priority habitats in Annex I of the European Habitats Directive. As they occur at low altitudes, they are strongly affected by human activities, including cutting and transformation to arable land or plantations of conifers or black locust, or by an overabundance of wild ungulates (Herbich 2004, Borhidi et al. 2012, Chytrý 2013, Chytrý et al. 2019). They also harbour endangered light- and semi-shade-demanding spe-cies of plants and invertebrates, especially in the forest tracts that were formerly used for coppicing or wood pasture (Konvička et al. 2004, Šebek et al. 2013).

As a zonal vegetation that has developed across large areas (Bohn et al. 2000–2003, Leuschner & Ellenberg 2017), oak-hornbeam forests in central Europe have been studied by vegetation scientists for almost a century. The first local studies assessing their floristic variability appeared in the 1920s (e.g. Issler 1926, Klika 1928). Later, national overviews of oak-hornbeam forest vegetation were published for most of the central-European countries (e.g. Soó 1940, Klika 1948, Oberdorfer 1957, Traczyk 1962, Neuhäuslová-Novotná 1964, Passarge & Hofmann 1968). Afterwards, several synthetic studies were prepared. The first coarse classification scheme covering a large part of Europe was proposed by Neuhäusl (1977), while Passarge (1978) provided a list of previ-ously described syntaxa from central-European oak-hornbeam forests. At the turn of the millennium, new vegetation surveys presenting critically revised syntaxonomic systems of oak-hornbeam forests based on numerical analyses of large datasets were published (e.g. Keller et al. 1998, Knollová & Chytrý 2004, Willner & Grabherr 2007). However, as for most other vegetation types, a study spanning the whole of central Europe and based on results of numerical analysis of an extensive relevé dataset is still missing.

Classification of oak-hornbeam forests usually reflects both biogeographical and ecological sources of variation in species composition (Knollová & Chytrý 2004). Biogeographical delineation prevails at the alliance level (e.g. Mucina et al. 2016) since these forests contain many nemoral species with distinct distributions, probably tracking gla-cial refugia of forest biota (Meusel & Jäger 1989, Willner et al. 2009, Postolache et al. 2017). The majority of central-European oak-hornbeam forests have been traditionally united into a single alliance *Carpinion betuli* (class *Carpino-Fagetea sylvaticae*, order *Carpinetalia*; Mucina et al. 2016), with a distribution core in central Europe and marginal occurrences in adjacent areas such as Great Britain (Rodwell 1991–2000), France (Noirfalise 1968), Denmark (Lawesson 2004), Sweden (Diekmann 1994), Romania (Coldea 2015) and Ukraine (Onyshchenko 2009). An alternative approach with several alliances that reflect ecological differences was used rarely, especially in relatively small and homogeneous areas (e.g. Passarge & Hofmann 1968). At the association level, both sources of variability, biogeographical and ecological, are usually used for delineating the units. However, lack of numerical comparisons of oak-hornbeam forest vegetation led to an inflation of locally recognized associations that were poorly delimited by good diagnostic species, especially if considered in broader regional comparisons (e.g. Borhidi & Kevey 1996; see also Ewald 2003, Knollová & Chytrý 2004). A classification system with strictly geographically delimited associations was used, for instance, in the former Czech classification system (Neuhäuslová 2000). As it was also adopted in Annex I of the European Habitats Directive, it was used also in the national habitat manuals, for example in the Czech Republic (Chytrý et al. 2001), Poland (Herbich 2004) and Slovakia (Stanová & Valachovič 2002). However, in the case of Czech oak-hornbeam forests, numerical analysis of variability supported the system with associations delimited both ecologically and geographically (Knollová & Chytrý 2004).

Given the lack of a well-tested, data-supported international classification of the oak-hornbeam forests in central Europe, the aims of this paper are as follows: (i) to analyse the variability in species composition of oak-hornbeam forests and explore its main drivers, and (ii) to present a revised international syntaxonomic system with formally delimited associations.

Methods

Dataset

Phytosociological relevés (vegetation-plot records) were obtained from the European Vegetation Archive (Chytrý et al. 2016) supplemented by two additional sources (origi-nal field data by J. Roleček and relevés from Novák et al. 2017). Relevé sources are listed in Electronic Appendix 1. We used relevés from Austria, Czech Republic, Germany, Hungary, Luxembourg, Poland, Slovakia, Switzerland and the Transcarpathian Region of Ukraine. The relevés of oak-hornbeam forests were selected by an ad hoc expert sys-tem (see Electronic Appendix 2 for details). To prepare this expert system, we divided the relevés of deciduous forests from the mentioned sources into eight broad groups (oak-hornbeam, scree and ravine, beech, acidophytic oak, thermophytic oak, alluvial, swamp and willow riparian forests) generally following the original authors' assignments, while the relevés without assignment were not used. Lists of the most frequent species in each group were compiled. Then we applied the GRIMP algorithm (Tichý et al. 2019) to select among them the species that best discriminated each group from all the others, and such species were then used in the expert system. Afterwards, we applied this expert system to all the deciduous forest relevés from the above-mentioned sources. Prior to the selec-tion, vascular plant nomenclature was unified according to the Euro+Med PlantBase (www.emplantbase.org; accessed August 2018). We obtained a dataset of oak-hornbeam forest relevés (n = 10,511). Relevés with a plot size < 50 m^2 or > 1,000 m^2 or with missing geographical coordinates were omitted. However, the relevés for which plot size was not indicated were preserved, assuming that it was highly probably within the indicated range. Bryophytes and lichens were deleted since they were recorded only in a small pro-portion of relevés and have limited ecological importance in oak-hornbeam forests (Neuhäusl 1977, Leuschner & Ellenberg 2017). The taxa determined only at the genus level were omitted except for the genus *Crataegus*, which is taxonomically difficult but frequent in the dataset. Some taxa were merged into aggregates defined in Electronic Appendix 3. To decrease the effect of denser sampling in some areas on the analysis, relevés were stratified geographically in a grid of 6'N × 10'E (~11 × 12 km^2). Subse-quently, a heterogeneity-constrained random resampling (Lengyel et al. 2011) resulting in 10–20 relevés selected per grid cell was performed, with the number of selected relevés proportional to the beta-diversity within the cell measured by the mean Bray-Curtis simi-larity between relevé pairs (Wiser & De Cáceres 2013). Percentage cover values of spe-cies were log-transformed prior to the resampling and the number of random selections was set to 500. This procedure resulted in the final dataset of 6,212 relevés (Fig. 1, hereaf-ter "dataset").

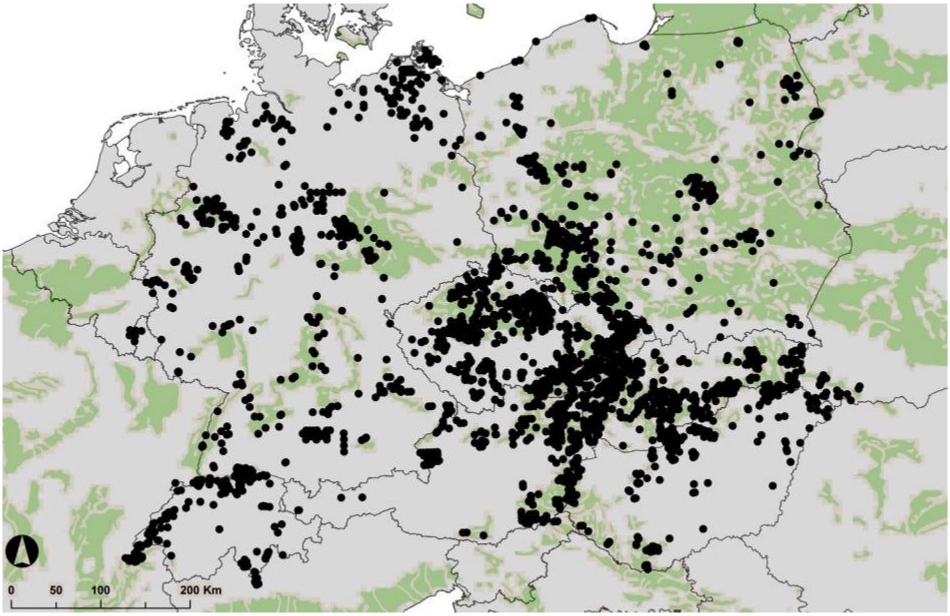


Fig 1. – Distribution of the relevés (n = 6,212) in the oak-hornbeam forest dataset. The areas in which oak-horn-beam forests are supposed to be natural vegetation (Bohn et al. 2000–2003) are shaded in green.

To show the link between species composition and site conditions of the associations, unweighted means of Ellenberg indicator values (hereafter "EIV") for light, moisture, nutrients, soil reaction and temperature (Ellenberg et al. 1992) as well as c-values for continentality (Berg et al. 2017) were calculated for each relevé. Climate variables (annual precipitation, mean annual temperature, temperature and precipitation seasonal-ity, and annual temperature amplitude) were obtained by intersection from the CHELSA climate dataset (Karger et al. 2017).

Data management and analyses were performed in Juice 7.0 (Tichý 2002) and R (ver-sion 3.4.1, www.r-project.org) using the package vegan (version 2.4-4, Oksanen et al. 2013).

Unsupervised classification and ordination

Several unsupervised classification analyses, based on different algorithms (both agglomerative and divisive hierarchical clustering), were performed to detect the main groups of relevés. Since each classification brought a unique insight into the structure of the dataset, the proposed classification system represents a compromise based on the results of these analyses. Of the agglomerative methods, we used flexible beta (with vari-ous values of beta) clustering with Sřrensen distance, and Ward's method with Euclidean distance, both with log-transformed percentage cover values. Of the divisive methods, we used modified TWINSPAN (Roleček et al. 2009) with Whittaker's beta as a measure of internal heterogeneity of clusters, and pseudospecies with 0-5-25% cover cut levels, as well as presence-absence data.

All the methods used yielded relatively similar results, indicating their robustness. OptimClass analysis based on a comparison of the number of diagnostic species of various partitions (Tichý et al. 2010) was used to evaluate the results more objectively. It sug-gested an optimal number of clusters between 10 and 12 for all the methods except Ward's clustering.

In this paper, we present the classification that produced the best results in terms of biogeographical and ecological interpretations of clusters. Vegetation types (associations) to be recognized by the formal definitions were chosen according to the results of the unsupervised classification analyses supplemented by detrended correspondence analysis (DCA). Species percentage covers were log-transformed prior to the analysis, and EIVs and climate variables were passively projected onto the ordination plot. Spearman correlations among vectors and the first two ordination axes were calculated. Significances of correlations of EIVs were checked using a modified permutation test proposed by Zelený & Schaffers (2012).

Cocktail classification

To provide explicit formulas defining each vegetation type (association), we applied the Cocktail method (Bruelheide 1995, 1997, 2000, Kočí et al. 2003). Sociological species groups are biogeographically and ecologically distinct and more or less correspond to the traditional concept of diagnostic species of certain associations. Initial members of sociological species groups were selected based on the results of unsupervised classification and expert knowledge of the authors. Afterwards, species were added to a group accord-ing to their statistical tendency to co-occur with species already included in the group, expressed as the phi coefficient (Chytrý et al. 2002). The number of species in a group required for its presence in a relevé was set empirically (Kočí et al. 2003). In the associa-tion formulas, membership conditions were connected by logical operators AND, OR and NOT (Bruelheide 1997). To keep a link between the recognized associations and their Cocktail formulas, the type relevé of each association had to unequivocally fulfil the formal definition of its association. Results of the supervised classification by formal def-initions were checked by semi-supervised K-mean clustering (Tichý et al. 2014), which showed that the relevés unclassified by the formal definitions did not form any new biogeographically or ecologically meaningful vegetation types.

Nomenclature of syntaxa was checked for compliance with the International Code of Phytosociological Nomenclature (Weber et al. 2000).

Results

Unsupervised classification and ordination

Of the several unsupervised classifications performed, we present the results of flexible beta classification (beta = –0.3) into 12 clusters. However, cluster 2 lacked diagnostic species, and therefore, we merged it with cluster 3 (see Electronic Appendix 4 for the full synoptic table and dendrogram). Consequently, we interpreted 11 clusters.

The classification indicated both ecological and geographical variation in central European oak-hornbeam forests. The main division clearly reflected ecological conditions, separating the moisture- and often nutrient-demanding types (4,624 relevés) from mesophytic and xerophytic, less nutrient-demanding types (1,588 relevés). Going deeper into the hierarchy, a geographical pattern also appeared. Cluster 1 (912 relevés) represented typical mesotrophic oak-hornbeam forests of the Bohemian Massif and Germany, as reflected by the diagnostic species *Galium sylvaticum* and *Hepatica nobilis*. Cluster 2 (1,468 relevés) included broadly distributed hygrophytic oak-hornbeam forests with moisture- and nutrient-demanding species (e.g. *Aegopodium podagraria*, *Ficaria verna*). Cluster 3 (398 relevés) contained xerophytic and thermophytic oak-hornbeam forests with the occurrence of thermophytic species of subcontinental and subcontinental-submediterranean distribution (e.g. *Cornus mas*). Cluster 4 (168 relevés) also represented thermophytic, but at the same time hygrophytic types (e.g. *Aristolochia clematitis*, *Fraxinus angustifolia*). Cluster 5 (202 relevés) included oak-hornbeam forests contain-ing both suboceanic and submediterranean species (e.g. *Hippocrepis emerus*, *Potentilla sterilis*) typical of western Switzerland. Clusters 6 (408 relevés) and 7 (639 relevés) included not very distinct types on slightly wet and nutrient-poor soils. Cluster 8 (429 relevés) comprised subboreal oak-hornbeam forests characteristic of the Polish Basin (e.g. *Rubus saxatilis*, *Trientalis europaea*). Cluster 9 (344 relevés) included suboceanic oak-hornbeam forests with mountain species (*Poa chaixii*). Cluster 10 (456 relevés) included nutrient-poor oak-hornbeam forests characterized by an admixture of species of dry acidophytic oak forests (e.g. *Calamagrostis arundinacea*, *Luzula luzuloides*). Finally, cluster 11 (788 relevés) comprised Western Carpathian oak-hornbeam forests with submediterranean and subcontinental influences (e.g. *Galium intermedium*, *Euphorbia amygdaloides*).

Comparing these results with the associations previously reported in the literature, we often found a good correspondence. Our syntaxonomic interpretation of the clusters of the presented classification was as follows: clusters 1 and 10 – *Galio sylvatici-Carpinetum*; clusters 2, 6 and 7 – *Stellario-Carpinetum*; cluster 3 – *Polygonato latifolii-Carpinetum* and *Primulo veris-Carpinetum*; cluster 4 – *Convallario-Carpinetum*; cluster 5 – *Lithospermo-Carpinetum*; cluster 8 – *Tilio-Carpinetum*; cluster 9 – *Poo chaixii-Carpinetum*; and cluster 11 – *Carici pilosae-Carpinetum*. All of these associations belong to the alliance *Carpinion betuli*. The alliance *Erythronio-Carpinion* was represented by a small number of relevés according to the authors' assignments. Its associations were not revealed in the 12-cluster solution of the unsupervised classification, but they were distinguished after a finer division of the dataset.

The DCA analysis (Fig. 2) showed the main gradient in species composition significantly correlated with the EIV for moisture ($r = -0.87$) and nutrients ($r = -0.82$). The sec-ond most important gradient in the dataset showed the highest correlation with EIVs for reaction ($r = -0.82$). Regarding the climate variables, the first ordination axis was best correlated with annual temperature amplitude ($r = 0.34$) and seasonality ($r = 0.24$), and the second with mean annual temperature ($r = -0.34$). Latitude was most closely corre-lated with the first ordination axis ($r = -0.44$) and also with the second axis ($r = 0.26$).

Cocktail classification and an overview of the recognized associations

Our Cocktail formal definitions of associations (Electronic Appendix 5) enabled the assignment of 3,413 relevés, i.e. 54.9% of the dataset. We recognized 13 associations of

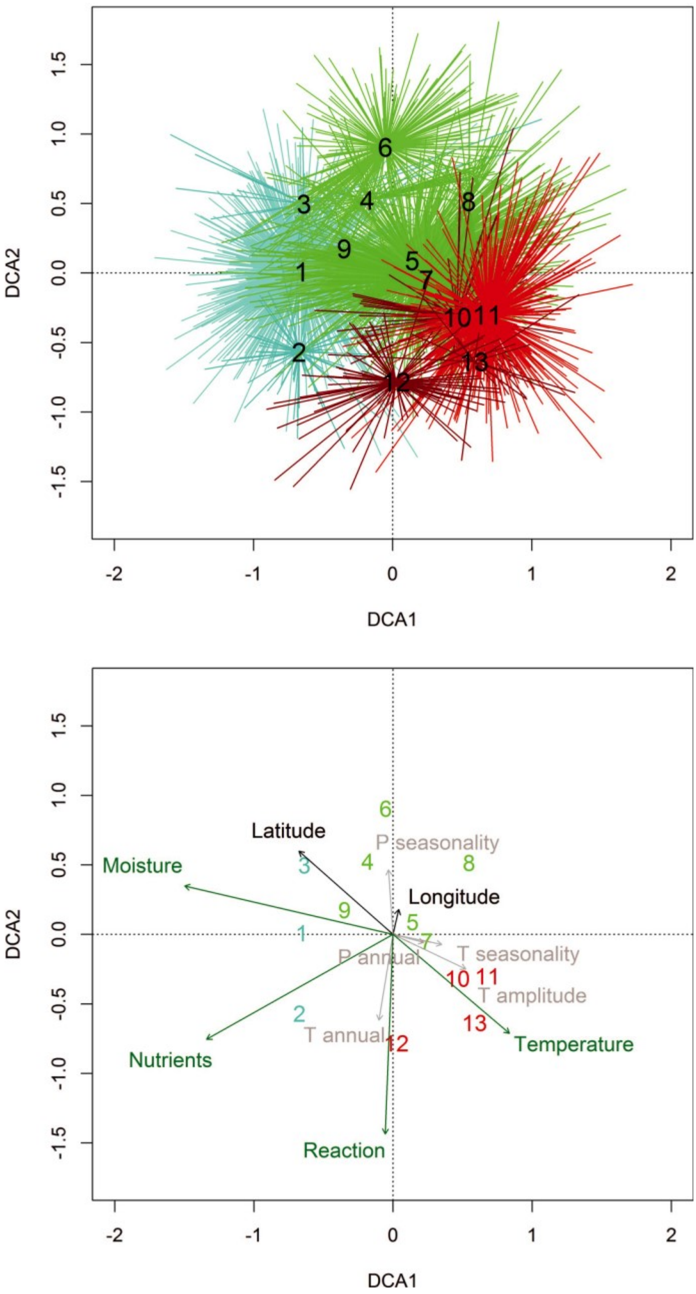


Fig. 2. – Detrended correspondence analysis of the subset of relevés classified by formal definitions. Spider plots with association centroids are plotted. The colours represent hygrophytic (blue), mesophytic (green) and xerophytic (red) associations. The second diagram shows the same ordination with vectors of geographical position (black), EIVs (green) and climate variables (grey) plotted together with the association centroids. All the plotted variables were significantly ($P < 0.05$) correlated with at least one of the two first ordination axes. The first axis explained 1.3% and the second 1.0% of the variability in the dataset. Association numbers: 1 – *Stellario-Carpinetum*, 2 – *Convallario-Carpinetum*, 3 – *Pseudostellario-Carpinetum*, 4 – *Poo-Carpinetum*, 5 – *Galio-Carpinetum*, 6 – *Tilio-Carpinetum*, 7 – *Carici-Carpinetum*, 8 – *Cruciato-Quercetum*, 9 – *Epimedio-Carpinetum*, 10 – *Lithospermo-Carpinetum*, 11 – *Primulo-Carpinetum*, 12 – *Polygonato-Carpinetum*, 13 – *Helleboro-Carpinetum*.

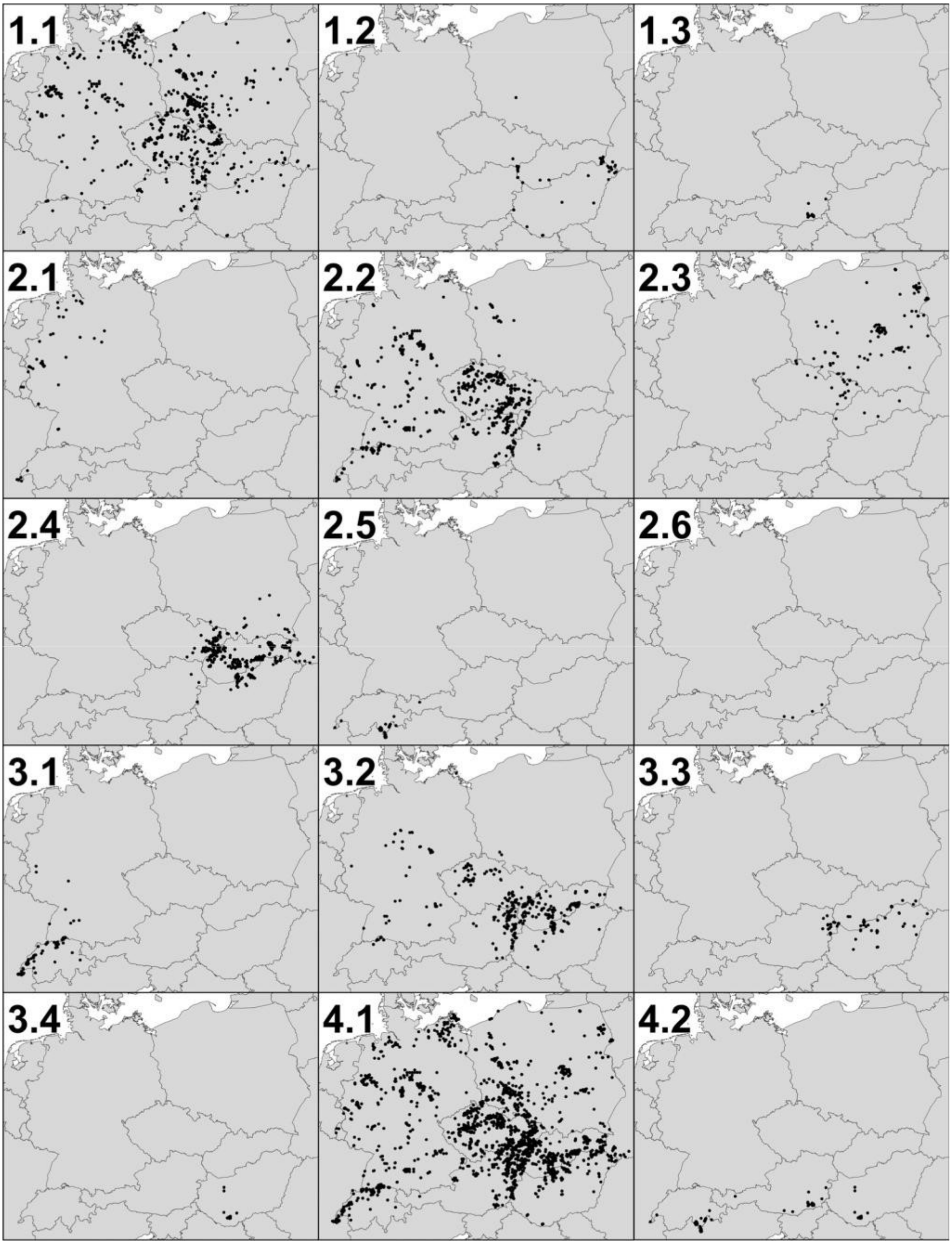


Fig 3. – Distribution of relevés assigned the particular associations by formal definitions (n = 3,413). 1.1 – *Stellario-Carpinetum*, 1.2 – *Convallario-Carpinetum*, 1.3 – *Pseudostellario-Carpinetum*, 2.1 – *Poo-Carpinetum*, 2.2 – *Galio-Carpinetum*, 2.3 – *Tilio-Carpinetum*, 2.4 – *Carici-Carpinetum*, 2.5 – *Cruciato-Quercetum*, 2.6 – *Epimedio-Carpinetum*, 3.1 – *Lithospermo-Carpinetum*, 3.2 – *Primulo-Carpinetum*, 3.3 – *Polygonato-Carpinetum*, 3.4 – *Helleboro-Carpinetum*, 4.1 – all relevés assigned to the *Carpinion betuli* associations, 4.2 – all relevés assigned to the *Erythronio-Carpinion* associations.

