

Phytosociological analysis of the lowland forests of peri-Pannonian Bosnia (SE Europe)

Pflanzensoziologische Analyse der Tieflandwälder des peri-pannonischen Bosniens (Südosteuropa)

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Abstract

Peri-Pannonian Bosnia was a forest-dominated landscape in the past. However, it has experienced extensive and continuous negative anthropogenic influence for over 200 years resulting in significant reduction and fragmentation of forest area. The remaining forests are not sufficiently studied, and little is known about their floristic composition, ecology and classification. In order to study the lowland forest from this area, Lijevče Polje (central part of the area) was chosen because of the relatively large patches of preserved forest. Phytosociological research was carried out from 2016 to 2023 using the Braun-Blanquet method, resulting in the compilation of a dataset consisting of 73 relevés of forest vegetation. These relevés were classified using TWINSpan into 15 units and afterwards merged into 8 groups, representing associations that were floristically and ecologically analyzed. One group, encompassing swamp alder forest, was identified as *Carici elongatae-Alnetum glutinosae*. Two groups represented forests with yearly fluctuations in soil moisture ranging from water-saturated to very dry soils. One of those groups, characterized by extreme soil moisture fluctuation, was attributed to *Pseudostellario-Quercetum roboris*, while the other group, with mild soil moisture fluctuation, was attributed to *Genisto elatae-Quercetum roboris*. Three groups were documented along streams and were attributed to: *Salicetum albae*, occupying the lowest river terraces; *Fraxino pannonicae-Ulmetum glabrae*, occurring on elevated river terraces; and *Stellario nemorum-Alnetum glutinosae*, confined to smaller streams. Two groups positioned in areas outside the flood zone were identified: *Convallario-Carpinetum*, occurring on old river terraces, and *Stellario-Carpinetum*, found on mountain foothills. Ellenberg indicator values were used to detect significant factors that shape the floristic composition of the analyzed plant communities. The distance from the nearest river and elevation were also useful in understanding ecological and topographic attributes of the communities. The driest and most widespread communities are those dominated by *Carpinus betulus* and *Quercus robur*. Riparian forests are confined to riverbanks while swamp forests are found in microdepressions that were not meliorated in the past. These findings contribute to the phytosociological understanding and classification of forest vegetation in peri-Pannonian Bosnia, providing a basis for future conservation efforts and classification.

Keywords: Braun-Blanquet method, Ellenberg indicator values, fluvisol, oak-hornbeam forests, plant communities, riparian habitats, wetlands

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

In the fifteenth century, around two-thirds of Bosnia was covered in dense forests, with the northern part standing out with well-preserved and quality forests (Begović 1960). This was abruptly changed by the large-scale deforestation that happened in the second half of the eighteenth century (Miklosich 1858, Jukić 1953, Mrgić 2007). By the end of the nineteenth century, intense exploitation had led to the disappearance of most of the large lowland oak forests in Bosnia and Herzegovina. This is testified by the fact that 3 260 000 oak trees were felled and exported in that period which was followed by the conversion of almost the entire lowlands into agricultural fields (Begović 1960, Memišević 2008). The last remaining old-growth *Quercus robur* forest in the country was cut down in 1895 (Begović 1960).

The vegetation of lowland forests in peri-Pannonian Bosnia can in fact mostly be attributed to azonal vegetation. This vegetation can be sequenced on several habitats including mesophilous *Quercus robur* and *Carpinus betulus* stands, mesohygrophilous stands of hardwood species composed of *Fraxinus angustifolia*, *Quercus robur*, *Ulmus minor*, *U. laevis* and softwood *Populus alba*, hygrophilous riverine stands dominated by softwood tree species such as *Salix alba*, *S. euxina* and *Populus nigra* and stands dominated by *Alnus glutinosa* both along small streams as well as in swamps (Glišić 1964, Stefanović et al. 1983, Stefanović 1989, Koljanin et al. 2023). These habitats are considered important from a conservation point of view and are listed under the EU Habitats Directive (Council of the European Communities 1992). However, in peri-Pannonian Bosnia forests are mostly fragmented, structurally degraded, and have altered water regimes due to long-lasting negative human impact which was mostly driven by the need for agricultural production. But even forest patches within typical lowland agricultural landscapes can serve as biodiversity hotspots and provide crucial ecosystem services such as water regulation, flood prevention, carbon sequestration, soil stabilization, timber, wild food production, etc. (Decocq et al. 2016). Several floristic studies on a national level have confirmed the importance of those forests for the survival of endangered plant species (Milanović et al. 2013, Koljanin et al. 2021).

Despite the ecological significance of lowland forests in peri-Pannonian Bosnia, they have remained phytosociologically insufficiently studied in contrast to neighboring Croatia where those forests are preserved, economically important and have a long history of studies (Vukelić 2012, Koljanin et al. 2023). In Bosnia, only six relevés of *Quercus robur* stands from this area have been published (Fukarek 1975) with the addition of several descriptions of lowland vegetation types (Glišić 1964, Obratil 1974, Fukarek 1975, Stefanović et al. 1983, Stefanović 1989). The lack of relevés had a significant effect, causing the peri-Pannonian Bosnia to be under-sampled (Košir et al. 2013, Novák et al. 2023) or even completely neglected (Douda et al. 2016) in large-scale phytosociological analyses which all lead to a gap in knowledge regarding floristic composition, ecology and the classification of those forests from this part of Europe. The situation is similar in other parts of Bosnia and Herzegovina where only several relevés (Fabijanić et al. 1963, Redžić et al. 1992,) and two synoptic tables (Ritter-Studnička & Grgić 1971, Milanović & Stupar 2017) of riparian forest

and scrub vegetation have been published. It should also be noted that swamp forest communities were completely neglected in the past and that there are no published relevés of this type of vegetation.

