Received: 20 July 2022 | Revised: 9 January 2023 | Accepted: 16 January 2023

DOI: 10.1111/avsc.12712

Applied Vegetation Science

IAVS

VEGETATION SURVEY

Classification of European oak–hornbeam forests and related vegetation types

Pavel Novák[1] | **Wolfgang Willner**[2] | **Idoia Biurrun**[3] | **Hamid Gholizadeh**[4] | **Thilo Heinken**[5] | **Ute Jandt**[6,7] | **Jozef Kollár**[8] | **Maria Kozhevnikova**[9] | **Alireza Naqinezhad**[4] | **Viktor Onyshchenko**[10] | **Remigiusz Pielech**[11] | **Valerijus Rašomavičius**[12] | **Pavel Shirokikh**[13] | **Kiril Vassilev**[14] | **Thomas Wohlgemuth**[15] | **Martin Večeřa**[1] | **Milan Chytrý**[1]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic
[2]Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
[3]Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain
[4]Department of Plant Biology, Faculty of Basic Sciences, University of Mazandaran, Babolsar, Iran
[5]General Botany, University of Potsdam, Potsdam, Germany
[6]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany
[7]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[8]Institute of Landscape Ecology, Bratislava, Slovakia
[9]Kazan, Russia
[10]M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine
[11]Department of Forest Biodiversity, University of Agriculture in Krakow, Kraków, Poland
[12]Institute of Botany, Nature Research Centre, Vilnius, Lithuania
[13]Ufa, Russia
[14]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria
[15]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

Correspondence
Pavel Novák, Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic.
Email: pavenow@seznam.cz

Funding information
Eusko Jaurlaritza; Grantová agentura České republiky

Co-ordinating Editor: Jörg Ewald

Abstract

Aims: Oak–hornbeam forests and related vegetation types (phytosociological order *Carpinetalia betuli*) are widespread in temperate western Eurasia. However, their national classification systems are poorly compatible, and a broad-scale classification based on numerical analyses is lacking. Therefore, we aimed to establish a unified formalized classification system based on a large data set of vegetation plots covering the entire range of these forests.

Location: Europe, Anatolia, Caucasus and northern Iran.

Methods: We compiled a data set of 15,817 vegetation plots from the European Vegetation Archive and the Hyrcanian Forest Vegetation Database, using the formal definition of the EUNIS habitat type T1E *Carpinus* and *Quercus* mesic deciduous forest. We classified the data set using TWINSPAN. Biogeographically and ecologically similar plot clusters were merged into oak–hornbeam forest types, which were interpreted as alliances. We also developed expert systems for automatically classifying vegetation at the alliance level for both the EuroVegChecklist (EVC) system and the revised classification. In addition, we calculated ordinations to show the major gradients in the species composition of the data set.

Results: We present a revised classification system of the order *Carpinetalia betuli* with nine alliances, including basic descriptions of their species composition, distribution, ecology and syntaxonomy. The analyses largely supported the biogeographic concept of classification, analogous to EVC. Compared to EVC, we recognized an additional alliance *Physospermo verticillati-Quercion cerridis* (southern Italy) but found no support for the alliances *Astrantio-Carpinion*, *Erythronio-Carpinion* and *Scillo-Quercion*. The greatest difference in species composition was found between the southern and northern-northeastern *Carpinetalia* types. Expert systems for the revised classification system (~89% of plots classified) and the EVC system (~72%) are also included.

Conclusions: We provide the first comprehensive overview of alliances of the order *Carpinetalia betuli* across its whole distribution range. The associated expert systems allow consistent application of the classification of these forests in nature conservation, habitat monitoring, and biodiversity and ecological research.

KEYWORDS
biogeography, *Carpinetalia betuli*, Europe, expert system, habitat, oak–hornbeam forest, phytosociology, syntaxonomy, vegetation classification, vegetation-plot database

1 | INTRODUCTION

Understanding the large-scale variability of vegetation types is central to effective biodiversity conservation, habitat monitoring, management planning, and basic biodiversity and ecological research (Dengler et al., 2008; Chytrý et al., 2011, 2020; Rodwell et al., 2018). In addition, ongoing climate change is likely to alter the distribution of trees and ecosystem properties in forests (Dyderski et al., 2017). Therefore, it is essential for ecosystem conservation to survey current forest biodiversity across extensive regions and provide a baseline for further observations of variation in species composition or overall ecosystem changes (Chytrý et al., 2011). Synthetic pan-European studies that provide a formalized classification of vegetation diversity are so far available only for a limited subset of vegetation types dominated by woody species, both zonal (Willner et al., 2017; Bonari et al., 2020) and azonal communities (Douda et al., 2016; Kalníková et al., 2021).

Oak–hornbeam forests and related vegetation types (OHFs; phytosociological orders *Carpinetalia betuli* and *Lathyro-Carpinetalia caucasicae* in Mucina et al., 2016 and Gholizadeh et al., 2020) represent a significant part of European mesophilous broad-leaved forest diversity (Neuhäusl, 1977; Bohn et al., 2000–2003; Košir et al., 2013; Mucina et al., 2016; Novák, Willner et al., 2020). They are estimated to potentially cover one-tenth of Europe and are considered zonal vegetation, occurring mainly at low elevations throughout much of its temperate region (Bohn et al., 2000–2003; Figure 1). However, in the southeastern part of their range, they can also occur at high elevations (Gholizadeh et al., 2020; Novák, Zukal et al., 2020). They are most common in temperate regions with subcontinental climate, mainly between 45° N and 55° N. Optimal conditions for OHF development are characterized by a mean annual temperature of ~9°C and annual precipitation of ~500–700 mm. They develop across a wide range of soil conditions, generally mesotrophic to eutrophic (Neuhäusl, 1977; Bohn et al., 2000–2003). Because they occur primarily at lower elevations, they have been affected by human interventions for millennia. They have traditionally been exploited in a variety of ways, such as coppicing, pollarding, litter raking, tanbark management and livestock grazing, which altered their species composition and physiognomy (Bohn et al., 2000–2003; Vera, 2000; Bergmeier et al., 2010). Even the expansion of *Carpinus betulus* in prehistoric times is locally attributed to human-induced forest disturbances (e.g. Ralska-Jasiewicz, 1964; Küster, 1997). In certain regions (e.g. central-western Europe), some authors assume that the present-day OHFs are secondary vegetation that has replaced natural beech (*Fagus sylvatica*) forests under relatively intensive, long-term anthropogenic pressure. However, this issue remains controversial (Klötzli, 1968; Frey, 1995; Leuschner, 1997; Bohn et al., 2000–2003; Leuschner & Ellenberg, 2017). OHFs are of key importance for biodiversity conservation because they serve as refugia for nemoral biota, especially in largely deforested lowlands (Vera, 2000; Kolb & Diekmann, 2004; Stefańska-Krzaczek et al., 2016; Chytrý et al., 2019). They harbour numerous narrow-range (limited to <20% of the study region, typically <10%) and relict forest plant species (Coldea, 2015; Novák et al., 2019, Novák,

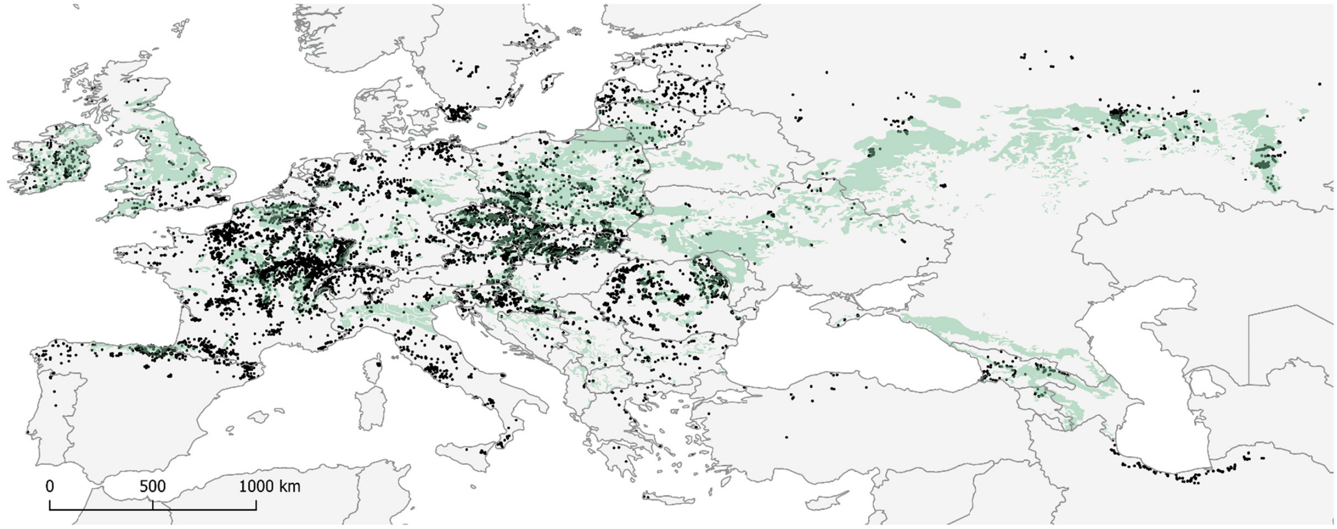


FIGURE 1 Distribution of vegetation plots in the data set (black dots; $n = 15{,}817$ plots) and areas where oak–hornbeam forests and related vegetation types are considered natural vegetation (green, according to mapping units F2, F3, F4, F6 (F164) and F7 in Bohn et al., 2000–2003; except for Anatolia and Iran, which are outside the geographic scope of this source).

Willner et al., 2020; Gholizadeh et al., 2020) as well as rare semi-shade species (Garbarino & Bergmeier, 2014; Miklín & Čížek, 2016; Kiedrzyński et al., 2017). They are classified as near threatened (NT) for EU28 and EU28+ countries, as their abiotic and biotic quality has decreased significantly over the last 50 years (Janssen et al., 2016). Declines of rare species of semi-shaded or oligotrophic sites as a consequence of habitat changes (e.g. canopy closure, eutrophication, nitrogen deposition) have been reported at numerous places across the continent (e.g. Vera, 2000; Hédl et al., 2010; Miklín & Čížek, 2016).

OHFs are named after their most frequent dominant trees, common hornbeam (*Carpinus betulus*) and oaks (mainly *Quercus petraea* aggr. and *Q. robur*). Many other trees are admixed, including broad-range species (e.g. *Acer campestre*, *Fagus sylvatica*, *Tilia cordata*) and regionally restricted species (e.g. *Ostrya carpinifolia*, *Quercus macranthera*, *Tilia tomentosa*). Mesophilous shade-tolerant forest (i.e. nemoral) species prevail in their understorey, although herb-layer diversity varies among biogeographic regions (Večeřa et al., 2019; Loidi et al., 2021). The moss layer usually has low cover or is absent (Neuhäusl, 1977; Bohn et al., 2000–2003). In the EuroVegChecklist (EVC; Mucina et al., 2016), most OHFs were included in the phytosociological order *Carpinetalia betuli*, while a separate order *Lathyro-Carpinetalia* (both included in the *Carpino-Fagetea* class) was recognized for the Caucasian stands. These two orders correspond well to EUNIS habitat type T1E *Carpinus* and *Quercus* mesic deciduous forest (Chytrý et al., 2020).

OHFs have attracted the interest of generations of vegetation scientists because of their broad distribution and great diversity. They have been studied phytosociologically since the 1920s and 1930s when the first associations of OHFs were introduced in the Braun-Blanquet system based on data from some areas of central, western and southeastern Europe (e.g. Issler, 1925; Domin, 1928; Horvat, 1938). *Carpinion betuli* was the first described alliance of OHFs (Issler, 1931), although it became broadly accepted only later. Subsequently, national overviews of OHF vegetation were published for most central and western European countries (e.g. Soó, 1940; Oberdorfer, 1957). The first synthesis of zonal OHF associations described in Europe was presented by Neuhäusl (1977). These forests have also been studied in eastern Europe (Schubert et al., 1979) and Iran (Djazirei, 1965). More recent studies have focused on relatively understudied regions in Euxinia, the Caucasus and northern Iran (Çoban & Willner, 2018; Novák et al., 2019, Novák, Zukal et al., 2020; Gholizadeh et al., 2020). Modern overviews of OHF diversity across large parts of Europe appeared in the last two decades (Onyshchenko, 2009; Košir et al., 2013; Novák, Willner et al., 2020). In EVC (Mucina et al., 2016), OHFs comprise 10 primarily biogeographically defined alliances. In fact, biogeography plays a crucial role in classifying a large proportion of European deciduous forests at the alliance level (Dierschke, 2004; Mucina et al., 2016; Willner et al., 2017). This seems to be mainly due to the distribution patterns of many narrow-range mesophilous forest species that reflect locations of forest refugia during Quaternary climatic fluctuations (Meusel & Jäger, 1989; Bohn et al., 2000–2003; Willner et al., 2009; Jiménez-Alfaro et al., 2018). This hypothesis has also been supported by phylogeographic (e.g. Bartha et al., 2015; Postolache et al., 2017; Volkova, Laczkó et al., 2020) and palaeoecological studies (e.g. Magyari, 2002; Muñoz Sobrino et al., 2018).

Pan-European vegetation overviews based on extensive vegetation-plot data sets have been prepared for several vegetation types at different levels of the syntaxonomic hierarchy. Most of them deal with the alliance level and provide a formalized classification that makes the classification repeatable (e.g. Douda et al., 2016; Willner et al., 2017; Bonari et al., 2020). Such an overview has been lacking for OHFs. To fill this gap, this study aims to: (1) identify the main gradients in species composition and the main types of OHFs in Europe and adjacent areas (i.e. Anatolia, Caucasus, northern Iran); (2) develop a revised syntaxonomic scheme at the alliance level including a formalized classification (i.e. a classification expert system); (3) describe the species composition, ecology and distribution of the recognized alliances; and (4) compare the revised classification with the current EVC classification system.

2 | METHODS

2.1 | Data set

Georeferenced vegetation-plot records were extracted from the European Vegetation Archive (Chytrý et al., 2016) and the Hyrcanian Forest Vegetation Database (Gholizadeh et al., 2019). The study area includes all of Europe, Anatolia, southern Caucasus (Armenia, Azerbaijan, Georgia) and Iran, i.e. the entire OHF distribution range (Bohn et al., 2000–2003; Mucina et al., 2016; Chytrý et al., 2020; Gholizadeh et al., 2020). The complete list of data sources can be found in Appendix S1. The taxonomy and nomenclature of vascular plants were standardized according to the Euro+Med PlantBase (2021), supplemented by The Plant List (2021) for species from Iran not included in the previous source. To reduce taxonomic bias (Jansen & Dengler, 2010), some species were grouped into ad hoc aggregates (see Appendix S2). Subspecies were generally merged at the species level except for species with only a single subspecies present in the data set. Non-vascular plants were omitted because they were recorded in a relatively small number of plots. Records of the same taxon in different vegetation layers were merged (Fischer, 2015). To select the vegetation plots of OHFs, we applied the formal definition of EUNIS habitat type T1E *Carpinus* and *Quercus* mesic deciduous forest (Chytrý et al., 2020) which are generally equal to the orders *Carpinetalia betuli* and *Lathyro-Carpinetalia* (Mucina et al., 2016). We additionally used the formal definition of Hyrcanian OHFs (Gholizadeh et al., 2020) because data from the Hyrcanian region were not considered when creating the EUNIS formal definition. Vegetation plots with a size smaller than 50 m^2 or larger than 1000 m^2 were deleted to avoid the negative effect of variation in plot sizes (Dengler et al., 2009). However, plots without size information were retained because ~95% of plots with known size were within the range of 50–1000 m^2, so we assumed a similar distribution for plots with unknown sizes. At this step, the preliminary data set contained 27,786 plots. To eliminate potential bias from the disproportionately high sampling density in some areas, the data set was stratified using a geographic grid of 6′ N × 10′ E (~11 × 12 km^2). Heterogeneity-constrained random resampling (Lengyel et al., 2011) was then conducted, resulting in up to 10–20 selected vegetation plots per grid cell, with the number of plots dependent on beta-diversity in the cell. Beta-diversity was expressed by the mean Bray–Curtis dissimilarity between pairs of plots (Wiser & De Cáceres, 2013). Percentage species covers were square-root transformed (Tichý et al., 2020), and the number of random selections was set to 100. This resampling resulted in a final data set of 15,817 vegetation plots (Figure 1, hereafter 'data set').

