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Classification and ecology of pedunculate oak–hornbeam forests at the southern margin of the Pannonian Basin

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Running title: CLASSIFICATION OF OAK–HORNBEAM FORESTS

Abstract – Pedunculate oak (*Quercus robur*) and common hornbeam (*Carpinus betulus*) forests represent one of the most widespread lowland forest vegetation types along the southern margin of the Pannonian Basin. However, their classification remains inconsistent across national borders due to differing phytosociological concepts. Therefore, we aimed to establish a unified classification system based on a dataset of vegetation plots covering the southern edge of the Pannonian Basin. A total of 608 phytosociological relevés from Slovenia, Croatia, Bosnia and Herzegovina, and Serbia were classified using the Two-Way Indicator Species Analysis (TWINSPAN) classification method to distinguish *Carpinetalia betuli* and *Alno-Fraxinetalia excelsioris*. Of these, 295 suitable relevés assigned to *Carpinetalia betuli* were subsequently classified into associations. Associations were further examined using detrended correspondence analysis (DCA) and characterised based on their floristic composition, climatic, and ecological properties. Five associations were distinguished: *Festuco drymeiae-Carpinetum*, representing mesophilous communities occurring in transitional habitats towards *Fagus sylvatica* and/or *Quercus petraea* forests; *Pseudostellario-Carpinetum betuli*, Illyrian mesohygrophilous forests dominated by *Carpinus betulus*; *Alno-Carpinetum betuli* occurring on elevated hills under relatively mild climatic conditions; *Lonicero caprifolii-Quercetum roboris*, mesothermophilous oak–hornbeam forests characteristic of eastern Croatia and Serbia; and *Convallario majalis-Carpinetum betuli*, riverine Pannonian hornbeam-dominated forests. These associations differ in their floristic composition as well as in their ecological and biogeographical characteristics. The results established a unified classification for pedunculate oak–hornbeam forests along the southern margin of the Pannonian Basin, improving cross-border comparability and providing a basis for future research, biodiversity conservation, sustainable forest management, and long-term habitat monitoring.

Keywords: *Carpinetalia betuli*, *Carpino betuli-Quercetum roboris*, *Carpinus betulus*, classification, lowland, phytosociological analysis, *Quercus robur*

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Introduction

Mixed pedunculate oak (*Quercus robur*) and common hornbeam (*Carpinus betulus*) forests, hereafter referred to as pedunculate oak–hornbeam forests, are among the most common forest habitats on the southern margin of the Pannonian Basin. These forests represent ecologically, physiognomically, and floristically complex communities that develop on moderately moist, deep soils, mostly in lowland and flat terrains (Stefanović 1989, Vukelić 2012, Koljanin et al. 2025a). Floristically, they belong to the group of mesophilous hornbeam forests and, according to modern classification systems (Košir et al. 2013, Mucina et al. 2016, Novák et al. 2020, 2023), are assigned to the class *Carpino-Fagetea sylvaticae* and the order *Carpinetalia betuli*. These forests differ ecologically from other common hornbeam-dominated forests due to high groundwater levels and/or periods of soil saturation during late autumn, winter, and early spring (Vukelić 2012). This is reflected in the dominance of moisture-demanding species such as *Quercus robur* or *Fraxinus angustifolia* in the upper tree layer. These species occur in sites where groundwater remains accessible even during prolonged drought. However, the lower tree layer is characterised by a high abundance of common hornbeam, a species intolerant of prolonged periods of wet soil (Vukelić 2012). Alongside common hornbeam, other mesophilous species are also present in the lower tree layer. For those ecologically different species to coexist, the soil must have an adequate groundwater level or have a heavy clay texture capable of retaining water to support the dominance of *Quercus robur* or *Fraxinus angustifolia*. However, at the same time, the upper soil layer must remain mesic at the beginning of the growing season to support the presence of common hornbeam and other species affiliated with the order *Carpinetalia betuli* (Koljanin et al. 2025a). Consequently, pedunculate oak–hornbeam forests persist at an ecological ecotone between azonal hardwood floodplain forests and zonal forests (Vukelić 2012).

In the study area, habitats of pedunculate oak–hornbeam forests were usually confined to deep, fertile soils of slightly elevated river terraces of lowland rivers beyond the reach of prolonged seasonal inundation or to deep soils of the lower part of diluvial deposits. Therefore, they have been subject to anthropogenic impacts since ancient times and have largely been converted to agricultural land. The most severe cases of deforestation are in the eastern and northeastern parts of the study area, in Vojvodina (northern Serbia), where agricultural land dominates, and forests occur only in very small areas, often composed of alien tree species. As the existence of this vegetation type often depends on the groundwater level, changes in hydrology have frequently been destabilising factors for these communities. Currently, oak–hornbeam forests are the most economically important lowland forest type on the southern margin of the Pannonian Basin (Klimo et al. 2008) and have high ecological value (Trinajstić 2008). Pedunculate oak–hornbeam forests are recognised as the Natura 2000 habitat type, indicating their importance for biodiversity conservation (Plišo Vusić et al. 2019).

Despite their ecological and economic importance, a comprehensive synthesis of available data and a harmonised classification of pedunculate oak–hornbeam forests are still lacking in this area. Previous comprehensive studies dealing with associations or alliances have covered only parts of this area (Purger et al. 2014) or have been based on a small number of phytosociological relevés sampled in this area (Košir et al. 2013, Novák et al. 2023). Consequently, various, fairly consistent classification systems are used in different countries. Furthermore, some associations still rely on concepts more than fifty years old, while others follow modern classification approaches, causing disproportion. Existing associations display inconsistent ecological and floristic breadth, and their geographical boundaries often coincide with national borders. Therefore, a revision of associations on the southern margin of the Pannonian Basin is necessary, followed by a description of their floristic, ecological, and geographical characteristics. This area was not covered by previous syntaxonomic revisions (Novák et al. 2020) and therefore represents a significant gap in the current understanding of

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pedunculate oak–hornbeam forest diversity. This study aims to provide a harmonised syntaxonomic classification of pedunculate oak–hornbeam forests along the southern margin of the Pannonian Basin and to clarify the floristic, ecological, and biogeographical differentiation of the associations occurring in this area.

Material and methods

Study area

The study was conducted on pedunculate oak–hornbeam forests along the southern margin of the Pannonian Basin, covering parts of Slovenia, Croatia, Bosnia and Herzegovina, and Serbia. This is a transitional zone that lies between the central part of the Pannonian Basin to the north and the Alpine, Dinaric, and Carpathian Mountains to the west, south, and east, respectively. It also represents a transitional area between central and southern Europe. The relief is predominantly lowland, with locally hilly areas and isolated low Pannonian mountains. Hilly topography is common near contact zones with the surrounding mountain ranges. The northeastern part of the study area has mostly been converted to agricultural land and has a much drier climate unsuitable for mesic forests, resulting in a lack of suitable sampling sites and, consequently, limited data from this area (Fig. 1).

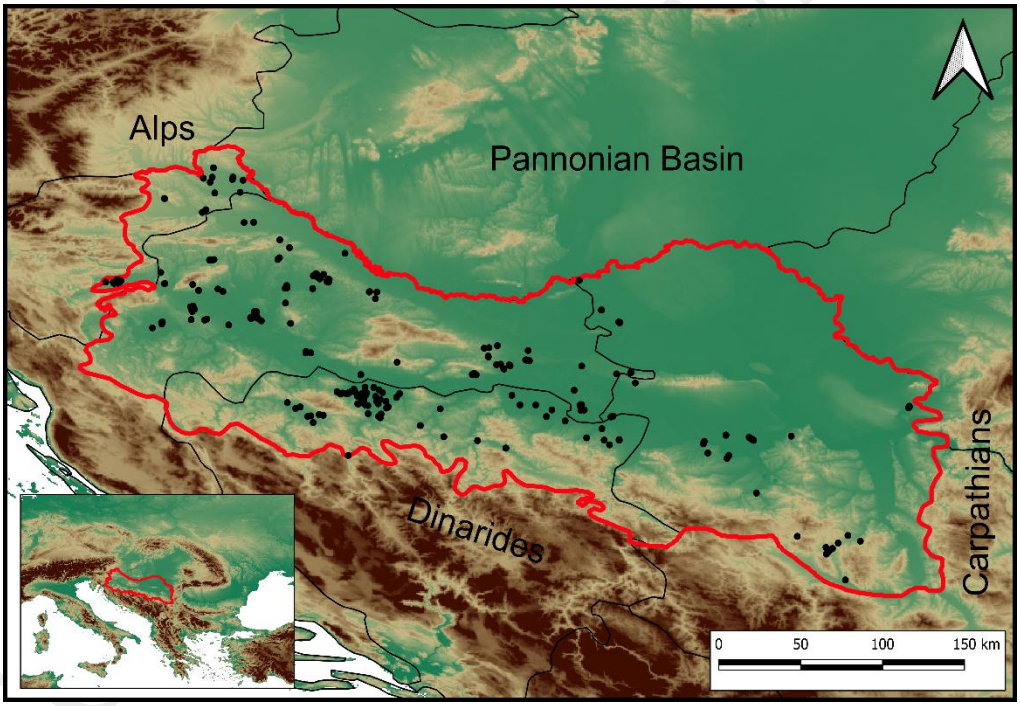


Fig. 1. Location of the study area along the southern margin of the Pannonian Basin. The background represents elevation derived from a digital elevation model (DEM). The study area is outlined with a red line. Black dots indicate the locations of classified pedunculate oak–hornbeam relevés belonging to the order *Carpinetalia betuli*. The inset map shows the location of the study area in Europe.