The research aims to clarify the floristic composition of the forests that are present in Lijevče, assess the ecological factors influencing their floristic composition and provide a classification scheme based on the collected data. Moreover, this study will contribute to a broader understanding of forest ecosystems in peri-Pannonian Bosnia and the Pannonian region by providing new data for future analyses

2. Methods

2.1 Study area

The majority of peri-Pannonian Bosnia (northern Bosnia and Herzegovina) is covered by flat surfaces that are parts of river floodplains. The soils are mostly developed on clay, sand and gravel substrates (Stefanović et al. 1983). The climate of this area is temperate with no pronounced dry season but with hot summer (Beck et al. 2018). The zonal vegetation of this part is attributed to the *Quercus petraea*-*Carpinus betulus* zonal forest that is differentiated from more southern vegetation zones by the presence of mesophilous European and Eurasian species (Stupar & Čarni 2017). From a floristic point of view, this zone lacks endemic Balkan species (Lubarda et al. 2014). In general, it is more similar to Central Europe which was recognised by Stefanović et al. (1983) who considered this part a Central European region.

The field research took place in Lijevče Polje (Fig. 1), located at the southwestern edge of the Pannonian plain. This flat, triangular area is bordered by the rivers Sava on the north, Vrbas on the east and south and Mount Kozara in the west. The total study area is around 465 km². The lowest point is at an elevation of 90 m which is located in the northeastern part of the study area at the place where the Vrbas flows into the Sava. Those two rivers had a significant impact in the past on the relief of Lijevče Polje depositing large amounts of alluvial material, thus forming the lower and middle, alluvial, terraces (Lepirica 2009). On the other hand, the higher, diluvial, terraces were created by the erosive processes from Mount Kozara (Cvijić 2018) that led to the accumulation of substrate and the formation of the Kozara foothills.

In Lijevče, deforestation was followed by the conversion into agricultural land and intensive hydro-meliorative works. Most of the hydro-meliorative works happened in the period from 1901 to 1980 (Mandić 2011) and included the construction of embankments along the rivers Sava and Vrbas, the establishment of a channel network, the construction of embankments around smaller watercourses, the installation of pumping stations, etc. Because of those works, natural and semi-natural flooding regimes were preserved only in narrow stripes along the rivers Vrbas and Sava. Today, this area has a complex network of natural and artificial streams that discharge either into the Vrbas or the Sava. These rivers play a crucial role in groundwater level dynamics (Marković et al. 2009). From a vegetation point of view, Lijevče is now mainly covered by non-forest vegetation (mostly arable land and meadows) with only around 15% of forests (European Environment Agency 2018) that are most often improperly managed and with altered flooding regimes (Mrgić 2007, Milanović et al. 2016, Mihaljčić 2018).

2.2 Data collection and preparation

In the period from 2016 to 2023 a total of 73 relevés have been made in Lijevče Polje using the Central European phytosociological method (Braun-Blanquet 1964). Only stands where no signs of recent logging or disturbance could be observed were sampled. During the vegetation survey, the following scale for vertical layers was applied: A – tree layer (more than 10 m), B – shrubs and young trees under 10 m and seedlings, C – herb layer. All collected relevés along with the recorded geographical coordinates (WGS84), soil type, bedrock, elevation and coverage per layer were entered