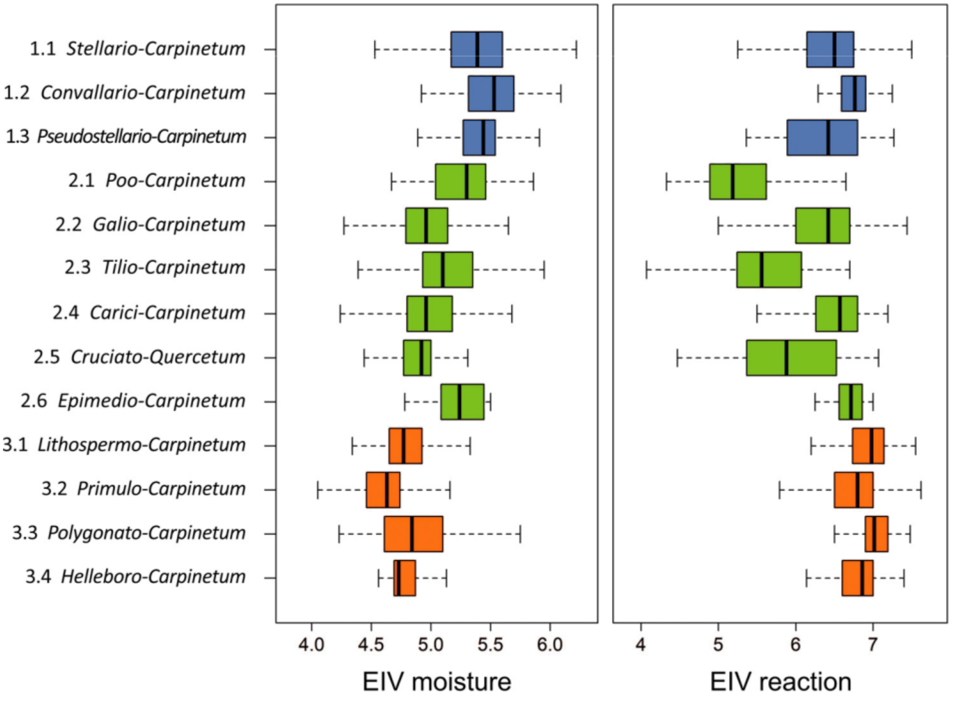


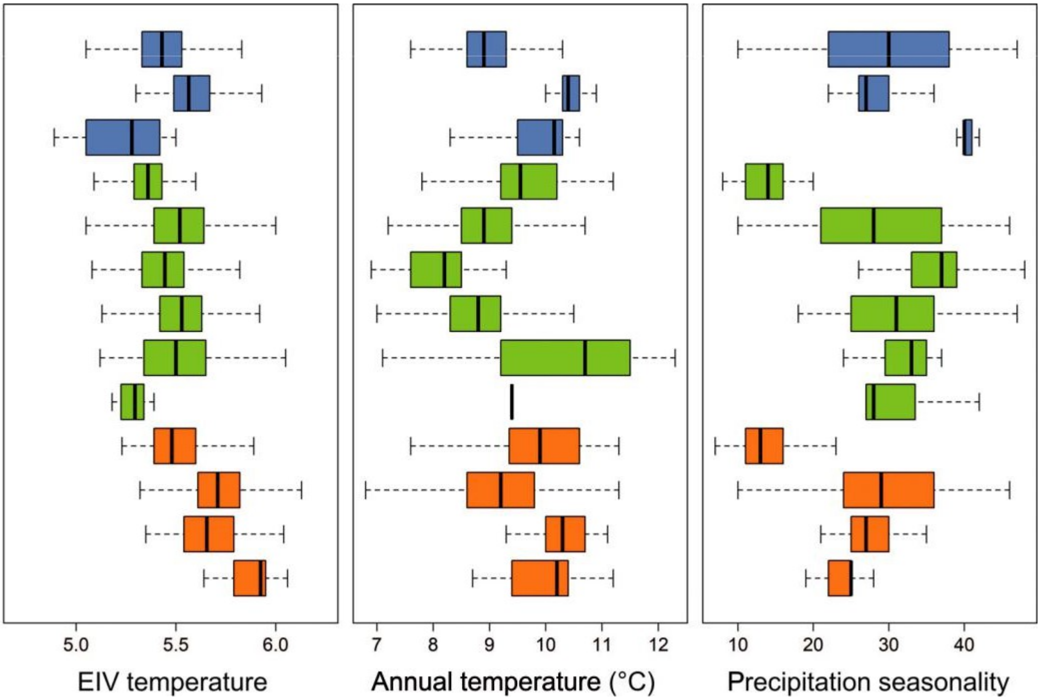
Fig. 4. – Comparison of the selected EIVs and climate variables among associations. Boxes indicate 25–75% interquartile range with their median (bold line), whiskers show the range of values without outliers.

oak-hornbeam forests in central Europe, nine in the *Carpinion betuli* alliance and four in the *Erythronio-Carpinion* alliance. They were based on previously described associations, whereas other associations frequently mentioned in the central-European phytosociological literature were mostly identified as their synonyms. Apart from the local environmental factors, biogeography played an important role in differentiating these communities.

The same species dominate the tree layer throughout the whole study area (e.g. *Carpinus betulus*, *Quercus petraea* agg., *Q. robur*) except in the southernmost part, where some sub-continental and submediterranean tree species are admixed (e.g. *Acer opalus*, *A. tataricum*, *Fraxinus angustifolia*, *Tilia tomentosa*).

In the following, we give brief descriptions of the recognized associations, including their distributions (Fig. 3), selected EIVs and climatic variables (Fig. 4), as well as a syn-optic table of the diagnostic species (Table 1, Electronic Appendix 6). A syntaxonomic framework and more detailed descriptions are given in the Syntaxonomic outline at the end of the paper.

The associations were divided into three ecological groups differing in soil moisture, which was indicated by the ordination analysis as the most important environmental gradient. We typified the association *Poo chaixii-Carpinetum* (*Carpinion betuli*).



We refrained from typifying the associations of the *Erythronio-Carpinion* (except *Pseudostellario-Carpinetum*) since the core area of their range lies outside the study area. The two above-mentioned associations were validated as well. Concerning higher syntaxonomic units, all the associations belong to the class *Carpino-Fagetea sylvaticae* and order *Carpinetalia betuli*.

Table 1. A shortened synoptic table summarizing percentage frequencies (constancies) of diagnostic species (shaded) of the distinguished associations (phi > 0.2 for diagnostic, phi > 0.5 for highly diagnostic species, in bold). The sizes of all clusters were virtually equalized (Tichý & Chytrý 2006). Two additional criteria were applied to increase the representativeness of the list of diagnostic species: (i) Fisher's exact test, excluding spe-cies with non-significant occurrence concentration in the association (P = 0.05), and (ii) the constancy ratio, excluding species with a constancy lower than 1.3× the constancy value in the association with the second high-est constancy value. The most frequent species in the dataset (frequency > 30%) that are not diagnostic for any of the clusters are listed at the bottom of the table. Diagnostic species are sorted by decreasing fidelity. Species with frequency lower than 20% in an association for which they are diagnostic are not shown. Alliance abbrevi-ations: Carp – *Carpinion betuli*, E-C *Erythronio-Carpinion*. Association abbreviations: StC – *Stellario-Carpinetum*, CoC – *Convallario-Carpinetum*, PsC – *Pseudostellario-Carpinetum*, PoC – *Poo-Carpinetum*, GaC – *Galio-Carpinetum*, TiC – *Tilio-Carpinetum*, CrQ – *Cruciato-Quercetum*, EpC – *Epimedio-Carpinetum*, LiC – *Lithospermo-Carpinetum*, PrC – *Primulo-Carpinetum*, PlC – *Polygonato-Carpinetum*, HeC – *Helleboro-Carpinetum*. The full version of this table is available in Electronic Appendix 6.

Association	1.1	1.2	1.3	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
	StC	CoC	PsC	PoC	GaC	TiC	CaC	CrQ	EpC	LiC	PrC	PlC	HeC
Alliance	Carp	Carp	E-C	Carp	Carp	Carp	Carp	E-C	E-C	Carp	Carp	Carp	E-C
Ecological group	hygrophytic			mesophytic						xerophytic			
Number of relevés	979	88	22	50	863	212	419	39	8	107	522	90	14
1.1 *Stellario-Carpinetum*													
Impatiens parviflora	32	20	–	4	10	5	8	3	–	1	7	4	–
Stachys sylvatica	35	26	–	12	10	8	9	–	–	7	6	23	–
1.2 *Convallario-Carpinetum*													
Fraxinus angustifolia	–	**72**	–	–	–	–	–	–	–	–	–	12	–
Aristolochia clematitis	–	**34**	–	–	–	–	–	–	–	–	1	6	–
Lysimachia nummularia	10	50	–	–	4	8	9	–	–	1	4	12	–
Rubus caesius	16	61	–	2	6	4	4	3	25	10	4	24	7
Rumex sanguineus	3	28	–	2	1	–	1	–	–	–	1	–	14
Circaea lutetiana	28	52	–	24	7	3	9	–	–	6	2	9	14
Carex remota	5	24	–	2	2	2	1	–	–	–	1	1	–
Carex muricata agg.	5	48	–	2	7	1	9	–	–	2	19	29	14
Cardamine impatiens	2	22	–	–	4	1	5	–	–	–	4	3	14
Lapsana communis	8	34	–	2	8	4	10	3	–	3	13	24	14
1.3 *Pseudostellario-Carpinetum*													
Erythronium dens-canis	–	–	**50**	–	–	–	–	–	–	–	–	–	–
Crocus vernus	–	1	**32**	–	–	–	–	–	–	–	–	–	–
Gentiana asclepiadea	–	–	**41**	–	1	–	1	3	13	–	–	–	–
Pseudostellaria europaea	–	–	**27**	–	–	–	–	–	–	–	–	–	–
Leucojum vernum	1	6	32	–	1	–	1	–	–	–	1	–	–
2.1 *Poo-Carpinetum*													
Lonicera periclymenum	5	–	–	**78**	1	–	–	–	–	7	1	–	–
Teucrium scorodonia	1	–	–	**54**	1	–	–	8	–	7	–	–	–
Poa chaixii	1	–	–	30	2	–	–	3	–	1	1	–	–
Holcus mollis	4	–	–	22	1	10	1	3	–	–	1	–	–
Galeopsis tetrahit	13	6	–	34	11	14	6	13	–	7	6	4	7
2.2 *Galio-Carpinetum*													
Galium sylvaticum	–	–	23	22	**85**	–	–	3	13	23	40	8	14
2.3 *Tilio-Carpinetum*													
Vaccinium myrtillus	2	–	–	6	3	**59**	1	18	–	3	1	–	–
Trientalis europaea	–	–	–	–	–	**32**	–	–	–	–	–	–	–
Rubus saxatilis	1	–	–	–	1	**33**	–	–	–	3	1	–	–
Maianthemum bifolium	24	27	50	22	18	87	31	15	50	7	7	8	–
Sorbus aucuparia	26	–	–	34	16	68	8	23	38	2	5	2	–
Betula pendula	15	–	–	8	12	43	9	18	–	2	7	–	–
Frangula alnus	9	25	–	20	5	52	7	10	13	9	7	7	–
Pinus sylvestris	6	1	5	2	7	36	5	–	13	15	5	1	–
Populus tremula	9	2	–	14	5	36	10	18	13	7	4	4	–
Calamagrostis arundinacea	3	1	9	4	19	32	5	21	–	1	15	–	–
Veronica officinalis	3	1	5	14	11	30	13	8	–	8	13	3	–
Dryopteris carthusiana agg.	9	5	18	18	3	33	5	–	25	2	1	–	14
2.4 *Carici-Carpinetum*													
Carex pilosa	2	1	14	–	15	18	71	3	13	1	23	14	36
Hacquetia epipactis	–	–	–	–	–	–	21	–	–	–	2	–	–
2.5 *Cruciato-Quercetum*													
Luzula nivea	–	–	–	–	–	–	–	**82**	–	–	–	–	–
Castanea sativa	1	–	–	2	–	–	–	**79**	–	–	1	–	–
Veronica urticifolia	–	–	–	–	–	–	–	**31**	–	–	–	–	–

Association	1.1	1.2	1.3	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
	StC	CoC	PsC	PoC	GaC	TiC	CaC	CrQ	EpC	LiC	PrC	PlC	HeC
Alliance	Carp	Carp	E-C	Carp	Carp	Carp	Carp	E-C	E-C	Carp	Carp	Carp	E-C
Ecological group	hygrophytic			mesophytic						xerophytic			
Number of relevés	979	88	22	50	863	212	419	39	8	107	522	90	14
Phyteuma betonicifolium	–	–	–	–	–	–	–	26	–	–	–	–	–
Asplenium adiantum-nigrum	–	–	–	–	–	–	1	26	–	–	–	–	–
Molinia caerulea agg.	1	–	–	16	1	5	1	38	–	8	1	–	–
Tilia cordata	46	34	32	12	43	49	42	95	25	12	35	28	7
Vinca minor	2	5	23	2	6	1	3	31	13	5	2	4	–
Robinia pseudoacacia	3	3	–	–	2	1	2	26	–	5	5	12	14
2.6 *Epimedio-Carpinetum*													
Anemone trifolia	–	–	–	–	–	–	–	–	**75**	–	–	–	–
Actaea spicata	4	–	5	–	7	9	7	5	**88**	1	4	6	–
Vicia oroboides	–	–	–	–	–	–	–	–	**38**	–	–	–	–
Alnus incana	1	–	–	–	1	–	1	–	**38**	–	–	–	–
Cirsium oleraceum	1	–	–	–	1	1	1	–	**38**	–	–	–	–
Pimpinella major	1	1	–	–	2	–	1	3	**50**	6	6	3	–
Polystichum aculeatum	1	–	–	–	1	–	1	5	**38**	–	1	–	–
Aquilegia vulgaris	1	–	5	–	1	1	1	–	**38**	4	1	–	–
Sanicula europaea	13	3	27	2	16	18	20	8	88	12	16	8	21
Geranium phaeum	1	–	–	–	–	–	1	–	25	–	–	1	–
Daphne mezereum	6	–	32	10	14	21	15	–	75	30	10	–	–
Salvia glutinosa	–	–	32	–	3	–	9	28	63	3	6	4	7
Clematis recta	1	1	–	–	1	–	1	8	38	–	5	10	–
Viola collina	1	–	–	–	1	1	1	–	25	1	1	–	–
Myosotis sylvatica	4	–	9	–	7	–	4	–	38	–	4	–	–
Dryopteris filix-mas	18	10	5	20	15	39	23	18	75	5	7	7	7
Chrysosplenium alternifolium	1	–	5	–	1	2	1	–	25	–	1	–	–
Corydalis solida	5	5	14	–	1	1	5	–	38	–	2	3	–
Paris quadrifolia	13	3	9	2	8	16	10	–	50	12	2	3	–
Ranunculus lanuginosus	11	–	23	2	9	17	13	–	50	–	2	3	7
Euonymus europaeus	40	60	32	10	21	14	19	51	100	50	28	70	7
Equisetum arvense	1	1	5	2	1	1	1	–	25	–	–	–	7
Neottia ovata	1	1	–	–	2	2	3	5	25	3	1	1	–
Aconitum lycoctonum	1	–	14	–	2	–	1	–	25	–	1	1	–
Pulmonaria officinalis agg.	41	36	36	2	48	30	67	15	100	29	43	31	57
Epilobium montanum	6	2	–	10	11	10	9	–	38	2	3	2	–
Brachypodium sylvaticum	40	76	9	28	35	17	24	41	100	64	46	69	29
Adoxa moschatellina	25	2	9	10	7	4	2	–	38	4	1	1	–
Acer pseudoplatanus	35	7	55	20	31	13	29	23	75	40	20	11	–
Campanula trachelium	17	18	41	4	29	9	35	36	75	22	37	54	21
Senecio nemorensis agg.	8	1	14	18	14	3	14	13	38	1	6	2	–
Viburnum opulus	13	20	5	24	12	24	12	5	50	36	10	8	–
Cyclamen purpurascens	–	–	18	–	9	–	–	10	25	–	5	2	–
Knautia drymeia	1	1	18	–	5	–	–	3	25	–	5	3	14
Polygonatum multiflorum	41	35	41	38	38	36	51	62	88	64	39	46	57
3.1 *Lithospermo-Carpinetum*													
Rosa arvensis	–	–	–	12	11	–	–	18	13	**81**	7	–	29
Carex flacca	1	–	–	6	1	–	1	10	13	**54**	1	–	–
Hippocrepis emerus	–	–	–	–	1	–	–	10	–	**43**	2	1	–
Viburnum lantana	1	–	5	2	6	1	5	18	38	**84**	21	31	14
Sorbus aria agg.	1	–	–	2	3	–	1	28	13	**60**	12	–	–
Lonicera xylosteum	10	2	–	12	25	22	15	13	38	90	27	19	–

Association	1.1	1.2	1.3	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
	StC	CoC	PsC	PoC	GaC	TiC	CaC	CrQ	EpC	LiC	PrC	PlC	HeC
Alliance	Carp	Carp	E-C	Carp	Carp	Carp	Carp	E-C	E-C	Carp	Carp	Carp	E-C
Ecological group	hygrophytic			mesophytic						xerophytic			
Number of relevés	979	88	22	50	863	212	419	39	8	107	522	90	14
Euphorbia dulcis	5	–	–	6	9	3	10	28	13	60	5	2	–
Phyteuma spicatum	5	–	27	6	17	9	8	3	13	51	5	2	–
Carex montana	1	–	–	12	12	8	11	8	13	50	25	1	7
Bromopsis ramosa agg.	5	2	–	4	15	3	13	–	–	43	30	30	7
Arum maculatum	7	5	–	12	10	–	2	–	–	24	4	3	–
Vicia sepium	8	22	–	22	20	5	7	3	25	43	19	6	–
Berberis vulgaris	1	2	–	–	2	3	1	8	13	24	8	11	–
Prunus spinosa	9	30	–	16	11	8	8	5	13	42	21	17	14
Malus sylvestris	2	3	–	4	2	7	3	8	13	22	4	9	–
3.2 *Primulo-Carpinetum*													
Tanacetum corymbosum	2	–	9	–	19	–	7	8	–	15	58	10	21
Primula veris	4	–	–	2	8	5	4	–	–	18	36	19	–
Campanula rapunculoides	4	–	–	2	18	3	26	–	13	7	39	23	14
Astragalus glycyphyllos	4	3	–	–	9	7	11	–	13	–	27	20	–
Hieracium sabaudum	3	–	–	–	14	11	19	–	–	5	27	4	14
Clinopodium vulgare	4	2	5	–	13	25	18	18	–	11	40	29	21
Fragaria moschata	6	1	5	–	14	3	18	–	13	1	26	13	–
3.3 *Polygonato-Carpinetum*													
Polygonatum hirtum	1	1	–	–	1	–	1	–	–	–	4	**81**	14
Viola mirabilis	4	2	–	–	7	17	8	3	13	16	22	**81**	–
Cruciata laevipes	1	3	–	–	1	–	2	–	–	–	6	20	7
Quercus cerris	–	9	–	–	3	–	6	–	–	–	20	28	14
Fallopia dumetorum	3	13	–	–	3	1	2	–	–	1	6	18	–
3.4 *Helleboro-Carpinetum*													
Tilia tomentosa	–	–	–	–	–	–	–	–	–	–	–	–	**79**
Fraxinus ornus	–	–	–	–	–	–	1	5	–	–	4	8	**86**
Helleborus odorus	–	–	–	–	–	–	–	–	–	–	–	–	**64**
Cardamine bulbifera	2	2	–	2	5	7	29	–	–	–	12	7	**79**
Luzula forsteri	–	–	–	–	–	–	–	3	–	–	–	–	**43**
Potentilla micrantha	–	–	–	–	1	–	1	3	–	3	1	–	**36**
Ruscus hypoglossum	–	–	–	–	–	–	–	–	–	–	–	–	**29**
Glechoma hirsuta	1	2	–	–	1	–	21	–	–	–	12	12	50
Viola alba	1	–	–	–	1	–	2	3	–	5	4	4	36
Arum besserianum	–	–	–	–	–	–	1	–	–	–	–	1	21
Waldsteinia geoides	–	–	–	–	–	–	6	–	–	–	5	2	21
Stellaria holostea	44	13	9	64	52	50	39	–	–	–	35	28	86
Melica uniflora	16	–	–	22	23	2	37	8	–	34	46	21	64
Corydalis cava	3	3	–	–	2	–	3	–	–	–	4	13	21
Allium ursinum	3	2	–	–	3	1	4	5	–	5	2	11	21
Diagnostic species for two or more associations													
Urtica dioica	51	56	9	14	12	23	10	–	13	2	8	16	14
Galium aparine	46	60	9	12	13	4	15	–	13	5	19	31	7
Ulmus minor	15	65	–	2	6	4	2	5	–	11	7	43	7
Acer tataricum	–	48	–	–	–	–	–	–	–	–	2	43	7
Quercus robur	78	91	50	58	41	82	23	21	88	39	30	68	–
Silene baccifera	1	11	–	–	–	–	–	–	–	–	1	11	–
Cornus sanguinea	24	70	5	14	23	14	28	23	63	75	41	57	29
Symphytum tuberosum	–	6	64	–	8	–	52	10	38	–	23	14	43

Association	1.1	1.2	1.3	2.1	2.2	2.3	2.4	2.5	2.6	3.1	3.2	3.3	3.4
	StC	CoC	PsC	PoC	GaC	TiC	CaC	CrQ	EpC	LiC	PrC	PlC	HeC
Alliance	Carp	Carp	E-C	Carp	Carp	Carp	Carp	E-C	E-C	Carp	Carp	Carp	E-C
Ecological group	hygrophytic			mesophytic						xerophytic			
Number of relevés	979	88	22	50	863	212	419	39	8	107	522	90	14
Aruncus dioicus	1	–	23	–	1	–	1	10	25	1	–	–	–
Alnus glutinosa	9	3	27	4	2	4	2	5	25	2	1	–	7
Picea abies	10	–	45	6	13	35	8	21	75	10	4	–	–
Aegopodium podagraria	49	16	59	–	25	38	34	8	88	8	9	20	7
Ilex aquifolium	1	–	–	38	1	–	–	10	–	23	1	–	–
Potentilla sterilis	–	–	–	24	8	–	–	–	–	38	1	–	–
Luzula pilosa	6	2	5	14	9	52	11	28	50	13	2	–	7
Galium intermedium	4	1	5	–	–	46	54	–	–	–	27	17	29
Euonymus verrucosus	1	–	–	–	2	39	12	–	13	–	25	37	14
Pteridium aquilinum	2	–	–	18	1	33	2	44	–	7	1	2	–
Cruciata glabra	1	1	5	–	1	24	39	13	**75**	–	16	3	7
Carex digitata	5	–	18	–	22	49	34	72	63	47	32	10	14
Prenanthes purpurea	1	–	14	–	4	–	3	31	25	7	1	–	–
Dioscorea communis	–	–	–	–	–	–	–	31	–	25	–	–	43
Vincetoxicum hirundinaria	4	1	5	–	7	2	5	31	–	14	39	22	–
Fagus sylvatica	28	3	27	56	40	–	46	21	75	68	31	3	14
Solidago virgaurea	3	–	9	16	13	21	5	44	50	52	18	3	–
Ligustrum vulgare	7	45	5	6	14	1	24	21	50	89	63	78	64
Acer campestre	33	84	14	10	41	1	55	36	50	92	75	88	64
Melittis melissophyllum	1	2	–	4	10	23	24	18	25	50	53	13	7
Sorbus torminalis	1	–	–	8	15	1	9	5	–	41	56	20	14
Primula acaulis	1	2	18	–	1	–	1	31	13	36	2	–	43
Cornus mas	1	–	–	–	2	–	9	26	–	2	37	31	21
Aegonychon purpurocaeruleum	1	1	–	–	1	–	1	–	–	17	25	26	7
Quercus petraea agg.	20	–	14	50	59	25	66	38	13	64	75	28	79
Viola odorata agg.	5	14	–	–	2	1	4	–	–	–	14	43	36
Oxalis acetosella	29	–	64	44	16	66	17	18	75	4	2	–	–
Euphorbia amygdaloides	–	2	5	10	4	–	50	3	13	44	19	9	43
Fraxinus excelsior	52	5	18	42	40	19	28	82	88	82	40	31	–
Hedera helix	21	28	9	54	27	8	24	72	–	93	26	31	71
Other frequent species (frequency > 30% across the whole dataset) sorted by decreasing frequency													
Carpinus betulus	75	77	100	92	86	81	94	21	75	69	82	71	86
Viola reichenbachiana agg.	65	88	32	62	61	81	73	62	63	84	54	50	64
Poa nemoralis	55	23	14	46	68	37	62	36	13	31	63	38	29
Crataegus species	40	77	9	36	41	22	44	56	50	95	74	82	57
Geum urbanum	64	88	5	20	30	26	35	10	63	21	46	76	57
Corylus avellana	43	20	32	60	41	68	37	90	75	63	43	47	7
Dactylis glomerata	42	55	5	30	40	16	43	13	–	12	60	62	71
Anemone nemorosa	55	22	82	58	41	67	21	28	63	66	19	1	–
Lathyrus vernus	13	15	27	4	47	34	57	8	38	63	59	26	57
Lamium galeobdolon	43	9	64	44	39	46	44	41	75	27	16	11	29
Galium odoratum	27	42	–	20	39	29	49	23	25	52	35	33	64
Melica nutans	23	–	14	4	44	70	31	28	63	53	41	32	–
Fragaria vesca	18	23	5	18	33	59	41	46	63	71	51	27	50
Convallaria majalis	20	49	5	22	41	47	23	10	–	38	53	61	14
Ajuga reptans	24	63	14	26	23	65	53	33	38	25	28	39	43

Hygrophytic group of associations

These forests are characterized by a frequent occurrence of nutrient-demanding (*Aegopodium podagraria*, *Geranium robertianum*, *Urtica dioica*) and/or moisture-demanding (*Circaea lutetiana*, *Stachys sylvatica*) species, partly winter annuals (*Galium aparine*, *Veronica hederifolia* agg.). Besides *Carpinus betulus*, *Quercus robur* is the key species of their tree layer. They are negatively delimited by the absence of typical mesophytic (e.g. *Galium sylvaticum*), thermophytic (e.g. *Melittis melissophyllum*) and acidophytic (e.g. *Luzula luzuloides*) species. In a landscape context, they are often confined to a broad transitional zone between mesophytic forests on slopes and alluvial forests on floodplains. They may occupy upper river terraces or poorly-drained plateaus.

* **1.1. *Stellario-Carpinetum***. Moisture- and nutrient-demanding oak-hornbeam forests distributed mainly in the western and central parts of central Europe. Especially lowland types have a well-developed vernal aspect with numerous geophytes.
* **1.2. *Convallario-Carpinetum***. Moisture- and nutrient-demanding oak-hornbeam forests of the Pannonian Basin. *Fraxinus angustifolia* is typically admixed in the tree layer and species characteristic of the Pannonian Basin (e.g. *Aristolochia clematitis*) are typical components of the herb layer.
* **1.3. *Pseudostellario-Carpinetum***. Hygrophytic Illyrian oak-hornbeam forests confined to moist soils covering soft sediments in the foothills of the south-eastern Alps and adjacent areas. Some moisture-demanding Illyrian elements (e.g. *Cardamine waldsteinii*, *Pseudostellaria europaea*) are among the most typical species. They include an admixture of mountain species (e.g. *Gentiana asclepiadea*).

Mesophytic group of associations

This group represents the core of the central-European oak-hornbeam forests. These asso-ciations are characterized by a frequent occurrence of forest mesophytes (e.g. *Carex pilosa*, *Galium sylvaticum*). In some types, acidophytes (e.g. *Luzula luzuloides*, *Vaccinium myrtillus*) are common. Moisture-demanding and thermophytic species are usually absent. Unlike in the previous group, *Quercus petraea* agg. most frequently co-occurs with *Carpinus betulus* in the tree layer.