Mean annual temperatures generally increases from west to east, ranging from approximately 10 – 12 °C (Fick and Hijmans 2017). Precipitation decreases from the west (approximately 1200 mm) to the east (approximately 600 mm). As a result, the climate forms a gradient from humid sub-Atlantic and moderately continental in the west towards a drier continental climate in the east (Škvorc et al. 2020). Soil conditions also follow a gradient.

Lowland areas adjacent to the Pannonian Basin are covered by neutral-to-slightly alkaline soils (ca. pH 6.5 – 7.5), associated with a drier climate and specific lithology (ESRI, 2023). Towards the southern and south-western hilly regions, soil pH decreases and moderately acidic soils prevail (pH < 5.5). Local discrepancies from the generalised models were anticipated, reflecting the influence of site-specific conditions such as riverine sediment deposition, heterogeneity in bedrock composition, and other local geological and geomorphological factors.

Data preparation and analysis

The initial dataset was compiled by collecting all available phytosociological relevés representing pedunculate oak–hornbeam forests assigned to the order *Carpinetalia betuli* and located within the study area. Relevés were retrieved from Turboveg databases of Slovenia (EU-SI-001), Croatia (EU-HR-002), Bosnia and Herzegovina (EU-BA-001), Serbia (EU-RS-003) and the SE Europe forest database (EU-00-021). Database codes follow the Global Index of Vegetation-Plot Databases (www.givd.info; accessed 11 July 2025).

For a relevé to be included in the initial dataset, at least one of the two specified selection criteria had to be met. The first selection criterion required relevés to be classified in the Turboveg database as pedunculate oak–hornbeam associations assigned to the alliances *Carpinion betuli* or *Erythronio-Carpinion*. The list of eligible associations was compiled from several sources, including Marinček and Čarni (2002) and Šilc and Čarni (2012) for Slovenia; Vukelić (2012) for Croatia; Tomić and Rakonjac (2011) for Serbia; and Koljanin et al. (2025a) for Bosnia and Herzegovina. Based on this criterion, the following names were included in the initial dataset: *Carpino betuli-Quercetum roboris*, *Stellario holosteae-Carpinetum betuli*, *Pseudostellario-Carpinetum betuli*, *Convallario majalis-Carpinetum betuli*, *Lonicero caprifolii-Quercetum roboris*, and *Circaeo-Carpinetum betuli*.

As interpretations of associations, alliances, and classes have changed over time (Willner 2006, Mucina et al. 2016, Willner 2020), a second selection criterion was applied to minimise the effects of the inconsistent assignment of relevés to phytosociological units. Therefore, all relevés containing *Fraxinus angustifolia* and/or *Quercus robur* were selected when the combined cover of mesophilous tree species characteristic of the class *Carpino-Fagetea* (Chytrý et al. 2024) exceeded 25%. These species included *Carpinus betulus*, *Tilia tomentosa*, *Tilia cordata*, *Tilia platyphyllos*, *Fagus sylvatica*, *Acer campestre*, *Ulmus minor* and *Prunus avium*. Species were selected based on their occurrence in the analysed vegetation type within the study area (Vukelić 2012, Tomić and Rakonjac 2011, Koljanin et al. 2025a). The combined cover of these species was calculated using the JUICE software (Tichý 2002).

Applying these two criteria resulted in the selection of 669 relevés for further selection, classification, and analysis. Relevés with plot areas smaller than 100 m² or larger than 1000 m² were excluded because variation in plot size can negatively affect vegetation classification. Subsequently, 608 relevés remained. Species nomenclature followed Euro+Med (2006–), whereas the nomenclature of higher syntaxonomic units followed Mucina et al. (2016). The nomenclature of associations followed Marinček (1994), Stupar (2020), and Novák et al. (2020). The full names of associations are provided in Appendix 2. Taxa not identified to the species level were removed. Taxonomically complex groups were merged into aggregates (Appendix 1). Bryophytes were excluded because of inconsistent sampling, and vegetation layers were merged into a single layer for the same reason.

To separate forests of the order *Carpinetalia betuli* from other syntaxonomic units that still met the initial criteria, we applied the TWINSPAN algorithm (Hill 1979) using presence/absence data. This data transformation proved useful in preventing species occurring with high cover values in both orders (eg. *Quercus robur*, *Fraxinus angustifolia*, *Acer campestre*, *Carex brizoides*, *Aegopodium podagraria*, etc.) from disproportionately driving the classification. Classical TWINSPAN was used to identify the principal floristic gradient and

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inspect the clusters produced at successive levels of division. After the inspection of TWINSPAN clusters, on several levels of division, it was determined based on floristic composition (On-line Suppl. Tab. 1) that the first level of division was sufficient. The first cluster belonged to the order *Alno-Fraxinetalia* (173 relevés), while the second belonged to the order *Carpinetalia betuli* (435 relevés). Relevés belonging to *Alno-Fraxinetalia* were excluded from further analysis, as this was out of the scope of this study. The dataset was further filtered to exclude other forest types within *Carpinetalia betuli* that were not pedunculate oak–hornbeam forests or that exhibited a transitional character. Relevés in which *Quercus cerris, Q. petraea, Q. frainetto, Fagus sylvatica,* or *Alnus glutinosa* had more than 50% cover were excluded from further analysis, as a high cover of these species typically indicates transitional stands to other types, successional stages (e.g., *Alnus glutinosa* stands), or strongly degraded stands. Consequently, 404 relevés remained.

Preliminary classification of *Carpinetalia betuli*, using different data transformations, linkage methods, and distance measures, revealed grouping by sampling time. As the optimal phenological window for the target vegetation type (*Carpinetalia betuli*) is late spring (Chytrý et al. 2024), all relevés recorded from July to November were excluded. Excluded late-season relevés were floristically incomplete due to the absence of spring geophytes and other short-cycle, early-flowering species, which are frequently diagnostic for common hornbeam-dominated associations (Košir et al. 2013, Novák et al. 2020, Koljanin et al. 2025a). An outlier analysis was conducted in PC-ORD 5.0 (McCune and Mefford 2006). Relevés whose floristic composition deviated by more than ±2 SD from the dataset mean (Euclidean distance) were removed.

Relevés containing fewer than five species were also excluded, as species-poor relevés cannot be reliably assigned to a phytosociological unit (Willner et al. 2017). The sampling-date and minimum species-number criteria were applied after the separation of the orders because the forest types included in the initial dataset differed significantly in their optimal sampling periods and species richness. Moreover, the assignment of these relevés to orders enabled a subsequent semi-supervised K-means reassignment of late-sampled and species-poor relevés belonging to *Carpinetalia betuli*, allowing a more detailed representation of the distribution of the associations and excluding the possibility that valid associations were excluded by these criteria. After all the selection steps, the final dataset comprised 295 relevés of pedunculate oak–hornbeam forests within the *Carpinetalia betuli* order, which was then used for the subsequent classification.

For the classification of relevés to associations, modified TWINSPAN (Roleček et al. 2009) was applied. Modified TWINSPAN was applied at the association level because it permitted the selection of any number of clusters without requiring their post hoc merging. Moreover, it also allowed the observation of the hierarchical relationships among the resulting clusters. As floristic variation among associations was less pronounced than floristic variation between higher syntaxonomic units, such as orders and classes, a transformation that also considered species cover was applied at this step. Cover values were transformed to an ordinal scale using thresholds of 0, 3, 5, 15, and 25, as Tichý et al. (2020) proposed for associations. For hierarchical clustering, Jaccard dissimilarity with the average linkage method was used. Several methods were tested, and this method produced the most floristically and ecologically interpretable results. The five-cluster solution was selected because it represented the highest hierarchical level at which clusters showed clear floristic differentiation, ecological coherence, and geographical consistency. Further divisions produced units with weak diagnostic species and limited ecological interpretability. This decision was supported by the classification crispness analysis (Botta-Dukát et al. 2005), which showed a peak at five clusters. Phi ≥ 0.25 was used for diagnostic species, and only those species that were significant according to Fisher's exact test ($P < 0.001$) were retained.

