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

Dubohabřiny střední Evropy: formalizovaná klasifikace a syntaxonomická revize

Pavel Novák[1], Wolfgang Willner[2,3], Dominik Zukal[1], Jozef Kollár[4], Jan Roleček[1,5], Krzysztof Świerkosz[6], Jörg Ewald[7], Thomas Wohlgemuth[8], János Csiky[9], Viktor Onyshchenko[10] & Milan Chytrý[1]

[1]*Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: pavenow@seznam.cz, dominikzukal@gmail.com, chytry@sci.muni.cz;* [2]*Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria, e-mail: wolfgang.willner@univie.ac.at;* [3]*Vienna Institute for Nature Conservation & Analyses, Gießergasse 6/7, 1090 Vienna, Austria;* [4]*Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, SK-814 99 Bratislava, Slovakia, e-mail: J.Kollar@savba.sk;* [5]*Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Lidická 25/27, CZ-602 00 Brno, Czech Republic, e-mail: honza.rolecek@centrum.cz;* [6]*Museum of Natural History, Wrocław University, Sienkiewicza 21, 50-355, Wrocław, Poland, e-mail: krzysztof.swierkosz@uwr.edu.pl;* [7]*Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, D-85354 Freising, Germany, e-mail: joerg.ewald@hswt.de;* [8]*Forest Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland, e-mail: thomas.wohlgemuth@wsl.ch;* [9]*Department of Ecology, Institute of Biology, Faculty of Sciences, University of Pécs, 7624 Pécs, Ifjúság útja 6, Hungary, e-mail: moon@ttk.pte.hu;* [10]*M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Tereshchenkivska str. 2, 01601 Kyiv, Ukraine, e-mail: labzap@ukr.net*.

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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-European 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 system. 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 central-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

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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, Marcenò 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 forest 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 species 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 previously 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 glacial 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 (original 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 system (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 selection, 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 proportion 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). Subsequently, 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 similarity between relevé pairs (Wiser & De Cáceres 2013). Percentage cover values of species 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, hereafter "dataset").

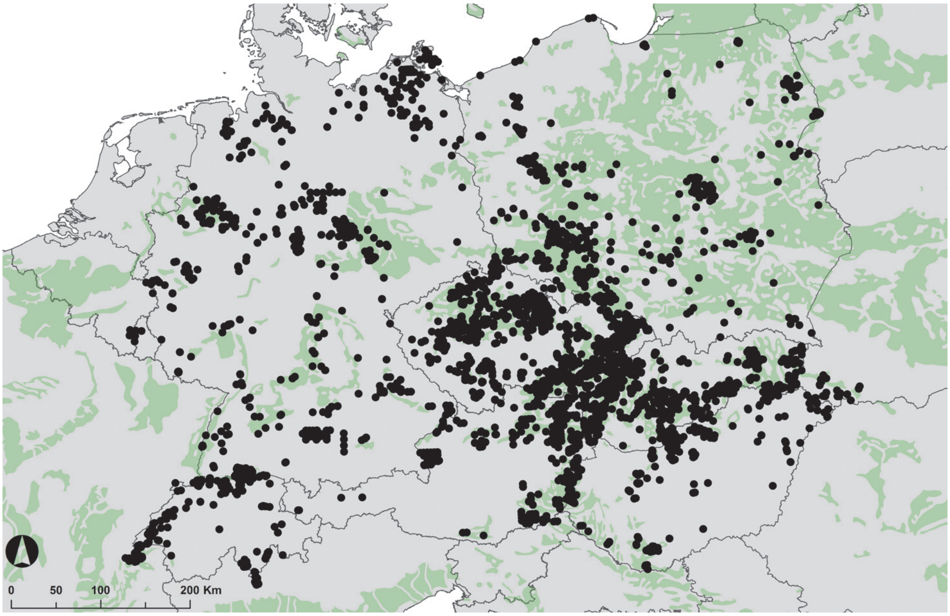


Fig 1. – Distribution of the relevés (n = 6,212) in the oak-hornbeam forest dataset. The areas in which oak-hornbeam forests are supposed to be natural vegetation (Bohn et al. 2000–2003) are shaded in green.