* **2.1 *Poo chaixii-Carpinetum***. Subatlantic mesophytic oak-hornbeam forests of westernmost central Europe. Species which in central Europe are usually associated with beech forests (e.g. *Poa chaixii*) are typical of their herb layer, coupled with suboceanic species such as the evergreen shrub *Ilex aquifolium*.
* **2.2 *Galio sylvatici-Carpinetum***. Mesophytic oak-hornbeam forests of the western and central parts of central Europe. *Galium sylvaticum* and *Hepatica nobilis* are among the most typical species in the herb layer.
* **2.3 *Tilio-Carpinetum***. Mesophytic subboreal oak-hornbeam forests growing mainly in the Polish Basin, often dominated by *Quercus robur* and *Tilia cordata*. A co-occur-rence of subcontinental (e.g. *Carex pilosa*) and subboreal (e.g. *Rubus saxatilis*) forest mesophytes is typical for the herb layer, whereas species characteristic of the Alps and Carpathians are missing.

* **2.4 *Carici pilosae-Carpinetum***. Mesophytic oak-hornbeam forests of the Western Carpathian foothills. The herb layer is characterized by a co-occurrence of subcontinental (e.g. *Carex pilosa*) and suboceanic-submediterranean (e.g. *Euphorbia amygda-loides*) species or species that occur mostly in the Carpathians within central Europe (e.g. *Hacquetia epipactis*).
* **2.5 *Cruciato glabrae-Quercetum***. Mesophytic Insubrian (southern Switzerland) oak-hornbeam forests mostly dominated by *Castanea sativa* and *Tilia cordata*. Since acidic bedrock prevails in this area, this association frequently contains acidophytes, including several species characteristic of the Alps (e.g. *Luzula nivea*, *Phyteuma betonicifolium*).
* **2.6 *Epimedio-Carpinetum***. Mesophytic Illyrian oak-hornbeam forests with the occur-rence of nemoral species typical of the south-eastern Alps and Dinarids (e.g. *Anemone trifolia*). They usually occur on calcareous soils since limestone bedrock prevails in this area. Within the study area, they are mainly confined to Carinthia (southern Austria).

Xerophytic group of associations

We recognized four associations within this group of xerophytic and often thermophytic types. In a cooler climate, they occupy sunny slopes, however, in the southern part of cen-tral Europe, they occur on slopes of other aspects or on flat land while thermophytic oak forests replace them on sunny slopes. A large portion of these forests is spatially or successionally connected with thermophytic oak forests (e.g. Chytrý 2013, Leuschner & Ellenberg 2017). They are more abundant on base-rich substrates such as limestone, loess and other calcareous sediments. On acidic bedrock, they represent a transition to acidophytic oak forests. In the shrub and herb layers, xerophytic and thermophytic species (e.g. *Cornus mas*, *Vincetoxicum hirundinaria*) occur frequently.

* **3.1 *Lithospermo-Carpinetum***. Xerophytic and thermophytic oak-hornbeam forests in western Switzerland with a combination of western submediterranean (e.g. *Helleborus foetidus*) and suboceanic (e.g. *Ilex aquifolium*) floristic influences.
* **3.2 *Primulo veris-Carpinetum***. Broadly distributed central-European xerophytic and thermophytic oak-hornbeam forests. Slightly thermophytic species with broad distributions (e.g. *Primula veris*, *Tanacetum corymbosum*, *Vincetoxicum hirundinaria*) are characteristic components of the herb layer.
* **3.3 *Polygonato latifolii-Carpinetum***. Pannonian Lowland oak-hornbeam forests occurring especially on loess and calcareous sand deposits on low hills in the marginal parts of the Pannonian Basin. They are rich in subcontinental thermophytic species (e.g. *Acer tataricum*, *Polygonatum hirtum*) and nitrophytes.
* **3.4 *Helleboro dumetorum-Carpinetum***. Southern Pannonian oak-hornbeam forests reaching their northern distribution limit in south-western Hungary, containing submediterranean species of the inner Balkan Peninsula forests (e.g. *Helleborus odorus*).

Discussion

Main sources of variability

The unsupervised classification and ordination indicated that the main gradient in species composition of oak-hornbeam forests is associated with soil moisture. Soil nutrient availability and base status also seem to be important. Analogous results were yielded by numerical analyses of the Czech oak-hornbeam forests (Knollová & Chytrý 2004), in which the main gradient in species composition, expressed by the first division of the unsupervised hierarchical divisive classification, distinguished mesic/dry from wet oak-hornbeam for-ests. A similar major division of oak-hornbeam forests reflecting soil moisture was used in some national overviews, e.g. by Schubert et al. (2001) for Germany, and Willner & Grabherr (2007) for Austria. The same gradient was also reflected in some pioneering phytosociological studies (e.g. Tüxen 1937, Soó 1962), which recognized two main units according to soil moisture, often named after *Quercus petraea* agg. (drier types) and *Q. robur* (wetter types). Soil moisture plays an important role in determining which of these two oak species becomes more abundant since *Q. robur* is better adapted to wetter soils while *Q. petraea* agg. is more common at drier sites with shallow soils. Traditional forest management probably had similar effects on both species, since oaks were preferred over other trees (e.g. *Acer campestre*, *Carpinus betulus*). In coppices with standards, oaks were usually the standards and the main source of acorns for pigs while other trees served as a source of firewood. Both species were also frequently planted, which changed their natu-ral distributions (Leuschner & Ellenberg 2017).

Besides ecological gradients, biogeography is highly important for the differentiation of oak-hornbeam forests. This is indicated by the occurrence of numerous species with distinctive distributions reflecting various floristic influences and regional vegetation histories (Horvat et al. 1974, Meusel & Jäger 1989, Willner et al. 2009). Our results indicate that at the scale of central Europe, latitude is more important for variation in species composition than longitude. The southern half of the study area (e.g. the Alps and the Pannonian Basin) exhibits very diverse environmental conditions resulting in a diverse forest vegetation that is rich in species with narrow distributions. The northern half of central Europe, by con-trast, is mostly characterized by slightly undulating or flat landscapes, geologically rather uniform. Moreover, a large part of these northern areas was covered by a continental ice sheet in the Pleistocene (McCann 2008, Leuschner & Ellenberg 2017). Even if we only consider the formerly non-glaciated areas, the distance from potential glacial refugia for nemoral plant species increases towards the north, which accounts for the lower number there of narrow-range forest specialists (Willner et al. 2009). In most of the central-Euro-pean national vegetation surveys (e.g. Willner & Grabherr 2007, Borhidi et al. 2012, Chytrý 2013) associations of oak-hornbeam forests are delimited both biogeographically and ecologically. However, a strictly biogeographical or strictly ecological classification might lead to schematic divisions, which do not reflect the often complex patterns in spe-cies composition (see also Knollová & Chytrý 2004).

Classification

On the basis of the unsupervised classification and ordination, we distinguished 13 basic vegetation types that could be identified with previously described associations. Applying an expert system based on formal definitions, we were able to classify ~55% of the data-set at the association level. The unclassified relevés may be classified with some level of uncertainty, e.g. by similarity indices (Tichý 2005) based on the relevés previously classified by the expert system, or can be classified at the alliance level.

Our approach tends to merge associations with minor differences in species composition (similarly to e.g. Roleček 2007, Douda et al. 2016). Therefore, we dismiss many of the previously described local associations (e.g. Michalko 1983, 1991, Šomšák & Kubíček 1995, Borhidi & Kevey 1996), which were mostly mentioned in local vegetation studies and lacked proper comparison with previously distinguished vegetation types (compare Knollová et al. 2006). Our decision not to recognize local associations was sup-ported by the results of the numerical analyses. Instead, we consider these units as parts of the variability of the 13 associations defined.

Moreover, some previously described associations (e.g. Moravec 1964 in the south-western Czech Republic) were based mainly on the absence of *Carpinus betulus* and some other typical trees of oak-hornbeam forests such as *Quercus petraea* agg. However, since their herb layer is very similar to the previously described associations, we do not distinguish them. In some cases, the absence of some trees is due to biogeographical rea-sons, but in other cases species composition of the tree layer of oak-hornbeam forests may strongly depend on recent or past management (Vera 2000, Müllerová et al. 2015, Leuschner & Ellenberg 2017).

We stick to the traditional approach of distinguishing two alliances of the *Carpinetalia* order within central Europe: widespread *Carpinion betuli* and northern Italian-Illyrian *Erythronio-Carpinion* (e.g. Wallnöfer et al. 1993, Borhidi et al. 2012, Mucina et al. 2016). The unsupervised classification did not distinguish *Carpinion betuli* from *Erythronio-Carpinion*, but this might have been due to the very limited subset of relevés of the *Erythronio-Carpinion* forests (according to original authors' assignment) in our dataset, which resulted from the fact that this alliance occurs only marginally in central Europe. The distribution centre of *Erythronio-Carpinion* is situated outside the study area, and many of its diagnostic species (e.g. *Omphalodes verna*, *Ostrya carpinifolia*, *Sesleria autumnalis*) are absent or very rare in central-European oak-hornbeam forests (Willner & Grabherr 2007, Willner et al. 2009, Borhidi et al. 2012, Košir et al. 2013). Nevertheless, some types of *Erythronio-Carpinion* formed coherent groups in finer divi-sions of our dataset, and Illyrian associations from Austria and Hungary were also well-reflected in the unsupervised classifications of data from Italy and the Balkan Peninsula in the study by Košir et al. (2013).

Regarding higher syntaxa, we do not group *Carpinion betuli* associations into geographical suballiances as proposed in some vegetation surveys (e.g. Oberdorfer 1957, Michalko et al. 1986) since they were not supported by our results. Instead, we suggest distinguishing three informal ecological groups of associations similar to the classification system proposed by Passarge & Hofmann (1968), who recognized alliances of oak-hornbeam forests defined by their soil properties (moisture, nutrients and reaction). A similar classification system with informal groups of alliances or orders taking into account macroclimatic, ecological, geographical or physiognomical characteristics was adopted in EuroVegChecklist (Mucina et al. 2016). We used Cocktail species groups reflecting the presence and absence of species (Bruelheide 1995, 1997, 2000, Kočí et al. 2003). This approach was recently applied in several vegetation surveys at national (e.g. Roleček 2007, Chytrý 2013) and supranational scales (e.g. Douda et al. 2016). We used a strategy that set a certain number of species of a sociological group that needed to be present in a relevé in order to consider the group as being present. This enabled us to prepare a more precise expert system, which better reflects the empirical fact that species may have different weights for the identification of an association. An alternative approach would be to compare the total cover values or the total number of species of par-ticular species groups (Willner 2011, Tichý et al. 2019, Willner et al. 2019), which is especially useful for classifying species-rich vegetation with several dominant species, such as grasslands.

So far, an expert system for the classification of oak-hornbeam forests has only been used in the Czech national vegetation classification (Chytrý 2013). Four associations were identified in this national classification, which we also recognize in our revised clas-sification. However, since our paper covers a much broader geographical range, our for-mal definitions of these four associations differ, although the resulting classification for the Czech Republic is very similar.

Syntaxonomic outline

Here we provide a syntaxonomic framework and more detailed descriptions of the 13 rec-ognized associations. For each of them, we give the protologue, name-giving taxa, nomen-clatural type, the most frequent synonyms occurring in central-European phytosocio-logical literature, and a brief description of its distribution, species composition and basic ecological characteristics.

1.1 *Stellario-Carpinetum* Oberdorfer 1957

P r o t o l o g u e: Oberdorfer (1957, p. 421–424): *Stellario-Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Stellaria holostea*.

N o m e n c l a t u r a l t y p e: Knapp (1946): Table 7, rel. 13, neotypus (designated in the study by Novák 2019, where the relevé was effectively published).

S y n o n y m s: *Alno-Carpinetum* Issler 1926 (potentially correct name, nomen ambi-guum rejiciendum propositum; Novák 2019), *Querceto-Carpinetum mogontiacense* Knapp 1946 (§34a), *Querceto-Carpinetum planare* Oberdorfer 1952 (§34a), *Melampyro nemorosi-Carpinetum* Passarge 1957 prov. (§3b), *Tilio-Carpinetum* Scamoni et Passarge 1959 p.p., *Melampyro nemorosi-Carpinetum* Passarge 1962, *Ulmo-Carpinetum* Mikyška 1963, *Dactylido-Carpinetum* Passarge et Hofmann 1968, *Milio effusi-Quercetum roboris* Willner, Starlinger et Grabherr ex Wallnöfer et Hotter 2008 p.p., *Tilio-Carpinetum* sensu auct. bohem. non Traczyk 1962 (pseudonym).

D e s c r i p t i o n: Hygrophytic central-European oak-hornbeam forests, which are usually dominated by *Carpinus betulus*, *Quercus robur* and *Tilia cordata*. Mesophytic (e.g. *Corylus avellana*, *Euonymus europaea*) and nitrophytic (mostly *Sambucus nigra*) species are the most frequent components of the shrub layer. Moisture- and/or nutrient-demanding species (e.g. *Geum urbanum*, *Lamium galeobdolon*, *Milium effusum*, *Urtica dioica*) are abundant in the herb layer. Some lowland types have a geophyte-rich vernal aspect (e.g. *Adoxa moschatellina*, *Corydalis cava*, *Gagea lutea*).

E c o l o g y: These forests mostly occur on upper river terraces, slope toes and poorly drained plateaus. Nevertheless, they are only rarely influenced by short-term floods.

They occur on moist and usually also nutrient-rich soils, typically gleysols and cambisols. They are more frequent in flat landscapes in the western and central part of central Europe, being rare or missing in areas with a rugged terrain (e.g. Alps, Carpathians) and dry lowlands (Pannonian Basin). They grow under a wide range of climatic conditions.

Nomenclatural note: Oberdorfer (1957) supposed this association to be a suboceanic type of *Carpinion*. However, he provided constancy tables with few suboceanic species (mainly *Arum maculatum* and *Potentilla sterilis*) accompanied by numerous moisture- and/or nutrient-demanding species with broader distributions. Therefore, this name was applied inconsistently in different countries. In Poland, *Stellario-Carpinetum* was considered to be a strictly suboceanic community, hence its range was recognized a priori to cover only the north-western and northern part of the country (Matuszkiewicz & Matuszkiewicz 1985). This resulted in a lack of truly differen-tial species between *Galio-Carpinetum* and *Stellario-Carpinetum* in Polish phytosocio-logical literature. This approach is still reflected in the recent Polish national vegetation handbooks (e.g. Matuszkiewicz 2001, 2007). In the Czech Republic, hygrophytic oak-hornbeam forests used to be assigned to other associations (e.g. Neuhäuslová 2000), e.g. *Tilio-Carpinetum*, mostly inconsistently with its original description (see below). Only in the recent national vegetation survey (Chytrý 2013), *Stellario-Carpinetum* was used in its original sense.

1.2 *Convallario-Carpinetum* Kevey 2008

Protologue: Kevey (2008, p. 234–237): *Convallario-Carpinetum* Kevey ass. nova.

Name-giving taxa: *Carpinus betulus*, *Convallaria majalis*.

Nomenclatural type: Kevey (2008): rel. on p. 234, *holotypus*.

Synonyms: *Querceto-Carpinetum hungaricum* Soó 1940 (§2b, §34a), *Querco robori-Carpinetum* Soó (1943) 1971 (§31), *Circaeo-Carpinetum* Borhidi 2003 (§2b), *Circaeo-Carpinetum* Borhidi ex Kevey 2008 (§3i), *Fraxino pannonicae-Carpinetum* sensu auct. austr. et slovak. non Borhidi et Soó in Soó 1962 (pseudonym).

Description: Hygrophytic Pannonian lowland oak-hornbeam forest dominated by *Carpinus betulus*, *Quercus robur*, with *Acer campestre* and *Fraxinus angustifolia* typ-ically admixed. *Acer tataricum* and *Ulmus minor* are frequent in the lower tree layer while *Cornus sanguinea* and *Euonymus europaeus* often form the shrub layer. A mixture of forest species typical of the Pannonian Lowland (e.g. *Aristolochia clematitis*, *Carex strigosa*) and common nutrient- and/or moisture-demanding species (e.g. *Geum urbanum*, *Lysimachia nummularia*, *Rubus caesius*) are found in the herb layer.

Ecology: These forests occur mainly on broad floodplains along lowland rivers where they inhabit places only slightly influenced by groundwater and rarely flooded. They are mainly developed on fluvisols.

Nomenclature note: Kevey (2008) split the association *Circaeo-Carpinetum*, invalidly described by Borhidi (2003) for Pannonian oak-hornbeam forests on wet soils, into four associations, mainly according to their soil properties. Kevey kept the name *Circaeo-Carpinetum* for the types recorded on wet floodplain soils, however, its name remained invalid (§3i). Therefore, we adopt the valid name *Convallario-Carpinetum,* which Kevey used for the Pannonian oak-hornbeam forests in wet interdunal depressions (species composition of these forests is similar to Borhidi's *Circaeo-Carpinetum*).

1.3 *Pseudostellario-Carpinetum* Accetto ex Novák et al. ass. nova hoc loco

P r o t o l o g u e: This paper.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Pseudostellaria europaea*.

N o m e n c l a t u r a l t y p e: Accetto (1973): Table 1, rel. 2, holotypus hoc loco designatus (effectively published below).

S y n o n y m s: *Pseudostellario-Carpinetum* Accetto 1973 (§1), *Pseudostellario-Carpinetum* Accetto 1974 (§2b).

D e s c r i p t i o n: Hygrophytic Illyrian oak-hornbeam forests. The tree layer is domi-nated by *Carpinus betulus* and *Quercus robur*, with an admixture of *Acer pseudo-platanus*, *Picea abies* and *Tilia cordata*. The herb layer includes moisture- and nutrient demanding species typical of the Illyrian Province (e.g. *Cardamine waldsteinii*, *Pseudo-stellaria europaea*) and widespread species with similar ecological requirements (e.g. *Aegopodium podagraria*, *Lamium galeobdolon*, *Polygonatum multiflorum*). These forests often have a distinct vernal aspect with submediterranean geophytes (e.g. *Crocus vernus*, *Erythronium dens-canis*). *Gentiana asclepiadea*, a species of mountain forests, occurs in places.

E c o l o g y: Forests of this association occur in environmental conditions similar to those recorded for *Stellario-Carpinetum*. They often occur on slightly wet soils of river terraces or slope toes. Soft Neogene sediments of the Styrian Basin mainly form the bed-rock.

N o m e n c l a t u r e n o t e: Marinček (1994) selected relevé 1 from the table of Accetto (1973) as "lectotype" of the *Pseudostellario-Carpinetum*. However, since this relevé was not published effectively, the name remained invalid. We selected the nomen-clature type from the same study (Accetto 1973), but we chose relevé 2 from the same table since it better fits the concept of *Carpinetalia* forests. Relevé 1 represents a transi-tion between oak-hornbeam and alluvial forest that could destabilize the nomenclature.

The type relevé of *Pseudostellario-Carpinetum*, *holotypus hoc loco designatus* (Accetto 1973; Table 1, rel. 2). Slovenia, Kostanjevica na Krki (Lower Sava Region), Krakovski Gozd Forest;

Tree layer 1 (90%): *Quercus robur* 3, *Carpinus betulus* 2; Tree layer 2 (10%): *Carpinus betulus* 1, *Acer campestre* +, *Pyrus pyraster* +; Shrub layer (20%): *Cornus sanguinea* 2, *Carpinus betulus* 1, *Corylus avellana* 1, *Euonymus europaea* [= *Euonymus europaeus*] 1, *Acer campestre* +, *Daphne mezereum* +, *Ulmus laevis* +, *Viburnum opulus* +; Herb layer (100%): *Anemone nemorosa* 2, *Pulmonaria stiriaca* 2, *Aegopodium podagraria* 1, *Crocus neapolitanus* [= *Crocus vernus* subsp. *vernus*] 1, *Dentaria bulbifera* [= *Cardamine bulbifera*] 1, *Ficaria verna* 1, *Galium odoratum* 1, *Paris quadrifolia* 1, *Pseudostellaria europaea* 1, *Ranunculus arvensis* [doubtful, perhaps rather *R. auricomus* coll.] 1, *Symphytum tuberosum* 1, *Ajuga reptans* +, *Aposeris foetida* +, *Arum maculatum* +, *Athyrium filix-femina* +, *Brachypodium sylvaticum* +, *Carex brizoides* +, *C. remota* +, *C. sylvatica* +, *Carpinus betulus* +, *Chrysosplenium alternifolium* +, *Fragaria vesca* +, *Gagea spathacea* +, *Glechoma hederacea* +, *Hedera helix* +, *Lamium galeobdolon* +, *Polygonatum multiflorum* +, *Pteridium aquilinum* +, *Quercus robur* +, *Rubus hirtus* +, *Viola riviniana* +, *Mercurialis perennis* r; species without cover value: *Carex pilosa*.

2.1 *Poo chaixii-Carpinetum* Oberdorfer ex Novák et al. ass. nova hoc loco

P r o t o l o g u e: This paper.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Poa chaixii*.

N o m e n c l a t u r a l t y p e: Schwickerath (1944): Table on p. 120–126, rel. 3, holotypus hoc loco designatus.

S y n o n y m s: *Querco-Carpinetum roboretosum, Poa chaxii*-Variante Faber 1933 (§31) p.p., *Querco-Carpinetum aceretosum pseudoplatani* Schwickerath 1944 (§31), *Querco-Carpinetum submontanum* Oberdorfer 1952 (§34a), *Querco-Carpinetum abietosum* Zeidler 1953 (§31), *Poo chaixii-Carpinetum* Oberdorfer 1957 prov. (§3b).

D e s c r i p t i o n: Mesophytic oak-hornbeam forests in the westernmost parts of central Europe. They are dominated by *Carpinus betulus*, *Quercus petraea* agg. and *Q. robur*. The shrub layer includes common mesophytic species (e.g. *Corylus avellana*) accompanied by evergreen *Ilex aquifolium* in places. The occurrence of species of beech forests (e.g. *Poa chaixii*, *Prenanthes purpurea*) coupled with suboceanic species (e.g. *Teucrium scorodonia*) is diagnostic for the herb layer. Moreover, these forests occur beyond the western distribution limits of some nemoral species characteristic of central-European oak-hornbeam forests (e.g. *Hepatica nobilis*).

E c o l o g y: These mesophytic forests usually occur on cambisols covering acidic par-ent rock. They grow in a relatively oceanic climate with rather high annual precipitation and narrow temperature amplitudes. Due to these specific climatic conditions, some herb species typical of central-European beech forests are present although these forests occur at relatively low altitudes.

2.2 *Galio sylvatici-Carpinetum* Oberdorfer 1957

P r o t o l o g u e: Oberdorfer (1957, p. 424–435): *Galio-Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Galium sylvaticum*.

N o m e n c l a t u r a l t y p e: Oberdorfer (1952): Table 2, rel. 86a, neotypus (designated by Willner & Grabherr 2007).

S y n o n y m s: *Querco pedunculatae-Carpinetum* Klika 1928 (potentially correct name, nomen ambiguum rejiciendum propositum; Novák 2019), *Querceto-Carpinetum boreonoricum* Knapp 1944 (§1, §34a), *Querceto-Carpinetum altovindobonense* Knapp 1944 (§1, §34a), *Stellario-Tilietum* Moravec 1964, *Festuco heterophyllae-Tilietum* Moravec 1964 prov., *Galio rotundifolii-Quercetum* Neuhäusl et Neuhäuslová 1968 prov. p.p., *Melampyro nemorosi-Carpinetum* sensu auct. bohem. non Passarge 1957 prov. (§3b; pseudonym), *Melampyro nemorosi-Carpinetum* sensu auct. bohem. et Wallnöfer et al. 1993 non Passarge 1962 (pseudonym), *Asperulo odoratae-Carpinetum* sensu Wallnöfer et al. 1993 non Wraber 1969 (pseudonym).

D e s c r i p t i o n: Mesophytic oak-hornbeam forests in western and central parts of central Europe. Their tree layer is mainly formed of *Carpinus betulus* and *Quercus petraea* agg. Species typical of this region (e.g. *Galium sylvaticum*, *Potentilla sterilis*) are diagnostic of their herb layer, which is dominated by common forest mesophytes. Since their distributions cover many regions where acidic bedrock prevails, forest acidophytes (e.g. *Hieracium murorum*, *Luzula luzuloides*) and less nutrient-demanding species (e.g. *Poa nemoralis*) are also typical of these forests.

E c o l o g y: These forests have a broad geographical range and tolerate a broad scale of ecological conditions. They usually grow on cambisols and luvisols.

2.3 *Tilio-Carpinetum* Traczyk 1962

P r o t o l o g u e: Traczyk (1962, p. 293–295): *Tilio-Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Tilia cordata*.

N o m e n c l a t u r a l t y p e: Kępczyński (1965): Table 3, rel. 15, neotypus (designated by Neuhäuslová 2000).

S y n o n y m s: *Corylo-Piceetum* Sokołowski 1973 p.p., *Melitti-Carpinetum* Sokołowski 1976.

D e s c r i p t i o n: North-eastern central-European zonal oak-hornbeam forests. *Carpinus betulus* and *Quercus robur* usually prevail in their tree layer, often accompanied by *Tilia cordata*. Moreover, *Picea abies* may also be a natural component. Besides common mesophytes (e.g. *Corylus avellana*), *Frangula alnus*, a species of oligotrophic substrates, is typical of the shrub layer. A co-occurrence of subcontinental (e.g. *Carex pilosa*, *Galium intermedium*) and subboreal (e.g. *Rubus saxatilis*, *Trientalis europaea*) species is characteristic of the herb layer. Acidophytes (e.g. *Luzula pilosa*) and ferns (e.g. *Dryo-pteris filix-mas*) are also frequent.

E c o l o g y: This association comprises zonal forests usually growing on acidic and deep soils (cambisols, gleysols, luvisols) on various glacial and fluvioglacial sediments. In eastern Poland, they also occur on Cretaceous marls. Locally, they are slightly influenced by groundwater. They occur in areas with a relatively continental climate as reflected by the lowest annual mean temperature and the highest precipitation seasonality of the recognized associations.