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Average unweighted Ellenberg indicator values were calculated for each relevé following Pignatti et al. (2005). To clarify the interpretation of the classification and to visualise floristic relationships among associations, a detrended correspondence analysis (DCA) was performed, with relevés projected into the ordination space. Before ordination, cover values were transformed to presence-absence. Ellenberg indicator values that showed statistically significant relationships with the ordination were passively fitted onto the DCA diagram. Altitude was also projected on the DCA space. The significance of correlations between Ellenberg indicator values and the first two DCA axes was assessed using the modified permutation test of Zelený and Schaffers (2012), with $p < 0.05$ as the significance threshold.
To map the distribution of associations and assess whether an association had been previously omitted due to the sampling date, phytosociological relevés that had been excluded earlier because of the sampling date or outlier elimination were reassigned using a semi-supervised K-means clustering approach. For this, cover values were transformed to an ordinal scale using thresholds of 0, 3, 5, 15, and 25. These relevés were assigned to five existing clusters, allowing the formation of an additional cluster when K-means found no suitable assignment to an existing cluster.

Results

Delimitation of *Carpinetalia betuli* forests within the initial dataset

At the first level of division, two clusters were formed. TWINSPAN separated the alluvial forests of the order *Alno-Fraxinetalia* (173 relevés) from those of the order *Carpinetalia betuli* (435 relevés). Diagnostic species for *Alno-Fraxinetalia* were hygrophilous and mesohygrophilous species such as *Carex remota*, *Galium palustre*, *Iris pseudacorus*, *Rubus caesius*, *Lysimachia nummularia*, etc. Diagnostic species for *Carpinetalia betuli* were mesophilous species that do not tolerate wet soil, such as *Stellaria holostea*, *Fagus sylvatica*, *Polygonatum multiflorum*, *Asarum europaeum*, *Anemone nemorosa*, etc. The full synoptic table is provided in On-line Suppl. Tab. 1.

Classification of pedunculate oak–hornbeam forests within the cluster assigned to the order *Carpinetalia betuli* resulted in five clusters (On-line Suppl. Fig. 1, Tab. 1). All five clusters were assigned to the already described associations. Cluster 1 comprises stands distributed in northern and northeastern Croatia, primarily occurring on lower hill slopes. The tree layer is characterised by the frequent occurrence of *Fagus sylvatica* and *Quercus petraea* alongside *Quercus robur* and *Carpinus betulus*. It corresponds to the *Festuco drymeiae-Carpinetum betuli* association. Cluster 2 comprises mesohygrophilous stands occurring in the cooler and more humid lowlands of Slovenia and north-western Croatia. These stands are characterised by the presence of Illyrian endemic forest species and correspond to the *Pseudostellario-Carpinetum betuli* association. Cluster 3 includes mesophilous and mesohygrophilous stands occurring at mountain foothills and on the highest river terraces with heavy soils, corresponding to the *Alno glutinosae-Carpinetum betuli* association. Cluster 4 corresponds to the *Lonicero caprifolii-Quercetum roboris* association. This association represents mesothermophilous and mesoxerophilous stands occurring in a drier continental climate of the Pannonian Basin. *Quercus frainetto* and *Quercus cerris* are sometimes present in the tree layer of this association. Cluster 5 comprises stands on river terraces under slightly warmer, drier continental conditions. Soils are base-rich, well-drained, and moist. The floristic composition comprises riparian and Pannonian species, such as *Fraxinus angustifolia* and *Acer tataricum*. This cluster corresponds to the *Convallario majalis-Carpinetum betuli* association.

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Tab. 1. Short synoptic table of the analysed associations (clusters). Cluster 1 – *Festuco drymeiae-Carpinetum betuli*, cluster 2 – *Pseudostellario-Carpinetum*, cluster 3 – *Alno glutinosae-Carpinetum betuli* (*Stellario-Carpinetum*), cluster 4 – *Lonicero caprifolii-Quercetum roboris*, and cluster 5 – *Convallario majalis-Carpinetum betuli*. Diagnostic species are highlighted in grey. Species frequency values are shown in full-sized numbers, whereas phi coefficients are given as superscript values. For each cluster, only the 10 diagnostic species with the highest phi values and frequencies greater than 20% are shown. A full synoptic table for analysed orders and associations is stored as online supplementary material (On-line Suppl. Tab. 2).

Cluster number	1		2		3		4		5	
Number of relevés	73		25		71		22		104	
Common tree and shrub species										
Quercus robur	96	---	100	---	100	---	100	---	95	---
Carpinus betulus	100	---	100	---	100	---	95	---	91	---
Acer campestre	75	---	68	---	49	---	86	---	95	24
Quercus petraea agg.	42	24	36	---	.	---	32	---	1	---
Prunus avium	59	---	60	---	45	---	41	---	50	---
Fraxinus angustifolia s. lat.	.	---	4	---	18	---	18	---	32	25
Tilia tomentosa	22	---	.	---	6	---	36	---	12	---
Tilia platyphyllos	8	---	16	---	18	---	9	---	24	---
Tilia cordata	22	---	8	---	32	---	.	---	15	---
Hedera helix	67	24	20	---	24	---	50	---	57	---
Cornus sanguinea	36	---	44	---	18	---	50	---	54	14
Rubus hirtus s. lat.	52	---	28	---	58	18	41	---	20	---
1- *Festuco drymeiae-Carpinetum betuli* Vukelić 1991 Marinček 1994										
Euphorbia amygdaloides	66	54	4	---	10	---	23	---	5	---
Carex pilosa	58	52	4	---	7	---	14	---	6	---
Fagus sylvatica	81	49	28	---	34	---	27	---	3	---
Cardamine bulbifera	62	47	28	---	4	---	14	---	6	---
Platanthera bifolia	36	43	8	---	.	---	5	---	1	---
Galium odoratum	71	39	28	---	37	---	27	---	10	---
Melica uniflora	34	31	.	---	3	---	27	---	1	---
Dryopteris filix-mas	47	31	24	---	28	---	.	---	7	---
Asarum europaeum	66	31	36	---	25	---	32	---	23	---
Stellaria holostea	75	26	36	---	54	---	50	---	32	---
2 - *Pseudostellario-Carpinetum* Accetto ex Novák et al. 2020										
Pseudostellaria europaea	.	---	52	68	.	---	.	---	.	---
Gentiana asclepiadea	.	---	40	59	.	---	.	---	.	---
Euphorbia dulcis	14	---	52	56	1	---	.	---	1	---
Paris quadrifolia	7	---	56	53	8	---	.	---	12	---
Crocus heuffelianus agg.	.	---	48	46	14	---	.	---	12	---
Anemone nemorosa	23	---	92	45	51	---	32	---	38	---
Viburnum opulus	4	---	56	44	10	---	.	---	32	14
Athyrium filix-femina	34	---	64	42	34	---	.	---	1	---
Gagea spathacea	.	---	36	42	7	---	.	---	9	---
Luzula pilosa	18	---	40	40	3	---	5	---	1	---

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Tab. 1. continued

3 - *Alno glutinosae-Carpinetum betuli* Issler 1926								
Veronica montana	10	.	39	44	.		8	
Carex brizoides	22	48	72	41	.		23	
Galeopsis speciosa	12	.	34	34	.		13	
Frangula alnus	.	12	23	26	.		7	
4 - *Lonicero caprifoliae-Quercetum roboris* (Rauš 1971) Marinček 1994								
Quercus cerris	15	.	1		73	66	11	
Fraxinus ornus	.	.	.		45	62	1	
Clematis vitalba	1	.	.		50	62	4	
Viola hirta agg.	7	.	6		64	59	14	
Dactylis glomerata s. lat.	3	8	4		59	57	10	
Cruciata laevipes	3	.	.		41	55	2	
Helleborus odorus	14	.	4		59	55	11	
Aremonia agrimonoides	3	.	1		41	54	2	
Asperula taurina	1	.	1		41	50	8	
Lapsana communis	4	.	1		36	49	2	
5 - *Convallario-Carpinetum* Kevey 2008.								
Ulmus minor	7	4	20		14		52	42
Ligustrum vulgare	18	36	11		68		78	36
Sambucus nigra	34	4	21		5		50	32
Acer tataricum	7	.	37		55		62	32
Galium aparine	18	16	14		41		57	30
Arum maculatum agg.	8	20	15		45		56	30
Ficaria verna	14	52	28		50		69	27

A total of 69 relevés, previously omitted due to sampling date or outlier analysis, were assigned to the existing clusters for distribution mapping, whereas the remaining 40 formed a separate cluster. This additional cluster lacked diagnostic species, with *Quercus robur* and *Carpinus betulus* as the only constant species. Most relevés in this cluster were floristically poor, as 33 contained fewer than 10 species, while the remaining seven comprised 10 or 11 species. These characteristics indicate that the relevés are unsuitable for further analyses and cannot be interpreted as a distinct plant community.

Ecological differentiation

Temperature, light, moisture, and elevation were correlated with the first two DCA axes. In contrast, soil reaction was correlated with the third and fourth axes, while soil nutrients were correlated only with the fourth axis (On-line Suppl. Tab. 3). Associations located on the left side of the ordination space (Fig. 2) (*Festuco drymeiae-Carpinetum betuli*, *Pseudostellario-Carpinetum*, *Alno glutinosae-Carpinetum betuli*) have the lowest Ellenberg indicator values for light and temperature.