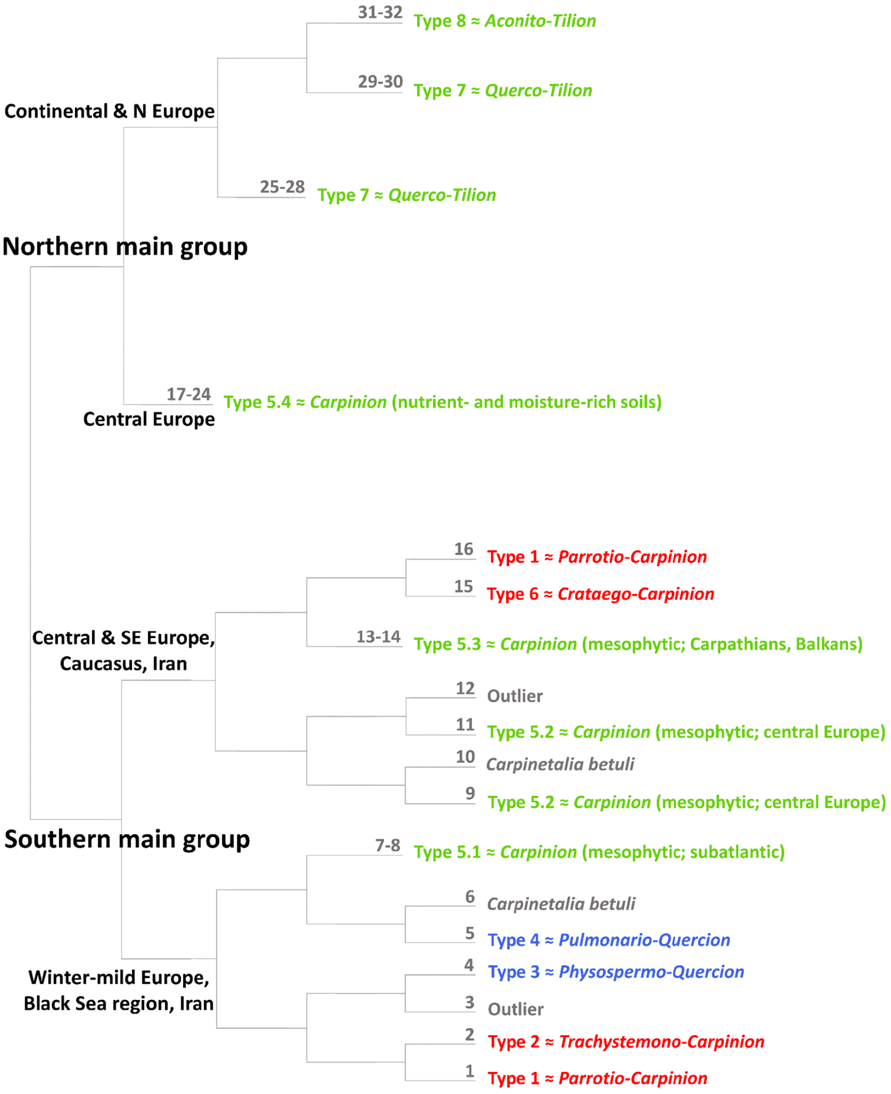
To provide an ecological context for the vegetation analyses, we used thematic maps of the following environmental variables. Topographic variables included elevation and terrain ruggedness calculated as a vector ruggedness measure (Sappington et al., 2007) based on the global digital elevation model with a spatial resolution of ~90 m (Jarvis et al., 2008). Climatic variables (~1 km spatial resolution) were extracted from the Chelsa Bioclim data set (BIO1–19, Karger et al., 2017, 2021). We delimited a circular buffer zone of 25 km^2 around each vegetation plot, calculated the mean value of each variable within the buffer and assigned it to the respective plot. We applied this buffer approach to smooth potentially extreme values of environmental variables (if a simple point extraction is applied) for plots with higher location uncertainty, for example, those georeferenced only into a relatively coarse spatial grid (Večeřa et al., 2019). Spatial data were managed in QGIS 3.8 (QGIS Development Team, 2021).

2.2 | Classification analyses

Data were stored and processed mainly in Juice 7.1 (Tichý, 2002). We performed unsupervised classification using the divisive hierarchical algorithm TWINSPAN, which translates the major gradients of species turnover into classification (Hill, 1979), using WinTWINS 2.3 (Hill & Šmilauer, 2005). This method produces well-interpretable classifications when species turnover in a data set is determined by distinct gradients and is therefore widely applied in similar broad-scale studies (e.g. Willner et al., 2017; Bonari et al., 2020; Kalníková et al., 2021). We defined pseudospecies using cut levels of 0%, 5% and 25% species covers. The minimal group size for the division was set at 10. Species with fewer than four occurrences in the data set (~38%) were excluded prior to the analysis to reduce noise. For further phytosociological interpretation, we selected the classification at the fifth level of division (i.e. 32 groups), where nearly all groups had their own diagnostic species. This classification was considered optimal according to the measure of classification crispness (Botta-Dukát et al., 2005).

In the final classification, we omitted the groups that did not belong to the target vegetation based on their species composition. We also merged some groups into OHF types based on their floristic, ecological and biogeographic similarities (Figure 2). These types were interpreted as alliances in the next step. We took a conservative approach by minimizing the changes to the circumscription of EVC alliances. Species-to-group fidelity was expressed by the phi (Φ) coefficient based on presence/absence data (Chytrý et al., 2002), with sizes of all plot groups virtually equalized (Tichý & Chytrý, 2006). In addition, Fisher's exact test ($p < 0.05$) was applied in combination with the Constancy Ratio criterion (CR ≥ 1.5; Dengler, 2003) to determine diagnostic species. Species that met both criteria with Φ as large as or larger than 0.2 were considered diagnostic, and those with Φ as large as or larger than 0.5 were considered highly diagnostic.

FIGURE 2 TWINSPAN classification dendrogram showing the correspondence between the TWINSPAN groups (numbers in grey) and the alliances of the revised classification system. Colours refer to groups of alliances (see Figure 3).



2.3 | Formalized classification (expert systems)

We have developed two alliance expert systems (for EVC classification and for our revised classification) that allow plots to be classified using unequivocal and reproducible assignment rules based on species composition. To develop the alliance formulas in the expert systems, we followed the principles of the Cocktail method (Bruelheide, 1995, 1997, 2000; Kočí et al., 2003). Two parallel expert systems provide the possibility to choose a classification strategy for the plots.

The 'EVC alliance expert system' provides formal definitions of all OHF alliances recognized in EVC (Mucina et al., 2016) as well as the alliance *Parrotio persicae-Carpinion betuli* from northern Iran (Gholizadeh et al., 2020). It served as a reference point for further work. The interpretations of the alliances and diagnostic species used in the sociological species groups (SSGs) were taken from authoritative literature sources, including the original descriptions of the alliances. Some of these SSGs were supplemented with additional species that tended to co-occur with species already present in the groups, statistically expressed by the phi coefficient (Chytrý et al., 2002) or based on our expert knowledge as the inclusion of some species with lower fidelity significantly increased classification success. The minimum number of species within an SSG required for the SSG to be considered present in a vegetation plot was determined empirically. In the alliance formulas, SSGs were combined using the logical operators AND, OR and NOT (Bruelheide, 1997).

The 'revised alliance expert system' is in line with our final classification. Here, diagnostic species of alliances (based on TWINSPAN groups organized into OHF types) served as the basis for the SSG definitions. In addition, the expert system followed analogous principles to the EVC alliance expert system. To strengthen the stability of the revised syntaxonomic system, the nomenclatural type relevé of each association that is the nomenclatural type of an alliance had to satisfy the formal definition of its alliance. The results of this supervised classification were examined by semi-supervised *K*-mean clustering (Tichý et al., 2014). Plots that remained unclassified by the formal definitions did not form a new biogeographically or ecologically characteristic unit that supported the concept of the revised classification system.

2.4 | Ordination

Detrended correspondence analysis (DCA) was performed to visualize the main gradients in species composition and the position of the recognized alliances along these gradients. In addition, we computed canonical correspondence analysis (CCA) using the Monte Carlo test with 999 unrestricted permutations to test the effects of each environmental variable on species composition. Species percentage covers were square-root transformed (Tichý et al., 2020). Analyses were performed in R 4.0.2 (R Core Team, 2020) using the libraries *vegan* 2.5-7 (Oksanen et al., 2020) and *goeveg* 0.4-2 (Goral & Schellenberg, 2018). The library *ggplot2* 3.3.5 (Wickham, 2016) was used to visualize the results.

2.5 | Syntaxonomy

The study focuses on the alliance level, the basic unit of EVC (Mucina et al., 2016) and a widely applied rank in pan-European phytosociological revisions (e.g. Peterka et al., 2017; Willner et al., 2017; Bonari et al., 2020). Willner (2020) proposed a revised definition of the phytosociological alliance concept that is respected in this study. We used EVC (Mucina et al., 2016) as the primary reference for the syntaxonomic nomenclature, which follows the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al., 2021). All accepted alliances and their type associations were checked for compliance with the ICPN.

3 | RESULTS

3.1 | TWINSPAN classification

We interpreted the TWINSPAN classification at the fifth level of division, that is, 32 groups of plots (see Appendix S3 for the synoptic table, Figure 2). The first TWINSPAN division separated two main biogeographically distinct groups of OHFs. The first main group ('southern', $n = 9384$ plots) encompassed mainly OHFs from the southern part of their range, including mountainous regions near the Black Sea, the Caucasus and northern Iran. This main group is internally more heterogeneous than the second group. The forests are rich in narrow-range species and often have a species-rich tree layer. The second main group ('northern', $n = 6433$) was associated with the northern and northeastern parts of the OHF distribution range. The proportion of narrow-range species was markedly lower, as was the number of species in the tree layer. Of the environmental variables analysed, the first division was well reflected in mean annual temperature (10.4°C for the southern main group vs 8.2°C for the northern main group), annual precipitation (833 mm vs 713 mm), and mean temperature of the coldest quarter (1.7°C vs −1.7°C). The best diagnostic species for the main groups reflected these biogeographic and environmental differences (*Crataegus monogyna*, *Dioscorea communis*, *Quercus petraea* aggr. vs *Acer platanoides*, *Aegopodium podagraria*, *Tilia cordata*). In the DCA (Figure 4, Appendix S4), latitude and associated climatic variables were strongly correlated with the main gradient in species composition expressed by the first ordination axis. This was also confirmed by the CCA tests (Table 1).

The second hierarchical level of TWINSPAN classification followed mainly biogeographic patterns within both main groups. In the southern main group, plots from northern Iran, the Black Sea region, Italy and southwestern and western Europe were separated from plots from the southern half of central Europe, southeastern Europe and the Caucasus (and several plots from Iran). In the northern main group, the division separated central European lowlands from the north temperate-continental region between the Baltic Sea and the Urals. The following two division steps reflected both biogeography and ecology, especially soil moisture and nutrient availability.

The southern main group included most of the EVC alliances, whereas the northern main group was more homogeneous and included only three alliances (*Aconito lycoctoni-Tilion cordatae*, *Carpinion betuli*, *Querco roboris-Tilion cordatae*). Two of the 32 TWINSPAN groups did not belong to the class *Carpino-Fagetea* at all — Group 3 (Mediterranean chestnut forests with evergreen woody plants) and Group 12 (subacidophilous oak forests of the Polish lowlands resembling the association *Potentillo albae-Quercetum*; Matuszkiewicz, 2001). Two other groups (6, 10) had OHF species composition but could not be classified into alliances due to their biogeographic and ecological heterogeneity. Therefore, we interpreted them at the order level only. The remaining 28 groups were merged into eight OHF types, which were subsequently interpreted as alliances (Figure 2). One broadly defined alliance (*Carpinion betuli*) with considerable internal heterogeneity was subdivided into four suballiances based on the TWINSPAN result. Furthermore, one alliance (*Paeonio dauricae-Quercion petraeae*) was accepted in the revised classification system due to its particular geographic location (Crimea) and a high number of diagnostic species, although it was not reproduced by the unsupervised classification, presumably due to the very limited number of vegetation plots available.

3.2 | Expert systems

The EVC alliance expert system (Appendix S6) served as a baseline for further work. We formally defined all 10 alliances listed in EVC (Mucina et al., 2016) and added the alliance *Parrotio-Carpinion* from the Hyrcanian region (Gholizadeh et al., 2020), which is outside the geographic scope of EVC. The expert system assigned ~72% of the plots in the data set (see Appendix S7 for the synoptic table). The revised alliance expert system (Appendix S8) was based on the interpretation of the TWINSPAN results. It classified ~89% of the plots (i.e. 14,038) in the data set into nine formally defined alliances. ~10% of the plots remained unclassified, while ~1% of the plots met formal definitions of two alliances. The results of this classification are documented by the geographic distribution of alliances (Figure 3), DCA (Figure 4), boxplots of environmental variables (Figure 5), and synoptic tables (Table 2, Appendix S9). Details of the syntaxonomy

TABLE 1 Effects of explanatory variables on species composition of oak–hornbeam forests.

Variable	PTV	*F*	*p*
Latitude	0.60	95.4	0.001
Mean annual air temperature (BIO1)	0.59	94.5	0.001
Mean daily mean air temperatures of the driest quarter (BIO9)	0.59	94.4	0.001
Mean daily mean air temperatures of the coldest quarter (BIO11)	0.59	94.3	0.001
Longitude	0.57	90.7	0.001
Mean daily minimum air temperature of the coldest month (BIO6)	0.56	88.9	0.001
Temperature seasonality (BIO4)	0.50	80.0	0.001
Annual range of air temperature (BIO7)	0.45	70.8	0.001
Mean daily mean air temperatures of the warmest quarter (BIO10)	0.44	70.0	0.001
Mean monthly precipitation amount of the coldest quarter (BIO19)	0.42	67.3	0.001
Mean daily maximum air temperature of the warmest month (BIO5)	0.37	59.1	0.001
Terrain ruggedness	0.37	58.2	0.001
Annual precipitation amount (BIO12)	0.33	52.3	0.001
Isothermality (BIO3)	0.31	50.0	0.001
Mean daily mean air temperatures of the wettest quarter (BIO8)	0.30	47.9	0.001
Mean monthly precipitation amount of the driest quarter (BIO17)	0.30	47.1	0.001
Precipitation amount of the driest month (BIO14)	0.29	45.8	0.001
Precipitation amount of the wettest month (BIO13)	0.29	45.6	0.001
Mean monthly precipitation amount of the wettest quarter (BIO16)	0.28	44.7	0.001
Elevation	0.27	43.1	0.001
Precipitation seasonality (BIO15)	0.27	42.7	0.001
Mean diurnal air temperature range (BIO2)	0.23	36.5	0.001
Mean monthly precipitation amount of the warmest quarter (BIO18)	0.21	33.5	0.001

Note: Geographic, topographic and climatic (Chelsa Bioclim data set BIO1–19) variables were included. Variables are sorted by decreasing percentage of the total variance (PTV). *F*-statistic and *p*-value are based on separate canonical correspondence analyses (CCA) for each variable using the Monte Carlo test. Correlations among variables are listed in Appendix S5.

of the alliances can be found in Appendices 1 and S8. The alliances were classified into three geographic groups considering the results of the classification and ordination analyses. A comparison of the results of the two expert systems is presented in Appendix S10.

3.3 | Revised classification system

3.3.1 | Subcontinental group of alliances

This group combines three alliances of central, southeastern and eastern Europe characterized by the occurrence of subcontinental species, including *Aegopodium podagraria*, *Asarum europaeum*, *Maianthemum bifolium* and *Pulmonaria officinalis* aggr. The proportion of narrow-range forest species is usually low.

Alliance 1.1. Carpinion betuli

The alliance comprises mainly the OHFs of central and southeastern Europe but also extends to western Europe, southernmost Scandinavia, the Baltic states and Ukraine. The tree layer is mostly co-dominated by *Carpinus betulus*, *Quercus petraea* aggr., *Q. robur* and, especially in the eastern part, *Tilia cordata*. The shrub layer contains deciduous species with broad distribution, locally enriched by subatlantic species (e.g. *Lonicera periclymenum*). The herb layer often combines subatlantic and subcontinental species. Narrow-range forest species (e.g. *Hacquetia epipactis*, *Hepatica transsilvanica*) are characteristic of the Carpathian and Illyric-Balkan stands. In accordance with the unsupervised classification, we have recognized four suballiances within this widespread alliance that exhibits considerable internal diversity (Appendices 1 and S11). The suballiances have their own biogeographic and, to some extent, also ecological meaning. Three suballiances were more zonal (subatlantic Europe; central Europe; Carpathians, Pannonian Basin, Balkans), while the fourth was confined to moist and nutrient-rich soils distributed almost throughout the range of the alliance.

Alliance 1.2. Querco roboris-Tilion cordatae

This alliance groups north temperate and subcontinental OHFs of northeastern and eastern Europe. Its range encompasses southern Scandinavia and the Eastern European Plain, i.e. the Baltic states, the northern half of Ukraine and the nemoral part of European Russia except for the Urals. The tree layer is dominated mainly by *Acer platanoides*, *Quercus robur* and *Tilia cordata*, which are accompanied, among others, by boreal species (e.g. *Picea abies*, *Sorbus aucuparia*).