N o m e n c l a t u r a l n o t e: In the original description of *Tilio-Carpinetum* (Traczyk 1962), three geographical races were recognized. Two of them were described from central and north-eastern Poland ("mazowiecka", "mazurska") and are a good fit to the concept of *Tilio-Carpinetum* as a subboreal and subcontinental type within *Carpinion*. The last one ("małopolska") unified oak-hornbeam forests in southern Poland, florist-ically influenced by the Western Carpathians. As emphasized by some authors (e.g. Neuhäuslová-Novotná 1963, Knollová & Chytrý 2004, Kącki et al. 2016), the species composition of this race resembles the Western Carpathian association *Carici pilosae-Carpinetum*. Our results also support the assignment of some oak-hornbeam forests in southern Poland within the association *Carici pilosae-Carpinetum*. Since *Tilio-Carpinetum* was typified by a relevé from central Poland (Neuhäuslová 2000), it is accepted as the correct name for subboreal and subcontinental oak-hornbeam forests (Knollová & Chytrý 2004).

2.4 *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964

P r o t o l o g u e: Neuhäusl & Neuhäuslová-Novotná (1964, p. 12–18): *Carici pilosae-Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Carex pilosa*, *Carpinus betulus*.

N o m e n c l a t u r a l t y p e: Neuhäusl & Neuhäuslová-Novotná (1964): Table 1, rel. 4, lectotypus (designated by Neuhäuslová 2000).

S y n o n y m s: *Querceto-Carpinetum caricetosum pilosae (praefatricum)* Mikyška 1939 (§34a), *Querco-Carpinetum vihorlaticum* Michalko 1957 (§34a) p.p., *Frangulo alni-Carpinetum* Michalko 1982 p.p., *Hacquetio-Carpinetum betuli* Michalko 1983, *Melico uniflorae-Tilietum cordatae* Šomšák et Kubíček 1995.

D e s c r i p t i o n: Zonal oak-hornbeam forests of the Western Carpathian foothills. They are dominated mainly by *Carpinus betulus* and *Quercus petraea* agg., which are frequently accompanied by *Tilia cordata* and *Fagus sylvatica* (mainly at higher alti-tudes). A co-occurrence of mesophytic forest species confined in central Europe mainly to the Western Carpathians (e.g. *Aremonia agrimonoides*, *Hacquetia epipactis*) or also to the Eastern Alps (e.g. *Euphorbia amygdaloides*, *Salvia glutinosa*) with subcontinental nemoral species (e.g. *Carex pilosa*, *Galium intermedium*) is diagnostic of the herb layer. Rhizomatous graminoids (mainly *Carex pilosa*, *Melica uniflora*) dominate in places.

E c o l o g y: These mesophytic oak-hornbeam forests usually form zonal vegetation on deep mesic soils, but can also occur on rocky slopes with shallow soils that can dry out in summer. Since limestone or calcareous flysch bedrocks are widespread in the Western Carpathians, basiphytic species (e.g. *Aremonia agrimonoides*, *Euphorbia amygdaloides*, *Hacquetia epipactis*) are typical of this association. Additionally, they can also occur on slightly acidic soils where a species-poor type dominated by *Carex pilosa* develops fre-quently.

2.5 *Cruciato glabrae-Quercetum* Ellenberg et Klötzli 1974

P r o t o l o g u e: Ellenberg & Klötzli (1974, p. 688–689): *Cruciato glabrae-Quercetum castanosum*.

N a m e - g i v i n g t a x a: *Cruciata glabra*, *Quercus* spp.

N o m e n c l a t u r a l t y p e: Not designated.

S y n o n y m s: *Querco-Castanetum insubricum* Lüdi 1941 p.p. (§34a), *Querco-Fraxinetum* Antonietti 1968 prov. (§3b).

D e s c r i p t i o n: Oak-hornbeam forests in Insubria (Lugano Prealps). The tree layer is mostly dominated by *Castanea sativa* and *Tilia cordata*, with *Carpinus betulus* and *Quercus petraea* agg. admixed. In the absence of *Castanea sativa*, oaks (*Quercus cerris*, *Q. pubescens* and *Q. robur*) and *Tilia cordata* would dominate. The herb layer contains several submediterranean species (e.g. *Asplenium adiantum-nigrum*, *Dioscorea communis*) coupled with species characteristic of the Alps (e.g. *Luzula nivea*, *Phyteuma betonici-folium*). Since they predominantly occur on acidic bedrock, acidophytes (e.g. *Pteridium aquilinum*, *Solidago virgaurea*) are also common.

E c o l o g y: This association includes mesophytic oak-hornbeam forests growing in the relatively warm and humid climate in the southern foothills of the Swiss Alps. They usually occur on acidic cambisols. The common occurrence and even dominance of *Castanea sativa* in these forests is frequently ascribed to its frequent cultivation in the region for at least two millennia.

2.6 *Epimedio-Carpinetum* (Horvat 1938) Borhidi ex Soó 1964

P r o t o l o g u e: Soó (1964, p. 25): *Epimedio-Carpinetum* (Horvat 1938) Borhidi 1963.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Epimedium alpinum*.

N o m e n c l a t u r a l t y p e: Horvat (1938): Table 1, rel. 14, lectotypus (designated by Marinček 1994).

S y n o n y m s: *Querco-Carpinetum croaticum* Horvat 1938 (§34a), *Carpinetum prae-alpinum* Marinček 1979, *Helleboro nigri-Carpinetum* Marinček in Mucina et al. 1993.

D e s c r i p t i o n: These Illyrian zonal oak-hornbeam forests are dominated mainly by *Carpinus betulus* and *Quercus robur*, with an admixture of *Fagus sylvatica* and *Fraxinus excelsior*. In the study area, they were only recorded rarely in southern Austria (Carinthia), where they are at the northern limit of their distribution. The presence of some forest mesophytes characteristic of the Illyrian region (e.g. *Anemone trifolia*, *Asperula taurina*, *Epimedium alpinum*) is highly diagnostic of their herb layer.

E c o l o g y: These forests inhabit the lowest part of the Klagenfurt Basin in the East-ern Alps. They usually grow there on calcareous soils covering Pleistocene terraces and moraines. They are very rare since the basin is largely deforested or covered by other for-est types (beech and coniferous forests).

3.1 *Lithospermo-Carpinetum* Oberdorfer 1957

P r o t o l o g u e: Oberdorfer (1957, p. 440–442): *Lithospermo-Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Lithospermum purpurocaeruleum* [= *Aegonychon purpuro-caeruleum*] (see Novák 2019), *Carpinus betulus*.

N o m e n c l a t u r a l t y p e: Issler (1926): Table 3, rel. 2, lectotypus (designated by Novák 2019).

S y n o n y m s: *Carpinetum betuli* Issler 1925 (potentially correct name, nomen ambiguum rejiciendum propositum; Novák 2019), *Carpinetum betuli* Issler 1926 (§31), *Lathyro-Quercetum* Richard 1961.

D e s c r i p t i o n: South-western central-European xerophytic oak-hornbeam forests. They are dominated by *Carpinus betulus*, *Quercus petraea* agg., with an admixture of *Fagus sylvatica* or *Quercus robur* in places. Other thermophytic woody species (e.g. *Acer opalus*, *Sorbus aria* agg., *S. torminalis*) are typical of the lower tree layer. They often have a species-rich shrub layer including, besides common mesophytic species (e.g. *Lonicera xylosteum*), also some thermophytic species (e.g. *Hippocrepis emerus*, *Viburnum lantana*). A co-occurrence of submediterranean (e.g. *Aegonychon purpuro-caeruleum*), suboceanic (e.g. *Potentilla sterilis*) and submediterranean-suboceanic (e.g. *Helleborus foetidus*) species is typical of the herb layer. Apart from forest mesophytes, they are accompanied by common thermophytic species (e.g. *Melittis melissophyllum*, *Viola hirta*).

E c o l o g y: These xerophytic oak-hornbeam forests mainly occur in the foothills of the Jura and adjacent areas in western Switzerland. They grow on soils of various reactions. Although limestone often forms the bedrock, a soil profile may be locally decalcified, especially when deep. They usually occur in the areas with a rather oceanic climate, including mild winters.

N o m e n c l a t u r a l n o t e: These forests in the foothills of the Swiss Jura were described as *Lathyro-Quercetum* by Richard (1961). This author included them among thermophytic oak forests (*Quercion pubescenti-petraeae* alliance). However, later authors classified them as transitional between thermophytic oak forests and mesophytic deciduous forests (e.g. Ellenberg & Klötzli 1974) or put them directly into oak-hornbeam forests of the *Carpinion* alliance (e.g. Moor 1967, Keller et al. 1998).

3.2 *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová ex Neuhäuslová-Novotná 1964

P r o t o l o g u e: Neuhäuslová-Novotná (1964, p. 48): *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová 1963.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Primula veris*.

N o m e n c l a t u r a l t y p e: Neuhäusl & Neuhäuslová-Novotná (1964): Table 2, rel. 15, lectotypus (designated by Neuhäuslová 2000).

S y n o n y m s: *Querceto-Carpinetum slovenicum* Dostál 1933 (§34a), *Querco-Carpinetum vihorlaticum* Michalko 1957 (§34a) p.p., *Festuco heterophyllae-Quercetum*

Neuhäusl et Neuhäuslová-Novotná 1964 p.p., *Querco-Carpinetum waldsteinietosum* Jakucs et Jurko 1967 p.p., *Galio sylvatici-Carpinetum bupleuretosum longifolii* Schlüter 1968, *Coronillo latifoliae-Carpinetum* (Michalko 1957) Michalko in Mucina et Maglocký 1985 p. p., *Waldsteinio-Carpinetum* (Jakucs et Jurko 1967) J. Michalko et M. Michalko in Mucina et Maglocký 1985 p.p., *Poo angustifoliae-Carpinetum* Michalko 1991 prov. p.p., "*Waldsteinio-Carpinetum* (Jakucs et Jurko 1967) Soó 1971" (a phantom name mentioned e.g. by Borhidi 2003 and Jarolímek et al. 2008).

D e s c r i p t i o n: These forests occur mainly in the southern half of central Europe. *Carpinus betulus* and *Quercus petraea* agg. are the most frequent dominants of their tree layer with an admixture of *Acer campestre* and *Sorbus torminalis*. Thermophytic species (e.g. *Cornus mas*, *Ligustrum vulgare*, *Prunus spinosa*) are typical components of the shrub layer. Herb layer is also rich in thermophytic species (e.g. *Primula veris*, *Tanacetum corymbosum*, *Vincetoxicum hirundinaria*, *Viola hirta*). Acidotolerant thermo-phytic species (e.g. *Carex montana*, *Festuca heterophylla*) are characteristic of these for-ests on slightly acidic soils.

E c o l o g y: Xerophytic and thermophytic central-European oak-hornbeam forests occur on various basic (e.g. calcareous flysch, limestone, loess) or slightly acidic (e.g. andesite) bedrock in warm regions in central Europe. Basic or neutral leptosols and cambisols are among the most typical soil types.

S y n t a x o n o m i c n o t e: In the vegetation surveys of Austria and Germany, this unit was often considered as a xeric subassociation of *Galio sylvatici-Carpinetum*.

3.3 *Polygonato latifolii-Carpinetum* Michalko et Džatko 1965

P r o t o l o g u e: Michalko & Džatko (1965, p. 73–76): *Polygonato* (*latifolii*)-*Carpinetum* ass. nova.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Polygonatum hirtum*.

N o m e n c l a t u r a l t y p e: Michalko & Džatko (1965): Table 17, rel. 16, lectotypus (designated by Willner & Grabherr 2007).

S y n o n y m s: *Aceri* (*campestri*)-*Querceteum petraeae-roboris* Fekete 1965 (§10a), "*Aceri campestris-Quercetum roboris* Fekete 1965" (phantom mentioned e.g. by Borhidi et al. 2012).

D e s c r i p t i o n: Pannonian Lowland oak-hornbeam forests with *Carpinus betulus* and *Quercus robur* as dominants in the tree layer, often with an admixture of *Acer campestre*, *A. tataricum*, *Quercus cerris* and *Ulmus minor*. The shrub layer is typically composed of a mixture of mesophytic (*Cornus sanguinea*, *Euonymus europaeus* and *E. verrucosus*) and thermophytic (*Ligustrum vulgare* and *Viburnum lantana*) species. The herb layer is characterized by forest species typical of the Pannonian Lowland (e.g. *Polygonatum hirtum*) and nitrophytes (e.g. *Geum urbanum*, *Veronica hederifolia* agg., *Viola odorata* agg.). Forest mesophytes are most frequently represented by *Campanula trachelium*, *Convallaria majalis* and *Galium odoratum*.

E c o l o g y: These forests typically grow on luvisols covering loess sediments on pla-teaus and gentle slopes. These soils are nutrient-rich, often spring-wet but summer-dry since they occur under the relatively continental climate of the Pannonian Basin. As flat parts of the basin are almost completely deforested, they usually occur in remnant forest patches surrounded by an agricultural landscape.

3.4 *Helleboro dumetorum-Carpinetum* Soó et Borhidi in Soó 1962

P r o t o l o g u e: Soó (1962, p. 356–357) *Helleboro* (*dumetorum*)-*Carpinetum* Soó et Borhidi nom. nov.

N a m e - g i v i n g t a x a: *Carpinus betulus*, *Helleborus dumetorum*.

N o m e n c l a t u r a l t y p e: Not designated.

S y n o n y m s: *Querceto robori-Carpinetum praeillyricum* Soó et Borhidi in Soó 1958 (§34a), *Querco petraeae-Carpinetum praeillyricum* Borhidi 1960 (§34a), *Querco petraeae-Carpinetum mecsekense* Horvát 1968.

D e s c r i p t i o n: Oak-hornbeam forests on hills in the southern Pannonian Basin. Their tree layer is dominated by *Carpinus betulus* and *Quercus petraea* agg. An admix-ture of thermophytic drought-tolerant trees *Fraxinus ornus* and *Tilia tomentosa* is highly diagnostic. Submediterranean species characteristic of the inner Balkan Peninsula (e.g. *Helleborus odorus*, *Ruscus hypoglossum*) are typical components of the herb layer. They are accompanied by common thermophytic (e.g. *Tanacetum corymbosum*) and meso-phytic (*Cardamine bulbifera*, *Viola reichenbachiana* agg.) species.

E c o l o g y: These forests represent a zonal forest community in relatively dry and warm hilly landscapes in south-western Hungary. They occur on a variety of bedrocks, usually basic (limestone, loess) or slightly acidic (sandstone).

See www.preslia.cz for Electronic Appendices 1–6

Acknowledgements

We thank the database custodians Henry Brisse, Jean-Claude Gégout, Ute Jandt, Florian Jansen, Zygmunt Kącki and Milan Valachovič for providing data, Lubomír Tichý for valuable comments on the expert systems, Andraž Čarni for providing Slovenian phytosociological literature and Ilona Knollová for data extraction from the European Vegetation Archive. PN and MCh were supported by the Czech Science Foundation (project no. 17-15168S), JCs was supported by the European Union, and cofinanced by the European Social Fund: Compre-hensive Development for Implementing Smart Specialization Strategies at the University of Pécs (project no. EFOP-3.6.1.-16-2016-00004).

Souhrn

Dubohabřiny (řád *Carpinetalia betuli*) představují široce rozšířený typ zonální lesní vegetace střední Evropy. Časté jsou zejména v níže položených oblastech se subkontinentálním klimatem. Jde o lesní vegetaci s domi-nancí habru obecného (*Carpinus betulus*) a dubů (nejčastěji *Quercus petraea* agg. a *Q. robur*), ve které se v růz-né míře objevují další opadavé listnaté dřeviny (např. *Acer campestre*, *A. platanoides* a *Tilia cordata*), některé ale jen v jižní části území (např. *Acer opalus*, *A. tataricum* a *Tilia tomentosa*). V bylinném patře převládají lesní mezofyty (*Carex pilosa*, *Galium sylvaticum*, *Stellaria holostea* a další). Tyto lesy byly studovány již od pionýr-ských dob výzkumu vegetace střední Evropy. Postupně bylo popsáno několik desítek asociací a jejich syntaxo-nomie na úrovni asociace se stala poměrně komplikovanou. Práce si klade za cíl vymezit hlavní typy/asociace středoevropských dubohabřin a pro každý typ vytvořit formální definici založenou na metodě Cocktail a dále zjistit hlavní ekologické faktory určující proměnlivost této vegetace. V analyzovaném datovém souboru bylo celkem 6212 fytocenologických snímků z Německa, Švýcarska, Rakouska, České republiky, Slovenska, Pol-ska, Maďarska a Zakarpatské Ukrajiny, které byly ve většině případů získány z vegetačních databází Evropské-ho vegetačního archivu. Na základě klasifikačních a ordinačních analýz bylo rozlišeno 13 asociací, 9 ze středo-evropského svazu *Carpinion betuli* a 4 z ilyrsko-severoitalského svazu *Erythronio-Carpinion*. Nově vytvořený expertní systém umožnil klasifikovat přibližně 55 % snímků do asociací. Numerické analýzy dále ukázaly, že hlavní gradient v druhovém složení studované vegetace je spjat s vlhkostí a úživností půd. Významnou roli hra-jí také zeměpisná šířka, roční teplotní amplituda (tj. kontinentalita klimatu) a průměrná roční teplota. Na zákla-dě této analýzy jsme rozlišili tři hlavní ekologické skupiny asociací: vlhkomilnou, mezofilní a suchomilnou.

Z vlhkomilných jde o asociace *Stellario-Carpinetum* (západo-středoevropské vlhkomilné dubohabřiny), *Convallario-Carpinetum* (panonské vlhkomilné dubohabřiny) a *Pseudostellario-Carpinetum* (ilyrské vlhkomilné dubohabřiny). Z mezofilní skupiny to jsou asociace *Poo chaixii-Carpinetum* (suboceanické mezofilní dubohabřiny), *Galio sylvatici-Carpinetum* (západo-středoevropské mezofilní dubohabřiny), *Tilio-Carpinetum* (mezofilní dubohabřiny polských nížin), *Carici pilosae-Carpinetum* (západokarpatské mezofilní dubohabřiny), *Cruciato-Quercetum* (insubrijské mezofilní dubohabřiny) a *Epimedio-Carpinetum* (ilyrské mezofilní dubohabřiny). V rámci suchomilných (a teplomilných) dubohabřin jsme definovali asociace *Lithospermo-Carpinetum* (suchomilné a teplomilné dubohabřiny západního Švýcarska), *Primulo veris-Carpinetum* (středoevropské suchomilné a teplomilné dubohabřiny), *Polygonato latifolii-Carpinetum* (panonské nížinné dubohabřiny) a *Helleboro-Carpinetum* (jihopanonské dubohabřiny). Oproti kompendiu Vegetace České republiky rozlišujeme na území ČR další dvě asociace, obě s centrem rozšíření v nížinách mimo naše území (*Convallario-Carpinetum*, *Tilio-Carpinetum*). Jejich výskyt byl zmíněn v literatuře již dříve a vzhledem ke zde prezentovaným výsledkům by bylo vhodné je začít na našem území prakticky rozlišovat.

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Received 15 July 2019
Revision received 21 November 2019
Accepted 30 November 2019

Electronic Appendix 5: Expert system
Electronic Appendix 5: Expert system for classification of central European oak-hornbeam forests (*Carpinetalia*) to associations.

This expert system can be run in the Juice 7 program after being transformed into plain text (.txt) format. It is expected that the analysed data will use species names following the Euro+Med PlantBase with modifications listed in Electronic Appendix 3. Species groups are provided followed by formulas of all the accepted associations. In the formulas, the number of species of a sociological group required for its presence is given by a two-digit number after "#". Sociological species groups are connected by logical operators AND, OR and NOT.

```
SECTION 1: Species aggregation
SECTION 1: End
SECTION 2: Species groups
### Boreal
     Equisetum pratense
     Trientalis europaea
     Lycopodium annotinum
     Vaccinium vitis-idaea
### Carinthia
     Anemone trifolia
     Galium laevigatum
     Vicia oroboides
### CE_sstr
     Galium sylvaticum
     Potentilla sterilis
     Rosa arvensis
     Phyteuma nigrum
     Cyclamen purpurascens
### CE_thermo
     Aegonychon purpurocaeruleum
     Anthericum ramosum
     Carex michelii
     Cornus mas
     Dictamnus albus
     Festuca heterophylla
     Ligustrum vulgare
     Melittis melissophyllum
     Primula veris
     Quercus cerris
     Quercus pubescens
     Sorbus torminalis
     Tanacetum corymbosum
     Trifolium alpestre
     Vincetoxicum hirundinaria
     Viola hirta
### CE_thermo_bas
     Aegonychon purpurocaeruleum
     Carex michelii
     Cornus mas
     Dictamnus albus
     Ligustrum vulgare
     Primula veris
     Quercus pubescens
     Viola hirta
### CE_thermo_neu
     Anthericum ramosum
     Festuca heterophylla
     Melittis melissophyllum
     Quercus cerris
     Sorbus torminalis
     Tanacetum corymbosum
     Trifolium alpestre
     Vincetoxicum hirundinaria
### Cont_nem
     Carex pilosa
     Cruciata glabra
     Euonymus verrucosus
     Galium intermedium
     Isopyrum thalictroides
     Viola mirabilis
```

```
### CWE_thermo
     Acer opalus
     Carex flacca
     Dioscorea communis
     Hippocrepis emerus
     Helleborus foetidus
     Ilex aquifolium
     Primula acaulis
     Rosa arvensis
     Sorbus aria aggr.
     Viburnum lantana
### E_C_mesic
     Anemone trifolia
     Asparagus tenuifolius
     Asperula taurina
     Dioscorea communis
     Doronicum orientale
     Erythronium dens-canis
     Galium aristatum
     Geranium nodosum
     Helleborus dumetorum
     Helleborus odorus
     Lamium orvala
     Luzula forsteri
     Luzula nivea
     Ostrya carpinifolia
     Phyteuma betonicifolium
     Polystichum setiferum
     Pulmonaria australis
     Pulmonaria stiriaca
     Ruscus aculeatus
     Ruscus hypoglossum
     Tilia tomentosa
     Veronica urticifolia
     Vicia oroboides
### Fagus_species
     Abies alba
     Fagus sylvatica
     Aruncus dioicus
     Veratrum album aggr.
     Prenanthes purpurea
### Galium_s_i
     Galium sylvaticum
     Galium intermedium
### Illyr_EA_Boh
     Knautia drymeia
     Cyclamen purpurascens
### Illyr_EA_Boh_vs_WC
     Galium sylvaticum
     Hepatica nobilis
     Hippocrepis emerus
     Knautia drymeia
     Cyclamen purpurascens
     Veratrum nigrum
### Mecsek
     Helleborus odorus
     Doronicum orientale
     Tilia tomentosa
     Fraxinus ornus
     Luzula forsteri
     Ruscus hypoglossum
### Oceanic
     Ilex aquifolium
     Luzula sylvatica
     Lonicera periclymenum
     Poa chaixii
     Pulmonaria montana
     Teucrium scorodonia
### Pannonia_thermo
     Acer tataricum
     Polygonatum hirtum
     Physalis alkekengi
     Viola mirabilis
### Pannonia_thermo_Qcerr
```

```
     Quercus cerris
### Pannonian_wet
     Fraxinus angustifolia
     Acer tataricum
     Aristolochia clematitis
     Carex strigosa
     Oenanthe banatica
### Styria
     Cardamine waldsteinii
     Crocus vernus
     Erythronium dens-canis
     Gentiana asclepiadea
     Pseudostellaria europaea
     Pulmonaria stiriaca
### Styria_sstr
     Cardamine waldsteinii
     Crocus vernus
     Erythronium dens-canis
     Pseudostellaria europaea
     Pulmonaria stiriaca
### Subboreal
     Dryopteris carthusiana aggr.
     Frangula alnus
     Luzula pilosa
     Maianthemum bifolium
     Oxalis acetosella
     Populus tremula
     Pteridium aquilinum
     Rubus saxatilis
     Sorbus aucuparia
     Vaccinium myrtillus
### Ticino
     Castanea sativa
     Geranium nodosum
     Veronica urticifolia
     Phyteuma betonicifolium
     Ostrya carpinifolia
     Luzula nivea
     Asplenium adiantum-nigrum
### Thermo_acido
     Calamagrostis arundinacea
     Carex montana
     Convallaria majalis
     Festuca ovina
     Genista tinctoria
     Hylotelephium maximum
     Hieracium lachenalii
     Hieracium murorum
     Hieracium sabaudum
     Hypericum montanum
     Lembotropis nigricans
     Luzula luzuloides
     Melampyrum pratense
     Veronica officinalis
     Avenella flexuosa
     Luzula campestris aggr.
     Solidago virgaurea
     Silene nutans
     Vaccinium myrtillus
### WCarp_only
     Aremonia agrimonioides
     Cardamine glanduligera
     Carex brevicollis
     Hacquetia epipactis
     Waldsteinia geoides
     Aconitum moldavicum
     Symphytum cordatum
### WCarp_typical
     Aposeris foetida
     Arum cylindraceum
     Carex alba
     Drymochloa drymeja
     Euphorbia amygdaloides
     Pulmonaria mollis
```

```
     Salvia glutinosa
     Stachys alpina
     Staphylea pinnata
     Symphytum tuberosum
### Wet_coll
     Aegopodium podagraria
     Anthriscus sylvestris
     Carex remota
     Carex sylvatica
     Circaea lutetiana
     Ficaria verna
     Lamium maculatum
     Prunus padus
     Stachys sylvatica
     Stellaria nemorum
     Urtica dioica
     Viburnum opulus
### Wet_low
     Adoxa moschatellina
     Alliaria petiolata
     Galium aparine
     Geranium robertianum
     Geum urbanum
     Glechoma hederacea
     Chaerophyllum temulum
     Sambucus nigra
     Urtica dioica
     Veronica hederifolia aggr.
#TC Carbet-woody
     Acer campestre
     Carpinus betulus
     Quercus robur
     Quercus petraea aggr.
     Tilia cordata
SECTION 2: End
SECTION 3: Group definitions
SECTION 3: Group definitions
5 01ShC Stellario-Carpinetum
(<#TC Carbet-woody GR25> AND (<#03 Wet_coll> OR <#03 Wet_low>)) NOT ((((((((((((<#01
Boreal> OR <#02 Cont_nem>) OR <#01 CE_sstr>) OR <#01 E_C_mesic>) OR <#02 Oceanic>) OR
<#03 CWE_thermo>) OR <#01 WCarp_only>) OR <#04 CE_thermo>) OR <#02 Pannonia_thermo>) OR
<#01 Pannonian_wet>) OR <#01 Styria_sstr>) OR <#01 Pannonia_thermo_Qcerr>) OR <#01
WCarp_typical>)

5 02CoC Convallario-Carpinetum
(<#TC Carbet-woody GR25> AND (<#02 Pannonian_wet> OR (<#01 Pannonian_wet> AND <#03
Wet_low>))) NOT (((((((<#01 Boreal> OR <#02 Cont_nem>) OR <#01 CE_sstr>) OR <#01
E_C_mesic>) OR <#02 Oceanic>) OR <#03 CWE_thermo>) OR <#01 WCarp_only>) OR <#04
CE_thermo>) OR <#02 Pannonia_thermo>)

5 03PeC Pseudostellario-Carpinetum
(<#TC Carbet-woody GR25> AND (<#02 Styria> OR (<#01 Styria_sstr> AND (<#01 WCarp_typical>
OR <#01 Illyr_EA_Boh>)))) NOT (<#01 WCarp_only> OR <#01 Pannonian_wet>)

5 04PcC Poo-Carpinetum
(<#TC Carbet-woody GR25> AND <#02 Oceanic>) NOT ((<#03 CWE_thermo> OR <#04 CE_thermo>) OR
<#01 E_C_mesic>)

5 05GsC Galio-Carpinetum
(<#TC Carbet-woody GR25> AND <#01 CE_sstr>) NOT (<#03 Subboreal> OR ((((((((<#04
CE_thermo> OR <#01 Ticino>) OR <#01 E_C_mesic>) OR <#02 WCarp_typical >) OR <#02
Cont_nem>) OR <#02 Oceanic>) OR <#03 CWE_thermo>) OR <#02 Galium_s_i>) OR <#01
Pannonian_wet>) OR <#01 WCarp_only>)

5 06TcC Tilio-Carpinetum
(<#TC Carbet-woody GR25> AND ((<#01 Cont_nem> AND <#03 Subboreal>) OR <#01 Boreal>)) NOT
((((<#01 WCarp_typical> OR <#01 WCarp_only>) OR <#01 Fagus_species>) OR <#01 CE_sstr>) OR
<#01 Oceanic>)

5 07CpC Carici-Carpinetum
(<#TC Carbet-woody GR25> AND ((<#02 Cont_nem> AND <#01 WCarp_typical>) OR <#01
WCarp_only>)) NOT ((((((<#01 E_C_mesic> OR <#04 CE_thermo>) OR <#01 CE_sstr>) OR <#02
Pannonia_thermo>) OR <
#01 Boreal>) OR <#01 Pannonian_wet>) OR <#01 Illyr_EA_Boh_vs_WC>)
```

```
5 08EaC Epimedio-Carpinetum
<#TC Carbet-woody GR25> AND (<#02 Carinthia> OR (<#01 Carinthia> AND (<#01 WCarp_typical>
OR <#01 Illyr_EA_Boh>)))

5 09CgQ Cruciato-Quercetum
<#TC Carbet-woody GR25> AND <#02 Ticino>

5 10LpC Lithospermo-Carpinetum
(<#TC Carbet-woody GR25> AND <#03 CWE_thermo>) NOT (((<#02 Cont_nem> OR <#01 Mecsek>) OR
<#01 Ticino>) OR <#01 Illyr_EA_Boh>)

5 11PvC Primulo-Carpinetum
(<#TC Carbet-woody GR25> AND (<#04 CE_thermo> OR (<#03 CE_thermo_bas> OR (<#02
Pannonia_thermo> AND <#04 Thermo_acido>)))) NOT (<#01 E_C_mesic> OR (<#03 CWE_thermo> OR
(<#02 Pannonia_thermo> NOT <#04 Thermo_acido>)))

5 12PlC Polygonato-Carpinetum
(<#TC Carbet-woody GR25> AND <#02 Pannonia_thermo>) NOT (<#01 E_C_mesic> OR (<#04
Thermo_acido> AND <#02 Pannonia_thermo>))

5 13HoC Helleboro-Carpinetum
<#TC Carbet-woody GR25> AND <#02 Mecsek>
SECTION 3: End
SECTION 4: Similarity
SECTION 4: End
```