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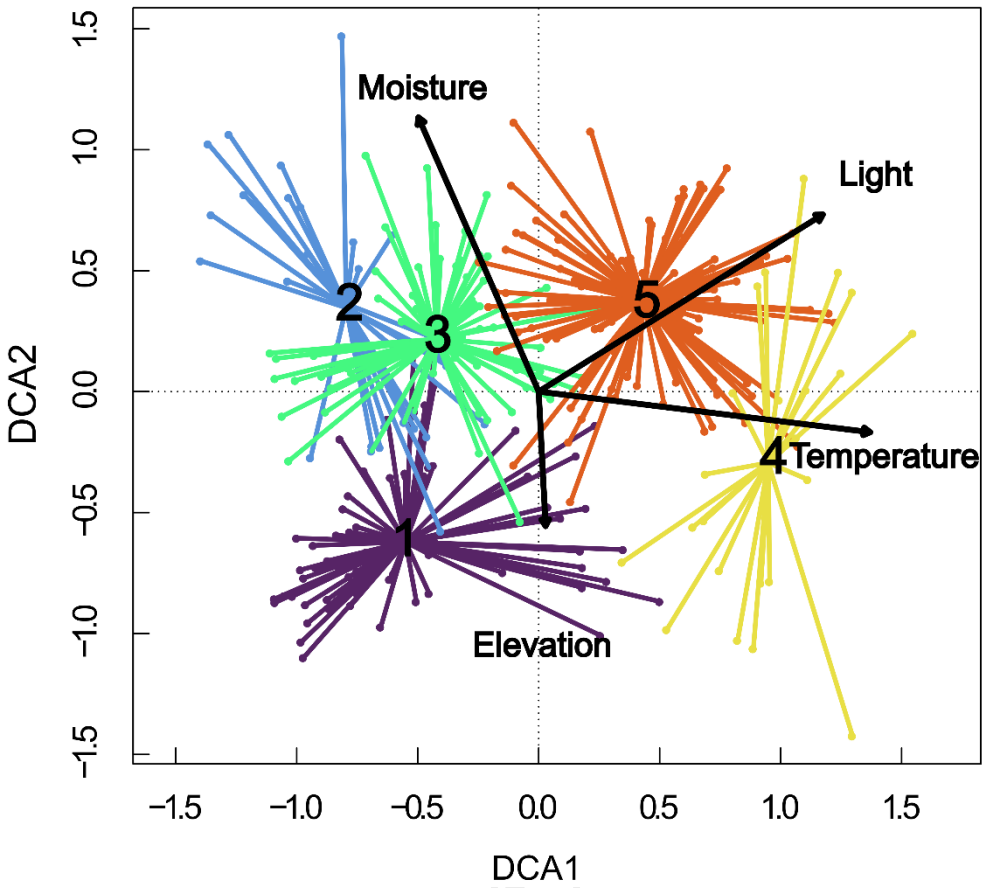


Fig. 2. DCA ordination diagram of the analysed associations: (1) *Festuco drymeiae-Carpinetum betuli* (purple), (2) *Pseudostellario-Carpinetum* (blue), (3) *Alno glutinosae-Carpinetum betuli* (green), (4) *Lonicero caprifolii-Quercetum roboris* (yellow), and (5) *Convallario majalis-Carpinetum betuli* (orange). Ellenberg indicator values that were significantly correlated with the first two ordination axes were passively plotted onto the DCA diagram along with elevation.

Among them, *Pseudostellario-Carpinetum* and *Alno glutinosae-Carpinetum betuli* occupy the wettest part of the gradient, which can be explained by a combination of more humid climatic conditions, soils with higher water-holding capacity, and supplementary moisture from lower elevations, such as groundwater influence or occasional river flooding. *Festuco drymeiae-Carpinetum* is typically developed on elevated terraces and, in some cases, on gentle slopes, where long-term water retention does not occur. *Lonicero caprifolii-Quercetum roboris* is located in the upper right part of the ordination space, showing the highest Ellenberg indicator values for temperature and light. The high values for light might be due to more open canopies, which could indicate a gradual transition from oak–hornbeam mesic forests (*Carpinetalia betuli*) to thermophilous oak forests of the forest-steppe zone (*Aceri tatarici-Quercion*). *Convallario majalis-Carpinetum* develops at sites influenced by supplementary moisture, which is reflected by its position in the moist part of the ordination diagram.

The study area spans the transition between continental and sub-Atlantic climatic regimes, with an almost twofold increase in annual precipitation across the region. The combination of climatic variables shows clear differentiation between associations (Fig. 3).

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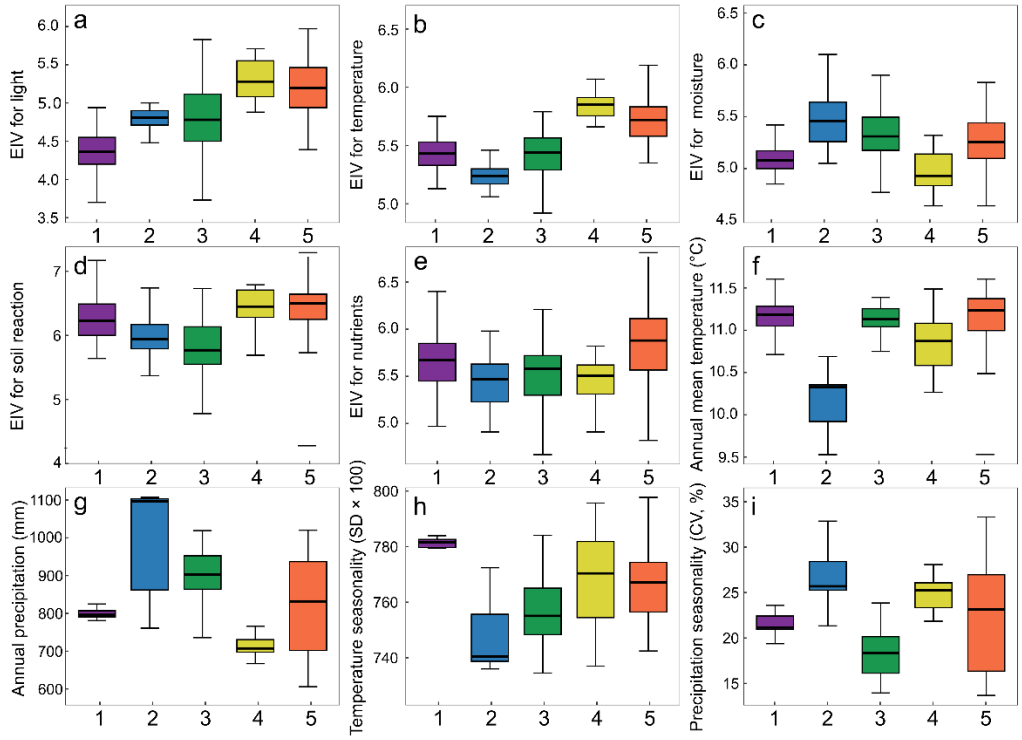


Fig. 3. Boxplots show the distributions of Ellenberg indicator values (EIVs; panels a–e) and climatic variables (panels f–i) among the five associations. Ellenberg indicator values are shown for (a) light, (b) temperature, (c) moisture, (d) soil reaction and (e) nutrients. Climatic variables are shown for (f) annual mean temperature (°C), (g) annual precipitation (mm), (h) temperature seasonality (standard deviation × 100) and (i) precipitation seasonality (coefficient of variation, %). Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers extend to the smallest and largest observations within 1.5 times the interquartile range. Numbers on the x-axes indicate the associations: (1) *Festuco drymeiae-Carpinetum betuli* (purple), (2) *Pseudostellario-Carpinetum* (blue), (3) *Alno glutinosae-Carpinetum* betuli (green), (4) *Lonicero caprifolii-Quercetum roboris* (yellow) and (5) *Convallario majalis-Carpinetum betuli* (orange).

Pseudostellario-Carpinetum betuli was found in the coldest climatic conditions, with the lowest annual mean temperatures. *Festuco drymeiae-Carpinetum betuli*, *Alno glutinosae-Carpinetum betuli*, *Lonicero caprifolii-Quercetum roboris*, and *Convallario majalis-Carpinetum betuli* occurred in comparatively warmer and mutually similar thermal conditions, with only minor variation in their mean temperatures. Patterns of temperature seasonality further distinguished those associations. *Pseudostellario-Carpinetum* and *Alno glutinosae-Carpinetum betuli* had the smallest seasonal variability in temperature. In contrast, *Festuco drymeiae-Carpinetum betuli*, *Lonicero caprifolii-Quercetum roboris*, and *Convallario majalis-Carpinetum betuli* exhibited the greatest temperature fluctuations, indicating a more continental-type annual temperature regime. Pronounced differences were also evident in annual precipitation. *Pseudostellario-Carpinetum* and *Alno glutinosae-Carpinetum betuli* occurred in the wettest climatic conditions. *Festuco drymeiae-Carpinetum betuli* and *Lonicero caprifolii-Quercetum roboris* were associated with the driest conditions, with median values near 800 mm and 700 mm, respectively. The variation in precipitation seasonality was highest in *Pseudostellario-Carpinetum* and *Lonicero caprifolii-Quercetum roboris*. However, because *Pseudostellario-Carpinetum* receives substantially higher annual precipitation, pronounced drought periods are not common, which may not be the case for *Lonicero caprifolii-Quercetum*

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roboris. The lowest variation was recorded in *Festuco drymeiae-Carpinetum betuli* and *Alno glutinosae-Carpinetum betuli*. *Convallario majalis-Carpinetum betuli* was highly variable across the analysed precipitation variables, mainly because soil moisture does not depend on precipitation but is influenced by the groundwater level.