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 seasonality, 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 (version 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 various values of beta) clustering with Sørensen 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 suggested 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 according 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 association 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 definitions 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 containing 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 second 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 correlated 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

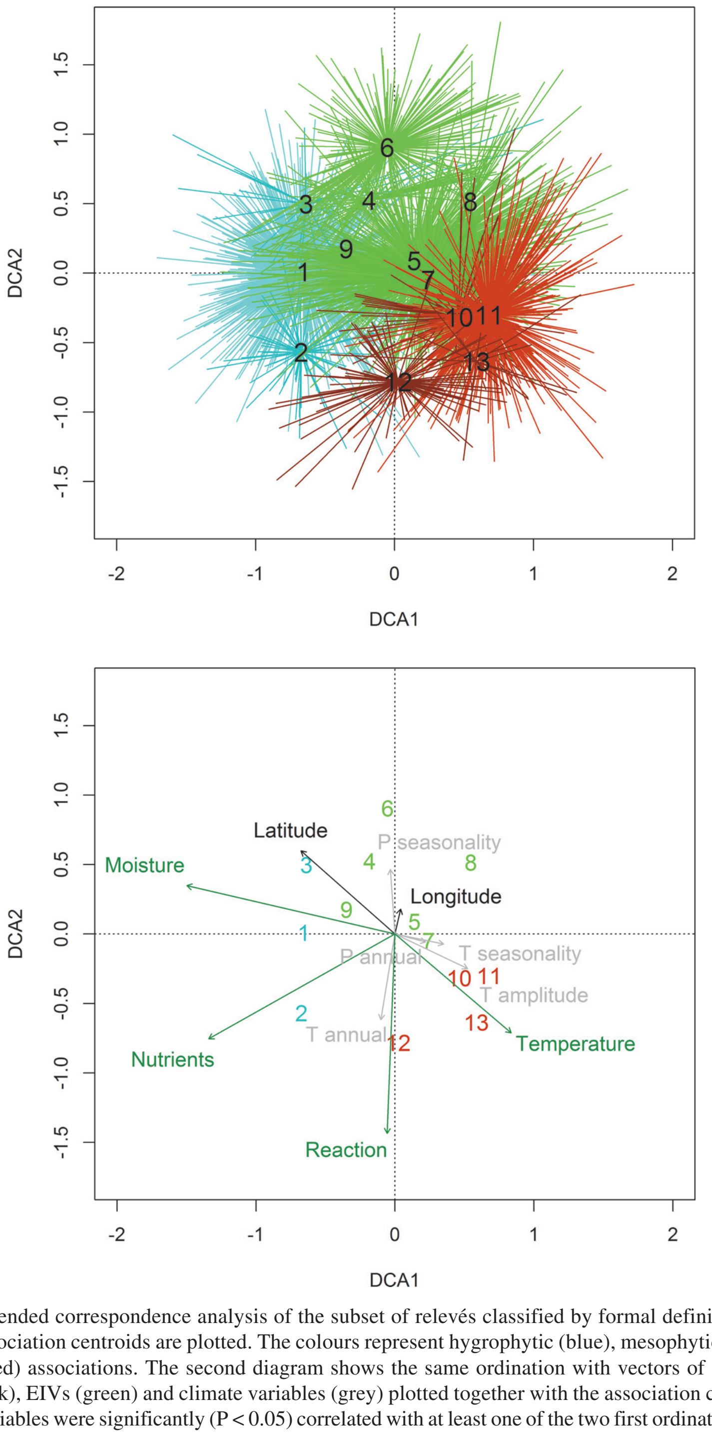


Fig. 2. – Detrended correspondence analysis of the subset of relevés classified by formal definitions. Spider plots with association centroids are plotted. The colours represent hygrophytic (blue), mesophytic (green) and xerophytic (red) associations. The second diagram shows the same ordination with 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*.