7.6. Paper 6

Kollár J. & Novák P. (2020): *Carpinetalia betuli* P. Fukarek 1968. – In: Kliment J., Valachovič M., Hegedűšová Vantarová K. (eds), Rastlinné spoločenstvá Slovenska 6, Lesná a krovinová vegetácia [Plant communities of Slovakia 6, Forest and shrub vegetation], Veda, Bratislava (*in press*). [in Slovak]

Spracovali: J. Kollár, P. Novák

Carpinetalia betuli P. Fukarek 1968
Dubovo-hrabové lesy

Tabuľka 1, stĺpce 1–4 (provizórne číslovanie)

Charakteristické taxóny: *Carex pilosa* (transgr.), *Carpinus betulus*, *Cerasus avium*
Diferenciálne taxóny: *Crataegus laevigata*, *Galium schultesii*, *Melica uniflora*, *Poa nemoralis*, *Pulmonaria officinalis* agg., *Ranunculus auricomus* agg., *Symphytum tuberosum* agg.

Rad *Carpinetalia betuli* združuje zonálne listnaté lesy mierneho pásma Európy, ktoré sa vyskytujú na hlbších a živných pôdach. Zvyčajne dominuje hrab a duby, najmä *Quercus petraea* agg. a *Q. robur* agg. Pre bylinné poschodie sú typické lesné mezofyty, napr. *Campanula rapunculoides*, *Carex digitata*, *Galium odoratum*, *Lathyrus vernus*, *Viola reichenbachiana* a pod. Súčasťou radu je viacero fytogeograficky podmienených zväzov. Na Slovensku a vo väčšine strednej Európy ide o zväz *Carpinion betuli*, v submediteránnej oblasti sú typické zväzy *Pulmonario longifoliae-Quercion roboris* Rivas-Mart. et Izco in Rivas-Mart. et al. 2002, *Erythronio-Carpinion* (Horvat 1958) Marincek in Wallnofer et al. 1993, *Castaneo sativae-Carpinion orientalis* Quezel, Barbero et Akman ex Quezel et al. 1993, *Paeonio dauricae-Quercion petraeae* Didukh 1996 a na subkontintálny región sa viažu zväzy *Querco roboris-Tilion cordatae* Solomeshch et Laivins ex Bulokhov et Solomeshch in Bulokhov et Semenishchenkov 2015, *Scillo sibericae-Quercion roboris* Onyshchenko 2009, *Aconito lycoctoni-Tilion cordatae* Solomeshch et Grigoriev in Willner et al. 2016. Dubovo-hrabové lesy zväzu *Carpinion* sa u nás tradične zaraďovali do radu *Fagetalia sylvaticae* . V tomto prehľade rešpektujeme európsky vegetačný prehľad (Mucina et al. 2016).

Carpinion betuli Issler 1931
Mezofilné dubovo-hrabové lesy

PFM: *Carpinetion* (Issler 1931: 83–90)

Tabuľka 1, stĺpce 1–4 (provizórne číslovanie)

DST: zhodná s DST radu

Zväz *Carpinion betuli* zahŕňa klimaxové lesy nižších polôh s relatívne teplou klímou, v ktorých zvyčajne prevládajú *Carpinus betulus*, *Quercus petraea* agg., *Q. robur* agg.; častou prímesou sú *Acer campestre*, *Cerasus avium, Tilia cordata* a ďalšie dreviny. V karpatskej oblasti sa hojne uplatňuje *Fagus sylvatica*. Poschodie krovín je vyvinuté rôzne, v závislosti od presvetlenia porastov, pôdy a vplyvov lesného hospodárstva. Bylinné poschodie tvoria najmä mezofilné druhy, ktoré v závislosti od konkrétnej jednotky sprevádzajú teplomilné, kyslomilné či mezohygrofilné druhy. Machové poschodie je zvyčajne nevýrazné. Častejšie sa uplatňujú bežné lesné druhy ako *Atrichum undulatum*, *Brachythecium velutinum*, *Hypnum cupressiforme*, *Plagiomnium undulatum* a *Polytrichum formosum.*
Dubovo-hrabové lesy tvoria samostatný vegetačný stupeň, ktorý sa vo svojej dnešnej podobe vyvinul pravdepodobne v subboreáli po expanzii hraba. Centrom rozšírenia zväzu je stredná

Európa, ale jeho areál presahuje aj do východnej časti západnej Európy (Leuschner, Ellenberg 2017), na východe do Bieloruska a Ukrajiny a na juhu do Rumunska a severnej časti Balkánskeho polostrova (Matuszkiewicz 2003; Novák et al. 2020). Na Slovensku sú rozšírené na celom území, od nížin cez sprašové pahorkatiny po kolínny (zriedka až submontánny) stupeň. Dlhodobo sú značne poznačené človekom. Ich drevinové zloženie je ovplyvnené lesným hospodárením, pretože hrab sa často odstraňoval ako nežiaduca drevina, pričom vznikali čisté dubové lesy. Na druhej strane bol hrab vďaka dobrému zmladzovaniu z pňov zvýhodnený pri tradičnom historickom hospodárení, kedy sa stromy obnovovali vegetatívne (ako hospodársky tvar lesa prevažoval nízky a stredný les). Osobitne to platí v porastoch, ktoré sú v kontakte s bučinami, kde hrab profitoval na úkor buka. Podľa niektorých autorov (napr. Boublík et al. 2007; Leuschner, Ellenberg 2017) by preto potenciálne rozšírenie bučín zasahovalo aj do nižších nadmorských výšok, kde sa v súčasnosti uplatňujú dubovo-hrabové lesy. Rozsiahle plochy dubo-hrabín boli odlesnené a premenené na poľnohospodársku pôdu, najmä v nížinách a sprašových pahorkatinách. Z niektorých typov sa preto zachovali len malé zvyšky (*Convallario-Carpinetum*, *Polygonato latifolii-Carpinetum*). Ich potenciálny výskyt sa predpokladá aj vo vyššie položených kotlinách, ako Liptovská a Popradská kotlina (Michalko et al. 1986), ktoré sú v súčasnosti odlesnené, resp. výrazne antropicky pozmenené.

Dubovo-hrabové lesy majú pomerne širokú ekologickú valenciu. Centrum rozšírenia majú v mezotrofných podmienkach, ale vytvárajú aj prechodné fytocenózy k teplomilným dúbravám (*Polygonato-Carpinetum*, *Primulo veris-Carpinetum*), kyslomilným dúbravám (*Carici pilosae-Carpinetum luzuletosum*), tvrdým lužným lesom (*Convallario-Carpinetum*), sutinovým lesom (*Carici pilosae-Carpinetum dryopteridetosum*) a bučinám (*Carici pilosae-Carpinetum*).

Syntaxonomická poznámka:
Predložená klasifikácia zväzu *Carpinion* rešpektuje tradičný prístup, v ktorom sa uplatňuje jednak charakter stanovištných podmienok, jednak fytogeografický aspekt. V porovnaní s predchádzajúcim vegetačným prehľadom (Jarolímek et al. 2008) však chápeme jednotlivé asociácie širšie, a preto nižšie uvedené spoločenstvá nerozlišujeme.

- Asociáciu *Hacquetio-Carpinetum*, ktorú M. Michalko (1983) opísal z Bielych Karpát, považujeme za lokálny variant asociácie *Carici pilosae-Carpinetum.* Výskyt druhu *Galium sylvaticum* (namiesto *G. schultesii*) však svedčí o určitej príbuznosti so stredo-západoeurópskou asociáciou *Galio sylvatici-Carpinetum* Oberd. 1957. K tejto asociácii sa ešte viac približujú niektoré porasty z Malých Karpát, kde sa popri *Galium sylvaticum* vyskytujú aj *Hepatica nobilis* a *Knautia drymeia*, a ktoré rovnako chápeme ako súčasť asociácie *Carici pilosae-Carpinetum*.
- Asociácia *Stellario-Carpinetum* Oberd. 1957 zahŕňa relatívne vlhkomilné dubovo-hrabové lesy s centrom rozšírenia v strednej a západnej Európy. V dostupnej databáze (CDF) sa síce nachádzajú fytocenologické zápisy s vyšším zastúpením vlhkomilnejších druhov a vysokým zastúpením *Quercus robur* agg. (najmä zo Záhoria), ale ide o malé množstvo údajov, pričom nižšie zastúpenie alebo absencia druhov karpatských dubo-hrabín môže vyplývať z faktu, že ide o čiastočne pozmenené porasty. Považujeme ich preto za súčasť variability spoločenstva *Carici pilosae-Carpinetum*.

- Šomšák a Kubíček (1995) zaradili porasty dubovo-hrabových lesov z terás rieky Rudavy (Borská nížina) do novoopísanej asociácie *Melico uniflorae-Tilietum* *cordatae*. Autori upozornili na určitú podobnosť týchto porastov so (sub)oceánickými typmi dubo-hrabín. Vyskytujú sa tu však typické prvky karpatských dubo-hrabín, ako *Carex pilosa* a *Galium schultesii*. Celý areál asociácie má navyše rozlohu iba niekoľko hektárov. Tieto porasty preto považujeme za súčasť variability asociácie *Carici pilosae-Carpinetum*.

- Asociácia *Coronillo latifoliae-Carpinetum* (J. Michalko 1957) J. Michalko in Mucina et Maglocký 1985 bola opísaná ako východoslovenský typ teplomilnej dubo-hrabiny. Takéto porasty považujeme za súčasť iných asociácií teplomilných dubohrabín a dubín.

- Z karbonátových pôd Slovenského krasu sa uvádza asociácia *Waldsteinio-Carpinetum* (Jakucs et Jurko 1967) Soó 1971 zo stanovíšť, ktoré nadväzujú na sutinové lesy a teplomilné dúbravy. Tento typ porastov považujeme za súčasť teplomilných dubín (*Quercion pubescenti-petraeae*) a dubo-hrabín (*Primulo veris-Carpinetum*).

- Podobný charakter majú porasty z karbonátových plytkých pôd Silickej planiny, ktoré Šomšák a Háberová (1979) uviedli pod menom *Melico uniflorae-Quercetum petraeae* Gergely 1962. Toto meno pre dané porasty nepovažujeme za správne, pretože pôvodne bolo použité pre dubovo-hrabové lesy Sedmohradska s druhmi ako *Aposeris foetida*, *Hepatica nobilis*, *Lathyrus transsilvanicus* a pod. Väčšina týchto porastov patrí medzi teplomilné dubiny zväzu *Quercion pubescenti-petraeae* Br.-Bl. 1932 a teplomilné dubo-hrabiny asociácie *Primulo veris-Carpinetum*.

- Asociácia *Festuco heterophyllae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1964 je na Slovensku tradične vymedzovaná pre teplomilné a subacidofilné dubo-hrabiny a tvorí prechod k teplo- a kyslomilným dubinám. Väčšinu takto hodnotených porastov považujeme za súčasť teplomilných subacidofilných dúbrav zväzu *Quercion petraeae*, najmä asociácie *Sorbo torminalis-Quercetum*.

- *Tilio-Carpinetum* Traczyk 1962 je asociácia subboreálnych dubo-hrabín opísaná z nížin Poľska. Z územia Slovenska nie sú k dispozícii zápisy, ktoré by zodpovedali tejto jednotke.

- *Frangulo alni-Carpinetum* je spoločenstvo, ktoré Michalko (1991) opísal z kotlín Slovenska ako prechod k široko chápanej asociácii *Potentillo albae-Quercetum*. Aspoň sčasti však pravdepodobne ide o pôvodne nátržníkové dúbravy, ktoré sa sukcesne menia na mezofilnejšie typy. Tento trend je opísaný z viacerých regiónov Európy (Roleček 2007). Michalko (1991) opísal na základe troch zápisov z Rimavskej a Lučeneckej kotliny aj asociáciu *Poo angustifoliae-Carpinetum* prov. (čl. 3b), ktorá sa svojím floristickým zložením blíži k teplomilným dubovým lesom.

Osobitým a nedoriešeným problémom sú dubo-hrabiny vyššie položených kotlín (Liptovská, Popradská), kde sa prírode blízke porasty nezachovali, a nie sú tak k dispozícii žiadne zápisy. Pri zostavovaní mapy potenciálnej vegetácie (Michalko et al. 1986) sa pre tieto polohy navrhla asociácia *Tilio cordatae-Piceetum* J. Michalko in J. Michalko et al. 1980, ktorá predstavuje pomyselný prechod od dubovo-hrabových lesov lipových k smrekovým a jedľovo-smrekovým lesom. Ide však o neplatné meno (čl. 2b).

1. *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964

Syn.: *Querco-Carpinetum vihorlaticum* Michalko 1957 p. p. (čl. 34a)
Syntax. syn.: *Hacquetio-Carpinetum betuli* Michalko 1983, *Melico uniflorae-Tilietum cordatae* Šomšák et Kubíček 1995
Incl.: *Querceto-Carpinetum caricetosum pilosae* (*praefatricum*) Mikyška 1939

Tabuľka 1, stĺpec 1 (provizórne číslovanie)

Diferenciálne taxóny: *Carex pilosa* (dom., konšt.), *Fagus sylvatica* (E_{3-1}), *Hieracium murorum*, *Luzula luzuloides*, *Mycelis muralis* (konšt.), *Rubus fruticosus* agg., *Symphytum tuberosum* agg.
Konštantne sprievodné taxóny: *Acer campestre*, *Ajuga reptans*, *Carpinus betulus* (E_{3-1}, dom.), *Galium odoratum* (dom.), *Lathyrus vernus*, *Poa nemoralis* (dom.), *Pulmonaria officinalis* agg., *Quercus petraea* agg. (E_3, dom.), *Viola reichenbachiana*

Nomenklatorický typ: Neuhäsl & Neuhäuslová-Novotná 1964: tab. 1, z. 4, lektotyp (Neuhäuslová 2000: 89)

SM, SF: V stromovom poschodí prevládajú *Carpinus betulus* a *Quercus petraea* agg., zriedkavejšie aj *Q. robur* agg. a *Tilia cordata*. V kontakte s bučinami môže kodominovať *Fagus sylvatica*. Vtrúsene sa vyskytuje *Acer campestre*, v južných častiach Slovenska aj *Quercus cerris* a niektoré ďalšie dreviny. Miestami hrab takmer chýba, čo býva spôsobené lesohospodárskymi zásahmi (preferencia dubov). Krovinové poschodie je v závislosti od zapojenia stromového poschodia rôzne vyvinuté. Okrem zmladených stromov sa často vyskytujú kry, ako napríklad *Corylus avellana*, druhy rodu *Crataegus*, *Euonymus europaeus*, *E. verrucosus*, *Ligustrum vulgare*, *Rosa canina* agg., *Swida sanguinea*. Bylinné poschodie je spravidla dobre zapojené. Charakteristická je kombinácia subkontinentálnych druhov (napr. *Carex pilosa*, *Galium schultesii*) a lesných mezofytov typických pre Karpaty a Alpy (napr. *Salvia glutinosa*, *Tithymalus amygdaloides*). Ekologické spektrum druhového zloženia je pomerne široké a popri mezofytoch sa tu v závislosti od podmienok stanovíšť uplatňujú v rôznej miere aj termofyty a acidofyty (v subasociácii *luzuletosum*), či mezohygrofyty a (hemi)nitrofyty (v subasociácii *dryopteridetosum*). V typickej podobe má podrast trávovitý vzhľad, ktorý mu dodávajú dominanty *Carex pilosa*, *Melica uniflora* a *Poa nemoralis*. Jarný aspekt je vyvinutý rôzne, chudobný je najmä v relatívne kyslomilných a suchších porastoch. Tvoria ho typické jarné efemeroidy. V zápise sa priemerne vyskytuje 39 druhov. Fenologický vrchol dosahuje spoločenstvo v apríli až máji v čase kvitnutia vyššie uvedených dominánt. Poschodie machorastov je nevýrazné.

SE: Dubovo-hrabové lesy asociácie *Carici pilosae-Carpinetum* sú rozšírené v kolínnom stupni karpatskej oblasti na rôznorodom geologickom substráte. Väčšina údajov pochádza z nadmorskej výšky 300 – 600 m. Uprednostňujú kambizeme, prípadne luvizeme dobre zásobené vodou a živinami. Vyhýbajú sa príliš vlhkým a suchým pôdam. Sú plošne najrozšírenejšou a ekologicky najširšou asociáciou zväzu *Carpinion* na Slovensku.

SD: Dynamika dubovo-hrabových lesov je značne ovplyvnená historickým výmladkovým hospodárením, často s krátkou obnovnou dobou. Dodnes tak majú mnohé porasty charakter nízkeho alebo stredného lesa, i keď sa značná časť porastov postupne previedla na vysoké lesy. Výmladkové hospodárenie zvýhodňovalo hrab na úkor dubov. Hrab ako menej atraktívna drevina býva naopak v niektorých porastoch v rámci výchovných zásahov odstraňovaný a vznikajú tak čisté dubiny. Vyššie zastúpenie hraba zvyšuje zatienenie a naopak, ak prevláda dub, svetlo dobre preniká aj do nižších poschodí. Zmeny v stromovom poschodí tak sprevádzajú sukcesné zmeny krovinového a najmä bylinného poschodia. V spodnej časti vertikálneho gradientu nadväzujú na lesy planárneho stupňa, vo vrchnej časti pozvoľna prechádzajú do bučín (najmä asociácie *Carici pilosae-Fagetum*). Na vlhkostnom gradiente nadväzujú najmä lužné lesy, v suchších polohách sú vystriedané teplomilnými dubo-hrabinami a teplomilnými dubovými lesmi. Na pôdach so zvýšeným obsahom skeletu hraničia so sutinovými lesmi. Náhradnou vegetáciou sú mezofilné travinno-bylinné porasty.

SC: Asociácia sa uvádza z karpatskej časti Českej republiky (Moravec et al. 2000; Chytrý 2013), z Ukrajiny (Onyshchenko 2009) a Maďarska (Borhidi et al. 2012). Časť porastov z južného Poľska (malopoľský región), ktoré sú označované ako *Tilio cordatae-Carpinetum betuli* (Matuszkiewicz 2001), sú podľa názoru niektorých autorov (Knollová, Chytrý 2004; Chytrý 2013) taktiež súčasťou *Carici pilosae-Carpinetum*. Názory na syntaxonomické hodnotenie porastov z východnej časti Rakúska sa líšia. Podľa aktuálneho prehľadu rakúskej lesnej vegetácie (Willner, Grabherr 2007) však už patria do západo-stredoeurópskej asociácie *Galio sylvaticae-Carpinetum*.
Na Slovensku je táto jednotka bohato zdokumentovaná z kolínneho až submontánneho stupňa prakticky celých Západných Karpát, zriedka aj z Borskej nížiny (Šomšák, Kubíček 1995). Najviac zápisov pochádza z Malých Karpát, Chvojnickej pahorkatiny, Bielych Karpát, Štiavnických vrchov a Slovenského krasu.

ST: V rámci asociácie možno rozlíšiť 3 subasociácie, ktoré sa líšia najmä nárokmi na vlhkosť resp. živiny a pôdnu reakciu:
Subasociácia ***Carici pilosae-Carpinetum typicum* Neuhäusl et Neuhäuslová 1968** (bez vlastných diferenciálnych druhov) predstavuje centrálnu časť spoločenstva. Jej charakteristika je totožná s charakteristikou asociácie.

Subasociácia ***Carici pilosae-Carpinetum luzuletosum* Neuhäuslová-Novotná 1964** predstavuje prechod ku kyslomilným dúbravám zväzu *Quercion roboris* a k teplomilným subacidofilným dúbravám zväzu *Quercion petraeae*. Viaže sa na kambizeme vyvinuté na kyslých substrátoch. Diferenciálnymi druhmi sú: *Astragalus glycyphyllos*, *Calamagrostis arundinacea*, *Campanula persicifolia*, *Clinopodium vulgare*, *Festuca heterophylla*, *Genista tinctoria*, *Hieracium lachenalii*, *H. murorum*, *H. sabaudum*, *Lathyrus niger*, *Luzula luzuloides*, *Melampyrum pratense*, *Pyrethrum corymbosum*, *Trifolium flexuosum*, *Veronica chamaedrys* agg., *V. officinalis*.

Subasociácia ***Carici pilosae-Carpinetum dryopteridetosum* Neuhäuslová-Novotná 1964** zahŕňa relatívne vlhkomilné a nitrofilné porasty, ktoré sa vyskytujú buď na skeletnatých pôdach, kde sú kontaktnou fytocenózou k sutinovým lesom, alebo na plošinách s vyššou hladinou podzemnej vody (napr. terasy vodných tokov). Typické je hojnejšie zastúpenie (hemi)nitrofytov a mezohygrofytov. Medzi diferenciálne druhy patria: *Acer pseudoplatanus*, *Actaea spicata*, *Aegopodium podagraria*, *Athyrium filix-femina*, *Circaea lutetiana*, *Dryopteris filix-mas*, *Galeobdolon luteum* agg., *Maianthemum bifolium*, *Oxalis acetosella*, *Paris quadrifolia*. Pre porasty nadväzujúce na sutinové lesy sú typické skeletnaté kambizeme až rankre, pre porasty ovplyvnené vodou kambizeme pseudoglejové a glejové.

SO: Ide o najmenej ohrozený typ dubo-hrabín na Slovensku, aj keď boli značné plochy v minulosti premenené na poľnohospodársku pôdu. Rizikovými faktormi sú najmä necitlivé lesné hospodárstvo a invázne druhy, z ktorých sú najbežnejšie *Impatiens parviflora* a *Robinia pseudacacia*. Výskyt ohrozených druhov je zriedkavejší, častejšie sa vyskytuje *Convallaria majalis*, menej *Lilium martagon* a lesné druhy vstavačovitých, najmä *Cephalanthera damasonium*, *C. longifolia* a *Epipactis helleborine*.