The tree species with eastern distribution limits in eastern central Europe (e.g. *Carpinus betulus*, *Quercus petraea* aggr.) are absent. The species composition of their shrub and herb layers combines subcontinental (e.g. *Euonymus verrucosus*, *Galium intermedium*) and north temperate species (e.g. *Maianthemum bifolium*, *Rubus saxatilis*) with large distribution ranges. Of the common nemoral species, *Hepatica nobilis*, *Lathyrus vernus* and *Stellaria holostea* are among the most frequent.

Alliance 1.3. Aconito lycoctoni-Tilion cordatae

This alliance unites mesophilous deciduous forests of the Southern Urals, a northeastern outpost of OHF vegetation. The canopy is dominated by broadly distributed noble hardwood trees (e.g. *Acer platanoides*, *Tilia cordata*) and *Quercus robur*. Tall forbs of Euro-Siberian distribution (e.g. *Crepis sibirica*, *Parasenecio hastatus*) coupled with continental forest species (e.g. *Carex pediformis*, *Stellaria bungeana*) are diagnostic. Many otherwise frequent species of European OHFs (e.g. *Carpinus betulus*, *Hepatica nobilis*, *Mercurialis perennis*) are absent.

3.3.2 | Southwestern group of alliances

This group combines two alliances from western and southwestern Europe and Italy. Due to mild winters, they contain Mediterranean and Mediterranean-oceanic woody species (*Castanea sativa*, *Rubus ulmifolius*, *Ruscus aculeatus*). The representation of narrow-range forest species is intermediate.

Alliance 2.1. Pulmonario longifoliae-Quercion roboris

The alliance comprises Atlantic OHFs of western and southwestern Europe. *Quercus petraea* aggr., *Q. robur*, *Fraxinus excelsior* and *Castanea sativa* often form the tree layer, while *Carpinus betulus* is generally absent. In the understorey, Atlantic and subatlantic species (e.g. *Arum maculatum*, *Lonicera periclymenum*, *Potentilla sterilis*), including narrow-range forest species (e.g. *Pulmonaria longifolia*, *Saxifraga hirsuta*), are diagnostic of the alliance. Evergreen mesophilous woody plants (e.g. *Hedera helix* aggr., *Ilex aquifolium*) that prefer relatively warm and humid winters are also characteristic.

Alliance 2.2. Physospermo verticillati-Quercion cerridis

This alliance includes OHFs from central and southern Italy. *Carpinus betulus* and *Castanea sativa* are the most frequent dominant species in the canopy, often accompanied by *Quercus cerris* as the most common oak species. Narrow-range forest species (e.g. *Anemone apennina*, *Cyclamen repandum*, *Teucrium siculum*) and common forest mesophytes (e.g. *Melica uniflora*, *Primula acaulis*) are well represented in the herb layer. These forests are influenced by the Mediterranean climate, as evident by the occurrence of geophytes (e.g. *Arum italicum*, *Cyclamen hederifolium*) and evergreen woody plants (e.g. *Quercus ilex*) typical of Mediterranean forests.

3.3.3 | Southeastern group of alliances

This group combines alliances from the Black Sea region, the Caucasus and northern Iran. Its alliances share several southeastern species (e.g. *Fagus orientalis*, *Lathyrus aureus*, *Lathyrus laxiflorus*) coupled with frequent submediterranean forest species (e.g. *Dioscorea communis*, *Viola alba*). The number of relict and narrow-range species is high, including dominant species in all vegetation layers (e.g. *Hedera colchica*, *Quercus castaneifolia*, *Rhododendron ponticum*).

Alliance 3.1. Paeonio dauricae-Quercion petraeae

The forests of this alliance are restricted to Crimea. They form a narrow elevation belt (450–800 m) on the carbonate bedrock of the Crimean Mountains. The tree layer is co-dominated by *Quercus petraea* and mesophilous species (mainly *Carpinus betulus* and *Fraxinus excelsior*). Common submediterranean species (e.g. *Dioscorea communis*, *Physospermum cornubiense*) accompanied by Eastern Mediterranean-Pontic species, often geophytes (e.g. *Arum elongatum*, *Ornithogalum ponticum*), and Euxino-Caucasian species (e.g. *Galanthus plicatus*, *Paeonia daurica*) constitute its diagnostic species combination.

Alliance 3.2. Crataego rhipidophyllae-Carpinion caucasicae

OHFs of the Caucasus, except for the precipitation-rich western part. They inhabit a broad elevation range, locally reaching the timberline in the continental part of the mountain range. *Carpinus betulus* (syn. *Carpinus caucasica*) usually dominates the tree layer, with a frequent admixture of *Fagus orientalis* and *Quercus petraea* (subsp. *iberica*). The narrow-range tree *Quercus macranthera* occurs at high elevations. Caucasian endemics of the forest herb layer (e.g. *Brunnera macrophylla*, *Polygonatum glaberrimum*) are often combined with submediterranean species. Compared to the following alliance, Euxinian species are mostly absent, although there is a large group of shared species (e.g. *Campanula alliariifolia*, *Helleborus orientalis*).

Alliance 3.3. Trachystemono orientalis-Carpinion betuli

These Euxinian OHFs are distributed along the mostly precipitation-rich southern coast of the Black Sea between Bulgaria and the western Caucasus. The canopy consists mainly of *Carpinus betulus*, *Castanea sativa* and *Quercus petraea*. Narrow-range species, both evergreen (e.g. *Ilex colchica*, *Rhododendron ponticum*) and deciduous (*Hypericum xylosteifolium*, *Vaccinium arctostaphylos*), often form the shrub layer. Herbs and lianas include species of the Euxinian floristic element (e.g. *Hedera colchica*, *Trachystemon orientalis*). Submediterranean forest species (e.g. *Potentilla micrantha*, *Viola alba*) are common.

Alliance 3.4. Parrotio persicae-Carpinion betuli

This alliance of the Hyrcanian region includes the southeasternmost type of OHFs. These forests inhabit a narrow strip on the mountain slopes above the Caspian Sea coast. Hyrcanian and Hyrcanian-Caucasian species (*Acer velutinum*, *Parrotia persica*, *Quercus castaneifolia*) co-dominate the tree layer together with

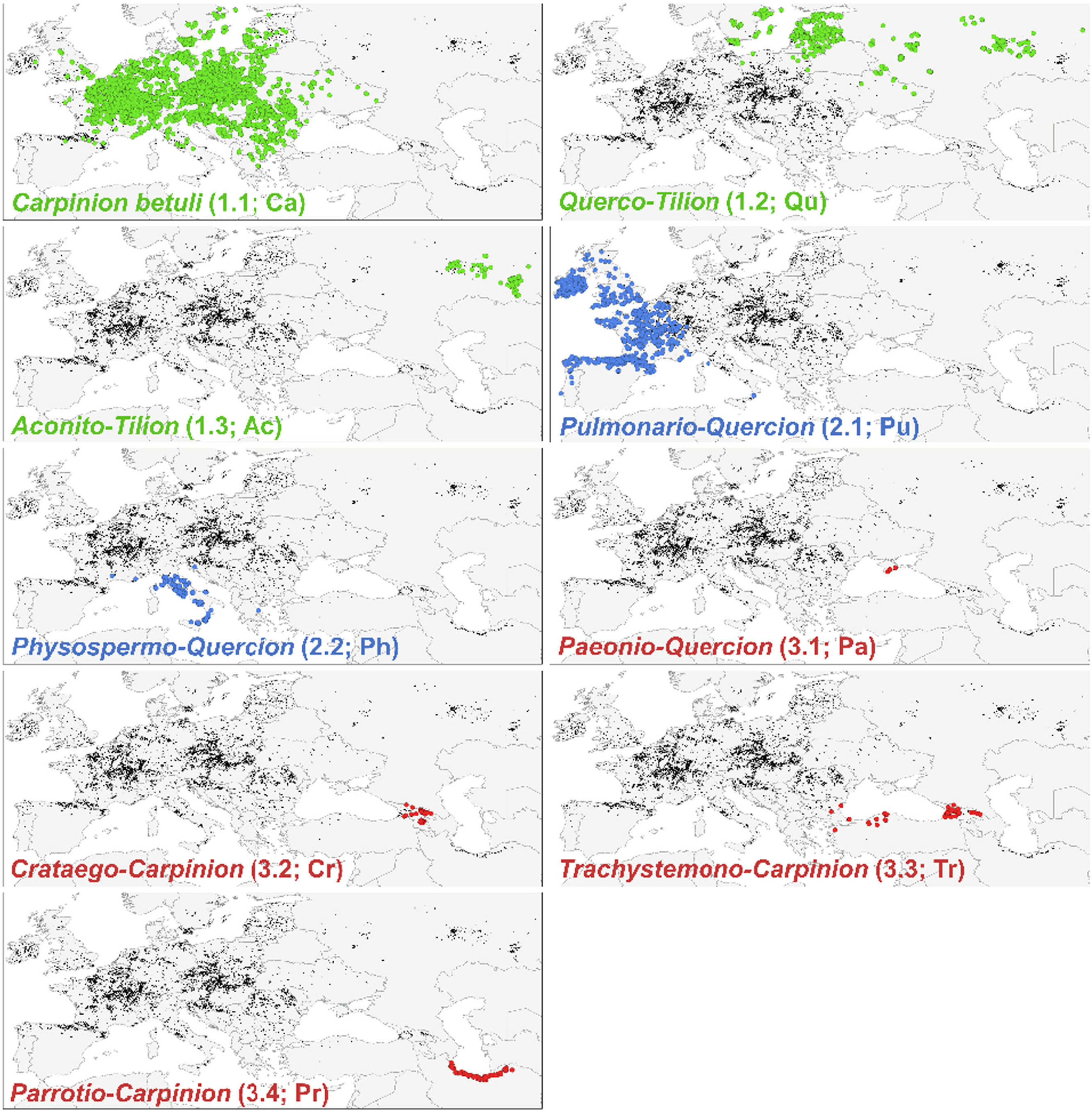


FIGURE 3 Distribution of the vegetation plots of the alliances following the revised classification system. Colours refer to groups of alliances (green, subcontinental; blue, southwestern; red, southeastern). The small black dots correspond to all the plots in the data set. See Appendix S6 for the distribution of alliances following the EVC classification system.

common species (e.g. *Carpinus betulus*). Compared to the Euxinian OHFs, the occurrence of evergreen shrubs is lower, although this group includes some endemics (e.g. *Danae racemosa*, *Ilex spinigera*). Narrow-range species are regularly found in the herb layer (e.g. *Primula heterochroma*, *Viola caspia*), along with common forest species. Due to their outpost character, some species characteristic of a considerable fraction of European OHFs are absent (e.g. *Castanea sativa*, *Cornus mas*, *Quercus petraea*).

4 | DISCUSSION

4.1 | Comparison of the revised and the EVC classification systems

This study presents two parallel systems for a broad-scale classification of OHFs, which provide complementary perspectives on this widespread type of mesophilous forests.

The EVC classification system for OHFs was proposed without data analysis across the entire range of OHFs and is based mainly on biogeographic patterns. Expert-based classifications such as the EVC are poorly reproducible because they lack consistent assignment rules (De Cáceres et al., 2015) and do not allow automatic classification of vegetation plots (Chytrý et al., 2020). Therefore, the major advantage of our revised classification system is that it is based on the results and interpretations of the analysis of a comprehensive data set of vegetation plots from the complete distribution range of OHFs. In some regions (e.g. the Balkans, Caucasus and eastern Europe), data were sparse, which may have biased our results toward patterns found in areas densely covered with vegetation plots. However, we reduced this bias by using a stratified resampling of the data set. In addition, we accepted the geographically and floristically distinct OHFs of Crimea as a separate alliance, even though they were not represented by the TWINSPAN classification.

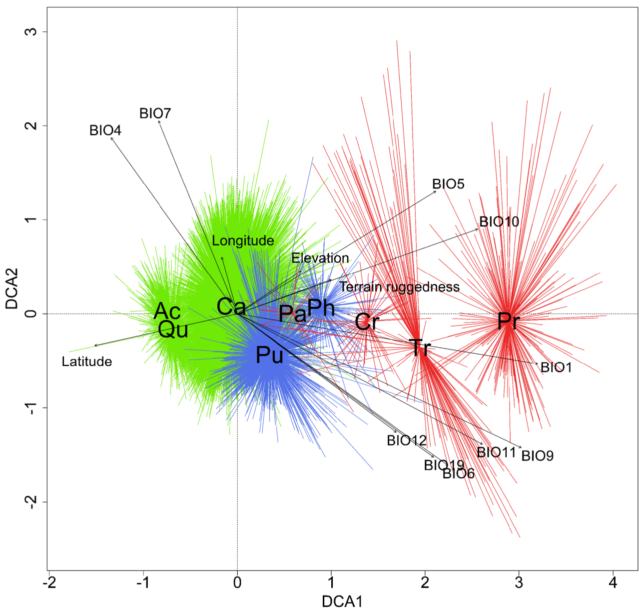


FIGURE 4 Detrended correspondence analysis (DCA) of all classified vegetation plots ($n = 14{,}038$) based on the revised alliance expert system. Plots are assigned to alliances, and centroids of each alliance are shown. The line tips indicate the position of the plots. The vectors represent geographic and topographic variables, as well as the 10 most important climatic variables identified in the canonical correspondence analysis (CCA) tests (Table 1). The first and second ordination axes explained 0.63% (length 5.82 SD units) and 0.69% (5.28) of the variance in species composition, respectively. The third ordination axis (not shown) explained 0.53% of the variance (4.79). See Figure 3 for explanations of colours and alliance acronyms.

The revised classification system brings several significant changes to the EVC system. The range of the Atlantic alliance *Pulmonario longifoliae-Quercion roboris* has been expanded, as our TWINSPAN analysis clearly showed that OHFs from the British Isles and western France belong to this alliance. This is supported by the co-occurrence of western European narrow-range forest species (e.g. *Hyacinthoides non-scripta*, *Pulmonaria longifolia*) and Mediterranean-oceanic species (e.g. *Conopodium majus*, *Hypericum androsaemum*, *Rubia peregrina*; Noirfalise, 1968; Webb, 1983).

The stands from central and southern Italy are placed in a separate alliance *Physospermo verticillati-Quercion cerridis*. This assignment was supported by many narrow-range species (e.g. *Anemone apennina*, *Cyclamen repandum*, *Pulmonaria vallarsae*, *Teucrium siculum*) occurring in local OHF types (Biondi et al., 2008). An analogous solution was proposed by Košir et al. (2013), but with *Erythronio-Carpinion* instead of *Carpinion betuli* in northern Italy. In EVC (Mucina et al., 2016), *Physospermo verticillati-Quercion cerridis* was considered a syntaxonomic synonym of *Crataego laevigatae-Quercion cerridis*, which is an alliance of thermophilous oak forests of the *Quercetea pubescentis* class. However, the typification of *Physospermo-Quercion* supports its assignment to *Carpino-Fagetea*.

The most striking difference between the EVC and the revised classification system is the absence of three alliances that were not

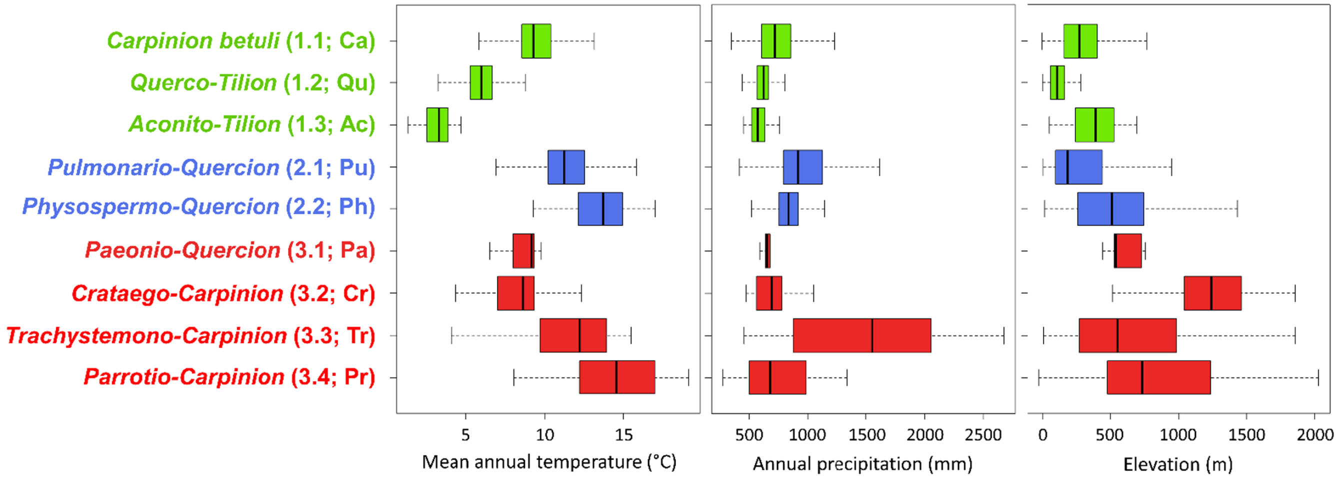


FIGURE 5 Boxplots of mean annual temperature, annual precipitation and elevation for the alliances of the revised classification system. Boxes indicate the interquartile range, bold lines represent the median, and whiskers indicate the range of values without outliers. See Figure 3 for explanations of colours. For boxplots of all environmental variables, see Appendix S8.