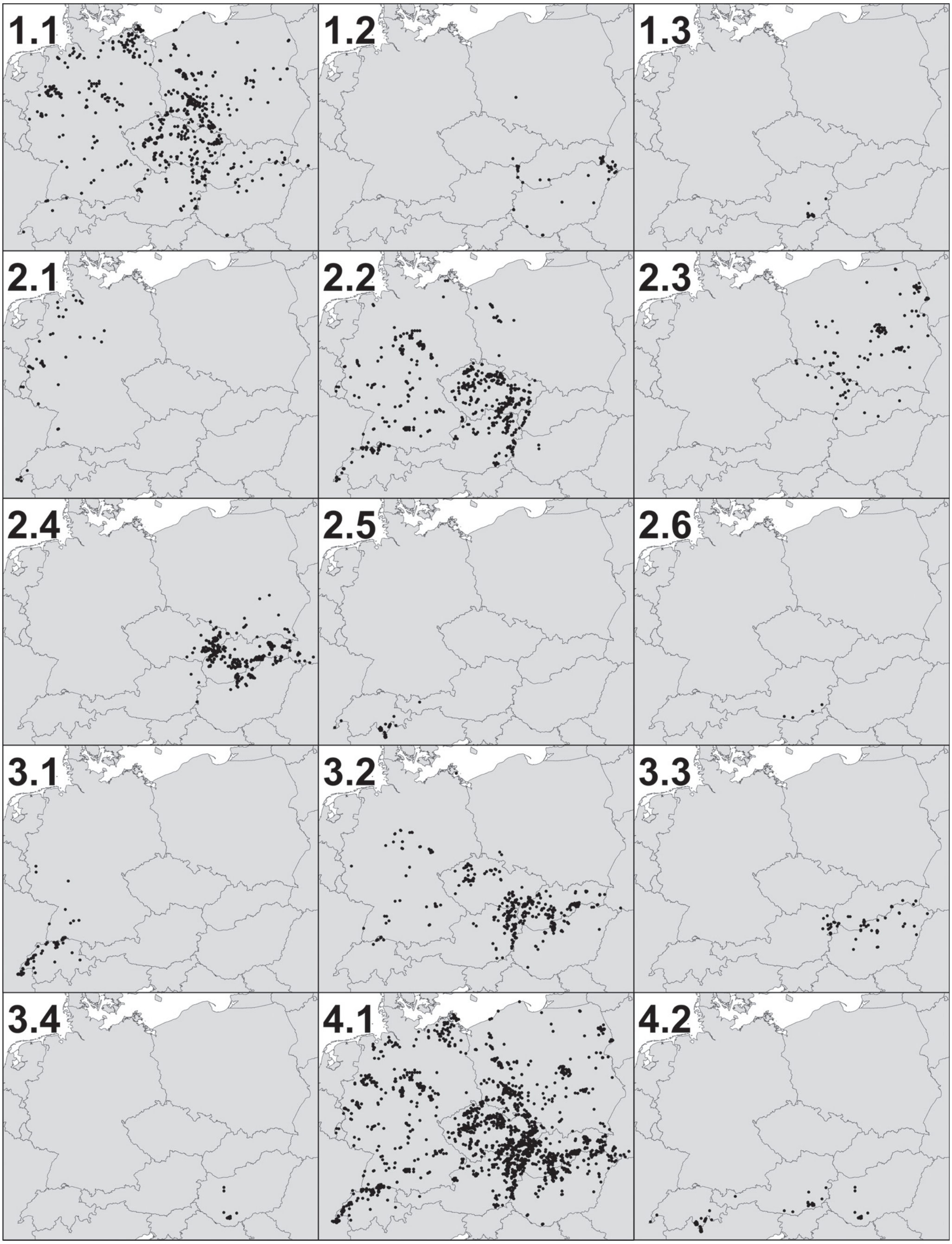


Fig 3. – Distribution of relevés assigned the particular associations by formal definitions (n = 3,413). 1.1 – *Stellario-Carpinetum*, 1.2 – *Convallario-Carpinetum*, 1.3 – *Pseudostellario-Carpinetum*, 2.1 – *Poo-Carpinetum*, 2.2 – *Galio-Carpinetum*, 2.3 – *Tilio-Carpinetum*, 2.4 – *Carici-Carpinetum*, 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.