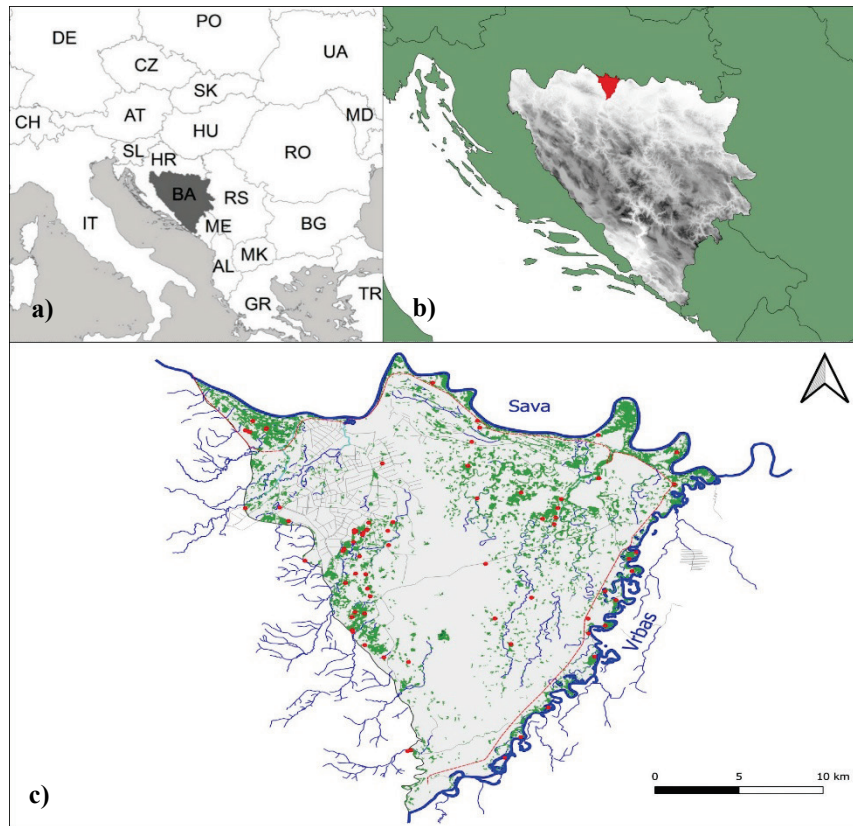


Fig. 1. a) Location of Bosnia and Herzegovina in Southeastern Europe. **b)** Position of the study area (red) in Bosnia and Herzegovina. **c)** Location of the study area (grey) and the rivers Sava and Vrbas. Wooded areas are indicated by green colour. Red dots indicate the position of relevés used in the present analysis. The red line indicates the position of the river embankment. Blue lines indicate watercourses. Grey lines indicate canals.

Abb. 1. a) Lage von Bosnien-Herzegowina in Südosteuropa. **b)** Lage des Untersuchungsgebiets (rot) in Bosnien und Herzegowina. **c)** Lage des Untersuchungsgebiets (grau) und der Flüsse Sava und Vrbas. Bewaldete Flächen sind durch grüne Farbe gekennzeichnet. Rote Punkte zeigen die Position der in der vorliegenden Studie verwendeten Vegetationsaufnahmen an. Die rote Linie markiert die Flussufer. Die blauen Linien zeigen Wasserläufe und die grauen Kanäle an.

into a Turboveg database (Hennekens & Schaminée 2001) and exported to Juice software (Tichý 2002) for further analysis. Species nomenclature followed Euro+Med (2006–) while syntaxonomical concepts and nomenclature of higher syntaxa followed Mucina et al. (2016). Taxonomically complex groups or species that could not always be certainly determined were aggregated: *Galium palustre* agg. (*G. palustre* and *G. elongatum*), *Fraxinus americana* agg. (*F. americana* and *F. pennsylvanica*), *Ranunculus auricomus* agg. and *Rubus fruticosus* agg. Taxa that could not be identified at the species level were excluded from the analysis. As a part of the preparation for the subsequent numerical analysis and in order to eliminate the possibility of inconsistent layer sampling, species found in multiple layers were merged into a single layer. The dataset used in analyses is available in the supplements E1 and E2. Before numerical analysis, species appearing in one or two relevés were removed, as this proved to be beneficial in reducing noise in the statistical analysis (Juvan et al. 2013, Stupar et al. 2015, Koljanin et al. 2023).

2.3 Data analysis

Classification of the dataset was done using the TWINSpan algorithm (Hill 1979) with pseudo-species levels set at 0, 5, 10, 25, and 50%. A minimum group size was set at five relevés. Resulting TWINSpan clusters were then combined based on expert judgement to form ecologically and floristically homogeneous groups corresponding to association levels. Combining was done only with sister clusters. Although imperfectly formalized, this method has often been used and proved to be effective in forming clusters interpretable as ecologically and floristically coherent groups that correspond to predefined units (Bergmeier 2002, Roleček 2005, Gholizadeh et al. 2019, Novák et al. 2023). Diagnostic species for each group were determined by calculating fidelity using the ϕ (Φ) coefficient (Tichý & Chytrý 2006), considering species with $\Phi \geq 0.40$ as diagnostic. Species whose diagnostic value lacked statistical significance at the level of $p < 0.05$ determined via Fisher's test, were not considered diagnostic. Constant species were those occurring in over 50% of the relevés. Dominant species were defined as those with over 50% cover in more than half of the relevés from the group. Average unweighted Ellenberg indicator values (EIV) were calculated for each relevé, following Pignatti et al. (2005). Shortest straight line distances from the relevé plot to the nearest large river (Sava or Vrbas) and elevation were measured in QGIS (QGIS Geographic Information System, Version 3.12.3, www.qgis.org). To detect the main ecological factors and topographical properties driving the differentiation of clusters, statistically significant differences in ecological factors and measured data between sister clusters were identified. This was done only at the first two levels of the TWINSpan division because of the small number of relevés. Statistical significance ($p < 0.05$) in measured data (elevation and distance from the nearest river) between sister clusters was determined using the Mann-Whitney U test in Statistica Version 14.0 (TIBCO Software Inc.), while analysis of variance (ANOVA) for calculated data (EIV) was performed using a modified permutation test (Zelený & Schaffers 2012) in Juice. To clarify the classification and relationships between groups in the dataset, the relevés were projected onto a DCA (Detrended Correspondence Analysis) diagram. Data was transformed with pseudospecies levels set at 0, 5, 10, 25, and 50%. Measured parameters and calculated data that proved to be statistically significant were passively projected on the DCA diagram. Statistical significance ($p < 0.05$) of calculated values concerning the first two DCA axes was tested using a modified permutation test (Zelený & Schaffers 2012) in Juice while statistical significance ($p < 0.05$) of measured values was determined using Spearman's correlation coefficient in Statistica software.