Spatial distribution of the associations

The spatial distribution of the five analysed associations (Fig. 4) shows a geographical differentiation along the southern margin of the Pannonian Basin.

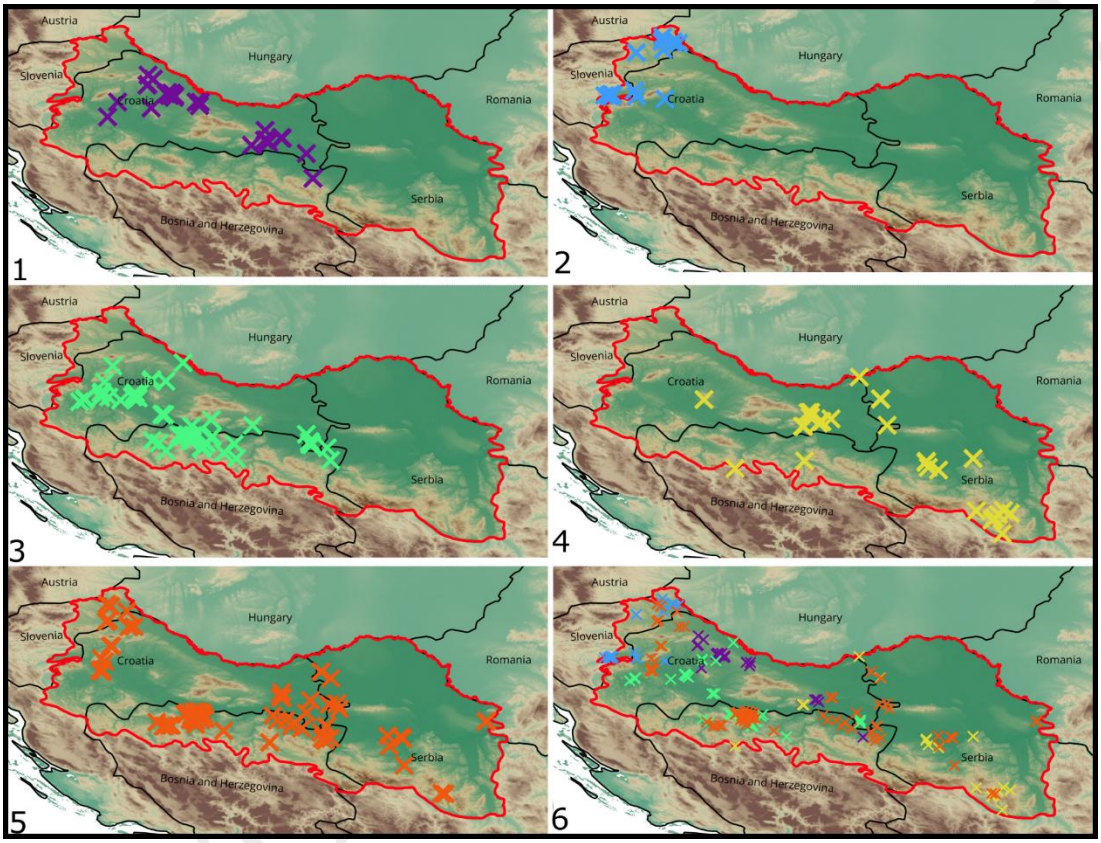


Fig. 4. Spatial distribution of the analysed associations along the southern margin of the Pannonian Basin. Maps 1–5 show the distribution of individual associations, including relevés assigned using the k-means method: (1) *Festuco drymeiae-Carpinetum betuli* (purple), (2) *Pseudostellario-Carpinetum* (blue), (3) *Alno glutinosae-Carpinetum betuli* (green), (4) *Lonicero caprifolii-Quercetum roboris* (yellow) and (5) *Convallario majalis-Carpinetum betuli* (orange). Numbers 1–5 correspond to the cluster numbers (associations) used in Tab. 1, Figs. 2 and 3, and On-line Suppl. Tabs. 1 and 2. Map 6 shows the combined distribution of all five associations but excludes relevés assigned using the k-means method. The red line indicates the boundary of the study area.

Festuco drymeiae-Carpinetum betuli is concentrated mainly in hilly areas and the foothills of northern and north-eastern Croatia, with an isolated relevé in Bosnia and Herzegovina. *Pseudostellario-Carpinetum betuli* is restricted to the westernmost part of the study area (Slovenia and Croatia). *Alno glutinosae-Carpinetum betuli* has a broader western-to-central distribution and is associated mainly with heavy, clay-rich soils in cooler, more humid foothill areas and on elevated terraces. At the same time, it is absent from the driest eastern part of the study area. In contrast, *Lonicero caprifolii-Quercetum roboris* is concentrated mainly in the eastern part of the study area, where continental conditions are

present. *Convallario majalis-Carpinetum betuli* is the most widespread association, occurring along rivers and streams in flat valleys throughout the study area, although it is absent in the western part.

Discussion

Biogeographical and ecological gradients

Similar to patterns observed at a broader spatial scale (Košir et al. 2013), the differentiation of associations along the southern margin of the Pannonian Basin is driven by a combination of ecological and biogeographical factors. From west to east, a floristic and ecological gradient can be observed, in which mesophilous Central European species gradually replace hygrophilous and Illyrian species. Further east, these species are replaced by Pannonian mesoxerophilous species. This gradient is locally interrupted by river systems, which modify the soil humidity regime as well as soil pH and nutrient gradients. In such areas, riverine species become prominent in the species composition.

Festuco drymeiae-Carpinetum betuli

Relevés from elevated sites without the influence of groundwater, located toward the Pannonian Basin, belonging to cluster 1, were classified as *Festuco drymeiae-Carpinetum betuli*. This name was first used by Vukelić (1991) to describe stands of sessile oak (*Quercus petraea*) and hornbeam with beech (*Fagus sylvatica*) in the Pannonian part of Croatia. The description of this association was later revised by Marinček (1994). In the table presented by Vukelić (1991), the *quercetosum roboris* subassociation is also described, encompassing the most hygrophilous stands within the association, which corresponds well with cluster 1. The *quercetosum roboris* subassociation develops on lower parts of hill slopes, where water flow from higher positions results in increased soil moisture, allowing the occurrence of pedunculate oak (Vukelić 2012). Our findings suggest that this subassociation is more widely distributed than previously known. However, further comparison with sessile oak–hornbeam forests is needed to determine the status of this subassociation and even association, as well as their relationship to other sessile oak–hornbeam forests such as *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná 1964 and *Epimedio-Carpinetum* (Horvat 1938) Borhidi ex Soó 1964.

The tree layer is composed of *Quercus robur* and *Carpinus betulus,* with a frequent occurrence of *Fagus sylvatica* and *Quercus petraea*. The association is floristically characterised by a combination of species typical of mesophilous beech and sessile oak-common hornbeam forests (*Melica uniflora, Galium odoratum, Cardamine bulbifera, Asarum europaeum, Dryopteris filix-mas, Carex pilosa,* etc.). These species indicate deep, well-drained soils on slopes and foothills, where waterlogging rarely occurs. Mesoxeric thermophilous and mesohygrophilous species are rare in this association. Such a floristic composition suggests an ecological transition toward beech and sessile oak forests. Climatic variables associated with these plots indicate a mean annual precipitation of approximately 800 mm (Fig. 3), with around 250 mm falling during the warmest quarter of the year.

Pseudostellario-Carpinetum betuli

Stands containing Illyrian endemics and subendemics, as defined by Koljanin et al. (2025b), developed in the western part of the study area were classified as *Pseudostellario-Carpinetum betuli*. Spatially, this association is in contact with *Pruno padi-Carpinetum*, which is developed on slightly elevated and often inclined sites (Marinček and Čarni 2002). However, more data should be collected, and further research is needed to distinguish these two associations. *Pseudostellario-Carpinetum betuli* has been described and studied in Slovenia, close to the Croatian border (Accetto 1974, Marinček and Čarni 2002), but has not been recorded in Croatia until now.