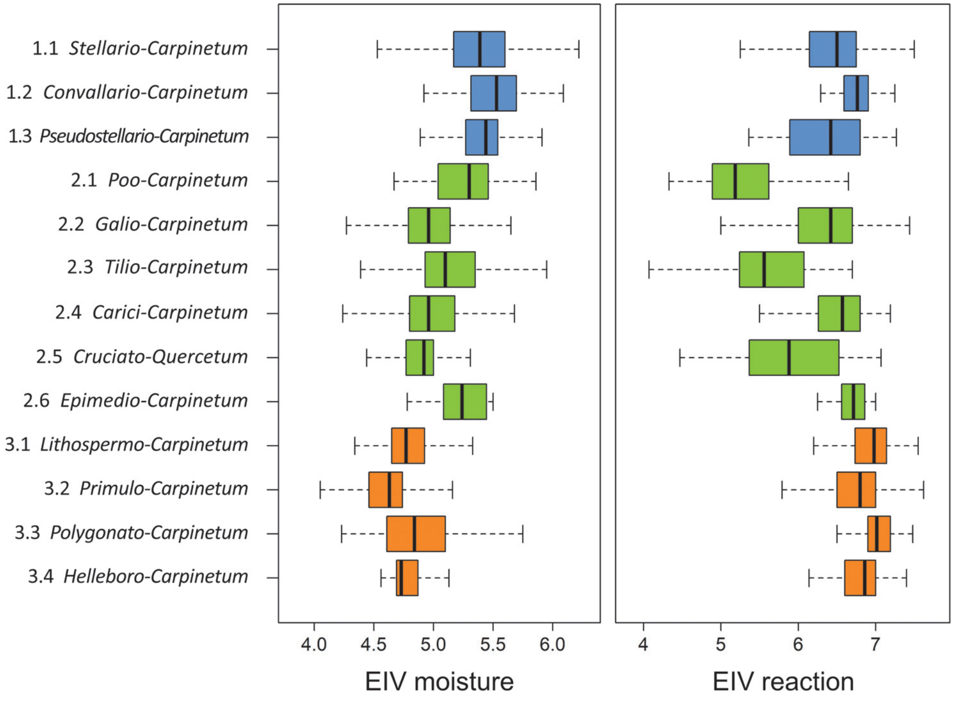


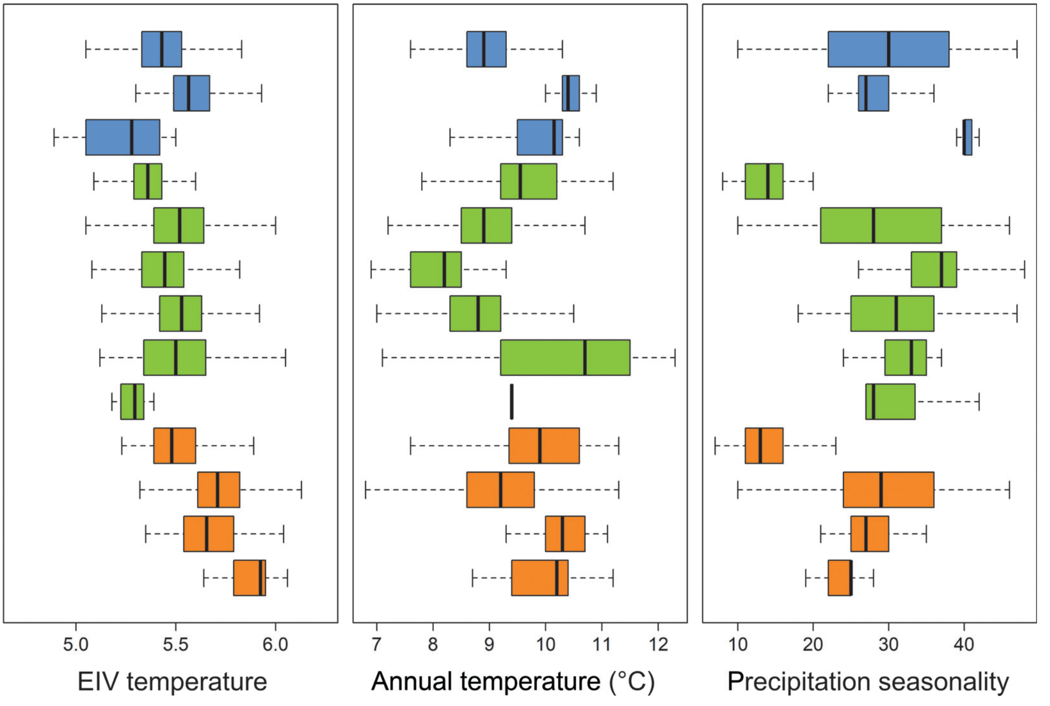
Fig. 4. – Comparison of the selected EIVs and climate variables among associations. Boxes indicate 25–75% interquartile range with their median (bold line), whiskers show the range of values without outliers.

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 subcontinental 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 synoptic 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 species 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 highest 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 abbreviations: 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 StC	1.2 CoC	1.3 PsC	2.1 PoC	2.2 GaC	2.3 TiC	2.4 CaC	2.5 CrQ	2.6 EpC	3.1 LiC	3.2 PrC	3.3 PlC	3.4 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 associations 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-occurrence 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 amygdaloides*) 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 occurrence 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 central 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 forests. 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 natural 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 contrast, 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-European 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 species 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 dataset 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 supported 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 southwestern 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 reasons, 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 divisions 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 particular 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 classification. However, since our paper covers a much broader geographical range, our formal 