3. Results

3.1 Classification

Using TWINSpan, the dataset was divided up to the fourth level. The eighth cluster from the third level was not further divided because of the lack of a minimum number of relevés for division. This resulted in the forming of fifteen initial TWINSpan clusters. Upon revising these clusters, eight ecologically and floristically homogeneous groups corresponding to association level were created. A representation of the subjective combination of sister clusters is shown in the dendrogram, supplemented by the average values of calculated and measured values which, upon comparing sister clusters, were found to be statistically significant (Fig. 2). A short synoptic table is also presented (Table 1). At the first level, regularly flooded and light-demanding forests were separated from rarely flooded and shaded forests. This is supported by the fact that the differences in EIV for light and moisture between sister clusters were statistically significant at this level. At the second level, four distinct units were formed. The first unit encompasses forests where water stagnates for a long period while the soils are relatively poor in nutrients and bases. The second unit comprises shorter flooded stands that are richer in bases and nutrients. The differences in values for temperature, moisture, soil reaction, and distance from the river proved to be

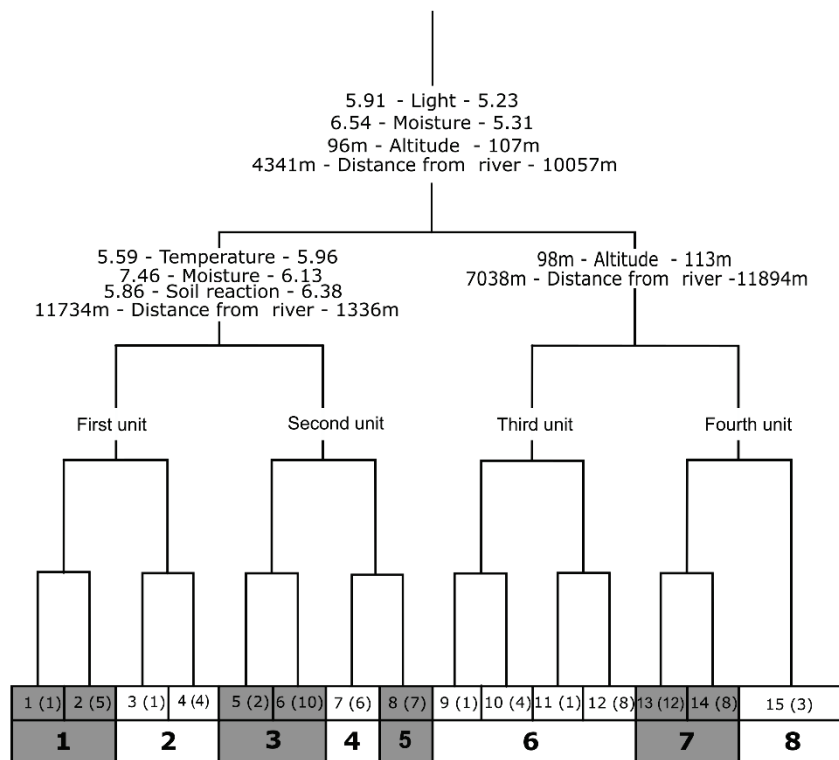


Fig. 2. TWINSPAN classification dendrogram. Statistically significant differences of Ellenberg values and measured parameters between sister clusters are shown with mean values. The numbers in the upper part of the table in front of the parentheses represent the sequence number of the TWINSPAN cluster, while the numbers in parentheses show the number of relevés in the TWINSPAN cluster. The bold numbers in the lower part of the table correspond to numbers of vegetation units used in Figures 2–4 and to group numbers used in the text. First unit – forests with long stagnation of water. Second unit – forests on nutrient-rich soils near rivers, moderately to shortly flooded. Third unit – rarely flooded forests on nutrient-rich pseudogley soils. Fourth unit – forests on dystrophic, deep soils at foothills with weak influence of floods.

Abb. 2. Dendrogramm der TWINSPAN-Klassifizierung. Statistisch signifikante Unterschiede der Ellenberg-Werte und der gemessenen Parameter zwischen Schwestergruppen werden im Dendrogramm mit Mittelwerten angezeigt. Die Zahlen im oberen Teil der Tabelle vor den Klammern sind die Nummer der TWINSPAN-Cluster, während die Zahl in Klammern die Anzahl der Vegetationsaufnahmen im TWINSPAN-Cluster anzeigt. Die fett gedruckten Zahlen im unteren Teil der Tabelle entsprechen den Nummern der Vegetationseinheiten in Abbildungen 2–4 und den im Text verwendeten Gruppennummern. Erste Einheit: Wälder mit langer Wasserüberstauung. Zweite Einheit: Wälder auf nährstoffreichen, mäßig bis kurz überfluteten Böden in der Nähe von Flüssen. Dritte Einheit: selten überflutete Wälder auf nährstoffreichen Pseudogley-Böden. Vierte Einheit: Wälder an Gebirgsausläufern auf nährstoffarmen, tiefgründigen Böden mit schwachem Überschwemmungseinfluss.

Table 1. Abbreviated synoptic table of the analysed vegetation of Lijevče Polje. The table shows all diagnostic species and the fifteen most frequent species in the dataset. Frequencies of species in each group are presented as percentages, with phi values multiplied by 100 shown in superscript. Diagnostic species (*phi* values higher than 0.40) for each group are shaded. Group numbers correspond to those used throughout the text.