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The soils are clay-rich and consequently moist (Accetto 1974). The climate is characterised by comparatively low mean annual temperatures and the highest precipitation among all analysed units, at approximately 1150 mm annually (Fig. 3), including around 350 mm during the warmest quarter. Stands typically form a two-layered tree canopy, with *Quercus robur* dominating the upper tree layer and *Carpinus betulus* forming the lower tree layer (Accetto 1974). A combination of Illyrian mesohygrophilous and mesophilous species, including *Pseudostellaria europaea*, *Crocus heuffelianus*, *Hacquetia epipactis*, *Epimedium alpinum*, and indicators of colder climates and humid conditions, such as *Geum rivale*, *Gentiana asclepiadea*, *Leucojum vernum*, and *Aegopodium podagraria*, characterise this association. Pannonian elements such as *Quercus cerris*, *Tilia tomentosa*, *Asperula taurina*, *Fraxinus angustifolia*, *Acer tataricum*, and *Ruscus hypoglossum* are absent.

Alno glutinosae-Carpinetum betuli

Alno glutinosae-Carpinetum betuli comprises pedunculate oak–hornbeam stands occurring under moderately humid and relatively cold climatic conditions. The original description of this association was based on relevés from Western Europe (Issler 1924). However, the association was subsequently recorded in other parts of Europe, with its distribution extending eastwards to the northern edge of the Pannonian Basin (Novák et al. 2020). Although cluster 3 exhibits some local floristic variations that are not included in the original relevés from Western Europe, such as the occurrence of *Acer tataricum*, it can nevertheless be assigned to the broadly circumscribed association as defined by Novák et al. (2020). Furthermore, the floristic relationship between the Pannonian *Convallario-Carpinetum* and the sub-Atlantic *Alno glutinosae-Carpinetum*, previously documented in Central Europe (Novák et al. 2020), is also evident in the study area, where both associations remain floristically distinct. This association was recorded for the first time in northern Bosnia and Herzegovina under the name *Stellario holosteae-Carpinetum betuli* (Koljanin et al. 2025a). The nomenclature interpretation of this association is complex and has been discussed in several papers (Novák 2019, Novák et al. 2020, Willner et al. 2024). The name *Alno glutinosae-Carpinetum betuli* is likely the valid one, and *Stellario holosteae-Carpinetum betuli* is a synonym.

Topographically, this association typically occupies wet, flat mountain foothills, hill slopes, or high river terraces with heavy soil structure that retains water. Due to positions on lower slopes and elevated river terraces, soils are generally deep, clay-rich, and capable of retaining water for prolonged periods (Koljanin et al. 2025a). However, because these stands mostly develop away from active floodplain influence, riparian species dependent on groundwater are typically absent. This association exhibits lower Ellenberg values for temperature and higher Ellenberg values for moisture than other associations associated with the more continental part of the Pannonian Basin (Fig. 2). Therefore, this community is floristically defined by mesophilous oak–hornbeam forest species such as *Lamium galeobdolon* s. lat., *Polygonatum multiflorum*, *Stellaria holostea*, *Viola reichenbachiana*, combined with species tolerant of clay-rich, slow-draining soils (*Carex brizoides*, *Frangula alnus*). It lacks Illyrian endemics and sub-endemics, thermophilous and mesothermophilous Pannonian species, as well as beech-forest and riverine species, which negatively differentiate this association.

Lonicero caprifolii-Quercetum roboris

Mesothermophilous and mesoxerophilous oak-hornbeam forests were classified as *Lonicero caprifolii-Quercetum roboris*. This interpretation is consistent with both the designation of the nomenclatural type by Marinček (1994) and the syntaxonomic concept

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proposed by Vukelić (2012), who restricted the application of the name *Lonicero caprifolii-Quercetum roboris* to the warmest and driest expression of this vegetation type.

This association is often in contact with *Carpino betuli-Quercetum frainetto*, especially in the easternmost part of the distribution area. However, *Carpino betuli-Quercetum frainetto* (mesophilous *Quercus frainetto* dominated forests) is characterised by the domination of *Quercus frainetto* found on inclined slopes (Stupar 2020), while *Lonicero caprifolii-Quercetum roboris* is usually confined to lower slopes and areas with additional humidity. It should be mentioned that the floristic composition of *Lonicero caprifolii-Quercetum roboris* partly corresponds to the *Helleboro dumetorum-Carpinetum* association as characterised by Novák et al. (2020). However, substantial floristic differences are evident. Most notably, *Quercus robur* is a constant species in *Lonicero caprifolii-Quercetum roboris*, while it is completely absent in *Helleboro dumetorum-Carpinetum* (Novák et al. 2020). Novák et al. (2020) also noted that pedunculate oak is present in the *Polygonato latifolii-Carpinetum* association. However, this association has a rare frequency of thermophilous and mesothermophilous species (Novák et al. 2020) such as *Fraxinus ornus*, *Tilia tomentosa*, *Viola hirta* and *Helleborus odorus*. Therefore, cluster 4 was assigned to *Lonicero caprifolii-Quercetum roboris*. It is probably more widespread than the results indicate, since some relevés with a similar floristic composition were excluded due to plot size and late sampling.

Lonicero caprifolii-Quercetum roboris occurs in a dry continental climate typical of the eastern part of the study area. It exhibits mesoxerophilous and mesothermophilous characteristics (Fig. 2). It usually occupies flat or gently sloping terrain with slightly higher soil moisture compared to the surrounding zonal vegetation, which is often dominated by xerophilous oak forests and forest-steppe vegetation (Tomić 2004). Climatic conditions are characterised by low annual precipitation (approximately 700 mm) (Fig. 3), with about 200–250 mm falling during the warmest quarter of the year. Mean annual temperatures range between 11 and 11.5 °C. Under such climatic regime, the presence of supplementary moisture plays a crucial role in allowing the development of pedunculate oak–hornbeam forests. This association is characterised by a mixture of mesothermophilous and mesoxerophilous species such as *Tilia tomentosa, Cornus mas, Fraxinus ornus, Potentilla micrantha, Polygonatum odoratum, Viola hirta* agg., *Festuca heterophylla*, accompanied by mesophilous oak–hornbeam elements such as *Asperula taurina, Polygonatum multiflorum*, etc. Typical mesohygrophilous species are rare.

Convallario majalis-Carpinetum betuli

Stands characterised by the presence of mesothermophilous Pannonian elements and nitrophilous species, developed along rivers throughout the entire scope and in moist areas in the eastern part, were classified within a Pannonian *Convallario majalis-Carpinetum betuli* association. This association was previously recorded in northern Bosnia (Koljanin et al. 2025a). In Croatia, along the Drava River, this association has been reported under the name *Circaeo-Carpinetum* (Purger 2008). In a nomenclature revision, Novák et al. (2020) consider the name *Circaeo-Carpinetum* to be a synonym of *Convallario-Carpinetum betuli*.

Convallario majalis-Carpinetum betuli is usually confined to rivers and streams with flat valleys in the majority of the research area. However, it is absent in cooler areas within the study area (Fig. 4). This association occurs on medium to highly elevated river terraces influenced by the groundwater. Such sites are nutrient-rich and often base-rich. However, in the eastern part, where soils are more base-rich (ESRI 2023), it also develops in wet areas out of the typical floodplain. These stands are confined to water-permeable substrates that prevent long-term stagnation of surface water. Short flood events may still occur irregularly, during maximum water levels. As groundwater availability compensates for precipitation deficits and permeable soil for excess water, the development of these forests is only weakly dependent on

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rainfall, resulting in a similar vegetation composition across different precipitation regimes. The most common soil type is humofluvisol, and in some cases pseudogleys (Koljanin et al. 2025a). This association is distinguished by a combination of riverine and groundwater-dependent species such as *Fraxinus angustifolia*, *Ficaria verna*, and *Polygonatum hirtum*, together with mesothermophilous shrubs, including *Acer tataricum*, *Ligustrum vulgare*, and nitrophilous *Sambucus nigra*. *Acer campestre* often dominates the lower tree layer. A notable feature of this community is the frequent occurrence of nitrophilous species that can sometimes reach high cover, including *Veronica hederifolia*, *Galium aparine* and *Geum urbanum.*

Connection to the previous classification systems

The analysis only partly supports the previously applied classification concepts. The majority of relevés in the dataset were originally assigned to *Carpino betuli-Quercetum roboris*. However, Marinček (1994) determined that this name is invalid and designated *Lonicero caprifolii-Quercetum roboris* as the valid name for a floristically and ecologically very heterogeneous association that had previously been known as *Carpino betuli-Quercetum roboris*. Since Rauš (1975) published relevés of the *quercetosum cerris* and *tilietosum tomentosae* subassociations first, and only later published the *typicum* subassociation Marinček (1994) designated *quercetosum cerris*, the older subassociation, as the nomenclature type. Our results indicate a clear separation of mesothermophilous pedunculate oak–hornbeam forests corresponding to the *quercetosum cerris* subassociation and, consequently, to the *Lonicero caprifolii-Quercetum roboris* association from the rest of the dataset. The taxonomic interpretation of Vukelić (2012), proposing to restrict the name *Lonicero caprifolii-Quercetum roboris* to the driest and most thermophilous stands of pedunculate oak–hornbeam forests, is supported by the present analysis, as cluster 4 resembles the type relevé of *Lonicero caprifolii-Quercetum roboris*.