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 recognized associations. For each of them, we give the protologue, name-giving taxa, nomenclatural type, the most frequent synonyms occurring in central-European phytosociological literature, and a brief description of its distribution, species composition and basic ecological characteristics.

1.1 *Stellario-Carpinetum* Oberdorfer 1957

Protologue: Oberdorfer (1957, p. 421–424): *Stellario-Carpinetum* ass. nova.

Name-giving taxa: *Carpinus betulus*, *Stellaria holostea*.

Nomenclatural type: Knapp (1946): Table 7, rel. 13, neotypus (designated in the study by Novák 2019, where the relevé was effectively published).

Synonyms: *Alno-Carpinetum* Issler 1926 (potentially correct name, nomen ambiguum 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).

Description: 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*).

Ecology: 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 differential species between *Galio-Carpinetum* and *Stellario-Carpinetum* in Polish phytosociological 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* typically 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**

Protologue: This paper.

Name-giving taxa: *Carpinus betulus*, *Pseudostellaria europaea*.

Nomenclatural type: Accetto (1973): Table 1, rel. 2, holotypus hoc loco designatus (effectively published below).

Synonyms: *Pseudostellario-Carpinetum* Accetto 1973 (§1), *Pseudostellario-Carpinetum* Accetto 1974 (§2b).

Description: Hygrophytic Illyrian oak-hornbeam forests. The tree layer is dominated by *Carpinus betulus* and *Quercus robur*, with an admixture of *Acer pseudoplatanus*, *Picea abies* and *Tilia cordata*. The herb layer includes moisture- and nutrient demanding species typical of the Illyrian Province (e.g. *Cardamine waldsteinii*, *Pseudostellaria 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.

Ecology: 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 bedrock.