Syntaxonomická poznámka: Porasty z plochého reliéfu s vyššou hladinou podzemnej vody sú zaraďované do subasociácie *primuletosum elatioris* Neuhäusl et Neuhäuslová-Novotná 1972, ktorá je charakteristická vyšším zastúpením vlhkomilných druhov. Túto jednotku však nebolo možné v zápisoch z územia Slovenska uspokojivo floristicky definovať a členitý karpatský reliéf ani nedáva predpoklady na výraznejšie rozšírenie takéhoto typu. Magic (1968) opísal zo Slovenského rudohoria subasociáciu *festucetosum drymejae*, ktorú v tomto prehľade nerozlišujeme. Väčšina zápisov s *Festuca drymeja* je súčasťou subasociácie *luzuletosum*.

Primulo veris-Carpinetum Neuhäusl et Neuhäuslová ex Neuhäuslová-Novotná 1964

PFM: *Primulae veris-Carpinetum* (Neuhäuslová-Novotná 1964: 48)
Syntax. syn.: *Waldsteinio-Carpinetum* (Jakucs et Jurko 1967) J. Michalko et M. Michalko in Mucina et Maglocký 1985 p. p, *Coronillo latifoliae-Carpinetum* (J. Michalko 1957) J. Michalko et M. Michalko in Mucina et Maglocký 1985 p. p., *Poo nemoralis-Quercetum dalechampii* Šomšák et Háberová 1979 p. p.)
Inkl.: *Querco petraeae-Carpinetum melicetosum uniflorae* (Mikyška 1939) Klika 1942 p. p., *Querco petraeae-Carpinetum poetosum nemoralis* (Mikyška 1939) Klika 1951 p. p.,
Pseud.: *Melico uniflorae-Quercetum petraeae* sensu Šomšák & Háberová 1979 non Gergely 1962 p. p.

Tabuľka 1, stĺpec 2 (provizórne číslovanie)

Diferenciálne taxóny: *Campanula rapunculoides*, *Cornus mas* ($E_{2,\ 1}$, konšt.), *Cruciata glabra* (konšt.), *Fraxinus excelsior* ($E_{3,1}$), *Glechoma hirsuta* (konšt.), *Lilium martagon*, *Melittis melissophyllum*, *Mercurialis perennis*, *Pyrethrum corymbosum*, *Sorbus torminalis* (E_3), *Symphytum angustifolium*, *Vincetoxicum hirundinaria*, *Waldsteinia geoides*

Konštantne sprievodné taxóny: *Acer campestre* (E_1), *Bromus benekenii*, *Campanula trachelium*, *Carpinus betulus* ($E_{3,\ 1}$, dom.), *Dactylis glomerata* agg., *Fragaria vesca*, *Galium schultesii*, *Geum urbanum*, *Lathyrus niger*, *L. vernus*, *Ligustrum vulgare* (E_1), *Melica uniflora* (dom.), *Poa nemoralis*, *Pulmonaria officinalis* agg., *Quercus petraea* agg. ($E_{3,\ 1}$, dom.), *Tithymalus amygdaloides*

Nomenklatorický typ: Neuhäusl & Neuhäuslová-Novotná 1964: tab. 2, z. 15, lektotyp (Neuhäuslová 2000: 99)

SM, SF: Stromové poschodie tvoria *Carpinus betulus* a *Quercus petraea* agg., ktoré sú sprevádzané druhmi *Acer campestre*, *Quercus cerris*, *Sorbus torminalis*, *Tilia cordata* a i. Krovinové poschodie je druhovo bohaté, najmä v porastoch na karbonátových pôdach.

Ekologicky typické sú teplomilné druhy ako *Cornus mas* a *Euonymus verrucosus*, avšak vyskytujú sa tu aj mezofyty, napr. *Swida sanguinea*. Pre bylinné poschodie je príznačná kombinácia teplomilných druhov tried *Trifolio-Geranietea* a *Festuco-Brometea* s mezofytmi (*Campanula rapunculoides*, *C. trachelium*, *Galium odoratum*, *G. schultesii*, *Lathyrus vernus*, *Viola reichenbachiana*) a (hemi)nitrofytmi, ako sú *Ajuga reptans*, *Glechoma hirsuta*, *Mercurialis perennis*, *Waldsteinia geoides* a ďalšie. Dominantnými druhmi sú najčastejšie *Carex pilosa*, *Galium odoratum*, *Melica uniflora* a *Poa nemoralis*. Priemerný počet druhov v zápise je 44. Skorý jarný aspekt je vyvinutý rôzne, výrazný je najmä na karbonátových pôdach s vyšším obsahom skeletu. Tvoria ho druhy rodu *Corydalis*, *Isopyrum thalictroides*, zriedkavejšie aj *Ficaria bulbifera* a *Galanthus nivalis*, ku ktorým sa neskôr pripájajú najmä *Dentaria bulbifera*, *Primula veris*, *Viola hirta*, *V. mirabilis* a pod. Koncom zimy, resp. v predjarí vytvára nápadný aspekt hojne sa vyskytujúci žltokvitnúci drieň *Cornus mas*. Fenologický vrchol však spoločenstvo dosahuje vo vrcholnej jari v čase kvitnutia dominánt. Machové poschodie je nevýrazné.

SE, SD: Spoločenstvo sa viaže na relatívne teplé a suché stanovištia, ako sú pahorkatiny a kolínny až submontánny stupeň pohorí južnejších častí Slovenska. Väčšina údajov pochádza z nadmorskej výšky 300 – 600 m, ale na špecifických stanovištiach (Slovenský kras) vystupujú takéto porasty aj vyššie. Z pôd sú typické rendziny (vápencové časti Karpát) a v sprašových polohách hnedozeme; pre kyslomilnejšie typy je to najmä kambizem vyvinutá prevažne na sopečných horninách. V chladnejších oblastiach sa vyskytujú na výslnných teplých svahoch, zatiaľ čo v nižších polohách môžu osídľovať aj inak orientované svahy, keďže najteplejšie časti pokrývajú primárne teplomilné dúbravy. Na vlhkostnom a teplotnom gradiente porasty spoločenstva nadväzujú na mezofilné dubo-hrabiny asociácie *Carici pilosae-Carpinetum* a predstavujú prechod k teplomilným dúbravám asociácie *Corno-Quercetum*, na kyslom substráte k spoločenstvám zväzu *Quercion petraeae*. Na karbonátových substrátoch so zvýšeným obsahom skeletu v pôde susedia so sutinovými lesmi zväzu *Melico-Tilion platyphylli*.

SC, ST: Centrom rozšírenia asociácie sú pahorkatiny a nižšie pohoria severného a severozápadného okraja panónskej oblasti. Okrem Slovenska sa vyskytuje na južnej Morave (Moravec 2000), ale v novších prácach sa uvádza aj z teplých oblastí Čiech (Chytrý 2013). V Rakúsku sa názory na klasifikáciu teplomilných dubo-hrabín rôznia, pričom niektoré národné prehľady túto jednotku akceptujú (Mucina et al. 1993). Z Maďarska sa spoločenstvo neuvádza, ale podobné porasty sa tu nachádzajú a sú klasifikované do viacerých asociácií (Borhidi et al. 2012). Zriedkavo boli zaznamenané aj na neovulkanitoch Zakarpatskej Ukrajiny (Novák et al. 2017).

Na Slovensku je asociácia zdokumentovaná z viacerých regiónov. Najväčší počet zápisov pochádza zo Slovenského krasu, ďalšie údaje sú z Myjavskej pahorkatiny, Malých Karpát, Bielych Karpát, Podunajskej pahorkatiny, Považského Inovca, Štiavnických vrchov , Tribča , Burdy, Hornonitrianskej kotliny, Krupinskej planiny, Javoria, Rimavskej kotliny, Revúckej vrchoviny, Zemplínskych vrchov a Vihorlatu.

V rámci jednotky sú zastúpené porasty s vyšou účasťou druhov náročných na živiny, najmä *Asarum europaeum* a *Hedera helix*. Prechody medzi nimi sú však pozvoľné, nižšie jednotky preto nerozlišujeme.

SO: Porasty asociácie predstavujú druhý najrozšírenejší typ dubo-hrabín na Slovensku. Keďže sa vyskytujú aj na strmších svahoch a pôdach s vyšším obsahom skeletu, neboli tak postihnuté premenou na poľnohospodársku pôdu ako nasledujúce dve asociácie. Rizikovými faktormi sú najmä necitlivé lesné hospodárstvo a prienik inváznych druhov. Z ohrozených druhov sa vzácne vyskytuje *Lathyrus transsilvanicus* a *Waldsteinia geoides*, iné druhy ako *Clematis recta*, *Convallaria majalis*, *Epipactis helleborine*, *Lilium martagon*, a *Symphytum angustifolium* bývajú častejšie.

***Polygonato latifolii-Carpinetum* Michalko et Džatko 1965**

Tabuľka 1, stĺpec 3 (provizórne číslovanie)

Charakteristické taxóny: *Arum alpinum* (konšt.)

Diferenciálne taxóny: *Alliaria petiolata* (konšt., dom.), *Chaerophyllum temulum* (konšt.), *Corydalis cava* (konšt.), *Dictamnus albus*, *Fallopia convolvulus* (konšt.), *Galium aparine* (konšt.), *Leopoldia comosa*, *Lithospermum purpurocaeruleum*, *Lonicera xylosteum* (E_2, konšt.), *Ornithogalum kochii*, *Polygonatum latifolium*, *Vinca minor* (dom.), *Viola odorata*

Konštantne sprievodné taxóny: *Acer campestre* (E_2), *Convallaria majalis*, *Cornus mas* (E_2), *Crataegus monogyna* ($E_{2,\ 1}$), *Euonymus europaeus* ($E_{2,\ 1}$), *Impatiens parviflora*, *Ligustrum vulgare* ($E_{2,\ 1}$), *Melica uniflora* (dom.), *Polygonatum multiflorum*, *Quercus petraea* agg. (E_3, dom.)

Nomenklatorický typ: Michalko, Džatko 1965: tab. 17, z. 16 lektotyp (Willner, Grabher 2007: 232)

SM, SF: Panónske dubovo-hrabové lesy. V stromovom poschodí prevláda *Quercus robur* agg. a hojne sú zastúpené aj *Acer campestre* a *Ulmus minor*. S vyššou stálosťou sa uplatňuje aj *Quercus cerris*. Samotný hrab je zriedkavejší a je len primiešanou drevinou, rovnako ako *Acer tataricum*. Poschodie krovín je vyvinuté rôzne, často je bohaté a prevládajú tu teplomilné druhy (*Ligustrum vulgare*, *Prunus spinosa*, *Viburnum lantana*) a druhy náročné na živiny (*Sambucus nigra*). Bylinné poschodie je dobre zapojené. Priemerný počet druhov v zápise je 32. Prevládajú v ňom bežné lesné druhy a nitrofyty znášajúce zatienenie. S vysokou stálosťou sa uplatňuje invázny druh *Impatiens parviflora*. Teplomilné druhy ako *Dictamnus albus*, *Lithospermum purpurocaeruleum*, *Polygonatum latifolium*, *Viola mirabilis* poukazujú na blízkosť asociácie k teplomilným dubinám. V spoločenstve je nápadný skorý jarný aspekt, ktorý tvorí predovšetkým dominanta *Corydalis cava* a miestami sa vyskytujú fácie s dominanciou *Vinca minor*. Zo skorých jarných druhov sa bežne vyskytujú aj *Arum alpinum*, *Ficaria bulbifera* a druhy rodu *Viola.* Neskôr je nápadná fenofáza s *Alliaria petiolata*. Fenologický vrchol dosahuje spoločenstvo vo vrcholnej jari v čase kvitnutia dominanty *Melica uniflora*.

SE, SD: Porasty asociácie sa typicky vyskytujú na hnedozemiach vyvinutých na sprašiach v nadmorskej výške do 200 m. Predstavujú prechod medzi nížinnými lesmi a mezofilnými lesmi pahorkatín. Väčšina stanovíšť spoločenstva bola premenená na ornú pôdu.

SC: Spoločenstvo je zdokumentované zo sprašových pahorkatín Podunajska. Opísané bolo z lesa Dubník pri Seredi, odkiaľ pochádza väčšina zápisov (Michalko, Džatko 1965; Hrabovský et al. 2010; Roleček ined.). Jeho výskyt sa uvádza aj zo severovýchodného Rakúska (Willner, Grabherr 2007). V Maďarsku sú podobné porasty zaraďované do iných jednotiek (Borhidi et al. 2012).

ST: Vzhľadom na malé množstvo údajov a rozšírenie nižšie jednotky nerozlišujeme. Jednotka je pomerne problematická, keďže sa na sprašových pahorkatinách Slovenska zachovalo len málo lesných porastov. Predstavuje prechod k teplomilným dubinám. Osobitne je potrebné doriešiť vzťah k asociácii *Convallario-Quercetum*, ako ju charakterizovali Roleček (2005) a Hrabovský et al. (2010).

SO: Keďže sa asociácia viaže na úrodné pôdy teplých oblastí, v súčasnosti sú zachované len malé fragmenty chránené vysokým stupňom územnej ochrany (NPR Dubník). Sú obklopené poľnohospodárskou pôdou so zvýšeným rizikom synantropizácie, ktorú podporuje prítomnosť agátov. Zmeny v druhovom zložení sú spôsobené aj zmenou využívania a sú sprevádzané ústupom svetlomilných druhov. Spolu s asociáciou *Convallario-Carpinetum* predstavujú najmenej rozšírený typ dubo-hrabín na Slovensku. Z ohrozených druhov sa vyskytuje *Dictamnus albus.*

***Convallario-Carpinetum* Kevey 2008**

Pseud.: *Fraxino pannonicae-Carpinetum* sensu Jarolímek et al. 2008 non Soó et Borhidi in Soó 1962, *Querco robori-Carpinetum* Soó et Pócs (1931) 1959 sensu Berta 1970 non Klika 1928

Tabuľka 1, sĺpec 4 (provizórne číslovanie)

Diferenciálne taxóny: *Acer tataricum* (E_2, konšt.), *Aristolochia clematitis*, *Cardamine impatiens*, *Carex brizoides*, *C. remota*, *C. sylvatica* (konšt.), *Cerastium sylvaticum*, *Circaea lutetiana*, *Cucubalus baccifer*, *Deschampsia cespitosa*, *Fraxinus angustifolia* ($E_{3, 2}$), *G. spathacea* (konšt.), *Leucojum vernum*, *Lysimachia nummularia*, *Maianthemum bifolium* (konšt.), *Melampyrum nemorosum*, *Milium effusum*, *Ophioglossum vulgatum*, *Platanthera bifolia* (konšt.), *Quercus robur* agg. ($E_{3, 2}$, konšt.), *Rubus caesius* (konšt.), *Scrophularia nodosa* (konšt.), *Torilis japonica* (konšt.), *Ulmus minor* ($E_{3, 2,}$ konšt.), *Viburnum opulus* (E_2), *Vicia sepium*

Konštantne sprievodné taxóny: *Acer campestre* ($E_{3, 2}$), *Ajuga reptans*, *Brachypodium sylvaticum*, *Carex muricata* agg., *Carpinus betulus* ($E_{3, 2,}$ dom.), *Convallaria majalis*, *Crataegus laevigata* (E_2), *Euonymus europaeus* (E_2), *Galium odoratum*, *Geranium robertianum*, *Geum urbanum* (konšt.), *Ligustrum vulgare* (E_2), *Polygonatum multiflorum*, *Ranunculus auricomus* agg., *Swida sanguinea* (E_2, konšt.), *Viola reichenbachiana*

Nomenklatorický typ: Kevey 2008: 234, holotyp

SM, SF: V stromovom poschodí dominuje *Carpinus betulus*, hojne sa vyskytuje aj *Quercus robur* agg. S vyššou stálosťou sa uplatňujú *Acer campestre* a *Ulmus minor*. Ekologicky a fytogeograficky významná je účasť *Fraxinus angustifolia*. Z krov je popri zmladených stromovitých drevinách nápadné vysoké zastúpenie *Swida sanguinea*. S vysokou stálosťou sa uplatňujú aj *Acer tataricum* a bežné, prevažne mezofilné kroviny triedy *Crataego-Prunetea*.

Ekologické pomery dobre dokresľuje aj výskyt *Viburnum opulus*. Pre bylinné poschodie je charakteristické, že popri mezofilných druhoch *Brachypodium sylvaticum*, *Convallaria majalis*, *Galium odoratum* a *Viola reichenbachiana* sú zastúpené aj vlhkomilnejšie druhy, ako napr. *Carex sylvatica*, *Circaea lutetiana*, *Rubus caesius* a iné. Priemerný počet druhov v zápise je 42. V niektorých porastoch je nápadný skorý jarný aspekt, ktorý s najvyššou stálosťou tvoria *Gagea spathacea* a *Leucojum vernum*, zriedkavejšie aj *Anemone nemorosa*. Fenologické optimum je však vo vrcholnej jari v čase kvitnutia dominantných druhov, najma *Convallaria majalis*, *Galium odoratum* a *Viola reichenbachiana*.

SE, SD: Spoločenstvo predstavuje najvlhkomilnejší typ dubo-hrabín, ktorý nadväzuje na tvrdé lužné lesy. S nimi pravdepodobne aj vývojovo súvisí, keďže typickou pôdou je na inundácie viazaná fluvizem. Na vlhkostnom gradiente naň nadväzujú mezofilné porasty asociácie *Carici pilosae-Carpinetum*. Údaje pochádzajú z nadmorskej výšky ca 105 – 130 m.

SC: Spoločenstvo je rozšírené v panónskej oblasti v Maďarsku (Borhidi et al. 2012), na Slovensku, okrajovo aj v Rakúsku (Willner, Grabherr 2007), v Českej republike (Vicherek 2000; Novák et al. 2020) a na Zakarpatskej Ukrajine (Onyshchenko 2009; Novák et al. 2017). Na Slovensku má centrum rozšírenia na Východoslovenskej nížine (Michalko 1957, 1991; Berta 1970). Keďže ide väčšinou o staršie údaje (prelom 50. a 60. rokov 20. storočia), bolo by potrebné ich aktualizovať.

SO: Keďže sa porasty asociácie viažu na úrodné pôdy v nížinných oblastiach, do značnej miery boli premenené na poľnohospodársku pôdu a ich súčasné rozšírenie je len zlomkom potenciálneho stavu. Z ohrozených druhov sa častejšie vyskytujú *Cerastium sylvaticum*, *Gagea spathacea*, *Leucojum verum* a *Ophioglossum vulgatum*.

Syntaxonomická poznámka: Otázka správneho mena asociácie je zložitá. Väčšina fytocenologických zápisov zo Slovenska pochádza od Bertu (1970), ktorý ich zaradil do asociácie *Querco robori-Carpinetum* Soó et Pócs (1931) 1957. Ide však o mladšie homonymum (čl. 31), keďže už skôr použil meno *Querco pedunculatae-Carpinetum* (= *Querco robori-Carpinetum*) Klika (1928) pre mezofilné dubo-hrabiny Českého krasu (Novák 2019). Jarolímek et al. (2008) akceptovali ako správne meno *Fraxino pannonicae-Carpinetum* Soó et Borhidi in Soó 1962. Táto asociácia však bola opísaná z južného Maďarska, kde sa uplatňujú vo väčšej miere aj submediteránne druhy. V aktuálnom prehľade maďarskej vegetácie (Borhidi et al. 2012) je preto zaradená do ilýrskeho zväzu *Erythro-Carpinion* (Horvat 1958) Marinček in Mucina et al. 1993 a pre analogické porasty zo stredného a severného Maďarska sa použil názov *Circaeo-Carpinetum* Borhidi 2003. Kevey (2008) túto asociáciu, ktorú neplatne opísal Borhidi (2003) pre panónske dubovo-hrabové lesy na vlhkých pôdach, rozdelil do štyroch asociácií, pričom jeho delenie vychádzalo najmä z pôdnych vlastností. Názov *Circaeo-Carpinetum* ponechal pre porasty z vlhkých aluviálnych pôd, ale aj ním publikované meno bolo validizované neplatne (čl. 3i). V našom prehľade preto preberáme názor Nováka et al. (2020). Uvedený vegetačný typ hodnotia ako asociáciu *Convallario-Carpinetum*. Predstavuje panónske vlhkomilné dubovo-hrabové lesy medzidunových depresií s druhovým zložením, ktoré sa približuje Borhidiho poňatiu asociácie *Circaeo-Carpinetum*.

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English summary

The presented book chapter provides the first detailed overview of oak-hornbeam forests in Slovakia, including a syntaxonomic revision. Slovak oak-hornbeam forests represent the variability of the *Carpinion* alliance in the eastern part of its range. They are one of the broadest distributed forest vegetation types in Slovakia occurring usually up to 600 m a.s.l. The tree layer is mostly dominated by *Carpinus betulus*, *Quercus petraea* and *Q. robur*. *Fagus sylvatica* is frequently admixed especially near the upper boundary of their vertical distribution. Forest mesophytes prevail in the shrub and herb layer. The moss layer is mostly sparse or missing. Similarly to the other central European oak-hornbeam forests, Slovak oak-

hornbeam forests were traditionally used for coppicing, litter raking or pasture of domestic animals. They have been studied by Braun-Blanquet methods since 1930s (e.g. Dostál 1933, Klika 1937). In the second half of the 20th century, numerous studies were published. They investigated oak-hornbeam forest diversity and their syntaxonomy at various spatial scales (e.g. Neuhäusl & Neuhäuslová-Novotná 1964, Michalko & Džatko 1965, Mucina & Maglocký 1985, Michalko et al. 1986). Nowadays, a representative subset of phytosociological relevés of oak-hornbeam forests is available for the most of the country. In the list of Slovak vegetation units, 14 associations were recognized (Jarolímek et al. 2008). Howevre, the majority of them were difficult to distinguish from the others since they lacked a sufficient number of good diagnostic species or had diagnostic species with only local validity. We revealed main vegetation units by numerical analyses of the variability, mainly by unsupervised classification analyses, applied to an extensive relevé dataset (n = 1180). We significantly reduced the number of the associations, mostly by merging similar associations. We also performed a nomenclatural revision to find out the oldest valid names for the distinguished units. Simultaneous work on the central European oak-hornbeam forest synthetic study (paper 5) helped to better present Slovak *Carpinion* associations in the central European context. We recognized four associations, one with three subassociations, the rest without subordinate units. In the manuscript, we present their species composition, structure, distribution, ecology, management, syntaxonomy, the importance for nature conservation and threats. Their brief descriptions are provided below.

The association *Carici pilosae-Carpinetum* includes zonal oak-hornbeam forests of the Carpathian foothills (mostly 300–600 m a.s.l.). It represents the central unit of Slovak *Carpinion* vegetation (n = 950 relevés). It was described from south-central Slovakia. Its herb layer is characteristic by a co-occurrence of nemoral species of two distinct biogeographical groups, subcontinental (e.g. *Carex pilosa* and *Galium intermedium*) and southern (e.g. *Euphorbia amygdaloides* and *Salvia glutinosa*). As this association has a relatively high internal variability, we distinguished three subassociations reflecting various soil properties. The subassociation *Carici pilosae-Carpinetum luzuletosum* comprises slightly acidophilous types (e.g. with *Hieracium* sp. div. and *Luzula luzuloides*) of acidic bedrock like neovolcanic rocks of the southern half of the country. The subassociation *Carici pilosae-Carpinetum dryopteridetosum* includes types of slightly wet and nutrient-rich soils (e.g. with *Aegopodium podagraria* and *Dryopteris filix-mas*) which occur, for instance, in the Carpathian river valleys. The subassociation *Carici pilosae-Carpinetum typicum* is considered as its central subassociation, occurring across the whole Slovak distribution of the association.

The association *Primulo veris-Carpinetum* unifies slightly thermophilous types of oak-hornbeam forests (n = 185). It was described from south-central Slovakia together with the previous association. They preferentially occupy neutral or basic soils of the warmer parts of the Western Carpathian foothills. The tree layer is usually dominated by *Carpinus betulus* and *Quercus petraea*. Species-rich shrub layer (e.g. with *Cornus mas* and *Euonymus verrucosa*) and admixture of thermophilous species (e.g. *Primula veris* and *Vincetoxicum hirundinaria*) in the field layer are their typical atributes.

The association *Polygonato latifoliae-Carpinetum* involves oak-hornbeam forests of loess hills and plateaus in the Pannonian Basin. As the Slovak part of the basin was highly deforested in the past, these forests are rare (n = 11) and often represent the last forest remnants surrounded by agricultural landscape. The tree layer is dominated mainly by *Acer campestre*, *Quercus robur* and *Ulmus minor*. Thermophilous and/or subcontinental species (e.g. *Acer tataricum* and *Quercus cerris*) are often admixed. Subcontinental species (e.g. *Polygonatum hirtum* and *Viola mirabilis*) accompanied by nitrophytes (e.g. *Alliaria petiolata* and *Chaerophyllum temulum*) are typical for their herb layer. Spring geophytes (e.g. *Arum* *alpinum* and *Corydalis cava*) are common. They occur mainly in the Danube Lowland in southwestern Slovakia where the association was described.

The association *Convallario-Carpinetum* includes Pannonian slightly wet oak-hornbeam forests (n = 34). It was described in the lowland of northeastern Hungary. In the tree layer, *Carpinus betulus* and *Quercus robur* prevail, with a frequent admixture of submediterranean *Fraxinus angustifolia* and subcontinental *Acer tataricum*. Nutrient- and moisture-demanding lowland species (e.g. *Aristolochia clematitis*, *Cucubalus baccifer* and *Rubus caesius*) are typical of the herb layer. In Slovakia, they were recorded almost exclusively in the Eastern Slovak Lowland.

Tab. 1. Synoptická tabuľka radu *Carpinetalia* a zväzu *Carpinion*
Tab. 1. Synoptic table of the* Carpinetalia *order and* Carpinion *alliance

Percentuálne frekvencie taxónov v asociáciách.
Percentage frequencies of taxa in the associations.

Priemerná pokryvnosť taxónu (r, +, 1-5; Braun-Blanquetova stupnica) je uvedená v hornom indexe u jeho frekvencie.
Mean cover value of a taxon (r, +, 1-5; the Braun-Blanquet scale) is provided in superscript at its frequency.