Tabelle 1. Gekürzte Übersichtstabelle der analysierten Vegetation von Lijevče Polje. Die Tabelle zeigt alle diagnostischen Arten und die fünfzehn häufigsten Arten im Datensatz. Die Stetigigkeiten der Arten in jeder Einheit werden als Prozentsätze dargestellt, mit *Phi*-Werten (mit 100 multipliziert) in hochgestellter Schrift. Diagnostische Arten (*Phi*-Werte größer als 0,40) für jede Einheit sind grau hinterlegt. Die Nummern der Vegetationseinheiten entsprechen den im Text verwendeten.

Group no.	1	2	3	4	5	6	7	8
No. of relevés in the group	6	5	12	6	7	14	20	3
Tree species								
<i>Quercus robur</i>	100 ⁻⁻⁻	20 ⁻⁻⁻	100 ^{29.6}	33 ⁻⁻⁻	29 ⁻⁻⁻	86 ⁻⁻⁻	95 ^{25.7}	33 ⁻⁻⁻
<i>Alnus glutinosa</i>	---	100 ^{60.6}	---	---	14 ⁻⁻⁻	---	10 ⁻⁻⁻	100 ^{60.6}
<i>Fraxinus angustifolia</i> subsp. <i>oxycarpa</i>	17 ⁻⁻⁻	100 ^{38.1}	100 ^{38.1}	---	57 ⁻⁻⁻	64 ⁻⁻⁻	25 ⁻⁻⁻	33 ⁻⁻⁻
<i>Ulmus minor</i>	---	40 ⁻⁻⁻	92 ^{30.7}	67 ⁻⁻⁻	57 ⁻⁻⁻	71 ⁻⁻⁻	15 ⁻⁻⁻	67 ⁻⁻⁻
<i>Salix alba</i>	---	---	---	100 ¹⁰⁰	---	---	---	---
<i>Ulmus laevis</i>	---	20 ⁻⁻⁻	33 ⁻⁻⁻	67 ^{47.3}	14 ⁻⁻⁻	7 ⁻⁻⁻	5 ⁻⁻⁻	---
<i>Acer negundo</i>	---	40 ⁻⁻⁻	25 ⁻⁻⁻	67 ³⁵	71 ^{39.1}	---	5 ⁻⁻⁻	---
<i>Juglans regia</i>	---	---	---	17 ⁻⁻⁻	71 ^{69.5}	7 ⁻⁻⁻	---	---
<i>Populus alba</i>	17 ⁻⁻⁻	---	17 ⁻⁻⁻	---	43 ^{42.9}	---	---	---
<i>Populus nigra</i>	---	---	---	33 ⁻⁻⁻	43 ^{42.9}	---	---	---
<i>Acer campestre</i>	---	20 ⁻⁻⁻	75 ⁻⁻⁻	---	43 ⁻⁻⁻	100 ^{41.8}	55 ⁻⁻⁻	67 ⁻⁻⁻
<i>Fagus sylvatica</i>	---	---	---	---	---	---	25 ^{47.5}	---
<i>Tilia platyphyllos</i>	---	---	---	---	---	---	20 ^{42.4}	---
<i>Carpinus betulus</i>	67 ⁻⁻⁻	---	17 ⁻⁻⁻	---	---	71 ⁻⁻⁻	100 ^{42.3}	100 ⁻⁻⁻
<i>Prunus avium</i>	---	---	---	---	29 ⁻⁻⁻	79 ⁴⁴	75 ⁴¹	33 ⁻⁻⁻
<i>Tilia cordata</i>	17 ⁻⁻⁻	---	---	---	---	7 ⁻⁻⁻	35 ⁴⁰	---
Group 1								
<i>Carex elongata</i>	100 ^{73.2}	60 ^{36.1}	8 ⁻⁻⁻	---	---	---	---	---
<i>Poa palustris</i>	50 ^{68.3}	---	---	---	---	---	---	---
<i>Juncus effusus</i>	83 ^{68.2}	20 ⁻⁻⁻	8 ⁻⁻⁻	---	---	---	20 ⁻⁻⁻	---
<i>Lysimachia vulgaris</i>	83 ^{58.6}	40 ⁻⁻⁻	8 ⁻⁻⁻	33 ⁻⁻⁻	---	---	---	---
<i>Glyceria fluitans</i>	50 ^{55.2}	20 ⁻⁻⁻	---	---	---	---	---	---
<i>Frangula alnus</i>	100 ^{52.7}	80 ^{36.7}	17 ⁻⁻⁻	17 ⁻⁻⁻	---	---	25 ⁻⁻⁻	33 ⁻⁻⁻
Group 2								
<i>Stachys palustris</i>	17 ⁻⁻⁻	100 ^{78.7}	17 ⁻⁻⁻	17 ⁻⁻⁻	---	---	---	---
<i>Euphorbia palustris</i>	---	60 ^{75.3}	---	---	---	---	---	---
<i>Persicaria hydropiper</i>	17 ⁻⁻⁻	80 ^{65.3}	17 ⁻⁻⁻	17 ⁻⁻⁻	---	---	---	---
<i>Carex elata</i>	17 ⁻⁻⁻	60 ^{64.7}	---	---	---	---	---	---
<i>Salix cinerea</i>	17 ⁻⁻⁻	60 ^{64.7}	---	---	---	---	---	---
<i>Echinocystis lobata</i>	---	100 ^{57.8}	42 ⁻⁻⁻	50 ⁻⁻⁻	43 ⁻⁻⁻	---	5 ⁻⁻⁻	---
<i>Calystegia sepium</i>	---	60 ^{56.9}	---	33 ⁻⁻⁻	---	---	---	---
<i>Lythrum salicaria</i>	50 ^{26.3}	80 ^{53.9}	25 ⁻⁻⁻	17 ⁻⁻⁻	---	---	---	---
<i>Solanum dulcamara</i>	17 ⁻⁻⁻	60 ^{53.7}	8 ⁻⁻⁻	17 ⁻⁻⁻	---	---	---	---
<i>Lycopus europaeus</i>	33 ⁻⁻⁻	60 ^{53.7}	8 ⁻⁻⁻	---	---	---	---	---
<i>Dryopteris carthusiana</i>	33 ⁻⁻⁻	60 ^{45.7}	---	---	---	---	---	33 ⁻⁻⁻
<i>Galium palustre</i> agg.	50 ⁻⁻⁻	80 ^{42.8}	67 ^{31.7}	33 ⁻⁻⁻	---	---	---	---