According to the previous classification system, *Pseudostellario-Carpinetum* was considered to be restricted to Slovenia (Accetto 1974) and was not recorded in Croatia (Vukelić 2012). However, our results indicate that this association also occurs in northwestern Croatia. The rest of the dataset was classified as *Convallario-Carpinetum betuli* or *Alno-Carpinetum*.
The name *Carpino betuli–Quercetum roboris* has been widely used throughout the study area and includes numerous subassociations such as *typicum*, *fagetosum*, *quercetosum cerridis*, *tilietosum tomentosae*, *quercetosum frainetto*, *brachypodietosum sylvaticae*, and *fraxinetosum angustifoliae* (Vukelić 2012, Tomić and Rakonjac, 2011). A considerable number of relevés in the dataset were not assigned to any subassociation. Among the assigned relevés, many were based on late-season surveys or large-area plots and were therefore excluded from the analysis. The assignment of subassociations was often subjective and varied substantially among authors. Consequently, an exact correspondence between the previous and the newly proposed system cannot be fully established.

Nevertheless, some general correspondences can be identified. The *Alno-Carpinetum* association largely corresponds to *Carpino betuli–Quercetum roboris typicum* and *fagetosum*, particularly on wetter, heavier, and poorly permeable soils, as described by Vukelić (2012). *Convallario-Carpinetum betuli*, including its internal variability, encompasses part of the *typicum* subassociation as well as *brachypodietosum sylvaticae*, as described by Rauš and Vukelić (1993). This association has also been reported under the name *Circaeo-Carpinetum* (Purger 2008). Furthermore, the *quercetosum cerridis*, *quercetosum frainetto*, and *tilietosum tomentosae* subassociations, as described by Rauš (1971) and Tomić and Rakonjac (2011), correspond well to the variability of *Lonicero-Quercetum roboris*. *Festuco-Carpinetum* was already recognised in the previous system. However, some relevés previously assigned *to Carpino betuli–Quercetum roboris fagetosum* are classified within this association in the present study.

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Syntaxonomic interpretation and relationship with alliances

In the present analysis, higher-level clusters were not interpreted as alliances. The first reason is that the analysis of alliances requires the inclusion of stands in which pedunculate oak is not the dominant species, a condition not met in this case. The type of association of the alliance *Erythronio-Carpinion* is *Epimedio-Carpinetum betuli*, in which sessile oak rather than pedunculate oak usually dominates alongside hornbeam. The second reason is that the southern margin of the Pannonian Basin represents a transitional zone between alliances (Koljanin et al. 2025b). Therefore, the final assignment of those associations to alliances is still to be determined in a more comprehensive study of hornbeam forests, including typical stands.

Conclusion

This study provides a harmonised syntaxonomic classification of pedunculate oak–hornbeam forests along the southern margin of the Pannonian Basin. Five associations were distinguished, reflecting clear floristic, ecological, and biogeographical differentiation across the study area. The results resolve several inconsistencies among previously applied national classification systems and improve the comparability of vegetation data across political borders. The proposed classification framework provides a basis for future phytosociological, biogeographical, and conservation studies of lowland forests in southeastern Europe. Further research should focus on the relationships of these associations to other oak–hornbeam forest types in Europe and on the syntaxonomic position of the corresponding alliances.

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Author contribution statement

DK, VS, and AČ conceived the research idea. All authors contributed data and additional relevés. DK performed the statistical analyses and prepared the figures. DK, AČ and VS wrote the first version of the manuscript. All authors contributed to the interpretation of the results, critically revised the manuscript, and approved the final version.

References

Accetto, M., 1974: Združbi gabra in evropske gomoljčnice (*Pseudostellario-Carpinetum*) ter doba in evropske gomoljčnice (*Pseudostellario-Quercetum*) v Krakovskem gozdu [The communities of hornbeam and European false birthwort (*Pseudostellario-Carpinetum*) and pedunculate oak and European false birthwort (*Pseudostellario-Quercetum*) in Krakovski gozd]. Gozdarski Vestnik 32, 357–369.

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.

Chytrý, M., Řezníčková, M., Novotný, P., Holubová, D., Preislerová, Z., Attorre, F., Biurrun, I., Blažek, P., Bonari, G., Borovyk, D., Čeplová, N., Danihelka, J., Davydov, D.,

ACCEPTED MANUSCRIPT

Dřevojan, P., Fahs, N., Guarino, R., Güler, B., Hennekens, S.M., Hrivnák, R., Kalníková, V., Kalusová, V., Kebert, T., Knollová, I., Knotková, K., Koljanin, D., Kuzemko, A., Loidi, J., Lososová, Z., Marcenò, C., Midolo, G., Milanović, D., Mucina, L., Novák, P., von Raab-Straube, E., Reczyńska, K., Schaminée, J.H.J., Štěpánková, P., Świerkosz, K., Těšitel, J., Těšitelová, T., Tichý, L., Vynokurov, D., Willner, W., Axmanová, I., 2024: FloraVeg.EU — an online database of European vegetation, habitats and flora. Applied Vegetation Science 27, e12798. https://doi.org/10.1111/avsc.12798

Esri, 2023: World Soils 250m pH. ArcGIS Living Atlas of the World, tiled imagery layer. Retrieved August 10, 2025 from https://www.arcgis.com/home/item.html?id=0961138215b8460e9f4e436d38c3b3b4

Euro+Med, 2006: Euro+Med PlantBase — The information resource for Euro-Mediterranean plant diversity. Retrieved June 11, 2025 from

http://ww2.bgbm.org/EuroPlusMed/query.asp

Fick, S. E., Hijmans, R. J., 2017: WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315. https://doi.org/10.1002/joc.5086

Hill, M. O., 1979: TWINSPAN — a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Computer software.

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, Nouvelle Série 17, 1–66.

Klimo, E., Hager, H., Matić, S., Anić, I., Kulhavý, J. (eds.), 2008: Floodplain forests of the temperate zone of Europe. Lesnická Práce, Kostelec nad Černými lesy.

Koljanin, D., Stupar, V., Čarni, A., 2025b: Defining Illyrian forests: The role of biogeographical patterns and species co-occurrence. Journal of Biogeography 52, e70078. https://doi.org/10.1111/jbi.70078

Koljanin, D., Stupar, V., Milanović, Đ., Šikuljak, T., Brujić, J., 2025a: Phytosociological analysis of the lowland forests of peri-Pannonian Bosnia (SE Europe). Tuexenia 45, 9–36. https://doi.org/10.14471/2025.45.002

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

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

Marinček, L., Čarni, A., 2002: Commentary to the vegetation map of forest communities of Slovenia in a scale of 1:400,000. Založba ZRC, ZRC SAZU Biološki inštitut Jovana Hadžija, Ljubljana.

McCune, B., Mefford, M. J., 2006: PC-ORD. Multivariate analysis of ecological data, Version 5.0 for Windows. MjM Software, Gleneden Beach, Oregon, USA.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., Gavilán García, R., Chytrý, M., Hájek, M., Di Pietro, R.,

ACCEPTED MANUSCRIPT

Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J. H. J., Lysenko, T., Didukh, Y. P., Pignatti, S., Rodwell, J. S., Capelo, J., Weber, H. E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S. M., Tichý, L., 2016: Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19, 3–264. https://doi.org/10.1111/avsc.12257

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

Novák, P., Willner, W., Biurrun, I., Gholizadeh, H., Heinken, T., Jandt, U., Kollár, J., Kozhevnikova, M., Naqinezhad, A., Onyshchenko, V., Pielech, R., Rašomavičius, V., Shirokikh, P., Vassilev, K., Wohlgemuth, T., Večeřa, M., Chytrý, M., 2023: Classification of European oak–hornbeam forests and related vegetation types. Applied Vegetation Science 26(1), e12712. https://doi.org/10.1111/avsc.12712

Novák, P., Willner, W., Zukal, D., Kollár, J., Roleček, J., Świerkosz, K., Ewald, J., Wohlgemuth, T., Csiky, J., Onyshchenko, V., Chytrý, M., 2020: Oak-hornbeam forests of central Europe: a formalized classification and syntaxonomic revision. Preslia 92(1), 1–34. https://doi.org/10.23855/preslia.2020.001

Pignatti, S., Menegoni, P., Pietrosanti, S., 2005: Valori di bioindicazione delle piante vascolari della flora d'Italia. Braun-Blanquetia 39, 1–97.