TABLE 2 Shortened synoptic table of the alliances of the revised classification system.

Alliance number	**1.1**	**1.2**	**1.3**	**2.1**	**2.2**	**3.1**	**3.2**	**3.3**	**3.4**
Alliance acronym	Ca	Qu	Ac	Pu	Ph	Pa	Cr	Tr	Pr
Number of plots	10,612	925	196	1630	248	19	62	127	219
***Carpinion betuli* (1.1, Ca)**									
Luzula luzuloides	14	.	.	.	.	.	.	.	.
Acer pseudoplatanus	21	.	.	8	2	.	2	1	.
Galium sylvaticum	11	.	.	1	.	.	.	.	.
***Querco-Tilion* (1.2, Qu)**									
Picea abies	10	**43**	.	1	.	.	.	.	.
Equisetum pratense	1	**30**	2	.	.	.	.	.	.
Lonicera xylosteum	17	56	21	13	4	.	.	.	.
Prunus padus	6	28	.	1	.	.	.	.	.
Hepatica nobilis	14	38	.	6	10	.	.	.	.
Convallaria majalis	27	44	8	1	.	5	6	.	.
Ranunculus auricomus coll.	15	33	6	2	.	.	.	.	.
Ribes alpinum	3	19	.	3	.	.	.	.	.
Actaea spicata	5	28	14	1	1	.	6	.	1
Geum rivale	1	16	3	1	.	.	.	.	.
Dryopteris carthusiana	9	25	4	5	.	.	5	1	.
Crepis paludosa	1	12	.	1	.	.	.	.	.
***Aconito-Tilion* (1.3, Ac)**									
Aconitum lycoctonum subsp. *septentrionale*	.	4	**73**	.	.	.	.	.	.
Crepis sibirica	.	1	**47**	.	.	.	.	.	.
Lactuca macrophylla	.	1	**47**	.	.	.	2	.	.
Viola collina	1	3	**48**	.	.	.	.	.	.
Drymochloa sylvatica	2	2	**45**	1	.	.	.	.	.
Conioselinum tataricum	.	1	**35**	.	.	.	.	.	.
Milium effusum	26	31	**76**	9	5	16	.	.	.
Bupleurum longifolium	1	1	**31**	.	.	.	.	.	.
Pulmonaria mollis	1	.	30	.	.	.	2	.	.
Ulmus glabra	9	38	79	7	2	5	29	10	23
Geranium sylvaticum	1	18	41	1	.	.	3	.	.
Lathyrus gmelinii	.	.	24	.	.	.	.	.	.
Parasenecio hastatus	.	1	23	.	.	.	.	.	.
Heracleum sphondylium	8	2	45	7	.	16	.	.	.
Brachypodium pinnatum	3	6	36	5	1	.	2	3	.
Calamagrostis arundinacea	6	17	40	1	.	.	5	1	.
Campanula latifolia	1	10	32	1	1	.	3	.	.
Valeriana wolgensis	.	1	20	.	.	.	.	.	.
Urtica dioica	18	26	63	9	2	11	16	9	8
Galium boreale	1	5	24	.	.	.	.	.	.
Rubus idaeus	9	20	39	1	.	.	.	2	.
Stachys sylvatica	15	19	47	5	7	5	5	.	1
Stellaria bungeana	.	1	17	.	.	.	.	.	.
Carex pediformis	1	7	22	.	.	.	.	.	.
Veratrum lobelianum	1	.	17	.	.	.	2	.	.

(Continues)

TABLE 2 (Continued)

Digitalis grandiflora	3	.	17	.	.	.	.	.	.
Lathyrus pisiformis	.	1	14	.	.	.	.	.	.
Glechoma hederacea	16	17	42	12	.	.	3	6	.
Omphalodes scorpioides	1	.	12	.	.	.	.	.	.
Lilium martagon	7	1	23	3	3	.	.	2	
Impatiens noli-tangere	6	9	25	.	.	.	6	1	.
***Pulmonario-Quercion* (2.1, Qu)**									
Lonicera periclymenum	10	.	.	**54**	.	.	.	.	.
Hyacinthoides non-scripta	1	.	.	**29**	.	.	.	.	.
Ilex aquifolium	4	.	.	38	19	.	.	.	.
Potentilla sterilis	6	.	.	27	.	.	.	.	.
Pulmonaria longifolia	1	.	.	14	.	.	.	.	.
Conopodium majus	1	.	.	12	.	.	.	.	.
Rosa arvensis	13	.	.	26	11	.	.	1	.
Teucrium scorodonia	4	.	.	22	11	.	.	.	.
***Physospermo-Quercion* (2.2, Ph)**									
Fraxinus ornus	4	.	.	.	**44**	.	.	.	.
Lathyrus venetus	2	.	.	.	**42**	.	.	1	.
Anemone apennina	1	.	.	.	**34**	.	.	.	.
Festuca heterophylla	10	.	.	8	**46**	.	.	2	.
Quercus cerris	5	.	.	.	32	.	.	.	.
Quercus ilex	1	.	.	5	30	.	.	.	.
Cyclamen repandum	.	.	.	.	22	.	.	.	.
Cyclamen hederifolium	1	.	.	.	22	.	.	.	.
Rubus ulmifolius	1	.	.	16	35	.	.	.	.
Ranunculus lanuginosus	6	4	.	.	31	.	.	.	.
Daphne laureola	1	.	.	8	28	.	.	.	.
Melica uniflora	21	.	.	23	52	.	15	3	5
Acer opalus aggr.	1	.	.	1	19	.	.	.	.
Asparagus acutifolius	.	.	.	.	18	.	.	.	.
Lonicera etrusca	.	.	.	.	18	.	.	.	.
Ostrya carpinifolia	1	.	.	.	18	.	.	.	.
Pulmonaria vallarsae	1	.	.	.	17	.	.	.	.
Teucrium siculum	.	.	.	.	16	.	.	.	.
Sorbus domestica	1	.	.	1	16	.	.	.	.
Digitalis lutea	1	.	.	1	15	.	.	.	.
Quercus pubescens	1	.	.	5	19	.	.	1	.
Clematis vitalba	7	.	.	12	29	.	.	6	.
Symphytum tuberosum	11	.	.	7	25	.	.	1	.
Allium pendulinum	.	.	.	.	11	.	.	.	.
Aristolochia lutea	1	.	.	.	11	.	.	.	.
Scutellaria columnae	1	.	.	.	11	.	.	.	.
Lilium bulbiferum	1	.	.	.	11	.	.	.	.
Poa trivialis	3	1	.	6	22	.	3	2	1
Geranium versicolor	.	.	.	.	10	.	.	.	.
***Paeonio-Quercion* (3.1, Pa)**									
Arum elongatum	.	.	.	.	.	**79**	.	.	.

TABLE 2 (Continued)

Ranunculus villosus subsp. *constantinopolitanus*	1	.	.	.	.	**63**	.	2	.
Scilla bifolia	4	.	.	1	2	**68**	2	.	1
Cardamine quinquefolia	1	1	.	.	.	**79**	27	.	.
Physospermum cornubiense	1	.	.	1	4	**79**	23	2	.
Allium cyrilli	.	.	.	.	.	**53**	.	.	.
Galanthus plicatus	.	.	.	.	.	**47**	.	.	.
Crocus tauricus	.	.	.	.	.	**47**	.	.	.
Smyrnium perfoliatum	1	.	.	.	1	**47**	.	.	.
Paeonia daurica	.	.	.	.	.	**42**	.	.	.
Polygonatum odoratum	8	9	9	2	2	**58**	.	.	.
Cornus mas	9	.	.	3	24	**68**	16	6	.
Scilla siberica	1	1	.	.	.	**32**	.	.	.
Mercurialis perennis	21	42	8	21	13	**84**	.	.	17
Corydalis cava	3	2	.	1	2	32	2	.	.
Polygonatum hirtum	4	.	.	.	.	26	.	1	.
Ornithogalum ponticum	.	.	.	.	.	21	.	.	.
Lathyrus aureus	1	.	.	.	.	32	3	9	.
Lathyrus rotundifolius	.	.	1	.	.	21	.	1	.
Quercus petraea aggr.	45	.	.	22	16	79	42	48	.
Crataegus rhipidophylla	6	3	.	5	.	32	5	.	.
Primula acaulis	5	.	.	15	24	58	16	31	.
Fraxinus excelsior	38	47	.	52	2	84	40	9	21
Platanthera chlorantha	1	2	.	1	1	21	5	.	.
Vincetoxicum scandens	1	.	.	.	.	26	.	2	17
Lathyrus niger	12	2	.	2	2	26	.	2	.
Chaerophyllum nodosum	1	.	.	.	.	11	.	.	.
Anthriscus sylvestris	4	9	14	2	4	32	5	2	3
Viola suavis	1	.	.	1	5	16	.	1	.
***Crataego-Carpinion* (3.2, Cr)**									
Fagus orientalis	.	.	.	.	.	.	**61**	26	24
Campanula alliariifolia	.	.	.	.	.	.	31	10	.
Lathyrus roseus	.	.	.	.	.	.	24	3	1
Polygonatum glaberrimum	.	.	.	.	.	.	18	.	.
Carex depressa	1	.	.	1	.	.	18	2	.
Quercus macranthera	.	.	.	.	.	.	16	.	1
Lapsana communis	8	3	.	4	3	26	50	21	10
Primula veris	6	9	29	7	.	5	44	.	.
Veronica multifida	.	.	.	.	.	.	15	.	.
Achillea biserrata	.	.	.	.	.	.	15	.	.
Pimpinella tripartita	.	.	.	.	.	.	18	4	.
Lonicera caucasica	.	.	.	.	.	.	23	12	.
Securigera varia	1	1	.	.	.	.	19	6	1
Pimpinella anthriscoides	.	.	.	.	.	.	11	.	.
Corydalis angustifolia	.	.	.	.	.	.	11	.	.
Valeriana tiliifolia	.	.	.	.	.	.	13	2	.
Veronica peduncularis	.	.	.	.	.	.	16	6	.

(Continues)

TABLE 2 (Continued)

Salvia glutinosa	7	.	.	.	9	11	39	23	13
Sedum stoloniferum	.	.	.	.	.	.	21	11	5
***Trachystemono-Carpinion* (3.3, Tr)**									
Hedera colchica	.	.	.	.	.	.	.	**44**	.
Smilax excelsa	.	.	.	.	.	.	.	**57**	21
Trachystemon orientalis	.	.	.	.	.	.	.	27	.
Rhododendron ponticum	.	.	.	.	.	.	.	26	.
Prunus laurocerasus	.	.	.	1	.	.	.	25	1
Hypericum xylosteifolium	.	.	.	.	.	.	.	23	.
Ruscus colchicus	.	.	.	.	.	.	.	22	.
Daphne pontica	.	.	.	.	.	.	.	21	1
Vinca major	.	.	.	.	1	.	.	20	.
Ilex colchica	.	.	.	.	.	.	.	18	.
Potentilla micrantha	2	.	.	1	11	11	15	35	.
Potentilla indica	1	.	.	.	.	.	.	13	.
Vaccinium arctostaphylos	.	.	.	.	.	.	.	13	1
Calystegia silvatica	1	.	.	.	.	.	10	24	12
***Parrotio-Carpinion* (3.4, Pr)**									
Acer velutinum	.	.	.	.	.	.	.	.	**69**
Viola caspia	.	.	.	.	.	.	.	.	**65**
Ruscus hyrcanus	.	.	.	.	.	.	.	.	**51**
Quercus castaneifolia	.	.	.	.	.	.	.	.	**50**
Crataegus microphylla	.	.	.	.	.	.	.	3	**47**
Primula heterochroma	.	.	.	.	.	.	.	.	**44**
Parrotia persica	.	.	.	.	.	.	.	.	**44**
Hedera pastuchovii	.	.	.	.	.	.	3	3	**39**
Diospyros lotus	.	.	.	.	.	.	2	18	**48**
Prunus cerasifera	1	.	.	1	.	.	.	.	**32**
Polystichum aculeatum	1	.	.	1	.	.	3	4	35
Clinopodium umbrosum	.	.	.	.	.	.	16	16	46
Ilex spinigera	.	.	.	.	.	.	.	.	23
Scutellaria tournefortii	.	.	.	.	.	.	.	.	20
Danae racemosa	.	.	.	.	.	.	.	.	20
Solanum kieseritzkii	.	.	.	.	.	.	.	.	19
Hypericum androsaemum	1	.	.	17	2	.	.	9	37
Microstegium vimineum	.	.	.	.	.	.	.	.	17
Crataegus germanica	1	.	.	4	8	.	26	13	44
Alnus subcordata	.	.	.	.	.	.	.	.	16
Viscum album	1	.	.	1	.	.	.	1	17
Zelkova carpinifolia	.	.	.	.	.	.	.	2	17
Asplenium adiantum-nigrum	1	.	.	6	22	.	5	23	43
Carex strigosa	1	.	.	1	.	.	.	.	15
Campanula odontosepala	.	.	.	.	.	.	.	.	14
Cyclamen coum	.	.	.	.	.	.	3	5	21
Viola sintenisii	.	.	.	.	.	.	.	.	12
Vicia crocea	.	.	.	.	.	.	.	.	11
Gleditsia caspia	.	.	.	.	.	.	.	.	11

TABLE 2 (Continued)

Polystichum woronowii	.	.	.	.	.	.	.	11	19
Carpesium cernuum	1	.	.	.	.	.	.	2	13
Species diagnostic for two alliances									
Maianthemum bifolium	19	29	4	.	.	.	.	.	.
Aegopodium podagraria	23	75	**97**	.	2	.	.	4	.
Acer platanoides	18	73	**94**	1	.	.	15	2	.
Sorbus aucuparia	18	60	47	5	1	11	5	4	.
Tilia cordata	28	73	**93**	4	5	11	5	2	.
Asarum europaeum	23	51	**79**	.	2	.	.	.	.
Rubus saxatilis	2	34	43	1	.	.	.	.	.
Paris quadrifolia	13	33	28	3	.	.	.	.	.
Viola mirabilis	7	46	**79**	1	.	5	.	.	.
Pulmonaria officinalis aggr.	31	48	**72**	1	2	5	.	.	.
Betula pendula	9	30	38	3	.	.	.	.	.
Stellaria holostea	34	55	**86**	26	.	.	6	5	7
Lathyrus vernus	23	47	**93**	.	2	.	3	6	.
Euonymus verrucosus	8	32	17	.	.	37	2	1	.
Galium odoratum	30	21	76	6	8	32	58	6	28
Lamium album	1	1	45	.	.	.	19	2	46
Crataegus monogyna	34	.	.	61	51	.	5	9	.
Hedera helix aggr.	35	1	.	81	74	47	3	28	.
Ruscus aculeatus	2	.	.	32	50	.	.	13	.
Rubia peregrina	1	.	.	20	29	.	.	.	.
Castanea sativa	5	.	.	23	62	.	2	44	.
Luzula forsteri	2	.	.	9	41	.	2	30	13
Lonicera caprifolium	2	.	.	.	25	.	23	5	.
Campanula rapunculoides	9	3	1	1	.	.	**63**	38	.
Acer cappadocicum	.	.	.	.	.	.	40	19	61
Oplismenus hirtellus subsp. *undulatifolius*	.	.	.	.	.	.	2	43	44
Pteris cretica	.	.	.	.	.	.	.	26	40
Asplenium scolopendrium	1	.	.	9	3	.	5	30	46
Other frequent species (frequency > 30%) sorted by decreasing frequency									
Carpinus betulus	77	.	.	31	45	95	98	74	87
Corylus avellana	49	73	11	70	36	32	32	35	1
Viola reichenbachiana aggr.	55	17	.	46	45	5	34	19	.
Quercus robur	47	63	61	57	10	.	.	2	.
Poa nemoralis	41	29	23	17	4	32	53	13	53
Acer campestre	40	4	.	35	48	84	58	26	5
Anemone nemorosa	40	28	.	24	11	.	.	.	.
Polygonatum multiflorum	37	31	49	17	11	21	34	6	.
Geum urbanum	33	36	61	26	17	42	24	8	29
Brachypodium sylvaticum	31	13	41	39	48	16	42	34	49
Fagus sylvatica	37	.	.	27	10	21	.	.	.