Group no.	1	2	3	4	5	6	7	8
No. of relevés in the group	6	5	12	6	7	14	20	3
Group 3								
<i>Leucojum aestivum</i>	---	20	83 ^{72.3}	17	---	---	---	---
<i>Ranunculus auricomus</i> agg.	---	---	83 ⁶³	---	---	50 ^{30.6}	15	---
<i>Clematis viticella</i>	---	---	42 ⁶²	---	---	---	---	---
<i>Cardamine pratensis</i>	---	---	67 ^{54.9}	---	14	---	5	33
<i>Amorpha fruticosa</i>	---	40	75 ^{54.9}	33	---	---	---	---
<i>Convallaria majalis</i>	---	---	42 ^{52.7}	---	---	7	5	---
<i>Genista tinctoria</i>	---	---	25 ^{47.5}	---	---	---	---	---
<i>Carex remota</i>	---	60	83 ^{45.7}	33	---	14	5	33
<i>Rhamnus cathartica</i>	---	---	33 ^{43.7}	---	14	---	---	---
Group 4								
<i>Parthenocissus quinquefolia</i>	---	20	---	50 ^{48.6}	14	---	---	---
<i>Silene baccifera</i>	---	---	---	33 ^{43.7}	14	---	---	---
Group 5								
<i>Brachypodium sylvaticum</i>	---	---	---	---	71 ^{58.4}	14	5	33
<i>Aegopodium podagraria</i>	---	---	---	17	71 ^{55.5}	7	5	33
<i>Poa trivialis</i>	17	---	33	---	57 ^{46.3}	7	---	---
<i>Hedera helix</i>	---	40	25	50	100 ^{45.1}	71 ^{23.2}	10	33
<i>Erigeron annuus</i>	---	---	8	---	29 ^{43.2}	---	---	---
Group 6								
<i>Corydalis cava</i>	---	---	---	---	---	43 ^{62.9}	---	---
<i>Ligustrum vulgare</i>	---	---	8	17	43	100 ^{60.2}	25	33
<i>Viola odorata</i>	---	---	---	---	---	43 ^{58.8}	5	---
<i>Viola reichenbachiana</i>	---	---	8	---	---	64 ^{58.2}	30	---
<i>Primula acaulis</i>	---	---	---	---	---	36 ^{57.2}	---	---
<i>Polygonatum hirtum</i>	---	---	---	---	---	36 ^{57.2}	---	---
<i>Geum urbanum</i>	---	---	---	---	14	57 ^{56.4}	15	---
<i>Veronica hederifolia</i>	---	---	---	---	29	57 ^{52.6}	10	---
<i>Arum maculatum</i>	---	---	8	17	57	100 ^{52.4}	25	67
<i>Scilla bifolia</i>	---	---	---	---	---	29 ^{50.9}	---	---
<i>Anemone ranunculoides</i>	---	---	8	---	---	43 ^{50.1}	10	---
<i>Carex sylvatica</i>	---	---	8	---	43	57 ^{45.1}	10	---
<i>Smyrnium perfoliatum</i>	---	---	---	---	---	21 ^{43.9}	---	---
<i>Galium aparine</i>	---	---	33	67	86 ^{31.5}	100 ^{42.4}	35	33
<i>Adoxa moschatellina</i>	---	---	8	---	---	64 ⁴²	20	67
<i>Geranium phaeum</i>	---	---	---	---	---	29 ^{41.9}	10	---
Group 7								
<i>Veratrum album</i>	---	---	---	---	---	---	55 ⁵³	33
<i>Anemone nemorosa</i>	17	---	---	---	---	50	70 ⁴⁵	33
<i>Polygonatum multiflorum</i>	---	---	8	---	---	29	60 ^{44.8}	33
Group 8								
<i>Athyrium filix-femina</i>	---	---	---	---	---	---	15	67 ^{70.5}
<i>Stellaria holostea</i>	17	---	---	---	---	50	65 ³⁰	100 ^{59.2}
<i>Carex brizoides</i>	67	---	---	---	---	21	65 ^{27.1}	100 ^{55.6}
<i>Solidago gigantea</i>	17	---	---	33	14	---	---	67 ^{51.4}
<i>Urtica dioica</i>	---	80 ^{30.9}	42	33	57	7	---	100 ^{46.4}