Nomenclature note: 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 nomenclature 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 transition 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**

Protologue: This paper.

Name-giving taxa: *Carpinus betulus*, *Poa chaixii*.

Nomenclatural type: Schwickerath (1944): Table on p. 120–126, rel. 3, holotypus hoc loco designatus.

Synonyms: *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).

Description: 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*).

Ecology: These mesophytic forests usually occur on cambisols covering acidic parent 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

Protologue: Oberdorfer (1957, p. 424–435): *Galio-Carpinetum* ass. nova.

Name-giving taxa: *Carpinus betulus*, *Galium sylvaticum*.

Nomenclatural type: Oberdorfer (1952): Table 2, rel. 86a, neotypus (designated by Willner & Grabherr 2007).

Synonyms: *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).

Description: 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.

Ecology: 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

Protologue: Traczyk (1962, p. 293–295): *Tilio-Carpinetum* ass. nova.

Name-giving taxa: *Carpinus betulus*, *Tilia cordata*.

Nomenclatural type: 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. *Dryopteris 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, floristically 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 altitudes). 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.

Ecology: 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 frequently.

2.5 *Cruciato glabrae-Quercetum* Ellenberg et Klötzli 1974

Protologue: Ellenberg & Klötzli (1974, p. 688–689): *Cruciato glabrae-Quercetum castanosum*.

Name-giving taxa: *Cruciata glabra*, *Quercus* spp.

Nomenclatural type: Not designated.

Synonyms: *Querco-Castanetum insubricum* Lüdi 1941 p.p. (§34a), *Querco-Fraxinetum* Antonietti 1968 prov. (§3b).

Description: 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 betonicifolium*). Since they predominantly occur on acidic bedrock, acidophytes (e.g. *Pteridium aquilinum*, *Solidago virgaurea*) are also common.

Ecology: 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

Protologue: Soó (1964, p. 25): *Epimedio-Carpinetum* (Horvat 1938) Borhidi 1963.

Name-giving taxa: *Carpinus betulus*, *Epimedium alpinum*.

Nomenclatural type: Horvat (1938): Table 1, rel. 14, lectotypus (designated by Marinček 1994).

Synonyms: *Querco-Carpinetum croaticum* Horvat 1938 (§34a), *Carpinetum praealpinum* Marinček 1979, *Helleboro nigri-Carpinetum* Marinček in Mucina et al. 1993.

Description: 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 Eastern 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 forest 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 purpurocaeruleum*] (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 purpurocaeruleum*), 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).

Description: 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 thermophytic species (e.g. *Carex montana*, *Festuca heterophylla*) are characteristic of these forests on slightly acidic soils.

Ecology: 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.

Syntaxonomic note: 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

Protologue: Michalko & Džatko (1965, p. 73–76): *Polygonato* (*latifolii*)-*Carpinetum* ass. nova.

Name-giving taxa: *Carpinus betulus*, *Polygonatum hirtum*.

Nomenclatural type: Michalko & Džatko (1965): Table 17, rel. 16, lectotypus (designated by Willner & Grabherr 2007).

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

Description: 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*.

Ecology: These forests typically grow on luvisols covering loess sediments on plateaus 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 admixture 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 mesophytic (*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

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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 dominancí habru obecného (*Carpinus betulus*) a dubů (nejčastěji *Quercus petraea* agg. a *Q. robur*), ve které se v různé 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 pionýrských dob výzkumu vegetace střední Evropy. Postupně bylo popsáno několik desítek asociací a jejich syntaxonomie 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, Polska, Maďarska a Zakarpatské Ukrajiny, které byly ve většině případů získány z vegetačních databází Evropského vegetačního archivu. Na základě klasifikačních a ordinačních analýz bylo rozlišeno 13 asociací, 9 ze středoevropského 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 hrají také zeměpisná šířka, roční teplotní amplituda (tj. kontinentalita klimatu) a průměrná roční teplota. Na základě 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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