Plišo Vusić, I., Šapić, I., Vukelić, J., 2019: Prepoznavanje i kartiranje šumskih staništa Natura 2000 u Hrvatskoj (II) — 91F0, poplavne šume s vrstama *Quercus robur*, *Ulmus laevis*, *Ulmus minor*, *Fraxinus angustifolia*; 91L0, hrastovo-grabove šume ilirskoga područja [Identification and mapping of Natura 2000 forest habitats in Croatia (II) — 91F0, floodplain forests with *Quercus robur*, *Ulmus laevis*, *Ulmus minor*, *Fraxinus angustifolia*; 91L0, Illyrian oak-hornbeam forests]. Šumarski list 143, 461–467. https://doi.org/10.31298/sl.143.9-10.7

Purger, D., Lengyel, A., Kevey, B., Lendvai, G., Horváth, A., Tomić, Z., Csiky, J., 2014: Numerical classification of oak forests on loess in Hungary, Croatia and Serbia. Preslia 86(1), 47–66.

Purger, J. J. (ed.), 2008: Biodiversity studies along the Drava river. University of Pécs, Pécs, 328 pp.

Rauš, Đ., 1971: Fitocenološke osobine šuma na obroncima zapadnog dijela Fruške gore [Phytocoenological characteristics of forests on the slopes of the western part of Fruška gora]. Radovi Centra JAZU Vinkovci 1, 37–147.

Rauš, Đ., 1975: Vegetacijski i sinekološki odnosi šuma u bazenu Spačva [Vegetational and synecological relationships of forests in the Spačva basin]. Glasnik za šumske pokuse 18, 225–346.

Rauš, Đ., Vukelić, J., 1993: Šumska vegetacija u području utjecaja HE »Novo Virje« (Forest vegetation in the impact area of the »Novo Virje« power plant). Glasnik za šumske pokuse, posebno izdanje 4, 391–404.

Roleček, J., Tichý, L., Zelený, D., Chytrý, M., 2009: Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20, 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

ACCEPTED MANUSCRIPT

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

Škvorc, Ž., Ćuk, M., Zelnik, I., Franjić, J., Igić, R., Ilić, M., Krstonošić, D., Vukov, D., Čarni, A., 2020: Diversity of wet and mesic grasslands along a climatic gradient on the southern margin of the Pannonian Basin. Applied Vegetation Science 23, 676–697. https://doi.org/10.1111/avsc.12497

Stefanović, V., 1989: Cenološki dijapazon lužnjaka (*Quercus robur*) u Bosni i Hercegovini [Coenological range of pedunculate oak (*Quercus robur*) in Bosnia and Herzegovina]. Godišnjak Biološkog Instituta Univerziteta u Sarajevu 42, 73–84.

Stupar, V., 2020: Mesophilous *Quercus frainetto* dominated forests from western Balkans. South-East European Forestry 11(2), 97–110. https://doi.org/10.15177/seefor.20-15

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

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. https://doi.org/10.1111/avsc.12510

Tomić, Z., 2004: Šumarska fitocenologija [Forest phytocoenology]. Šumarski fakultet Univerziteta u Beogradu, Beograd.

Tomić, Z., Rakonjac, L., 2011: Survey of syntaxa of forest and shrub vegetation of Serbia. Folia Biologica et Geologica 52, 111–140.

Trinajstić, I., 2008: Biljne zajednice Republike Hrvatske [Plant communities of the Republic of Croatia]. Akademija šumarskih znanosti, Zagreb.

Vukelić, J., 1991: Šumske zajednice i staništa hrasta kitnjaka (*Quercus petraea* Liebl.) u gorju sjeverozapadne Hrvatske [Forest communities and habitats of sessile oak (*Quercus petraea* Liebl.) in the mountains of northwestern Croatia]. Glasnik za šumske pokuse 27, 1–82.

Vukelić, J., 2012: Šumska vegetacija Hrvatske [Forest vegetation of Croatia]. Šumarski fakultet, Sveučilište u Zagrebu, Državni zavod za zaštitu prirode, Zagreb.

Willner, W., 2006: The association concept revisited. Phytocoenologia 36, 67–76. https://doi.org/10.1127/0340-269X/2006/0036-0067

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

Willner, W., Čarni, A., Fernández-González, F., Pallas, J., Terzi, M., Theurillat, J.-P., 2024: Report 3 of the Committee for Change and Conservation of Names (CCCN). Vegetation Classification and Survey 5, 257–265. https://doi.org/10.3897/VCS.142803

Willner, W., Jiménez-Alfaro, B., Agrillo, E., Biurrun, I., Campos, J. A., Čarni, A., Casella, L., Csiky, J., Ćušterevska, R., Didukh, Y. P., Ewald, J., Jandt, U., Jansen, F., Kącki, Z., Kavgacı, A., Lenoir, J., Marinšek, A., Onyshchenko, V., Rodwell, J. S., Schaminée, J. H. J., Šibík, J., Škvorc, Ž., Svenning, J.-C., Tsiripidis, I., Turtureanu, P. D., Tzonev, R., Vassilev, K., Venanzoni, R., Wohlgemuth, T., Chytrý, M., 2017: Classification of European beech forests: A Gordian Knot? Applied Vegetation Science 20, 494–512. https://doi.org/10.1111/avsc.12299

ACCEPTED MANUSCRIPT

Zelený, D., Schaffers, A. P., 2012: Too good to be true: Pitfalls of using mean Ellenberg indicator values in vegetation analyses. Journal of Vegetation Science 23, 419–431. https://doi.org/10.1111/j.1654-1103.2011.01366.x

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Appendix 1. List of aggregated taxa

Aggregates (agg.)
Aconitum lycoctonum agg. = *Aconitum lycoctonum* subsp. *ranunculifolius*, *Aconitum lycoctonum* subsp. *vulparia*.
Arum maculatum agg. = *Arum maculatum*, *Arum italicum*, *Arum orientale*.
Carex muricata agg. = *Carex muricata*, *Carex divulsa*, *Carex spicata*.
Cardamine pratensis agg. = *Cardamine pratensis*, *Cardamine dentata*, *Cardamine matthioli*.
Crocus heuffelianus agg. = *Crocus heuffelianus*, *Crocus napolitanus*, *Crocus vernus*.
Helleborus atrorubens agg. = *Helleborus atrorubens*, *Helleborus croaticus*, *Helleborus dumetorum*.
Malus sylvestris agg. = *Malus pumila*, *Malus sylvestris*.
Myosotis palustris agg. = *Myosotis palustris*, *Myosotis scorpioides*.
Oxalis corniculata agg. = *Oxalis corniculata*, *Oxalis fontana*, *Oxalis stricta*.
Quercus petraea agg. = *Quercus petraea*, *Quercus dalechampii*.
Rubus fruticosus agg. = *Rubus fruticosus*, *Rubus plicatus*.
Stellaria media agg. = *Stellaria media*, *Stellaria neglecta*.
Viola hirta agg. = *Viola alba*, *Viola hirta*.

Species in broad sense (s. lat.)

Dactylis glomerata s. lat. = *Dactylis glomerata*, *Dactylis glomerata* subsp. *lobata*.
Fraxinus angustifolia s. lat. = *Fraxinus angustifolia*, *Fraxinus angustifolia* subsp. *oxycarpa*.
Lamium galeobdolon s. lat. = *Lamium galeobdolon* subsp. *galeobdolon*, *Lamium galeobdolon* subsp. *montanum*.
Melittis melissophyllum s. lat. = *Melittis melissophyllum*, *Melittis melissophyllum* subsp. *carpatica*.
Prunus spinosa s. lat. = *Prunus spinosa*, *Prunus spinosa* subsp. *dasyphylla*.
Pyrus communis s. lat. = *Pyrus communis* subsp. *communis*, *Pyrus communis* subsp. *pyraster*.
Ranunculus polyanthemos s. lat. = *Ranunculus polyanthemos*, *Ranunculus polyanthemos* subsp. *serpens*.
Symphytum tuberosum s. lat. = *Symphytum tuberosum*, *Symphytum tuberosum* subsp. *angustifolium*.

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Appendix 2. List of associations used throughout the text with authorship indicated

Alno glutinosae-Carpinetum betuli Issler 1924

Carici pilosae-Carpinetum betuli Neuhäusl et Neuhäuslová-Novotná 1964

Carpino betuli-Quercetum frainetto Stupar 2020

Carpino betuli-Quercetum roboris Anić 1959 em. Rauš 1969

Circaeo lutetianae-Carpinetum betuli Borhidi 2003

Convallario majalis-Carpinetum betuli Kevey 2008

Epimedio-Carpinetum betuli (Horvat 1938) Borhidi ex Soó 1964

Festuco drymeiae-Carpinetum Vukelić ex Marinček 1994

Helleboro dumetorum-Carpinetum Soó et Borhidi in Soó 1962

Lonicero caprifolii-Quercetum roboris (Rauš 1971) Marinček 1994

Polygonato latifolii-Carpinetum Michalko et Džatko 1965

Pruno padi-Carpinetum betuli (Marinček & Zupančič 1982) Marinček 1994

Pseudostellario-Carpinetum Accetto ex Novák et al. 2020

Stellario holosteae-Carpinetum betuli Oberdorfer 1957

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