Group no.	1	2	3	4	5	6	7	8
No. of relevés in the group	6	5	12	6	7	14	20	3
Diagnostic species for more than one group								
<i>Peucedanum palustre</i>	83 ^{60.3}	---	8	---	---	---	---	67 ^{44.5}
<i>Carex riparia</i>	83 ^{53.3}	80 ^{50.3}	25	---	---	---	---	---
<i>Iris pseudacorus</i>	100 ^{41.1}	100 ^{41.1}	67 ^{15.8}	67	---	---	---	33
<i>Caltha palustris</i>	---	60 ^{41.5}	17	---	---	---	---	67 ⁴⁸
Other species with high frequency								
<i>Acer tataricum</i>	100	20	92	17	14	86	90 ^{19.9}	100
<i>Rubus caesius</i>	---	100 ^{28.5}	83 ^{15.4}	83	86	43	15	100
<i>Cornus sanguinea</i>	---	60	92 ^{22.2}	100 ^{28.7}	100 ^{28.7}	79	10	67
<i>Corylus avellana</i>	17	40	17	---	43	86 ^{31.3}	55	100
<i>Galeopsis speciosa</i>	17	80	33	33	57	43	45	33
<i>Crataegus monogyna</i>	---	---	75 ²⁵	17	71	79 ^{27.8}	30	67
<i>Ficaria verna</i>	---	---	17	---	57	79 ^{27.9}	85 ^{32.8}	100
<i>Sambucus nigra</i>	---	20	8	---	71	93 ^{38.8}	45	100
<i>Glechoma hederacea</i>	---	40	75 ^{27.5}	17	71	36	10	67
<i>Euonymus europaeus</i>	---	20	25	17	71	86 ^{37.4}	50	33
<i>Lysimachia nummularia</i>	17	40	75 ^{31.5}	83 ^{38.1}	29	---	5	33

statistically significant between these two clusters. The third unit is comprised of rarely flooded stands on shallow pseudogley soils formed on old river deposits. These soils are influenced by groundwater and have high values of bases and nutrients. The fourth unit encompasses stands at the foothills of Mount Kozara on deep and dystrophic soils. These soils are rarely flooded by water flowing from the mountain, resulting in limited nutrient deposition. Statistically significant differences between the third and fourth units are elevation and distance from the river.

Eight clusters appeared at the third level of division and fifteen clusters appeared at the fourth level of division revealing less distinct patterns. The fourth level was considered sufficient to form units corresponding to associations and therefore, no further division was made. Through the combination of 15 TWINSpan clusters of the last division level, eight groups were formed. Clusters 1 and 2 encompass stands dominated by *Quercus robur*, in which the herb layer is dominated by species characteristic for swamp forests. Clusters 3 and 4 consist of swamp stands of *Alnus glutinosa* in micro-depressions. Clusters 5 and 6 consist of stands dominated by *Fraxinus angustifolia* and usually *Quercus robur* with a mix of mesohygrophilous and marsh species in the understory. Cluster 7 contains *Salix alba* stands developed on the lowest terraces of large rivers. Cluster 8 encompasses a mixed stand of hardwood and softwood trees and is distributed on elevated, water-permeable terraces along large rivers. Clusters 9, 10, 11, and 12 encompass mesophilous to mesohygrophilous species-rich *Quercus robur* and *Carpinus betulus* forests with frequent occurrence of *Fraxinus angustifolia* on the middle and high alluvial terraces that are usually outside the flood zone. Clusters 13 and 14 include forests of *Quercus robur* and *Carpinus betulus*, with frequent occurrences of *Fagus sylvatica*, found in the Kozara foothills (diluvial terraces). Cluster 15 features *Alnus glutinosa* stands situated along small streams.

3.2 Syntaxonomical scheme

The suggested syntaxonomic interpretation of the groups is:

Class: *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946

Order: *Alnetalia glutinosae* Tx. 1937

All: *Alnion glutinosae* Malcuit 1929

Ass: *Carici elongatae-Alnetum glutinosae* Tüxen 1931 (group 2)

Class: *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968

Order: *Alno-Fraxinetalia excelsioris* Passarge 1968

All: *Alno-Quercion roboris* Horvat 1950

Ass: *Pseudostellario-Quercetum roboris* Accetto 1973 (group 1)

Ass: *Genisto elatae-Quercetum roboris* Horvat 1938 (group 3)

All: *Fraxino-Quercion roboris* Passarge 1968

Ass: *Fraxino pannonicae-Ulmetum glabrae* Aszod 1935 corr. Soo 1963
(group 5)

All: *Alnion incanae* Pawłowski et al. 1928

Ass: *Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957 (group 8)

Class: *Salicetea purpureae* Moor 1958

Order: *Salicetalia purpureae* Moor 1958

All: *Salicion albae* Soó 1951

Ass: *Salicetum albae* Issler 1926, (group 4)

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

Order: *Carpinetalia betuli* P. Fukarek 1968

All: *Carpinion betuli* Issler 1931

Ass: *Convallario majalis-Carpinetum betuli* Kevey 2008 (group 6)

Ass: *Stellario holosteae-Carpinetum betuli* Oberdorfer 1957 (group 7)

3.3 Overview of associations

***Carici elongatae-Alnetum glutinosae* (group 2)**

Number of relevés: 5.

Site conditions and distribution: microdepressions at lower, water-impermeable terraces of the Sava river (Kočićevo, Laminci, Bardača).