Note: Percentage frequencies (constancies) are shown. Diagnostic species ($\Phi \geq 0.2$) are shaded, and highly diagnostic ($\Phi \geq 0.5$) are shaded and bolded. Only species with $\Phi \geq 0.3$ or species with a frequency greater than 30% in the entire data set are shown. See Figure 3 for alliance acronyms and grouping. The full version of this table is available in Appendix S9.

supported by the unsupervised classification: *Erythronio-Carpinion*, *Scillo-Quercion roboris* and *Astrantio-Carpinion caucasicae*. In the case of the Illyrian alliance *Erythronio-Carpinion*, the Illyrian endemics indicated in the literature as key diagnostic species for the *Erythronio-Carpinion* (Wallnöfer et al., 1993; Marinček, 1994; Košir et al., 2013) are present in only a small fraction of the vegetation plots from this region, while the common OHF species strongly predominate, and the majority of species are shared with central European stands. Although the Illyrian region is one of the hotspots of narrow-range forest species in Europe (Meusel & Jäger, 1989; Willner et al., 2009; Jiménez-Alfaro et al., 2018; Večeřa et al., 2019), they are probably much more frequent in beech forests than in OHFs (Horvat et al., 1974; Trinajstić, 1992; Brus, 2010). Moreover, dry and moist OHFs in southeastern Europe were separated at the first division level. Thus, the moisture gradient is stronger than the biogeographic gradient in the OHFs of central and southeastern Europe. Consequently, *Erythronio-Carpinion* is included in the alliance *Carpinion betuli* in the revised system. The Ukrainian thermophilous lowland alliance *Scillo-Quercion* proved to be poorly supported by diagnostic species in all *Carpinetalia betuli* forests. In the national context in which it was described (Onyshchenko, 2009), recognition of two major lowland OHF types (alliances *Querco-Tilion* and *Scillo-Quercion*) may be a useful way to represent variability in these forests. However, the reported diagnostic species of *Scillo-Quercion*, at least the frequent ones, are common across central and eastern European stands (e.g. *Stellaria holostea*, *Tilia cordata*, *Torilis japonica*) or have a wider distribution in eastern Europe, the Caucasus and Anatolia (*Scilla siberica*, *Tulipa biebersteiniana*). In addition, few vegetation plots are available for *Scillo-Quercion*. Therefore, it was merged in the revised system with the alliance *Querco-Tilion*, which now includes all eastern European OHFs except those from the western half of Ukraine, Crimea and the Southern Urals. An analogous approach was used in the recent Ukrainian vegetation synopsis (Dubyna et al., 2019). The Caucasian OHFs are the only exception to the geographic classification of OHFs in EVC, as the azonal mountain alliance *Astrantio-Carpinion caucasicae* is distinguished within the distribution of the zonal alliance *Crataego rhipidophyllae-Carpinion caucasicae*. These two alliances are recognized along the elevation gradient, as the Caucasus is presumably the only area where OHFs locally occupy almost the entire elevation range of forest vegetation (Nakhutsrishvili, 2013; Novák, Zukal et al., 2020). We did not include the azonal alliance in the revised classification system for now because the TWINSPAN classification did not support its recognition even in a fine partition (64 groups) of the data set and its species composition is close to the zonal alliance. However, azonal Caucasian OHFs have been sampled at very few sites in a limited area (Passarge, 1981; Novák, Zukal et al., 2020), although they are probably distributed over a large territory for which vegetation-plot data are not available (Bohn et al., 2000–2003; Nakhutsrishvili, 2013; Fayvush & Aleksanyan, 2016).

We adopted the name *Trachystemono orientalis-Carpinion betuli* for the Euxinian OHFs instead of the EVC name *Castaneo sativae-Carpinion orientalis*, following a proposal by Çoban and Willner (2018). The latter name was typified by the association *Erico arboreae-Carpinetum orientalis* (Quézel et al., 1992), which includes dry forests dominated by *Carpinus orientalis* and the Mediterranean evergreen shrub *Erica arborea*, and thus certainly does not fall within the class *Carpino-Fagetea*. See Çoban and Willner (2018) for further explanation.

4.2 | Phytosociological framework of the revised system

The EVC concept of a separate Caucasian order *Lathyro-Carpinetalia caucasicae* Passarge 1981 alongside the order *Carpinetalia betuli* comprising the rest of the European OHFs (Mucina et al., 2016) did not find support in our classification analyses. Therefore, it should be united with the order *Carpinetalia betuli*, as previously proposed and explained in regional studies (Çoban & Willner, 2018; Novák, Zukal et al., 2020). Consequently, the revised classification system includes a single order, *Carpinetalia betuli*, for all OHFs.

Traditionally, OHF alliances were based almost entirely on biogeography, i.e. each European region had its own alliance. The EVC (Mucina et al., 2016) represents such an approach based strictly on biogeographic boundaries. The ecological approach to classification at the level of alliances, used for beech forests by several authors (e.g. Tüxen, 1955; Willner, 2002; Willner et al., 2017), was applied only sporadically in the case of OHFs and the alliances described were close to the concept of associations or small association groups (e.g. Passarge & Hofmann, 1968 for northeastern Germany; Julve, 1993 for France). Differences between ecologically delineated alliances reflected soil parameters, such as reaction (Julve, 1993) or nutrient availability combined with moisture (Passarge & Hofmann, 1968). The latter were also recognized as the most important environmental gradient for central European OHFs (Novák, Willner et al., 2020). However, biogeography and ecology should not be applied arbitrarily in vegetation classification but should be balanced according to the result of numerical analyses (Knollová & Chytrý, 2004). The presented revised classification system is mainly based on biogeography and follows the result of numerical analyses. Analogous patterns with a predominant biogeographic clustering at higher levels of the classification hierarchy have been found in some other types of forest vegetation in broad-scale studies (e.g. Douda et al., 2016; Bonari et al., 2020).

4.3 | Biogeographic patterns

The geographic boundaries between alliances are either with a broad transition zone or relatively sharp. Broad transition zones are characteristic of lowland areas with gradually changing species composition. They occur in flat landscapes north of the Alps, the Carpathians, the Black Sea region and the Caucasus. Towards the east, they are characterized by a gradual increase in climatic continentality and the associated increase in the number of continental and boreal species and the simultaneous decline of oceanic and submediterranean species. Narrow-range species are very rare there, while widespread species prevail (Meusel, 1969; Schubert et al., 1979; Willner et al., 2009; Leuschner & Ellenberg, 2017). This region was heavily modified by Quaternary climatic fluctuations; large areas were glaciated or directly influenced by the proximity of glaciers (Böse et al., 2012). Because of the flat topography without significant migration barriers, species could migrate relatively easily and recolonize large areas during the Holocene. The species diversity of mesophilous forests in this area generally decreases toward the east and north (Bohn et al., 2000–2003). Moreover, glacial refugia of forest species were probably very limited here (Hewitt, 1999; Palmé & Vendramin, 2002; Leroy & Arpe, 2007). The Southern Urals are an exception, as the OHFs there host numerous forest species that do not occur in the rest of the data set. However, most of these species are distributed in Siberia (Bohn et al., 2000–2003; Willner et al., 2016). On the other hand, the region has been recognized as a putative glacial refugium of broad-leaved forest vegetation (Volkova, Burlakov et al., 2020). Therefore, the isolated distribution of some forest species can be attributed to the specific history of local forests.

Towards the south, the picture is different. Southern OHFs are generally rich in narrow-range species due to the refugial nature of the region (Meusel, 1969; Meusel & Jäger, 1989; Willner et al., 2009; Jiménez-Alfaro et al., 2018). Climatic, topographic and biogeographic gradients are very complex. Consequently, geographic boundaries between alliances are generally sharp. This is supported by the relatively strong geographic isolation of some OHF types (e.g. northern Iran and southern Italy).

4.4 | Expert systems

The presented expert systems must be combined with the EUNIS expert system (EUNIS-ESy; Chytrý et al., 2020) in a two-step procedure. First, an analysed plot must be assigned to the EUNIS habitat T1E *Carpinus* and *Quercus* mesic deciduous forest, and only then can it be processed with the OHF alliance expert systems. Direct use of the alliance expert systems could result in misclassifications.

Although the revised alliance expert system was able to classify a relatively high percentage of vegetation plots (~89%), there were some areas where many plots remained unclassified. These were in: (1) transition zones between alliances, especially in the northern half of the study area (e.g. France, European Russia outside the Urals); (2) marginal areas with OHFs impoverished of typical species (e.g. the British Isles and the Mediterranean); and (3) areas with OHFs strongly altered by human activities and extremely low forest cover (e.g. the lowlands in northwestern Europe). Similarity indices (Tichý, 2005) based on previously classified vegetation plots can be used for an approximate assignment of unclassified plots.

4.5 | *Carpinion betuli* concept and its suballiances

Taking into account the unsupervised classification results in the revised classification, we adhere to the concept of the broadly conceived alliance *Carpinion betuli*, which was also accepted as such in EVC (there without Illyrian and Balkan stands). Its absolute character species group (sensu Willner, 2020) includes *Galium sylvaticum*, which occurs in some of its associations with high constancy and in some others with low to moderate constancy (Horvat et al., 1974; Novák, Willner et al., 2020). Splitting this unit into alliances corresponding to the accepted suballiances (Appendices 1 and S11) would establish alliances without absolute character species, an essential alliance condition according to Willner (2020). Unsupervised classification indicated that this broad alliance could be divided into four ecological-biogeographic units, which we present as suballiances. Suballiances within this alliance have already been proposed by several authors. Oberdorfer (1957) provisionally recognized two suballiances for the southern half of Germany and one for the eastern part of central Europe. Neuhäuslová-Novotná (1964) applied Oberdorfer's concept on classification of OHFs of Czechoslovakia. Michalko et al. (1986) presented three invalidly published suballiances for Slovak OHFs reflecting the biogeographic division of the national territory (Pannonian Basin, Carpathians, intermontane Carpathian basins). However, all these subdivisions were largely limited by national boundaries. In the last decades, additional suballiances were described under the alliance *Erythronio-Carpinion*, which is included in *Carpinion betuli* in our revised classification system. They were generally based on biogeographic criteria (Marinček, 1994; Košir et al., 2013). Nevertheless, TWINSPAN provided no support for their concept.

4.6 | Habitat conservation

Defining plant community types for conservation planning, management and monitoring is among the most important goals of vegetation classification (Janssen et al., 2016; Rodwell et al., 2018). OHFs remain at risk of local disappearance due to habitat changes such as large-scale logging and subsequent conversion to non-native tree plantations, eutrophication, an overabundance of wild ungulates or invasions by alien species, for example, vascular plants or various tree pathogens. Recreational pressure poses an additional threat in densely populated areas (Bohn et al., 2000–2003; Rodwell & Dring, 2001; Brasier & Jung, 2006; Chytrý et al., 2019). Traditionally, OHFs were managed as coppices or coppices-with-standards. These methods have been largely abandoned since the 18th century, especially in western and central Europe. Such managed stands often had the character of open-canopy woodlands (Vera, 2000; Konvička et al., 2004; Müllerová et al., 2014) containing species requiring semi-shade conditions, many of which are now rare and vanishing (Bohn et al., 2000–2003; Vodka et al., 2009; Sebek et al., 2015). Because contemporary OHFs can be mostly considered a legacy of the interplay between natural processes and traditional management, this habitat appears to be sensitive to both extremes of human intervention, that is, either too strong or no disturbances (Bohn et al., 2000–2003). Owing to their at least former connection to human management and their occurrence at lower elevations, they are poorly represented in primary forests throughout Europe, with Polish Białowieża and Niepołomice forests serving as rare examples (Sabatini et al., 2018). A strict conservation regime of non-intervention for the entire protected areas where OHFs are among target communities often leads to canopy closure and deletion of the scarce semi-shade species (Vera, 2000; Müllerová et al., 2014). Therefore, the optimal conservation strategy for this habitat would likely be a balanced regime with various active management measures combined with forest sections with avoided management (Sebek et al., 2015).

AUTHOR CONTRIBUTIONS

Pavel Novák and Milan Chytrý conceived the idea of the study; Pavel Novák compiled the data set, conducted the analyses and prepared the classification under the supervision of Milan Chytrý; Pavel Novák led the writing; Martin Večeřa processed spatial data using GIS; Wolfgang Willner assisted with the classification analyses and phytosociological nomenclature; all authors participated in the interpretation of the results, discussions and syntaxonomic outlines.

ACKNOWLEDGEMENTS

We thank EVA database custodians for providing data, namely Emiliano Agrillo, Erwin Bergmeier, Maxim Bobrovsky, Gianmaria Bonari, Jörg Brunet, Juan Antonio Campos, Laura Casella, János Csiky, Andraž Čarni, Mirjana Ćuk, Renata Ćušterevska, Els De Bie, Iris de Ronde, Michele De Sanctis, Panayotis Dimopoulos, Jörg Ewald, Federico Fernández-González, Úna FitzPatrick, Xavier Font, Jean-Claude Gégout, Stephan Hennekens, Adrian Indreica, Florian Jansen, Anni Jašková, Zygmunt Kącki, Jonathan Lenoir, Tatiana Lysenko, Vadim Prokhorov, John Rodwell, Eszter Ruprecht, Solvita Rūsiņa, Joop Schaminée, Joachim Schrautzer, Anna Szabó, Urban Šilc, Željko Škvorc, Emin Uğurlu and Roberto Venanzoni. We also thank Ilona Knollová and Lubomír Tichý for assistance with data processing, Yakiv P. Didukh for pictures of Ukrainian vegetation and Gianmaria Bonari and two anonymous reviewers for helpful comments on a previous version of the manuscript.

FUNDING INFORMATION

Pavel Novák, Martin Večeřa and Milan Chytrý were funded by the Czech Science Foundation (project no. 19-28491X). Idoia Biurrun was funded by the Basque Government (project no. IT1487-22).

DATA AVAILABILITY STATEMENT

Vegetation-plot data used in this study are available in the European Vegetation Archive (EVA; Chytrý et al., 2016) and the Hyrcanian Forest Vegetation Database (GIVD ID: AS-IR-006; Gholizadeh et al., 2019). They can be obtained upon request from the database administrators with reference to EVA project no. 5.

ORCID

Pavel Novák https://orcid.org/0000-0002-3758-5757
Wolfgang Willner https://orcid.org/0000-0003-1591-8386
Idoia Biurrun https://orcid.org/0000-0002-1454-0433
Hamid Gholizadeh https://orcid.org/0000-0002-3694-368X
Thilo Heinken https://orcid.org/0000-0002-1681-5971
Ute Jandt https://orcid.org/0000-0002-3177-3669
Jozef Kollár https://orcid.org/0000-0002-0069-4220
Maria Kozhevnikova https://orcid.org/0000-0002-8771-5679
Alireza Naqinezhad https://orcid.org/0000-0002-4602-6279
Viktor Onyshchenko https://orcid.org/0000-0001-9079-7241
Remigiusz Pielech https://orcid.org/0000-0001-8879-3305
Valerijus Rašomavičius https://orcid.org/0000-0003-1314-4356
Pavel Shirokikh https://orcid.org/0000-0003-1864-4878
Kiril Vassilev https://orcid.org/0000-0003-4376-5575
Thomas Wohlgemuth https://orcid.org/0000-0002-4623-0894
Martin Večeřa https://orcid.org/0000-0001-8507-791X
Milan Chytrý https://orcid.org/0000-0002-8122-3075

REFERENCES

Aita, L., Corbetta, F. & Orsino, F. (1977) Osservazioni fitosociologiche sulla vegetazione forestale dell'Appennino Lucano centrosettentrionale. I. Le cerrete [Phytosociological observations on forest vegetation of the northcentral Lucanian Appenines. I. *Quercus cerris* forests]. *Archivio Botanico e Biogeografico Italiano*, 53, 97–128.

Böse, M., Lüthgens, C., Lee, J.R. & Rose, J. (2012) Quaternary glaciations of northern Europe. *Quaternary Science Reviews*, 44, 1–25. Available from: https://doi.org/10.1016/j.quascirev.2012.04.017

Bœuf, R. (2010) Le référentiel des types forestiers d'Alsace: apports phytosociologiques. *Revue Forestière Française*, 62, 331–364.