Diferenciálne taxóny (zvýraznene) – rozdiel vo frekvenciách medzi asociáciami > 20 %, iba druhy s frekvenciou < 50 % v porovnávaných asóciáciách.
Differential taxa (in bold) – difference in frequencies among associations > 20%, only taxa with frequency < 50% in the compared associations.

D1-D4 diferenciálne taxóny asociací 1-4. D – diferenciálne taxony radu.
D1-D4 – differential taxa of the associations 1-4. D – differential taxa of the order.

Vegetačné poschodie: (E_3) – stromové, (E_2) – krovinové, ostatné taxóny – bylinné.
Vegetation layer: (E_3) – tree, (E_2) – shrub, other taxa – herb.

1. *Carici pilosae-Carpinetum*
2. *Primulo veris-Carpinetum*
3. *Polygonato latifolii-Carpinetum*
4. *Convallario-Carpinetum*

Stĺpec (column)		1	2	3	4
Počet zápisov (number of relevés)		950	185	11	34
Charakteristické taxóny asociácií **(Characteristic taxa of the associations)**					
Fagus sylvatica (E$_3$)	D1	**48**^{1}	22^{+}	.	.
Fagus sylvatica (E$_2$)	D1	**40**$^{+}$	13^{+}	.	.
Fagus sylvatica	D1	**50**$^{+}$	15^{+}	.	.
Mycelis muralis	D1	**51**$^{+}$	31^{+}	.	15^{+}
Rubus fruticosus agg.	D1	**34**$^{+}$	9^{+}	.	6^{+}
Luzula luzuloides	D1	**31**$^{+}$	5^{+}	.	.
Hieracium murorum	D1	**29**$^{+}$	12^{+}	.	.
Cornus mas (E$_2$)	D2	6^{+}	**69**^{1}	55^{+}	3^{+}
Cornus mas	D2	5^{+}	**46**$^{+}$	9^{+}	.
Fraxinus excelsior (E$_3$)	D2	4^{+}	**22**^{1}	.	.
Fraxinus excelsior	D2	24^{+}	**42**$^{+}$	9^{r}	.
Sorbus torminalis (E$_3$)	D2	6^{+}	**21**$^{+}$	.	.
Sorbus torminalis	D2	10^{+}	**23**$^{+}$	.	3^{+}
Glechoma hirsuta	D2	30^{+}	**57**^{1}	9^{r}	35^{+}
Cruciata glabra	D2	33^{+}	**54**$^{+}$	.	9^{+}
Melittis melissophyllum	D2	33^{+}	**50**$^{+}$	27^{r}	.
Campanula rapunculoides	D2	28^{+}	**50**$^{+}$	.	.
Mercurialis perennis	D2	20^{+}	**48**^{1}	.	.
Vincetoxicum hirundinaria	D2	10^{+}	**41**$^{+}$	18^{+}	.
Pyrethrum corymbosum	D2	10^{+}	**37**$^{+}$	.	.
Lilium martagon	D2	9^{+}	**32**$^{+}$	.	6^{1}
Waldsteinia geoides	D2	2^{+}	**49**^{1}	.	.
Symphytum angustifolium	D2	3^{+}	**18**$^{+}$	.	.
Arum alpinum	C3	4^{+}	2^{+}	**64**$^{+}$	.
Lonicera xylosteum (E$_2$)	D3	5^{+}	12^{+}	**55**$^{+}$	.
Galium aparine	D3	17^{+}	22^{+}	**73**$^{+}$	38^{1}
Alliaria petiolata	D3	15^{+}	34^{+}	**64**^{1}	26^{+}
Corydalis cava	D3	2^{+}	1^{1}	**55**^{1}	3^{1}
Fallopia convolvulus	D3	9^{+}	16^{+}	**55**$^{+}$	9^{+}
Chaerophyllum temulum	D3	3^{+}	15^{+}	**55**$^{+}$	12^{+}
Vinca minor	D3	3^{2}	1^{1}	**45**^{3}	12^{1}
Dictamnus albus	D3	.	.	**45**^{1}	.
Lithospermum purpurocaeruleum	D3	1^{1}	14^{+}	**45**$^{+}$	.
Polygonatum latifolium	D3	1^{+}	1^{1}	**45**$^{+}$	.
Viola odorata	D3	2^{+}	8^{+}	**36**$^{+}$	.
Ornithogalum kochii	D3	.	.	**36**$^{+}$	.
Leopoldia comosa	D3	.	.	**18**^{r}	.
Carex sylvatica	D4	20^{+}	3^{r}	.	**85**^{1}
Quercus robur (E$_3$)	D4	10^{1}	5^{2}	45^{3}	**82**^{1}
Quercus robur (E$_2$)	D4	2^{+}	2^{+}	.	**38**$^{+}$
Ulmus minor (E$_3$)	D4	1^{+}	1^{+}	36^{+}	**65**^{1}
Ulmus minor (E$_2$)	D4	1^{+}	1^{+}	36^{+}	**79**^{1}
Ulmus minor	D4	1^{+}	.	55^{+}	.
Scrophularia nodosa	D4	22^{+}	5^{+}	.	**71**$^{+}$
Rubus caesius	D4	1^{+}	.	.	**68**^{1}
Maianthemum bifolium	D4	20^{+}	10^{+}	.	**65**^{1}
Gagea spathacea	D4	1^{+}	.	.	**65**$^{+}$
Acer tataricum (E$_2$)	D4	1^{+}	3^{+}	9^{+}	**62**^{1}
Platanthera bifolia	D4	9^{+}	6^{r}	.	**62**$^{+}$
Lysimachia nummularia	D4	7^{+}	6^{+}	.	**50**^{1}
Milium effusum	D4	12^{+}	2^{+}	.	**50**$^{+}$
Viburnum opulus (E$_2$)	D4	1^{+}	.	.	**47**$^{+}$

Stĺpec (column)		1	2	3	4
Počet zápisov (number of relevés)		950	185	11	34
Leucojum vernum	D4	.	.	.	**44^{+}**
Melampyrum nemorosum	D4	10^{+}	15^{+}	.	**44^{+}**
Circaea lutetiana	D4	10^{+}	1^{r}	.	**38^{+}**
Carex brizoides	D4	1^{+}	.	.	**35^{1}**
Cardamine impatiens	D4	5^{+}	13^{+}	.	**35^{+}**
Vicia sepium	D4	8^{+}	8^{+}	.	**29^{+}**
Deschampsia cespitosa	D4	4^{+}	2^{+}	.	**29^{+}**
Cerastium sylvaticum	D4	.	.	.	**29^{+}**
Fraxinus angustifolia (E_3)	D4	.	.	.	**15^{1}**
Fraxinus angustifolia (E_2)	D4	.	.	.	**26^{+}**
Cucubalus baccifer	D4	1^{r}	.	.	**24^{+}**
Ophioglossum vulgatum	D4	.	.	.	**24^{+}**
Aristolochia clematitis	D4	.	.	.	**21^{+}**
Carex remota	D4	1^{r}	.	.	**21^{+}**
Carpinetalia betuli					
Carpinus betulus (E_3)	C	84^{3}	87^{3}	18^{+}	100^{5}
Carpinus betulus (E_2)	C	59^{+}	48^{+}	.	91^{1}
Carpinus betulus	C	69^{+}	64^{+}	18^{r}	3^{1}
Carex pilosa	tC,D1	**64^{2}**	4^{2}	.	3^{+}
Cerasus avium (E_3)	C	12^{+}	11^{+}	.	12^{1}
Cerasus avium (E_2)	C	7^{+}	5^{+}	.	15^{1}
Cerasus avium	C	44^{+}	36^{+}	.	.
Lathyrus vernus	tC	53^{+}	81^{+}	18^{r}	.
Pulmonaria officinalis agg.	D	70^{+}	52^{+}	.	32^{1}
Poa nemoralis	D	64^{+}	55^{+}	45^{+}	32^{+}
Melica uniflora	D	49^{1}	77^{3}	100^{3}	6^{+}
Galium schultesii	D	44^{+}	62^{+}	9^{+}	3^{1}
Symphytum tuberosum	D,D1	**38^{+}**	21^{+}	.	9^{1}
Crataegus laevigata (E_2)	D,D4	14^{+}	31^{+}	9^{+}	94^{+}
Crataegus laevigata	D	22^{+}	36^{+}	.	.
Ranunculus auricomus agg.	D,D4	21^{+}	15^{+}	.	**71^{+}**
Carpino-Fagetea					
Viola reichenbachiana		71^{+}	50^{+}	9^{+}	100^{2}
Galium odoratum		63^{1}	45^{1}	.	74^{2}
Tithymalus amygdaloides		40^{+}	56^{+}	.	6^{+}
Asarum europaeum		40^{1}	46^{1}	.	6^{+}
Dentaria bulbifera		36^{+}	32^{1}	18^{1}	6^{1}
Dryopteris filix-mas		35^{+}	16^{r}	.	35^{+}
Galeobdolon luteum agg.		33^{1}	29^{+}	.	3^{1}
Sanicula europaea		25^{+}	14^{+}	.	9^{+}
Acer pseudoplatanus (E_3)		5^{+}	5^{+}	.	.
Acer pseudoplatanus (E_2)		3^{+}	1^{+}	.	.
Acer pseudoplatanus		22^{+}	15^{+}	.	.
Actaea spicata		5^{+}	2^{+}	.	12^{+}
Hacquetia epipactis		5^{1}	1^{+}	.	.
Hordelymus europaeus		2^{+}	2^{+}	.	.
Quercetea pubescentis					
Quercus petraea agg. (E_3)		76^{3}	84^{3}	64^{4}	3^{1}
Quercus petraea agg. (E_2)		17	10^{+}	.	.
Quercus petraea agg.		66^{+}	55^{+}	45^{+}	3^{+}
Quercus cerris (E_3)		11^{1}	26^{1}	45^{+}	6^{2}
Quercus cerris		8^{+}	18^{+}	.	.
Ligustrum vulgare (E_2)		14^{+}	26^{+}	82^{1}	82^{1}
Ligustrum vulgare		32^{+}	51^{+}	73^{+}	.
Euonymus verrucosus (E_2)		2^{+}	16^{+}	9^{1}	.

Stĺpec (column)	1	2	3	4
Počet zápisov (number of relevés)	950	185	11	34
Euonymus verrucosus	5^+	39^+	36^r	.
Lathyrus niger	27^+	51^+	45^+	18^+
Clinopodium vulgare	18^+	28^+	9^+	9^1
Hieracium sabaudum	22^+	9^+	.	3^+
Fragaria moschata	16^+	22^+	9^+	.
Veronica officinalis	16^+	4^r	.	6^+
Astragalus glycyphyllos	14^+	18^+	.	12^+
Crataego-Prunetea				
Crataegus monogyna (E_2)	8^+	22^+	55^+	26^+
Crataegus monogyna	22^+	39^+	55^+	.
Swida sanguinea (E_2)	12^+	12^+	18^+	**100^2**
Swida sanguinea	24^+	11^+	18^r	.
Euonymus europaeus (E_2)	3^+	3^+	18^r	65^+
Euonymus europaeus	14^+	12^+	91^+	.
Rosa canina agg. (E_2)	2^+	1^+	9^+	44^+
Rosa canina agg.	17^r	29^r	18^r	.
Corylus avellana (E_2)	27^+	31^+	.	50^1
Corylus avellana	21^+	21^+	9^+	.
Ostatné taxóny (Other taxa)				
E_3				
Acer campestre	14^+	39^+	45^1	53^1
E_2				
Acer campestre	23^+	37^+	100^1	97^1
Sambucus nigra	4^+	3^+	27^2	15^+
E_1				
Acer campestre	59^+	78^+	82^+	3^+
Dactylis glomerata agg.	42^+	65^+	27^+	50^1
Polygonatum multiflorum	42^+	47^+	64^+	56^+
Geum urbanum	37^+	55^+	45^+	94^+
Campanula trachelium	31^+	51^+	9^+	38^+
Geranium robertianum	29^+	33^+	36^r	62^+
Brachypodium sylvaticum	24^+	33^+	45^+	**88^1**
Convallaria majalis	21^+	37^+	73^+	76^1
Hedera helix	18^+	31^+	9^+	18^2
Bromus benekenii agg.	13^+	51^+	27^+	18^+
Carex muricata agg.	11^+	15^+	18^r	**59^+**
Stachys sylvatica	11^+	2^+	27^+	44^+
Lapsana communis	9^+	15^r	9^+	29^+
Urtica dioica	9^r	4^r	45^+	29^+
Torilis japonica	7^+	13^+	9^+	**56^+**
Viola mirabilis	6^+	32^+	36^+	24^1
Ficaria bulbifera	6^+	3^+	27^2	21^+
Viola hirta	2^+	9^+	9^+	21^+
Veronica hederifolia agg.	1^+	2^1	27^1	9^+
Ajuga reptans	52^+	36^+	.	97^1
Fragaria vesca	48^+	55^+	.	50^+
Veronica chamaedrys agg.	42^+	38^+	.	44^+
Melica nutans	33^+	29^+	18^+	.
Stellaria holostea	32^1	45^+	.	12^+
Neottia nidus-avis	22^r	21^r	.	24^+
Heracleum sphondylium	18^+	41^+	.	32^+
Impatiens parviflora	15^+	9^+	64^+	.
Moehringia trinervia	14^+	12^+	.	26^+
Sambucus nigra	11^+	2^+	27^+	.

Stĺpec (column)	1	2	3	4
Počet zápisov (number of relevés)	950	185	11	34
Viburnum lantana	5^{+}	23^{+}	27^{r}	.
Festuca gigantea	4^{+}	3^{+}	.	**21^{+}**
Carex digitata	43^{+}	36^{+}	.	.
Tilia cordata	28^{+}	22^{+}	.	.
Acer platanoides	25^{+}	38^{+}	.	.
Campanula persicifolia	25^{+}	23^{+}	.	.
Lonicera xylosteum	13^{+}	32^{+}	.	.

Dodatky k tabuľke 1, rad *Carpinetalia*, zväz *Carpinion* (stĺpce 1 – 4)
Species with low frequencies (columns 1 – 4)

Stĺpec 1 (Column 1), ***Carici pilosae-Carpinetum***: **E_3**: *Abies alba* 4^{+}, *Acer platanoides* 6^{+}, *A. tataricum* 1^{1}, *Alnus glutinosa* 1^{+}, *Betula pendula* 2^{+}, *Clematis vitalba* 1^{+}, *Cornus mas* 1^{+}, *Crataegus laevigata* 1^{+}, *C. monogyna* 1^{+}, *Fraxinus* sp.1^{+}, *Juglans nigra* 1^{+}, *Larix decidua* 1^{+}, *Malus sylvestris* 1^{r}, *Picea abies* 2^{+}, *Pinus nigra* 1^{1}, *P. sylvestris* 6^{+}, *Populus tremula* 3^{1}, *Quercus rubra* 1^{2}, *Quercus* sp. 1^{1}, *Robinia pseudacacia* 1^{+}, *Salix caprea* 1^{1}, *Sorbus aria* 1^{r}, *S. aucuparia* 1^{+}, *Tilia cordata* 15^{1}, *Ulmus glabra* 1^{+}, *U. laevis* 1^{1}. – **E_2**: *Abies alba* 2^{+}, *Acer platanoides* 4^{+}, *Berberis vulgaris* 1^{+}, *Cerasus fruticosa* 1^{+}, *Clematis vitalba* 1^{r}, *Cotoneaster integerrimus* 1^{r}, *Crataegus* sp. 2^{+}, *Daphne mezereum* 1^{+}, *Frangula alnus* 1^{+}, *Fraxinus excelsior* 4^{+}, *Juglans regia* 1^{+}, *Malus domestica* 1^{+}, *M. sylvestris* 1^{r}, *Padus avium* 1^{+}, *Picea abies* 2^{+}, *Pinus sylvestris* 1^{r}, *Populus tremula* 1^{+}, *Prunus spinosa* 2^{+}, *Pyrus communis* agg. 2^{+}, *Quercus cerris* 1^{+}, *Q. rubra* 1^{+}, *Rhamnus cathartica* 1^{r}, *Ribes alpinum* 1^{+}, *R. uva-crispa* 2^{+}, *Robinia pseudacacia* 1^{+}, *Rosa arvensis* 1^{3}, *R. gallica* 1^{+}, *R. sherardii* 1^{r}, *Rosa* sp. 4^{+}, *Rubus fruticosus* agg.1^{r}, *R. idaeus* 1^{+}, *Rubus* sp. 1^{+}, *Sambucus racemosa* 1^{r}, *Sorbus aria* 1^{+}, *S. aucuparia* 1^{r}, *S. torminalis* 6^{+}, *Staphylea pinnata* 1^{+}, *Tilia cordata* 17^{+}, *T. platyphyllos* 2^{+}, *Ulmus glabra* 1^{+}, *U. laevis* 1^{1}, *Viburnum lantana* 2^{+}. – **E_1**: *Abies alba* 5^{+}, *Acer tataricum* 3^{r}, *Achillea distans* agg. 1^{+}, *A. millefolium* agg. 1^{+}, *A. nobilis* 1^{+}, *Acinos arvensis* 1^{+}, *Aconitum anthora* 1^{+}, *A. lycoctonum* 1^{+}, *A. moldavicum* 1^{+}, *Adoxa moschatellina* 1^{1}, *Aegopodium podagraria* 16^{+}, *Aesculus hippocastanum* 1^{+}, *Agrimonia eupatoria* 1^{+}, *Agrostis capillaris* 1^{r}, *Ajuga genevensis* 4^{+}, *Allium carinatum* 1^{+}, *A. oleraceum* 1^{+}, *A. scorodoprasum* 1^{+}, *A. ursinum* 1^{+}, *A. victorialis* 1^{2}, *Anemone nemorosa* 8^{+}, *A. ranunculoides* 3^{+}, *Archangelica officinalis* 1^{r}, *Angelica sylvestris*1^{+}, *Antennaria dioica* 1^{+}, *Anthericum ramosum* 2^{+}, *Anthoxanthum odoratum* 1^{1}, *Anthriscus *trichospermus* 1^{r}, *A.*

sylvestris 2^{+}, *Aposeris foetida* 6^{1}, *Aquilegia vulgaris* 1^{r}, *Arabis glabra* 1^{r}, *A. hirsuta* agg. 1^{+}, *A. turrita*1^{r}, *Arctium lappa*1^{r}, *A. minus*1^{r}, *A. nemorosum* 1^{r}, *Arctium* sp. 1^{r}, *A. tomentosum* 1^{r}, *Aremonia agrimonoides* 1^{+}, *Arrhenatherum elatius* 1^{+}, *Asplenium septentrionale* 1^{r}, *A. trichomanes* 1^{+}, *Astrantia major* 1^{+}, *Athyrium filix-femina* 11^{+}, *Atropa bella-donna* 1^{+}, *Avenella flexuosa* 3^{+}, *Berberis vulgaris* 1^{r}, *Betonica officinalis* 2^{+}, *Brachypodium pinnatum* 2^{+}, *Bromus hordeaceus* 1^{+}, *B. racemosus* 1^{r}, *Bupleurum falcatum* 1^{+}, *Calamagrostis arundinacea* 6^{+}, *C. epigejos* 1^{+}, *Campanula bononiensis* 1^{+}, *C. moravica* 1^{+}, *C. patula* 1^{r}, *Cardamine flexuosa* 1^{+}, *Cardamine* sp. 1^{r}, *Cardaminopsis arenosa* agg. 2^{+}, *Carex alba* 1^{+}, *C. caryophyllea* 1^{r}, *C. fritschii* 1^{+}, *C. hirta* 1^{r}, *C. humilis* 1^{+}, *C. michelii* 1^{+}, *C. montana* 11^{+}, *C. pallescens* 2^{+}, *C. pendula* 1^{r}, *C. pilulifera* 1^{+}, *Carex* sp. 1^{+}, *C. vesicaria* 1^{1}, *Castanea sativa* 1^{r}, *Cephalanthera damasonium* 4^{+}, *C. longifolia* 10^{+}, *C. rubra* 2^{+}, *Cephalanthera* sp. 1^{r}, *Cerasus mahaleb* 1^{r}, *Chaerophyllum aromaticum*1^{+}, *C. hirsutum*1^{+}, *Chamaecytisus hirsutus*1^{+}, *C. supinus*1^{r}, *Chamerion angustifolium*1^{r}, *Chelidonium majus* 3^{+}, *Chrysosplenium alternifolium* 1^{+}, *Circaea ×intermedia* 1^{+}, *Cirsium oleraceum* 1^{+}, *Clematis recta* 1^{r}, *C. vitalba* 5^{+}, *Colchicum autumnale* 1^{r}, *Convolvulus arvensis* 1^{+}, *Corallorhiza trifida* 1^{r}, *Corydalis intermedia* 1^{+}, *C. pumila* 1^{+}, *C. solida* 1^{+}, *Crataegus* sp. 2^{+}, *Cruciata laevipes* 2^{+}, *Cynoglossum germanicum* 1^{+}, *Cystopteris fragilis* 3^{+}, *C. montana* 1^{r}, *Dactylorhiza sambucina* 1^{r}, *Daphne mezereum* 8^{+}, *Daucus carota* 1^{+}, *Dentaria enneaphyllos* 1^{+}, *D. glandulosa* 1^{+}, *Dianthus deltoides* 1^{+}, *Digitalis grandiflora* 8^{+}, *Doronicum austriacum* 1^{r}, *Dryopteris carthusiana* agg. 3^{+}, *D. cristata* 1^{r}, *Epilobium collinum* 1^{+}, *E. hirsutum* 1^{+}, *E. lanceolatum* 1^{+}, *E. montanum* 11^{+} , *Epipactis atrorubens*1^{+}, *E. helleborine* agg. 6^{+}, *E. microphylla* 1^{+}, *E. pontica* 1^{+}, *E. purpurata* 2^{+}, *Epipactis* sp. 1^{r}, *Equisetum arvense* 1^{r}, *Equisetum* sp. 1^{r}, *E. sylvaticum* 1^{+}, *Eupatorium cannabinum* 1^{r}, *Fallopia dumetorum* 2^{+}, *Festuca altissima* 1^{1}, *F. drymeja* 5^{3}, *F. heterophylla* 6^{+}, *F. ovina* agg. 1^{+}, *Ficaria verna* agg. 2^{+}, *Fragaria* sp. 1^{+}, *F. viridis* 1^{+}, *Frangula alnus* 2^{+}, *Fraxinus *danubialis* 1^{+}, *F. ornus* 1^{r}, *Fraxinus* sp. 1^{+}, *Fumaria* sp. 1^{+}, *Gagea lutea* 1^{1}, *Galanthus nivalis* 1^{1}, *Galeobdolon argentatum* 1^{1}, *Galeobdolon* sp. 1^{r}, *Galeopsis ladanum* 1^{r}, *G. pubescens* 7^{r}, *Galeopsis* sp. 2^{r}, *G. speciosa* 1^{+}, *G. tetrahit* 4^{+}, *Galium austriacum* 1^{+}, *G. mollugo* agg. 2^{+}, *G. rotundifolium* 1^{1}, *Galium* sp. 1^{+}, *G. sylvaticum* 4^{+}, *G. verum* 3^{+}, *G. wirtgenii* 1^{+}, *Genista germanica* 1^{+}, *G. pilosa* 1^{+}, *G. tinctoria* 8^{+}, *Gentiana asclepiadea* 1^{+}, *Geranium phaeum* 1^{+}, *Gnaphalium sylvaticum* 1^{+}, *Gymnadenia conopsea* 1^{+}, *Gymnocarpium dryopteris* 1^{+}, *G. robertianum* 1^{+}, *Gypsophila muralis* 1^{+}, *Helleborus purpurascens* 1^{+}, *Hepatica nobilis* 2^{1}, *Hieracium bifidum* 1^{+}, *H. caesium* 1^{+}, *H. laevigatum* 1^{r}, *H. lachenalii* 10^{+}, *H. maculatum* 1^{+}, *H. racemosum* 4^{+}, *Hieracium* sp. 1^{+}, *H. umbellatum* 1^{+}, *H. vulgatum* 1^{+}, *Hylotelephium maximum* 7^{+}, *Hypericum hirsutum* 12^{+}, *H. maculatum* 1^{+}, *H. montanum* 3^{+}, *H. perforatum* 8^{+}, *Impatiens noli-tangere* 5^{+}, *Inula conyzae* 1^{1}, *Isopyrum thalictroides* 5^{+}, *Juglans regia* 3^{r}, *Juncus effusus* 1^{r}, *Juniperus communis* 1^{+}, *Knautia dipsacifolia* 1^{+}, *K. drymeia* 1^{+}, *Knautia* sp. 1^{+}, *Lactuca quercina* 1^{+}, *L. serriola* 1^{r}, *Lamium maculatum* 4^{+}, *Larix decidua* 1^{r}, *Laser trilobum* 1^{+}, *Laserpitium latifolium* 1^{r}, *Lathraea squamaria* 2^{+}, *Lathyrus pratensis* 1^{+}, *L. transsilvanicus*1^{1}, *Lembotropis nigricans*1^{+}, *Leucanthemum vulgare* agg. 1^{r}, *Listera ovata* 1^{r}, *Lonicera caprifolium* 1^{+}, *Lotus corniculatus* 1^{+}, *Lunaria rediviva* 1^{+}, *Lupinus polyphyllus* 1^{+}, *Luzula campestris* agg. 1^{+}, *L. luzulina* 1^{1}, *L. pilosa* 7^{+}, *L. sylvatica* 1^{+}, *Lychnis flos-cuculi* 1^{+}, *Lysimachia nemorum* 1^{r}, *L. punctata* 1^{r}, *L. vulgaris* 1^{r}, *Malus sylvestris* 2^{r}, *Medicago lupulina* 1^{+}, *Melampyrum cristatum* 1^{1}, *M. pratense* 7^{+}, *Melampyrum* sp. 1^{+}, *M. sylvaticum* 1^{1}, *Melica picta* 1^{1}, *Melilotus officinalis* 1^{r}, *Molinia caerulea* agg. 1^{+}, *Monotropa hypopitys* agg. 1^{+}, *Myosotis arvensis* 1^{r}, *M. ramosissima* 1^{+}, *Myosotis sparsiflora* 1^{+}, *Myosotis* sp. 1^{+}, *M. sylvatica* 6^{+}, *Omphalodes scorpioides* 1^{+}, *Orchis pallens* 1^{r}, *O. purpurea* 1^{+}, *Origanum vulgare* 1^{+}, *Orobanche* sp. 1^{r}, *Orthilia secunda* 1^{+}, *Oryzopsis virescens* 1^{1}, *Oxalis acetosella* 13^{+}, *Padus avium* 1^{r}, *Parietaria officinalis* 1^{+}, *Paris quadrifolia* 6^{+}, *Petasites hybridus* 1^{+}, *Peucedanum cervaria* 1^{1}, *Phegopteris connectilis* 1^{1}, *Phlomis tuberosa* 1^{+}, *Phyteuma spicatum* 6^{+}, *Picea abies* 3^{+}, *Pilosella bauhinii* 1^{+}, *Pimpinella major* 1^{r}, *P. saxifraga* 1^{+}, *Pinus nigra* 1^{+}, *P. sylvestris* 1^{r}, *Plantago major* 1^{r}, *Platanthera* sp. 2^{r}, *Poa annua* 1^{r}, *P. compressa* 1^{r}, *P. pratensis* agg. 4^{+}, *P. stiriaca* 1^{1}, *P. trivialis* 1^{+}, *Polygonatum odoratum* 6^{+}, *P. verticillatum* 1^{+}, *Polypodium vulgare* 3^{+}, *Polystichum aculeatum* 1^{+}, *Populus* sp. 1^{r}, *P. tremula* 4^{+}, *Potentilla erecta* 1^{+}, *P. recta* 1^{r}, *Prenanthes purpurea* 4^{+}, *Primula elatior* 4^{+}, *Primula* sp. 1^{+}, *P. vulgaris* 1^{+}, *Prunella vulgaris* 2^{+}, *Prunus spinosa* 6^{+}, *Pteridium aquilinum* 1^{+}, *Pulmonaria mollis* 2^{+}, *P. murinii* 1^{+}, *Pyrola media* 1^{+}, *P. minor* 1^{+}, *P. rotundifolia* 1^{+}, *Pyrus communis* agg. 4^{r}, *Quercus robur* agg. 6^{+}, *Q. rubra* 1^{r}, *Quercus* sp. 1^{1}, *Ranunculus acris* 1^{+}, *R. lanuginosus* 6^{+}, *R. nemorosus* 1^{r}, *R. platanifolius* 1^{2}, *R. polyanthemos* 1^{+}, *R. repens* 1^{+}, *Rhamnus cathartica* 1^{r}, *Ribes alpinum* 1^{+}, *R. nigrum* 1^{r}, *Ribes* sp. 1^{r}, *R. uva-crispa* 5^{+}, *Robinia pseudacacia* 2^{r}, *Roegneria canina* 1^{r}, *Rosa dumalis* 1^{r}, *R. gallica* 1^{+}, *R. pendulina* 1^{r}, *Rosa* sp. 16^{r}, *R. spinosissima* 1^{r}, *Rubus idaeus* 4^{+}, *Rubus* sp. 3^{+}, *Rumex conglomeratus* 1^{+}, *R. crispus*1^{r}, *R. obtusifolius* 1^{r}, *Rumex* sp. 1^{r}, *Ruscus hypoglossum* 1^{1}, *Salix caprea* 1^{+}, *Salvia* *glutinosa* 10^{+}, *Sambucus ebulus* 1^{+}, *S. racemosa* 1^{+}, *Scilla bifolia* agg. 1^{1}, *Scopolia carniolica* 1^{1}, *Scrophularia vernalis* 1^{+}, *Securigera elegans* 1^{+}, *S. varia* 4^{+}, *Selinum carvifolia* 1^{+}, *Senecio nemorensis* agg. 13^{+}, *S. sylvaticus* 1^{+}, *S. viscosus* 1^{+}, *Serratula tinctoria* 1^{+}, *Silene dioica* 1^{r}, *S. nemoralis* 1^{r}, *S. nutans* 1^{+}, *Silene* sp. 1^{r}, *S. viridiflora* 1^{+}, *S. vulgaris* 2^{+}, *Smyrnium perfoliatum* 1^{+}, *Solidago virgaurea* 3^{r}, *Sonchus arvensis* 1^{+}, *Sorbus aria* 2^{r}, *S. aucuparia* 7^{+}, *S. austriaca* 1^{+}, *S. domestica* 1^{r}, *Stachys alpina* 1^{+}, *Staphylea pinnata* 1^{+}, *Stellaria graminea* 1^{2}, *S. media* agg. 2^{+}, *S. nemorum* 1^{+}, *Stenactis annua* 1^{r}, *Steris viscaria* 1^{+}, *Swida sanguinea* 1^{2}, *Symphytum cordatum* 1^{1}, *S. officinale* 1^{r}, *Taraxacum erythrospermum* 1^{r}, *Taraxacum* sp. 3^{r}, *Teucrium chamaedrys* 1^{+}, *Thalictrum aquilegiifolium* 1^{+}, *Tilia platyphyllos* 7^{+}, *Tilia* sp. 1^{+}, *Tithymalus cyparissias* 2^{+}, *T. dulcis* 1^{+}, *T. epithymoides* 1^{+}, *Tithymalus villosus* 1^{+}, *Trifolium alpestre* 2^{+}, *T. aureum* 1^{r}, *T. campestre* 1^{r}, *T. flexuosum* 5^{+}, *T. montanum* 1^{+}, *T. ochroleucon* 1^{r}, *T. pallescens* 1^{+}, *T. rubens* 1^{r}, *T. striatum* 1^{+}, *Trisetum flavescens* 1^{1}, *Tussilago farfara* 1^{r}, *Ulmus glabra* 6^{r}, *Ulmus* sp. 1^{+}, *Vaccinium myrtillus* 1^{+}, *Valeriana *sambucifolia* 1^{+}, *V. stolonifera* 1^{r}, *Verbascum *austriacum* 1^{r}, *V. densiflorum*1^{+}, *V. lychnitis* 1^{r}, *Verbascum* sp. 1^{r}, *Veronica montana* 1^{+}, *Viburnum opulus* 11^{+}, *Vicia cassubica* 2^{+}, *V. cracca* agg. 1^{+}, *V. dumetorum* 1^{+}, *V. hirsuta* 1^{+}, *V. pisiformis* 1^{+}, *V. sativa* agg. 1^{+}, *Vicia* sp. 1^{r}, *V. sylvatica* 2^{+}, *Viola alba* 1^{+}, *V. canina* 1^{r}, *V. collina* 1^{+}, *V. riviniana* 8^{+}, *Viola* sp. 2^{+}, *V. ×scabra* 1^{1}, *V. suavis* 1^{+}, *V. tricolor* 1^{+}, *Xanthoxalis stricta* 1^{r}.