Bartha, L., Sramkó, G., Volkova, P.A., Surina, B., Ivanov, A.L. & Banciu, H.L. (2015) Patterns of plastid DNA differentiation in *Erythronium* (Liliaceae) are consistent with allopatric lineage divergence in Europe across longitude and latitude. *Plant Systematics and Evolution*, 301, 1747–1758. Available from: https://doi.org/10.1007/s00606-014-1190-x

Bergmeier, E., Petermann, J. & Schröder, E. (2010) Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodiversity and Conservation*, 19, 2995–3014. Available from: https://doi.org/10.1007/s10531-010-9872-3

Biondi, E., Allegrezza, M., Casavecchia, S., Galdenzi, D., Gigante, D. & Pesaresi, S. (2013) Validation of some syntaxa of Italian vegetation. *Plant Biosystems*, 147, 186–207. Available from: https://doi.org/10.1080/11263504.2013.773948

Biondi, E., Casavecchia, S. & Biscotti, N. (2008) Forest biodiversity of the Gargano peninsula and a critical revision of the syntaxonomy of the mesophilous woods of southern Italy. *Fitosociologia*, 45, 93–127.

Bonari, G., Fernández-González, F., Çoban, S., Monteiro-Henriques, T., Bergmeier, E., Didukh, Y.P. et al. (2020) Classification of the Mediterranean lowland to submontane pine forest vegetation. *Applied Vegetation Science*, 24, e12544. Available from: https://doi.org/10.1111/avsc.12544

Botta-Dukát, Z., Chytrý, M., Hájková, P. & Havlová, M. (2005) Vegetation of lowland wet meadows along a climatic continentality gradient in Central Europe. *Preslia*, 77, 89–111.

Brasier, C.M. & Jung, T. (2006) Recent developments in *Phytophthora* diseases of trees and natural ecosystems in Europe. In: Goheen, E.M. & Frankel, S.J. (Eds.) *Proceedings of the Third International IUFRO Working Party (S07. 02.09). Progress in research on Phytophthora* *diseases of forest trees. General technical report PSW-GTR-221*. Albany: Department of Agriculture, Forest Service, Pacific Southwest Research Station, pp. 101–115.

Bruelheide, H. (1995) Die Grünlandgesellschaften des Harzes und ihre Standortsbedingungen. Mit einem Beitrag zum Gliederungsprinzip auf der Basis von statistisch ermittelten Artengruppen. *Dissertationes Botanicae*, 244, 1–338.

Bruelheide, H. (1997) Using formal logic to classify vegetation. *Folia Geobotanica et Phytotaxonomica*, 32, 41–46.

Bruelheide, H. (2000) A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science*, 11, 167–178. Available from: https://doi.org/10.2307/3236796

Brus, R. (2010) Growing evidence for the existence of glacial refugia of European beech (*Fagus sylvatica* L.) in the South-Eastern Alps and north-western Dinaric Alps. *Periodicum Biologorum*, 112, 239–246.

Bulokhov, A.D. & Semenishchenkov, Y.A. (2015) Typification and correction of forest vegetation syntaxa of the southern Nechernozemye of Russia and adjacent regions (in Russian). *Bulletin of Bryansk Department of RBS*, 1(5), 26–32.

Chytrý, M., Hájek, M., Kočí, M., Pešout, P., Roleček, J., Sádlo, J. et al. (2019) Red List of Habitats of the Czech Republic. *Ecological Indicators*, 106, 105446. Available from: https://doi.org/10.1016/j.ecolind.2019.105446

Chytrý, M., Hennekens, S.M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F. et al. (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Applied Vegetation Science*, 19, 173–180. Available from: https://doi.org/10.1111/avsc.12191

Chytrý, M., Schaminée, J.H.J. & Schwabe, A. (2011) Vegetation survey: a new focus for Applied Vegetation Science. *Applied Vegetation Science*, 14, 435–439. Available from: https://doi.org/10.1111/j.1654-109X.2011.01154.x

Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A.M., Rodwell, J.S. et al. (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*, 23, 648–675. Available from: https://doi.org/10.1111/avsc.12519

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, J. (2002) Determination of diagnostic species with statistical fidelity. *Journal of Vegetation Science*, 13, 79–90. Available from: https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Çoban, S. & Willner, W. (2018) Numerical classification of the forest vegetation in the Western Euxine region of Turkey. *Phytocoenologia*, 49, 71–106. Available from: https://doi.org/10.1127/phyto/2018/0274

Coldea, G. (2015) Classe Carpino-Fagetea. In: Coldea, G., Indreica, A. & Oprea, A. (Eds.) *Les associations végétales de Roumanie, Tome 3, Les associations forestiéres et arbustives*. Cluj-Napoca: Presa Universitară Clujeană and Accent, pp. 70–125.

De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J. et al. (2015) A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science*, 18, 543–560. Available from: https://doi.org/10.1111/avsc.12179

Dengler, J. (2003) *Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation*. Nümbrecht: Martina Galunder Verlag.

Dengler, J., Chytrý, M. & Ewald, J. (2008) Phytosociology. In: Jørgensen, S.E. & Fath, B.D. (Eds.) *Encyclopedia of ecology*. Oxford: Elsevier, pp. 2767–2779.

Dengler, J., Löbel, S. & Dolnik, C. (2009) Species constancy depends on plot size–a problem for vegetation classification and how it can be solved. *Journal of Vegetation Science*, 20, 754–766. Available from: https://doi.org/10.1111/j.1654-1103.2009.01073.x

Didukh, Y.P. (1996) Nemoral forests of the mountain Crimea of the class *Querco-Fagetea* Br.-Bl. et Vlieg. 1937. *Ukrainian Phytosociological Journal, Series A*, 1, 34–51.

Dierschke, H. (2004) Sommergrüne Laubwälder (*Querco-Fagetea* s. lat.) in Europa - Einführung und Übersicht. *Tuexenia*, 24, 13–18.

Djazirei, M.H. (1965) Contribution à l'étude des forêts primaires de la Caspienne. *Bulletin de l'Institut Agronomique et des Stations de Recherches de Gembloux*, 33, 36–71.

Domin, K. (1928) The plant associations of the valley of Radotín. *Preslia*, 7, 3–68.

Douda, J., Boublík, K., Slezák, M., Biurrun, I., Nociar, J., Havrdová, A. et al. (2016) Vegetation classification and biogeography of European floodplain forests and alder carrs. *Applied Vegetation Science*, 19, 147–163. Available from: https://doi.org/10.1111/avsc.12201

Dubyna, D.V., Dziuba, T., Iemelianova, S., Bagrikova, N., Borysova, O., Borsukevych, L. et al. (2019) *Prodrome of the vegetation of Ukraine*. Kyiv: Naukova dumka.

Dyderski, M.K., Paź, S., Frelich, L.E. & Jagodziński, A.M. (2017) How much does climate change threaten European forest tree species distributions. *Global Change Biology*, 24, 1150–1163. Available from: https://doi.org/10.1111/gcb.13925

Euro+Med. (2021) *Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity*. Available from: http://ww2.bgbm.org/EuroPlusMed/query.asp [Accessed 1st March 2021]

Fayvush, G.M. & Aleksanyan, A.S. (2016) *Habitats of Armenia (in Russian)*. Yerevan: National Academy of Sciences of the Republic of Armenia – Institute of Botany.

Fischer, H.S. (2015) On the combination of species cover values from different vegetation layers. *Applied Vegetation Science*, 18, 169–170. Available from: https://doi.org/10.1111/avsc.12130

Frey, H.U. (1995) Waldgesellschaften und Waldstandorte im St. Galler Berggebiet. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel*, 126, 1–280.

Garbarino, M. & Bergmeier, E. (2014) Plant and vegetation diversity in European wood-pastures. In: Hartel, T. & Plieniger, T. (Eds.) *European wood-pastures in transition*. London: Earthscan Routledge, pp. 131–149.

Gholizadeh, H., Naqinezhad, A. & Chytrý, M. (2019) Hyrcanian forest vegetation database. *Phytocoenologia*, 49, 209–210. Available from: https://doi.org/10.1127/phyto/2018/0315

Gholizadeh, H., Naqinezhad, A. & Chytrý, M. (2020) Classification of the Hyrcanian forest vegetation, northern Iran. *Applied Vegetation Science*, 23, 107–126. Available from: https://doi.org/10.1111/avsc.12469

Goral, F. & Schellenberg, J. (2018) *goeveg* 0.4-2. Available from: https://cran.r-project.org/web/packages/goeveg/index.html [Accessed 1st December 2020].

Hédl, R., Kopecký, M. & Komárek, J. (2010) Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Diversity and Distributions*, 16, 267–276. Available from: https://doi.org/10.1111/j.1472-4642.2010.00637.x

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, 68, 87–112. Available from: https://doi.org/10.1006/bijl.1999.0332

Hill, M.O. (1979) *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Ithaca: Cornell University.

Hill, M.O. & Šmilauer, P. (2005) *TWINSPAN for Windows version 2.3*. Huntingdon: Centre for Ecology and Hydrology and České Budějovice: University of South Bohemia.

Horvat, I. (1938) Biljnosociološka istraživanja šuma u Hrvatskoj [Phytosociological research of forests in Croatia]. *Glasnik za Šumske Pokuse*, 6, 127–279.

Horvat, I., Glavač, V. & Ellenberg, H. (1974) *Vegetation Südosteuropas*. Stuttgart: Gustav Fischer.

Issler, E. (1924) Les associations végétales des Vosges méridionales et de la Plaine Rhénane avoisinante. Première Partie. Les forêts. A.

Les associations d'arbres feuillus. Diagnoses phytosociologiques. *Bulletin de la Société d'Histoire Naturelle de Colmar N. S.*, 17, 1–66.

Issler, E. (1925) Die Hartwälder der oberelsässischen Rheinebene. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens*, 81, 274–286.

Issler, E. (1926) Les associations végétales des Vosges méridionales et de la Plaine Rhénane avoisinante. Première Partie. Les forêts. Fin. Documents sociologiques. *Bulletin de la Société d'Histoire Naturelle de Colmar N. S.*, 19, 1–109.

Issler, E. (1931) Les associations silvatique haut-rhinoises. *Bulletin de la Société Botanique de France*, 73, 62–142.

Jansen, F. & Dengler, J. (2010) Plant names in vegetation databases – a neglected source of bias. *Journal of Vegetation Science*, 21, 1179–1186. Available from: https://doi.org/10.1111/j.1654-1103.2010.01209.x

Janssen, J.A.M., Rodwell, J.S., Criado, M.G., Gubbay, S., Haynes, T., Nieto, A. et al. (2016) *European Red List of Habitats: Part 2. Terrestrial and freshwater habitats*. Luxembourg: Publications Office of the European Union.

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) *Hole-filled SRTM for the globe version 4*. Available from the CGIAR-CSI SRTM 90m Database: http://srtm.csi.cgiar.org/ [Accessed 26th January 2021].

Jiménez-Alfaro, B., Girardello, M., Chytrý, M., Svenning, J.C., Willner, W., Gégout, J.C. et al. (2018) History and environment shape species pools and community diversity in European beech forests. *Nature Ecology & Evolution*, 2, 483–490. Available from: https://doi.org/10.1038/s41559-017-0462-6

Julve, P. (1993) Synopsis phytosociologique de la France (communautés de plantes vasculaires). *Lejeunia*, 140, 1–160.

Küster, H. (1997) The role of farming in the postglacial expansion of beech and hornbeam in the oak woodlands of Central Europe. *The Holocene*, 7, 239–242. Available from: https://doi.org/10.1177/095968369700700213

Kalníková, V., Chytrý, K., Biţa-Nicolae, C., Bracco, F., Font, X., Iakushenko, D. et al. (2021) Vegetation of the European mountain river gravel bars: a formalized classification. *Applied Vegetation Science*, 24, e12542. Available from: https://doi.org/10.1111/avsc.12542

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. Available from: https://doi.org/10.1038/sdata.2017.122

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2021) Data from: Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. Available from: https://doi.org/10.5061/dryad.kd1d4 [Accessed 12th January 2022].

Kavgacı, A., Čarni, A., Tecimen, H. & Özalp, G. (2011) Diversity of floodplain forests in the Igneada region (NW Thrace - Turkey). *Hacquetia*, 10, 73–93. Available from: https://doi.org/10.2478/v10028-011-0003-9

Kevey, B. (2008) Magyarország erdőtársulásai [Forest communities of Hungary]. *Tilia*, 14, 1–489.

Kiedrzyński, M., Kurowski, J.K. & Kiedrzyńska, E. (2017) Trade-off between light availability and soil fertility determine refugial conditions for the relict light-demanding species in lowland forests. *Acta Oecologica*, 85, 1–8. Available from: https://doi.org/10.1016/j.actao.2017.09.004

Klötzli, F. (1968) Über die soziologische und ökologische Abgrenzung schweizerischer Carpinion- von den Fagion-Wäldern. *Feddes Repertorium*, 78, 15–37.

Knollová, I. & Chytrý, M. (2004) Oak-hornbeam forests of the Czech Republic: geographical and ecological approaches to vegetation classification. *Preslia*, 76, 291–311.

Kočí, M., Chytrý, M. & Tichý, L. (2003) Formalized reproduction of an expert-based phytosociological classification: a case study of subalpine tall-forb vegetation. *Journal of Vegetation Science*, 14, 601–610. Available from: https://doi.org/10.1111/j.1654-1103.2003.tb02187.x

Košir, P., Casavecchia, S., Čarni, A., Škvorc, Ž., Zivkovic, L. & Biondi, E. (2013) Ecological and phytogeographical differentiation of oak-hornbeam forests in southeastern Europe. *Plant Biosystems*, 147, 84–98. Available from: https://doi.org/10.1080/11263504.2012.717550

Kolb, A. & Diekmann, M. (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science*, 15, 199–208. Available from: https://doi.org/10.1111/j.1654-1103.2004.tb02255.x

Konvička, M., Čížek, L. & Beneš, J. (2004) *Ohrožený hmyz nížinných lesů: ochrana a management [Endangered insect of lowland forests: conservation and management]*. Olomouc: Sagittaria.

Lengyel, A., Chytrý, M. & Tichý, L. (2011) Heterogeneity-constrained random resampling of phytosociological databases. *Journal of Vegetation Science*, 22, 175–183. Available from: https://doi.org/10.1111/j.1654-1103.2010.01225.x

Leroy, S.A. & Arpe, K. (2007) Glacial refugia for summer-green trees in Europe and south-west Asia as proposed by ECHAM3 time-slice atmospheric model simulations. *Journal of Biogeography*, 34, 2115–2128. Available from: https://doi.org/10.1111/j.1365-2699.2007.01754.x

Leuschner, C. (1997) Das Konzept der potentiellen natürlichen Vegetation (PNV): Schwachstellen und Entwicklungsperspektiven. *Flora*, 192, 379–391. Available from: https://doi.org/10.1016/S0367-2530(17)30809-5

Leuschner, C. & Ellenberg, H. (2017) *Ecology of Central European forests*. Berlin and Heidelberg: Springer.

Loidi, J., Chytrý, M., Jiménez-Alfaro, B., Alessi, N., Biurrun, I., Campos, J.A. et al. (2021) Life-form diversity across temperate deciduous forests of Western Eurasia: a different story in the understory. *Journal of Biogeography*, 48, 2932–2945. Available from: https://doi.org/10.1111/jbi.14254

Müllerová, J., Szabó, P. & Hédl, R. (2014) The rise and fall of traditional forest management in southern Moravia: a history of the past 700 years. *Forest Ecology and Management*, 331, 104–115. Available from: https://doi.org/10.1016/j.foreco.2014.07.032

Magyari, E. (2002) Holocene biogeography of *Fagus sylvatica* L. and *Carpinus betulus* L. in the Carpathian-Alpine Region. *Folia Historico-Naturalia Musei Matraensis*, 26, 15–35.

Marinček, L. (1994) Zur Nomenklatur der Hainbuchenwälder des *Erythronio-Carpinion*. In: Trinajstić, I. (Ed.) *Simpozij Pevalek, Flora i vegetacija Hrvatske, Čakovec*. Čakovec: Tiskarsko izdavački zavod Zrinski, pp. 57–62.

Martynenko, V.B., Yamalov, S.M., Zhigumov, O.Y. & Filinov, A.A. (2005) *Rastitelnost gosudarstvennogo prirodnogo zapovednika "Shulgan-Tash" [Vegetation of the state nature reserve "Shulgan-Tash"]*. Ufa: Gilem.

Matuszkiewicz, J.M. (2001) *Zespoły leśne Polski [Forest communities of Poland]*. Warszawa: Wydawnictwo Naukowe PWN.

Meusel, H. (1969) Chorologische Artengruppen der mitteleuropäischen Eichen-Hainbuchenwälder. *Feddes Repertorium*, 80, 113–132.

Meusel, H. & Jäger, E.A. (1989) Ecogeographical differentiation of the Submediterranean deciduous forest flora. *Plant Systematics and Evolution*, 162, 315–329.

Michalko, J., Berta, J. & Magic, D. (1986) *Geobotanická mapa ČSSR, Slovenská socialistická republika, textová časť [Geobotanical map of ČSSR., Slovak Socialist Republic, text part]*. Bratislava: Veda.

Miklín, J. & Čížek, L. (2016) Erasing a European biodiversity hot-spot: open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO Biosphere Reserve. *Journal for Nature Conservation*, 22, 35–41. Available from: https://doi.org/10.1016/j.jnc.2013.08.002

Muñoz Sobrino, C., García-Moreiras, I., Gómez-Orellana, L., Iriarte-Chiapusso, M.J., Heiri, O., Lotter, A.F. et al. (2018) The last hornbeam forests in SW Europe: new evidence on the demise of *Carpinus betulus* in NW Iberia. *Vegetation History and Archaeobotany*, 27, 551–576. Available from: https://doi.org/10.1007/s00334-017-0654-7

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A. et al. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19(Suppl. 1), 3–264. Available from: https://doi.org/10.1111/avsc.12257

Nakhutsrishvili, G. (2013) *The vegetation of Georgia (South Caucasus)*. Berlin: Springer.

Neuhäusl, R. (1977) Comparative ecological study of European oak-hornbeam forests. *Naturaliste Canadien*, 104, 109–117.

Neuhäusl, R. & Neuhäuslová-Novotná, Z. (1964) Vegetationsverhältnisse am Südrand des Schemnitzer Gebirges. *Biologické Práce*, 10(4), 1–77.

Neuhäuslová, Z. (2000) Svaz: *Carpinion* Issler 1931 [Alliance: *Carpinion* Issler 1931]. In: Moravec, J. (Ed.) *Přehled vegetace České republiky, Vol. 2, Hygrofilní, mezofilní a xerofilní opadavé lesy [Vegetation Survey of the Czech Republic, Vol. 2, Hygrophilous, mesophilous and xerophilous deciduous forests]*. Praha: Academia, pp. 70–115.

Neuhäuslová-Novotná, Z. (1964) Zur Charakteristik der *Carpinion*-Gesellschaften in der Tschechoslowakei. *Preslia*, 36, 38–54.

Noirfalise, A. (1968) Le *Carpinion* dans l'Ouest de l'Europe. *Feddes Repertorium*, 79, 69–85.

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. Available from: https://doi.org/10.1127/phyto/2019/0346

Novák, P., Willner, W., Zukal, D., Kollár, J., Roleček, J., Świerkosz, K. et al. (2020) Oak-hornbeam forests of Central Europe: a formalized classification and syntaxonomic revision. *Preslia*, 92, 1–34. Available from: https://doi.org/10.23855/preslia.2020.001

Novák, P., Zukal, D., Harásek, M., Vlčková, P., Abdaladze, O. & Willner, W. (2020) Ecology and vegetation types of oak-hornbeam and ravine forests of the eastern Greater Caucasus, Georgia. *Folia Geobotanica*, 55, 333–349. Available from: https://doi.org/10.1007/s12224-020-09386-0

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. Available from: https://doi.org/10.1127/phyto/2019/0250

Oberdorfer, E. (1957) Süddeutsche Pflanzengesellschaften. *Pflanzensoziologie*, 10, 1–564.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2020) *vegan 2.5-7*. Available from: https://cran.r-project.org/web/packages/vegan/index.html [Accessed 1st November 2020].

Onyshchenko, V. (2009) *Forests of order Fagetalia sylvaticae in Ukraine*. Kyiv: Alterpress.

Palmé, A.E. & Vendramin, G.G. (2002) Chloroplast DNA variation, postglacial recolonization and hybridization in hazel, *Corylus avellana*. *Molecular Ecology*, 11, 1769–1779. Available from: https://doi.org/10.1046/j.1365-294X.2002.01581.x

Passarge, H. (1981) Carpineta in kartalinischen Kaukasus. *Phytocoenologia*, 9, 533–545.

Passarge, H. & Hofmann, G. (1968) Pflanzengesellschaften des nordostdeutschen Flachlandes II. *Pflanzensoziologie*, 16, 1–298.

Peterka, T., Hájek, M., Jiroušek, M., Jiménez-Alfaro, B., Aunina, L., Bergamini, A. et al. (2017) Formalized classification of European fen vegetation at the alliance level. *Applied Vegetation Science*, 20, 124–142. Available from: https://doi.org/10.1111/avsc.12271

Postolache, D., Popescu, F., Paule, L., Ballian, D., Zhelev, P., Fărcaş, S. et al. (2017) Unique postglacial evolution of the hornbeam (*Carpinus betulus* L.) in the Carpathians and the Balkan Peninsula revealed by chloroplast DNA. *Science of the Total Environment*, 599–600, 1493–1502. Available from: https://doi.org/10.1016/j.scitotenv.2017.05.062

QGIS Development Team. (2021) *QGIS geographic information system. Open source geospatial foundation project*. Available from: http://qgis.osgeo.org [Accessed 10th February 2021].

Quézel, P., Barbéro, M. & Akman, Y. (1992) Typification de syntaxa décrits en région méditerranéenne orientale. *Ecologia Mediterranea*, 18, 81–87.

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: http://www.R-project.org [Accessed 20th December 2020].

Ralska-Jasiewicz, M. (1964) Correlation between the Holocene history of the *Carpinus betulus* and prehistoric settlement in North Poland. *Acta Societatis Botanicorum Poloniae*, 33, 461–468.

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M. et al. (2002) Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. *Itinera Geobotanica*, 15, 5–922.

Rivas-Martínez, S. & Loidi, J. (1988) Los robledales mesofíticos navarro-alaveses (*Crataego laevigatae-Quercetum roboris*). *Lazaroa*, 10, 81–88.

Rodwell, J.S. & Dring, J. (2001) European significance of British woodland types. *English Nature Research Reports*, 460, 1–98.

Rodwell, J.S., Evans, D. & Schaminée, J.H.J. (2018) Phytosociological relationships in European Union policy-related habitat classifications. *Rendiconti Lincei. Scienze Fisiche e Naturali*, 29, 237–249.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F. et al. (2018) Where are Europe's last primary forests? *Diversity and Distributions*, 24, 1426–1439. Available from: https://doi.org/10.1111/ddi.12778

Sappington, J.M., Longshore, K.M. & Thompson, D.B. (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, 71, 1419–1426. Available from: https://doi.org/10.2193/2005-723

Schubert, R., Jäger, E.J. & Mahn, E.-G. (1979) Vergleichende geobotanische Untersuchungen in der Baschkirischen ASSR. *Hercynia N.F.*, 16, 206–263.

Sebek, P., Bace, R., Bartos, M., Benes, J., Chlumska, Z., Dolezal, J. et al. (2015) Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests. *Forest Ecology and Management*, 358, 80–89. Available from: https://doi.org/10.1016/j.foreco.2015.09.008

Šilc, U. & Čarni, A. (2012) Conspectus of vegetation syntaxa in Slovenia. *Hacquetia*, 11, 113–164. Available from: https://doi.org/10.2478/v10028-012-0006-1

Soó, R. (1940) Vergangenheit und Gegenwart der pannonischen Flora und Vegetation. *Nova Acta Leopoldina*, 56(9), 1–49.

Stefańska-Krzaczek, E., Kącki, Z. & Szypuła, B. (2016) Coexistence of ancient forest species as an indicator of high species richness. *Forest Ecology and Management*, 365, 12–21. Available from: https://doi.org/10.1016/j.foreco.2016.01.012

Tüxen, R. (1955) Das System der nordwestdeutschen Pflanzengesellschaften. *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft, Neue Folge*, 5, 155–176.

The Plant List(2021) *The Plant List. Version 1.1*. Available from: http://www.theplantlist.org [Accessed 1st March 2021].

Theurillat, J.P., Willner, W., Fernández-González, F., Bültmann, H., Čarni, A., Gigante, D. et al. (2021) International Code of Phytosociological Nomenclature. 4th edition. *Applied Vegetation Science*, 24, e12491. Available from: https://doi.org/10.1111/avsc.12491

Tichý, L. (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science*, 13, 451–453. Available from: https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý, L. (2005) New similarity indices for the assignment of relevés to the vegetation units of an existing phytosociological classification. *Plant Ecology*, 179, 67–72. Available from: https://doi.org/10.1007/s11258-004-5798-8

Tichý, L. & Chytrý, M. (2006) Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science*, 17, 809–818. Available from: https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Tichý, L., Chytrý, M. & Botta-Dukát, Z. (2014) Semi-supervised classification of vegetation: preserving the good old units and searching for new ones. *Journal of Vegetation Science*, 25, 1504–1512. Available from: https://doi.org/10.1111/jvs.12193

Tichý, L., Hennekens, S.M., Novák, P., Rodwell, J.S., Schaminée, J.H.J. & Chytrý, M. (2020) Optimal transformation of species cover for vegetation classification. *Applied Vegetation Science*, 23, 710–717. Available from: https://doi.org/10.1111/avsc.12510

Trinajstić, I. (1992) A contribution to the phytogeographical classification of the Illyrian floral element. *Acta Botanica Croatica*, 51, 135–142.

Večeřa, M., Divíšek, J., Lenoir, J., Jiménez-Alfaro, B., Biurrun, I., Knollová, I. et al. (2019) Alpha diversity of vascular plants in European forests. *Journal of Biogeography*, 46, 1919–1935. Available from: https://doi.org/10.1111/jbi.13624

Vera, F. (2000) *Grazing ecology and forest history*. New York, NY: CABI Publishing.

Vodka, S., Konvicka, M. & Cizek, L. (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation*, 13, 553–562. Available from: https://doi.org/10.1007/s10841-008-9202-1

Volkova, P.A., Burlakov, Y.A. & Schanzer, I.A. (2020) Genetic variability of *Prunus padus* (Rosaceae) elaborates "a new Eurasian phylogeographical paradigm". *Plant Systematics and Evolution*, 306, 1–9. Available from: https://doi.org/10.1007/s00606-020-01644-0

Volkova, P.A., Laczkó, L., Demina, O., Schanzer, I. & Sramkó, G. (2020) Out of Colchis: the colonization of Europe by *Primula vulgaris* Huds. (Primulaceae). *Acta Societatis Botanicorum Poloniae*, 89, 89313. Available from: https://doi.org/10.5586/asbp.89313

Wallnöfer, S., Mucina, L. & Grass, V. (1993) *Querco-Fagetea*. In: Mucina, L., Grabherr, G. & Wallnöfer, S. (Eds.) *Die Pflanzengesellschaften Österreichs, Teil III, Wälder und Gebüsche*. Jena, Stuttgart and New York, NY: Gustav Fischer Verlag, pp. 85–236.

Webb, D.A. (1983) The flora of Ireland in its European context. *Journal of Life Sciences*, 1983, 143–160.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York, NY: Springer-Verlag.

Willner, W., Solomeshch, A., Čarni, A., Bergmeier, E., Ermakov, N. & Mucina, L.. (2016) Description and validation of some European forest syntaxa – a supplement to the EuroVegChecklist . *Hacquetia*, 15(1), 15–25. https://doi.org/10.1515/hacq-2016-0005

Willner, W. (2002) Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. *Phytocoenologia*, 32, 337–453. Available from: https://doi.org/10.1127/0340-269X/2002/0032-0337

Willner, W. (2020) What is an alliance? *Vegetation Classification and Survey*, 1, 139–144. Available from: https://doi.org/10.3897/VCS/2020/56372

Willner, W., Di Pietro, R. & Bergmeier, E. (2009) Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography*, 32, 1011–1018. Available from: https://doi.org/10.1111/j.1600-0587.2009.05957.x

Willner, W., Jiménez-Alfaro, B., Agrillo, E., Biurrun, I., Campos, J.A., Čarni, A. et al. (2017) Classification of European beech forests: a Gordian knot? *Applied Vegetation Science*, 20, 494–512. Available from: https://doi.org/10.1111/avsc.12299

Willner, W., Solomeshch, A.I., Čarni, A., Bergmeier, E., Ermakov, N. & Mucina, L. (2016) Description and validation of some European forest syntaxa – a supplement to the EuroVegChecklist. *Hacquetia*, 15, 15–25. Available from: https://doi.org/10.1515/hacq-2016-0005

Wiser, S.K. & De Cáceres, M. (2013) Updating vegetation classifications: an example with New Zealand's woody vegetation. *Journal of Vegetation Science*, 24, 80–93. Available from: https://doi.org/10.1111/j.1654-1103.2012.01450.x

Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T. et al. (Eds.). (2000–2003) *Karte der natürlichen vegetation Europas/Map of the natural vegetation of Europe. Maßstab/Scale 1:2500000*. Münster: Landwirtschaftsverlag.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Sources of vegetation plots of the data set.

Appendix S2. List of aggregated taxa in the data set.

Appendix S3. Frequency synoptic table with diagnostic species of the TWINSPAN groups.

Appendix S4. Detrended correspondence analysis (DCA) of the data set with the TWINSPAN groups.

Appendix S5. Correlations among climatic, topographic and geographic variables.

Appendix S6. EuroVegChecklist (EVC) *Carpinetalia betuli* alliance expert system and distribution maps of the alliances.

Appendix S7. Frequency synoptic table with alliance diagnostic species of the EuroVegChecklist (EVC) classification system.

Appendix S8. Revised *Carpinetalia betuli* alliance expert system, further data on the nomenclature, boxplots of environmental variables and photos of the alliances of the revised classification system.

Appendix S9. Full frequency synoptic table with alliance diagnostic species of the revised classification system.

Appendix S10. Matching between plot classification by the EuroVegChecklist (EVC) and revised alliance expert systems.

Appendix S11. Frequency synoptic table with diagnostic species of the suballiances within the alliance *Carpinion betuli*.

How to cite this article: Novák, P., Willner, W., Biurrun, I., Gholizadeh, H., Heinken, T., Jandt, U. et al. (2023) Classification of European oak–hornbeam forests and related vegetation types. *Applied Vegetation Science*, 26, e12712. Available from: https://doi.org/10.1111/avsc.12712

APPENDIX 1

A syntaxonomic overview of the alliances accepted for the revised classification system. For each alliance, we provide the following information: **Protologue, Nomenclatural type, Original diagnostic species** (an alphabetically ordered list of alliance diagnostic species published together with the valid description of the alliance), **Synonyms** (only those not listed in EVC; Mucina et al., 2016). See Appendix S8 for type relevés of the alliance type associations and photos of the alliances. Suballiances of the alliance *Carpinion betuli* are also formally described and full lists of their diagnostic species based on the results of unsupervised classification are provided in Appendix S11.

Carpino-Fagetea sylvaticae Jakucs ex Passarge 1968

Carpinetalia betuli P. Fukarek 1968

1.1 *Carpinion betuli* Issler 1931

Protologue: Issler (1931, p. 83): '*Carpinetion*' [recte: *Carpinion*].

Nomenclatural type: *Carpinetum betuli* Issler 1924–1926 (automatic type, Art. 20).

Carpinetum betuli Issler 1926 is a later homonym of *Carpinetum betuli* Issler 1925 (Novák, 2019), hence illegitimate (Art. 31). However, this does not affect the typification of the alliance, which is valid even if the type name is illegitimate (Art. 17). Moreover, the name *Carpinetum betuli* might have already been validly described in Issler (1924), but this interpretation is controversial. The name *Carpinetum betuli* Issler was found as the oldest valid name of the association *Lithospermo-Carpinetum betuli* described by Oberdorfer (1957), which was proposed for conservation (Novák, 2019).