StĺÍpec 2 (Column 2), ***Primulo veris-Carpinetum***: $\mathbf{E_3}$: *Acer platanoides* 14^{+}, *Betula pendula* 1^{+}, *Pinus sylvestris* 2^{+}, *Populus tremula* 1^{r}, *Pyrus communis* agg. 2^{+}, *Quercus pubescens* agg., 1^{r}, *Robinia pseudacacia* 1^{1}, *Sorbus aria* 4^{+}, *Tilia cordata* 12^{+}, *T. platyphyllos* 9^{1}, *Tilia* sp. 1^{+}, *Ulmus glabra* 2^{+}. – $\mathbf{E_2}$: *Acer platanoides* 5^{+}, *Berberis vulgaris* 1^{r}, *Fraxinus excelsior* 5^{+}, *F. ornus* 1^{r}, *Lonicera nigra* 1^{r}, *Malus sylvestris* 1^{+}, *Padus avium* 1^{+}, *Prunus spinosa* 2^{+}, *Pyrus communis* agg. 1^{+}, *Quercus virgiliana* 1^{r}, *Rhamnus cathartica* 1^{+}, *Ribes uva-crispa* 1^{+}, *Robinia pseudacacia* 1^{r}, *Rosa* sp. 5^{+}, *Sorbus aria* 6^{r}, *S. aucuparia* 1^{r}, *S. torminalis* 8^{+}, *Staphylea pinnata* 2^{+}, *Tilia cordata* 9^{+}, *T. platyphyllos* 6^{+}, *Ulmus glabra* 1^{r}, *U. laevis*1^{+}, *Viburnum lantana* 9^{+}. – $\mathbf{E_1}$: *Acer tataricum* 4^{+}, *Aconitum anthora* 5^{+}, *A. lycoctonum* 1^{+}, *A. moldavicum* 2^{2}, *Adenophora liliifolia* 1^{r}, *Adonis vernalis* 1^{+}, *Aegopodium podagraria* 11^{+}, *Aethusa cynapium* 1^{+}, *Ajuga genevensis* 1^{r}, *Allium ursinum* 1^{+}, *Anemo nenemorosa* 1^{+}, *A. ranunculoides* 6^{+}, *Anthriscus nitida* 1^{r}, *A. sylvestris* 2^{+} *Arabis glabra* 1^{r}, *A. turrita* 4^{r}, *Arctium lappa* 2^{r}, *Arctium* sp. 1^r, *Asplenium trichomanes* 6^+, *Avenella flexuosa* 1^+, *Berberis vulgaris* 3^r, *Betonica officinalis* 2^r, *Betula pendula* 1^r, *Brachypodium pinnatum* 2^+ *Bupleurum falcatum* 2^r, *B. longifolium* 2^+, *Calamagrostis arundinacea* 2^+, *C. epigejos* 1^1, *Calamintha menthifolia* 1^+, *Cardamine flexuosa* 1^+, *Cardaminopsis arenosa* 5^+, *C. halleri* 1^+, *Carex humilis* 1^1, *C. michelii* 3^+, *C. montana* 6^+, *Cephalanthera damasonium* 3^r, *C. longifolia* 3^r, *C. rubra* 2^r, *Cerasus mahaleb* 2^r, *Chaerophyllum hirsutum* 1^+, *Chelidonium majus* 4^+, *Cirsium vulgare* 1^r,*Clematis alpina* 1^+, *C. recta* 6^+, *C. vitalba* 5^+, *Corallorhiza trifida* 1^+, *Corydalis pumila* 2^+, *C. solida* 2^+, *Corydalis* sp. 1^1, *Cotoneaster integerrimus* 1^r, *Crataegus* sp. 1^r, *Cruciata laevipes* 1^+, *Cynoglossum germanicum* 1^r, *Cystopteris fragilis* 3^r, *Daphne mezereum* 7^+, *Daucus carota* 1^+, *Digitalis grandiflora* 8^+, *Dorycnium pentaphyllum* agg. 1^+, *Epilobium collinum* 1^+, *E. lanceolatum* 1^r, *E. montanum* 1^+, *Epipactis helleborine* 9^r, *E. microphylla* 1^+, *Epipactis* sp. 1^r, *Erysimum odoratum* 1^r, *Erythronium dens-canis* 1^1, *Fallopia dumetorum* 3^+, *Festuca altissima* 1^r, *F. heterophylla* 6^+, *F. rubra* agg. 1^+, *Festuca* sp. 1^+, *Filipendula vulgaris* 1^+, *Fragaria viridis* 3^1, *Frangula alnus* 1^+, *Fraxinus ornus* 3^+, *Galanthus nivalis* 2^+, *Galeobdolon* sp. 1^+, *Galeopsis ladanum* 2^+, *G. pubescens* 6^r, *Galeopsis* sp. 1^r, *G. tetrahit* 3^+, *Galium mollugo* agg. 3^+, *G. sylvaticum* 1^1, *G. verum* 8^+, *Genista germanica* 1^+, *G. tinctoria* 4^+, *Geum montanum* 1^+, *Hieracium caesium* 1^+, *H. laevigatum* 1^+, *H. lachenalii* 3^+, *H. racemosum* 5^+, *Hylotelephium maximum* 12^r, *Hypericum hirsutum* 9^+, *H. maculatum* 1^+, *H. montanum* 2^+, *H. perforatum* 4^+, *Inula conyzae* 1^+, *Iris graminea* 1^+, *Isopyrum thalictroides* 8^+, *Juglans regia* 2^r, *Juniperus communis* 1^r, *Lactuca quercina* 1^+, *Lamium album* 1^+, *L. maculatum* 4^+, *Laser trilobum* 1^+, *Laserpitium latifolium* 3^r, *Lathraea squamaria* 1^+, *Lathyrus sylvestris* 2^+, *L. transsilvanicus* 4^+, *Lembotropis nigricans* 1^+, *Loranthus europaeus* 1^+, *Luzula pilosa* 1^1, *Lysimachia nemorum* 1^+, *L. punctata* 1^r, *Malus sylvestris* 1^r, *Melampyrum pratense* 2^+, *Muscari botryoides* 1^1, *Myosotis sylvatica* 2^+, *Orchis purpurea* 1^+, *Origanum vulgare* 1^+, *Orobanche* sp. 1^+, *Oryzopsis virescens* 2^+, *Oxalis acetosella*2 $^+$, *Padus avium* 1 ^{r}, *Parietaria officinalis* 1^r, *Paris quadrifolia* 1^+, *Phyteuma spicatum* 1^1, *Picea abies* 1^r, *Pilosella bauhinii* 1^+, *P. cymosa* 1^+, *Pimpinella major* 1^r, *P. saxifraga* 1^+, *Platanthera* sp. 1^+, *Poa pratensis* agg. 6^+, *P. stiriaca* 4^1, *Polygala vulgaris* 1^+, *Polygonatum odoratum* 12^+, *P. verticillatum* 1^+, *Polypodium vulgare* 6^+, *Polystichum aculeatum* 1^r, *Populus tremula* 2^+, *Primula elatior* 8^+, *Prunella vulgaris* 1^+, *Prunus spinosa* 4^+, *Pulmonaria mollis* 6^+, *P. murinii* 1^r, *Pyrola minor* 1^+, *Pyrus communis* agg. 9^r, *Quercus robur* agg. 2^+, *Ranunculus lanuginosus* 1^r, *R. polyanthemos* 1^+, *Rhamnus cathartica* 7^+, *Ribes uva-crispa* 4^r, *Robinia pseudacacia* 1^r, *Roegneria canina* 1^{+}, *Rosa* sp. 17^{r}, *Rubus idaeus* 1^{r}, *Rubus* sp. 2^{+}, *Rumex* sp. 1^{+}, *Salvia glutinosa* 3^{r}, *Scilla bifolia* agg. 1^{+}, *Scrophularia umbrosa* 1^{+}, *S. vernalis* 1^{+}, *Securigera elegans* 2^{+}, *S. varia* 2^{+}, *Senecio nemorensis* agg. 3^{+}, *Silene nemoralis* 1^{r}, *S. viridiflora* 1^{+}, *S. vulgaris* 3^{r}, *Solidago virgaurea* 2^{r}, *Sorbus aria* 9^{r}, *S. aucuparia* 1^{r}, *Spiraea media* 1^{+}, *Stachys alpina* 1^{r}, *Staphylea pinnata* 3^{+}, *S. media* agg. 1^{1}, *S. nemorum* 1^{+}, *Taraxacum erythrospermum* 1^{r}, *Taraxacum* sp. 4^{+}, *Tilia platyphyllos* 18^{+}, *Tithymalus cyparissias* 8^{+}, *T. epithymoides* 2^{+}, *T. esula* 1^{+}, *T. villosus* 1^{+}, *Trifolium alpestre* 1^{r}, *T. flexuosum* 9^{+}, *T. montanum* 2^{+}, *T. striatum* 1^{+}, *Ulmus glabra* 6^{+}, *Valeriana tripteris* 4^{+}, *Verbascum* *austriacum 1^{+}, *V. phoeniceum* 1^{+}, *Verbascum* sp. 1^{+}, *Veronica teucrium* 1^{1}, *Viburnum opulus* 1^{+}, *Vicia cassubica* 1^{+}, *V. cracca* agg. 3^{+}, *V. dumetorum* 1^{+}, *V. pisiformis* 2^{+}, *V. sylvatica* 1^{+}, *Viola alba* 1^{+}, *V. collina* 1^{+}, *V. ×scabra* 1^{+}, *V. riviniana* 5^{+}, *Viola* sp. 1^{1}, *V. suavis* 1^{+}.

StÍpec 3 (Column 3), ***Polygonato latifolii-Carpinetum***: **E_3**: *Robinia pseudacacia* 18^{+}. – **E_2**: *Rosa* sp. 9^{+}, *Viburnum lantana* 8^{r}. – **E_1**: *Acer tataricum* 9^{1}, *Allium* sp. 9^{+}, *Anthriscus sylvestris* 9^{+}, *Arctium lappa* 8^{+}, *Ballota nigra* 18^{r}, *Chelidonium majus* 18^{r}, *Chenopodium album* agg. 9^{r}, *Clematis vitalba* 9^{+}, *Cruciata laevipes* 9^{+}, *Galeopsis pubescens* 9^{+}, *Humulus lupulus* 9^{+}, *Lamium maculatum* 9^{+}, *L. purpureum* 9^{+}, *Physalis alkekengi* 9^{+}, *Quercus robur* agg. 9^{+}, *Quercus* sp. 27^{+}, *Rhamnus cathartica* 18^{r}, *Robinia pseudacacia* 9^{+}, *Roegneria canina* 18^{+}, *Rosa* sp. 9^{r}, *Tithymalus cyparissias* 9^{r}, *Viola ×scabra* 9^{r}, *Viola* sp. 27^{+}.

StÍpec 4 (Column 4), ***Convallario-Carpinetum***: **E_3**: *Populus alba* 3^{1}, *P. nigra* 3^{1}, *P. tremula* 3^{+}, *Pyrus communis* agg. 3^{+}, *Salix fragilis* 3^{1}. – **E_2**: *Frangula alnus* 9^{+}, *Padus avium* 18^{+}, *Populus tremula* 3^{1}, *Prunus spinosa* 9^{+}, *Quercus cerris* 3^{+}, *Robinia pseudacacia* 3^{1}, *Tilia cordata* 9^{+}, *Ulmus glabra* 3^{+}, *U. laevis* 3^{+}. – **E_1**: *Aegopodium podagraria* 6^{+}, *Anemone nemorosa* 12^{2}, *A. ranunculoides* 3^{+}, *Angelica sylvestris* 12^{+}, *Anthoxanthum odoratum* 3^{1}, *Anthriscus sylvestris* 15^{+}, *Barbarea stricta* 3^{+}, *Betonica officinalis* 3^{1}, *Campanula patula* 3^{+}, *Carex pallescens* 6^{+}, *C. pendula* 3^{1}, *Clematis vitalba* 3^{+}, *Corydalis solida* 18^{+}, *Cruciata laevipes* 3^{+}, *Digitalis grandiflora* 3^{+}, *Epilobium montanum* 18^{+}, *Epipactis* sp. 24^{+}, *Fritillaria meleagris* 3^{1}, *Gagea lutea* 15^{+}, *Galeopsis pubescens* 15^{+}, *Hieracium umbellatum* 3^{+}, *Hylotelephium maximum* 6^{+}, *Hypericum hirsutum* 12^{+}, *H. perforatum* 3^{+}, *Lamium album* 6^{+}, *Lithospermum officinale* 3^{+}, *Luzula campestris* agg. 3^{+}, *Lychnis flos-cuculi* 6^{+}, *Oenanthe banatica* 3^{+}, *Parthenocissus quinquefolia* 3^{+}, *Poa trivialis* 18^{+}, *Prunella vulgaris* 3^{+}, *Pteridium aquilinum* 6^{+}, *Quercus* *robur* agg. 3^+, *Ranunculus repens* 3^+, *Rumex sanguineus* 3^+, *Selinum carvifolia* 3^1, *Senecio jacobaea* 3^+, *Taraxacum* sp. 3^+, *Tithymalus villosus* 3^1, *Vicia sylvatica* 3^+

8. Curriculum vitae

Personal details

Pavel Novák, born 3 May 1988, Litomyšl, Czech Republic

Education

2014–present Masaryk University, Doctoral degree programme: Ecological and Evolutionary Biology

2010–2013 Masaryk University, Master's degree programme: Ecological and Evolutionary Biology. Thesis: *Woodland vegetation of Krumlovský les Forest and its neighbourhood* (in Czech)

2007–2010 Masaryk University, Bachelor's degree programme: Systematic Biology and Ecology. Thesis: *Vegetation characteristics of the geographically distinct floral elements of the Litomyšl region* (in Czech)

1999–2007 Grammar School Gymnázium Aloise Jiráska Litomyšl

Employment history

2014–present Masaryk University, Faculty of Science, Department of Botany and Zoology, position: Researcher

Research interests

biogeography, Caucasus, central Europe, forest ecology, vascular plants, vegetation variability and classification

Membership in professional societies

Czech Botanical Society (*Česká botanická společnost*)
Czech Union for Nature Conservation (*Český svaz ochránců přírody*)

Research project membership

2014–2018 Plant Diversity Analysis and Synthesis Centre (PLADIAS) (Czech Science Foundation 14-36079G)

2019–present Centre for European Vegetation Syntheses (CEVS) (Czech Science Foundation 19-28491X)

Teaching

2015–present Protected areas of Central Europe (Masaryk University)

Academic stays

2018 University of Vienna, Department of Botany and Biodiversity Research (2 months)

Vegetation-plot database custodian

2020– GIVD AS-00-005 - Transcaucasian Vegetation Database

Publications

Publications in international peer-reviewed journals

Chytrý M., Tichý L., Hennekens S., Knollová I., Janssen J., Rodwell J., Peterka T., Marcenò C., Landucci F., Danihelka J., Hájek M., Dengler J., **Novák P.**, Zukal D., Jiménez-Alfaro B., Mucina L., Aćić S., Agrillo E., Attorre F., Bergmeier E., Biurrun I., Boch S., Bölöni J., Bonari G., Braslavskaya T., Bruelheide H., Campos J., Čarni A., Casella L., Ćuk M., Ćušterevska R., De Bie E., Delbosc P., Demina O., Didukh Ya., Dítě D., Dziuba T., Ewald J., Gavilán R., Gégout J.-C., Giusso del Galdo G. P., Golub V., Goncharova N., Goral F., Graf U., Indreica A., Isermann M., Jandt U., Jansen F., Jansen J., Pyykönen A., Jiroušek M., Kącki Z., Kalníková V., Kavgacı A., Khanina L., Korolyuk A., Kozhevnikova M., Kuzemko A., Küzmič F., Kuznetsov O., Laivinš M., Lavrinenko I., Lavrinenko O., Lebedeva M., Lososová Z., Lysenko T., Maciejewski L., Mardari C., Marinšek A., Napreenko M., Onyshchenko V., Pérez-Haase A., Pielech R., Prokhorov V., Rašomavičius V., Rodríguez-Rojo M. P., Rusina S., Schrautzer J., Šibík J., Šilc U., Škvorc Ž., Smagin V., Stančić Z., Stanisci A., Tikhonova E., Tonteri T., Uogintas D., Valachovič M., Vassilev K., Vynokurov D., Willner W., Yamalov S., Evans D., Palitzsch L., Spyropoulou R., Tryfon E., Schaminée J.: EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. – Appl. Veg. Sci.: https://doi.org/10.1111/avsc.12519.

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Dřevojan P., **Novák P.**, Doležal J., Lustyk P., Peterka T. & Šumberová K. (2020): Komentované fytocenologické snímky z České republiky 4. – Zprávy České botanické společnosti 55: 139–155.

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Novák P., Peterka T., Roleček J. & Švarcová M. (2015): Nález ostřice Davallovy (*Carex davalliana*) v Lubenském lese na Litomyšlsku a poznámky k vegetaci nové lokality a jejího okolí. – Východočeský sborník přírodovědný, Práce a studie, 22: 111–119.

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Peruzzi L. Viciani D., Agostini N., Angiolini C., Ardenghi N.M.G., Astuti G., Berdaro M.R., Bertacchi A., Bonari G., Boni S., Chytrý M., Ciampolini F., D'Antraccoli M., Domina G., Ferretti G., Guiggi A., Iamonico D., Laghi P., Lastrucci, Lazzaro L., Lazzeri V., Liguori P., Mannocci M., Marsiaj G., **Novák P.**, Nucci A., Pierini B., Roma-Marzio F., Romiti B., Sani A., Zoccola A., Zukal D. & Bedini G. (2016): Contributi per una flora vascolare di Toscana. VIII (440–506). – Atti della Società toscana di scienze naturali residente in Pisa. Memorie. Serie B, 123: 71–82.

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Books and book chapters

Chytrý M., Danihelka J., Michalcová D., Chytrá M., Daněk P., Grulich V., Hédl R., Jongepier J.W., Jongepierová I., Kočí M., **Novák P.**, Peterka T., Roleček J., Šumberová K. & Tichý L. (2015): Botanical Excursions in Moravia. – Masaryk University, Brno.

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International symposia

European Vegetation Survey meetings

2016 (25th EVS Workshop, 6–9 April 2016, Roma, Italy): **Novák P.** & project partners: Formalized classification of oak-hornbeam forest vegetation in Central and Western Europe: the first insights. Poster.

2017 (26th EVS Workshop, 13–16 September 2017, Bilbao, Spain): **Novák P.**, Zukal D., Kalníková V., Chytrý K. & Kavgacı A.: Vegetation of low-altitudinal mesophilous forests in south-western Georgia (Colchic Region). Oral presentation.

2018 (27th EVS Workshop, 23–26 May 2018, Wrocław, Poland): **Novák P.** and data contributors: Oak-hornbeam forests in Central Europe - New insights into old problems. Oral presentation.

2019 (28th EVS Workshop, 2–6 September 2019, Madrid, Spain): **Novák P.** and data contributors: Oak-hornbeam forests from the European perspective – Currently recognized alliances, a faithful mirror of their floristic variability? Oral presentation.

Symposium of the International Association for Vegetation Science

2015 (Brno): **Novák P.**: Vegetation of European oak-hornbeam forests – an introduction to the project. Poster.

International meetings of plant ecology Ph.D students

2014 (Karpacz, Poland): **Novák P.**: Vegetation of European oak-hornbeam forests. Oral presentation.

2016 (Tihany, Hungary): **Novák P.**: Syntaxonomy of oak-hornbeam forests in Central Europe. Oral presentation.