Original diagnostic species: *Ajuga genevensis*, *Convallaria majalis*, *Crataegus monogyna*, *Fragaria collina* [= *viridis*], *Primula officinalis* [= *veris*], *Scilla bifolia*, *Viola hirta*, *Viola riviniana*. Issler (1931) explicitly indicated only the above-mentioned species that are differential against the hygrophilous alliance *Alnion glutinosae* described therein. Moreover, as the alliance *Carpinion betuli* contained a single subordinate association, *Carpinetum betuli*, in the original publication, also its character species are to be considered as diagnostic species of the alliance if differential species against one alliance would not be sufficient (Art. 8). The species indicated as characteristic of the association are as follows: Tree layer: *Carpinus betulus*, *Pirus* [= *Pyrus*] *communis*, *Quercus sessilis* [= *petraea*], *Sorbus domestica*, *Sorbus torminalis*, *Tilia cordata*; shrub layer: *Acer campestre*, *Cornus sanguinea*, *Corylus avellana*, *Crataegus monogyna*, *Crataegus oxyacantha* [= *rhipidophylla*], *Evonymus* [= *Euonymus*] *europaeus*, *Ligustrum vulgare*, *Prunus spinosa*, *Rosa arvensis*, *Rosa caina* [= *canina*], *Rosa dumetorum*, *Rubus fruticosus* agg., *Viburnum lantana*; herb layer: *Ajuga genevensis*, *Aquilegia vulgaris*, *Asarum europaeum*, *Brachypodium pinnatum*, *Brachypodium silvaticum* [= *sylvaticum*], *Bromus asper ramosus* [= *Bromopsis benekenii* + *Bromopsis ramosa*], *Calamintha officinalis* [= *Clinopodium nepeta*], *Carex alba*, *Carex fritschii*, *Carex glauca* [= *flacca* subsp. *flacca*], *Carex montana*, *Carex ornithopoda*, *Carex tomentosa*, *Carex umbrosa*, *Carex ventricosa* [= *depauperata*], *Carex virens* [= *divulsa* subsp. *divulsa*], *Convallaria majalis*, *Coronilla* [= *Securigera*] *varia*, *Dactylis aschersoniana* [= *glomerata* subsp. *lobata*], *Euphorbia amygdalina* [= *amygdaloides*], *Euphorbia dulcis*, *Festuca heterophylla*, *Fragaria collina* [= *viridis*], *Galium silvaticum* [= *sylvaticum*], *Hedera helix*, *Helleborus foetidus*, *Hypericum montanum*, *Lathyrus niger*, *Lithospermum officinale*, *Lithospermum purpuro-coerul.* [= *Aegonychon purpurocaeruleum*], *Luzula forsteri*, *Melica nutans*, *Melittis melissophyllum*, *Mercurialis perennis*, *Muscari botryoides*, *Orchis purpureus* [= *purpurea*], *Poa chaixii*, *Potentilla opaca* [= *heptaphylla*], *Primula officinalis* [= *veris*], *Ranunculus silvaticus* [= *polyanthemos* subsp. *nemorosus*], *Scilla bifolia*, *Stellaria holostea*, *Vicia dumetorum*, *Vicia pisiforme* [= *pisiformis*], *Vinca minor*, *Viola alba*, *Viola hirta*, *Viola mirabilis*, *Viola riviniana*.

Synonyms: *Erythronio-Carpinion* (Horvat 1958) Marinček in Wallnöfer et al. 1993 p.p.

Carpinion betuli suballiances

1.1.1 *Eu-Carpinenion betuli*

The suballiance includes the subatlantic mesophilous OHFs with the distribution core in western Germany, northern Switzerland, Belgium and eastern and central France.

Nomenclatural type: Autonym (Art. 24b).

Diagnostic species: *Hedera helix*, *Ilex aquifolium*, *Lonicera periclymenum*, *Luzula pilosa*, *Potentilla sterilis*, *Rosa arvensis*, *Teucrium scorodonia*.

Synonym: *Pulmonario-Carpinenion* Oberdorfer 1957 nom. inval. (Art. 3b) p.p.

TWINSPAN groups 7–8 in this study.

The suballiance includes e.g. the associations *Lithospermo-Carpinetum* Oberdorfer 1957 and *Poo chaixii-Carpinetum* Oberdorfer ex Novák et al. 2020 (Novák, Willner et al., 2020), *Stellario holosteae-Quercetum petraeae* (Issler 1924) Bœuf et Simlerand in Bœuf 2010, *Glechomo hederaceae-Carpinetum betuli* (Timbal 1985) Bœuf et Simlerand in Bœuf 2010 (Bœuf, 2010).

1.1.2 *Galio-Carpinenion betuli* Oberdorfer ex Neuhäuslová-Novotná 1964

The suballiance comprises mesophilous, often rather mesotrophic, OHFs in central Europe (including central and eastern Germany, Czechia, western Poland, Austria, Slovakia), the Eastern Alps and northern Croatia.

Nomenclatural type: *Galio-Carpinetum* Oberdorfer 1957 (automatic type, Art. 20).

Diagnostic species: *Calamagrostis arundinacea*, *Campanula persicifolia*, *Galium sylvaticum*, *Hieracium murorum*, *Hieracium sabaudum*, *Luzula luzuloides*, *Melampyrum pratense*, *Veronica officinalis*.

Synonym: *Galio-Carpinenion* Oberdorfer 1957 nom. inval. (Art. 3b).

TWINSPAN groups 9 and 11 in this study.

The suballiance includes e.g. the associations *Epimedio-Carpinetum* (Horvat 1938) Borhidi ex Soó 1964, *Galio-Carpinetum* Oberdorfer 1957 (see Novák, Willner et al., 2020), *Carici albae-Carpinetum betuli* Čušin 2002 and *Helleboro nigri-Carpinetum* Marinček in Wallnöfer et al. 1993 (Šilc & Čarni, 2012).

1.1.3 *Tilio-Carpinenion betuli* Oberdorfer ex Neuhäuslová-Novotná 1964

The suballiance includes mesophilous, often nutrient-rich OHFs. They are distributed chiefly in the Carpathians, Romanian Moldavia, the Pannonian Basin and the Balkans.

Nomenclatural type: *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná in Neuhäuslová-Novotná 1964 (Neuhäuslová-Novotná, 1964, p. 46, lectotypus hoc loco).

Diagnostic species: *Acer campestre*, *Acer tataricum*, *Aegonychon purpurocaeruleum*, *Cornus mas*, *Crataegus monogyna*, *Dactylis glomerata*, *Euphorbia amygdaloides*, *Geum urbanum*, *Lapsana communis*, *Melica uniflora*, *Polygonatum hirtum*, *Polygonatum odoratum*, *Pulmonaria mollis*, *Tilia tomentosa*.

Synonyms: *Lonicero caprifoliae-Carpinenion betuli* Vukelić ex Marinček 1994, *Aceri tatarici-Carpinenion betuli* Košir et al. 2013 nom. inval. (Art. 2b, 18a).

TWINSPAN groups 13–14 in this study.

The suballiance comprises the Balkan and southern Pannonian associations of the alliance *Erythronio-Carpinion* (e.g. Košir et al., 2013) and the *Carpinion* associations *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná in Neuhäuslová-Novotná 1964, *Polygonato latifolii-Carpinetum* Michalko et Džatko 1965, *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová-Novotná in Neuhäuslová-Novotná 1964 (Novák, Willner et al., 2020) as well as associations from Romania [e.g. *Dentario quinquefoliae-Carpinetum* (Dobrescu et Kovács 1973) Täuber 1992, *Tilio tomentosae-Carpinetum* Doniţă 1968; Coldea, 2015].

Note :

The association name *Carici pilosae-Carpinetum* was published in two different papers in the same year (Neuhäusl & Neuhäuslová-Novotná, 1964; Neuhäuslová-Novotná, 1964). Most authors consider the latter as the first valid publication of the name. However, from the issue numbers of the two journals, it appears that the paper of Neuhäuslová-Novotná (1964) was published first. In any case, since there is no sufficient bibliographic reference between the two papers, the two publications are formally independent of each other. The paper of Neuhäuslová-Novotná (1964) only includes a synoptic table, which was partly based on the relevés published in Neuhäusl and Neuhäuslová-Novotná (1964). We, therefore, select the following relevé as the neotype for the *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná in Neuhäuslová-Novotná 1964: Neuhäusl and Neuhäuslová-Novotná (1964), Table 1, rel. 4, neotypus hoc loco. The same relevé was selected as lectotype for the *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964 by Neuhäuslová (2000), so our choice ensures that the two names are homotypic.

1.1.4 *Circaeo lutetianae-Carpinenion betuli* suball. nova

OHFs of nutrient-rich and mostly moist soils of the eastern part of western Europe, central Europe, Romania, Slovenia and northern Croatia.

Nomenclatural type: *Convallario-Carpinetum* Kevey 2008 (Kevey, 2008, p. 234, holotypus hoc loco).

Diagnostic species: *Adoxa moschatellina*, *Aegopodium podagraria*, *Athyrium filix-femina*, *Circaea lutetiana*, *Ficaria verna*, *Lamium galeobdolon*, *Maianthemum bifolium*, *Oxalis acetosella*, *Paris quadrifolia*, *Primula elatior*, *Ranunculus lanuginosus*, *Schedonorus giganteus*, *Urtica dioica*.

Synonym: *Pulmonario-Carpinenion* Oberdorfer 1957 nom. inval. (Art. 3b) p.p.

TWINSPAN groups 17–24 in this study.

The suballiance includes e.g. the associations *Convallario-Carpinetum* Kevey 2008, *Pseudostellario-Carpinetum* Accetto ex Novák et al. 2020, *Stellario-Carpinetum* Oberdorfer 1957 and *Tilio-Carpinetum* Traczyk 1962 (see Novák, Willner et al., 2020).

1.2 *Querco roboris-Tilion cordatae* Solomeshch et Laiviņš ex Bulokhov et Solomeshch in Bulokhov et Semenishchenkov 2015

Protologue: Bulokhov & Semenishchenkov (2015, p. 27): '*Querco roboris-Tilion cordatae* Bulokhov et Solomeshch all. nov. hoc loco'.

Nomenclatural type: *Mercuriali perennis-Quercetum roboris* Bulokhov et Solomeshch in Bulokhov et Semenishchenkov 2015 (holotypus).

Original diagnostic species: *Acer platanoides*, *Anemonoides* [= *Anemone*] *nemorosa*, *Corylus avellana*, *Carex digitata*, *Euonymus verrucosa* [= *verrucosus*], *Galeobdolon luteum* [= *Lamium galeobdolon*], *Galium intermedium*, *Hepatica nobilis*, *Luzula pilosa*, *Maianthemum bifolium*, *Oxalis acetosella*, *Picea abies*, *Quercus robur*, *Tilia cordata*.

Synonyms: *Querco-Tilion* Schubert et al. 1979 nom. nudum (Art. 5), *Scillo sibericae-Quercion roboris* Onyshchenko 2009 nom. nudum (Art. 5), *Scillo sibericae-Quercion roboris* Onyshchenko 2017.

1.3 *Aconito lycoctoni-Tilion cordatae* Solomeshch et Grigoriev in Willner et al. 2016

Protologue: Willner et al. (2016, p. 18): '*Aconito lycoctoni-Tilion cordatae* Solomeshch et Grigoriev all. nov. hoc loco'.

Nomenclatural type: *Stachyo sylvaticae-Tilietum cordatae* Martynenko et al. 2005 (holotypus).

Original diagnostic species: *Aconitum lycoctonum* (= *A. septentrionale*) [= *lycoctonum* subsp. *septentrionale*], *Anemone altaica*, *Bromopsis benekenii*, *Bupleurum longifolium*, *Campanula latifolia*, *Crepis sibirica*, *Drymochloa sylvatica*, *Geranium robertianum*, *Heracleum sphondylium* subsp. *sibiricum*, *Lactuca macrophylla* subsp. *uralensis*, *Lamium album*, *Parasenecio hastatus*, *Pleurospermum uralense*, *Stellaria bungeana*, *Tilia cordata*.

Synonyms: -

2.1 *Pulmonario longifoliae-Quercion roboris* Rivas-Martínez et Izco in Rivas-Martínez et al. 2002

Protologue: Rivas-Martínez & Izco in Rivas-Martínez et al. (2002, p. 178): '*Pulmonario longifoliae-Quercion roboris* all. nova hoc loco'.

Nomenclatural type: *Crataego laevigatae-Quercetum roboris* Rivas-Martínez et Loidi 1988 (holotypus).

Original diagnostic species: *Dryopteris aemula*, *Dryopteris corleyi*, *Epipactis phyllanthes*, *Hypericum androsaemum*, *Phyllitis* [= *Asplenium*] *scolopendrium*, *Pulmonaria longifolia*, *Quercus* ×*andegavensis* [= *Q. pyrenaica* × *robur*], *Quercus* ×*coutinhoi* [= *Q. faginea* × *robur*], *Quercus* ×*kerneri* nothosubsp. *kerneri* [= *Q. pubescens* × *robur*].

Synonyms: See Rivas-Martínez et al. (2002).

2.2 *Physospermo verticillati-Quercion cerridis* Biondi et al. 2013

Protologue: Biondi et al. (2013, p. 197): '*Physospermo verticillati-Quercion cerridis* Biondi et al. ex Biondi, Casavecchia et Biscotti all. nova'.

Nomenclatural type: *Physospermo verticillati-Quercetum cerris* [recte: *cerridis*] Aita, Corbetta et Orsino 1977 (holotypus).

Original diagnostic species: Character and differential species of the alliance *Physospermo verticillati-Quercion cerridis* (Biondi et al., 2008): *Acer obtusatum* subsp. *neapolitanum*, *Anemone apennina*, *Arum lucanum*, *Cyclamen repandum*, *Doronicum orientale*, *Festuca exaltata* [= *Drymochloa drymeja* subsp. *exaltata*], *Lathyrus jordanii*, *Physospermum verticillatum*, *Quercus cerris*, *Teucrium siculum*, *Viola odorata*.

Synonyms: *Erythronio-Carpinion* (Horvat 1958) Marinček in Wallnöfer et al. 1993 p.p., *Physospermo verticillati-Quercion cerris* [recte: *cerridis*] Biondi, Casavecchia et Biscotti 2008 nom. nudum (Art. 5). Although the vegetation of the type association of this alliance is typically dominated by *Quercus cerris*, its herb layer contains numerous forest mesophytes. Therefore, we assign it to the order *Carpinetalia betuli*. The dominance of oaks may be caused not only by environmental factors but also by current or past human management. The alliance also contains several associations dominated by *Carpinus betulus* (e.g. *Centaureo montanae-Carpinetum betuli*, *Doronico orientalis-Carpinetum betuli*; Biondi et al., 2013).

3.1 *Paeonio dauricae-Quercion petraeae* Didukh 1996

Protologue: Didukh (1996, p. 46): '*Paeonio dauricae-Quercion petraeae* all. nov.'.

Nomenclatural type: *Corno maris-Quercetum petraeae* Didukh 1996 (holotypus).

Original diagnostic species: *Allium auctum* [= *decipiens*], *Arum elongatum*, *Euonymus verrucosa* [= *verrucosus*], *Fraxinus excelsior*, *Galium verum*, *Geum urbanum*, *Mercurialis perennis*, *Milium effusum*, *Ornithogalum ponticum*, *Paeonia daurica*, *Polygonatum latifolium* [= *hirtum*], *Polygonatum multiflorum*, *Ranunculus constantinopolitanus* [= *villosus* subsp. *constantinopolitanus*], *Smyrnium perfoliatum*, *Tamus* [= *Dioscorea*] *communis*, *Vincetoxicum scandens*, *Viola hirta*.

Synonyms: -

3.2 *Crataego rhipidophyllae-Carpinion caucasicae* Passarge 1981

Protologue: Passarge (1981, p. 544): '*Crataego-Carpinion caucasicae* all. nov.'.

Nomenclatural type: *Corno-Carpinetum caucasicae* Passarge 1981 (holotypus).

Original diagnostic species: *Acer campestre*, *Acer laetum* [= *cappadocicum*], *Carex* cf. *euxina* [= *depressa* subsp. *transsilvanica*], *Crataegus kyrtostyla* and other species of this genus, *Cytisus caucasicus* [= *ruthenicus*], *Digitalis schischkinii*, *Lonicera caprifolium*, *Melica uniflora*, *Mespilus* [= *Crataegus*] *germanica*, *Quercus iberica* [= *petraea* subsp. *iberica*], *Sorbus torminalis*, *Ulmus foliaceus* [= *minor*], *Viola reichenbachiana*.

Synonyms: -

3.3 *Trachystemono orientalis-Carpinion betuli* Çoban et Willner 2018

Protologue: Çoban and Willner (2018, p. 102): '*Trachystemono orientalis-Carpinion betuli* all. nov. hoc loco'.

Nomenclatural type: *Trachystemono orientalis-Carpinetum betuli* Kavgacı et al. 2011 (holotypus).

Original diagnostic species: *Carpinus betulus*; *Mespilus* [= *Crataegus*] *germanica*; *Asperula involucrata*, *Campanula persicifolia*, *Daphne pontica*, *Epimedium pubigerum*, *Festuca heterophylla*, *Hypericum calycinum*, *Lathyrus hirsutus*, *Lathyrus niger*, *Salvia forskahlei* [= *forsskaolei*], *Smilax excelsa*, *Trachystemon orientalis*, *Viola sieheana*.

Synonyms: -

3.4 *Parrotio persicae-Carpinion betuli* Djazirei ex Gholizadeh, Naqinezhad et Chytrý 2020

Protologue: Gholizadeh et al. (2020, p. 112): '*Parrotio persicae-Carpinion betuli* Djazirei ex Gholizadeh, Naqinezhad et Chytrý 2020 all. nov. hoc loco'.

Nomenclatural type: *Querco castaneifoliae-Carpinetum betuli* Gholizadeh, Naqinezhad et Chytrý 2020 (holotypus).

Original diagnostic species: *Buxus sempervirens* subsp. *hyrcana*, *Oplismenus undulatifolius* [= *hirtellus* subsp. *undulatifolius*], *Parrotia persica*.

Synonyms: See Gholizadeh et al. (2020).