Diagnostic species: *Alnus glutinosa*, *Salix cinerea*, *Caltha palustris*, *Calystegia sepium*, *Carex elata*, *C. riparia*, *Dryopteris carthusiana*, *Echinocystis lobata*, *Euphorbia palustris*, *Galium palustre* agg., *Iris pseudacorus*, *Lycopus europaeus*, *Lythrum salicaria*, *Persicaria hydropiper*, *Solanum dulcamara* and *Stachys palustris*.

Constant species: *Alnus glutinosa*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Cornus sanguinea*, *Frangula alnus*, *Salix cinerea*, *Viburnum opulus*, *Rubus caesius*, *Caltha palustris*, *Calystegia sepium*, *Carex elata*, *C. elongata*, *C. remota*, *C. riparia*, *Dryopteris carthusiana*, *Echinocystis lobata*, *Euphorbia palustris*, *Galeopsis speciosa*, *Galium palustre* agg., *Iris pseudacorus*, *Lycopus europaeus*, *Lythrum salicaria*, *Persicaria hydropiper*, *Ranunculus repens*, *Solanum dulcamara*, *Stachys palustris* and *Urtica dioica*.

Dominant species: *Alnus glutinosa*.

This community occurs in microdepressions on the lowest clay terraces around cold-water streams (Ažaba and Matura) in the northeastern part of Lijevo (Fig. 3). During high water levels, these streams fill the microdepressions that retain water long after the streams have receded. The groundwater level is kept high by the river Sava which helps to keep high moisture levels in the soil even during the summer months. The soils are gleyic with all-year-round wet upper layers. *Alnus glutinosa* dominates the tree canopy, while *Fraxinus angustifolia* is usually present but always with small cover. The shrub layer is composed of hygrophytes such as *Frangula alnus* and *Salix cinerea*. The herb layer is dominated by hydrophilous species capable of tolerating long-lasting flood and oxygen deprivation. Therefore, graminoids such as *Carex elongata*, *C. riparia*, and *C. elata* dominate. Other helophytes, such as *Iris pseudacorus*, *Galium palustre* agg., *Stachys palustre*, *Lythrum salicaria*, etc., are commonly present.

***Pseudostellario-Quercetum roboris* (group 1)**

Number of relevés: 6.

Site conditions and distribution: microdepressions at the Kozara foothills (Elezačić and Berek).

Diagnostic species: *Frangula alnus*, *Carex elongata*, *C. riparia*, *Glyceria fluitans*, *Iris pseudacorus*, *Juncus effusus*, *Lysimachia vulgaris*, *Peucedanum palustre* and *Poa palustris*.

Constant species: *Acer tataricum*, *Carpinus betulus*, *Quercus robur*, *Frangula alnus*, *Carex brizoides*, *C. elongata*, *C. riparia*, *Iris pseudacorus*, *Juncus effusus*, *Lysimachia vulgaris* and *Peucedanum palustre*.

Dominant species: *Quercus robur*.

Those stands are confined to microdepressions on the flat foothills of Mount Kozara (Fig. 3). In early spring, those microdepressions are filled with atmospheric water and streams descending from nearby hills. The stands are developed on epigleyic or gleyic, nutrient-poor and base-poor soils (Fig. 4). The deeper parts of the soil are water saturated only in the autumn-spring period. As the soil consists of heavy clay, microdepressions retain water for a prolonged period. Sometimes, stagnation lasts until mid-summer. After water withdrawal, the upper layer of soil dries out, leading to extreme drought which shapes unique species composition. Typically, *Quercus robur* is present in the tree layer and is occasionally accompanied by *Populus tremula*. Other species known to survive in extreme wet conditions such as *Fraxinus angustifolia* and *Alnus glutinosa* are completely absent. The shrub layer is composed of *Acer tataricum* and *Frangula alnus*, while *Carpinus betulus*, although constant, is present mainly with a low cover value. As the wet period lasts very long, the herb layer is usually comprised of sedges capable of withstanding both extremely wet and dry periods such as *Carex elongata* and *C. riparia*. Other hydrophilous species such as *Iris pseudacorus*, *Peucedanum palustre* and *Poa palustris* are commonly present. Species characteristic for compact and heavy soils such as *Carex brizoides* and *Juncus effusus* are also common.

***Genisto elatae-Quercetum roboris* (group 3)**

Number of relevés: 12.

Site conditions and distribution: wet clay soils along the Sava river (Vrbaška, Milava, Poljanska, Dubrave, Mačkovac, Bajinci and Bardača) and the Jurkovića stream (Berek).

Diagnostic species: *Amorpha fruticosa*, *Rhamnus cathartica*, *Clematis viticella*, *Genista tinctoria*, *Cardamine pratensis*, *Carex remota*, *Convallaria majalis*, *Leucojum aestivum* and *Ranunculus auricomus* agg.

Constant species: *Acer campestre*, *A. tataricum*, *Amorpha fruticosa*, *Cardamine pratensis*, *Carex remota*, *Cornus sanguinea*, *Crataegus monogyna*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Galium palustre* agg., *Glechoma hederacea*, *Iris pseudacorus*, *Leucojum aestivum*, *Lysimachia nummularia*, *Quercus robur*, *Ranunculus auricomus* agg., *R. repens*, *Rubus caesius* and *Ulmus minor*.

Dominant species: *Fraxinus angustifolia* subsp. *oxycarpa*.

This community is distributed in concave micro-relief shapes adjacent to the Sava river or, more rarely, along smaller tributaries (Fig. 3). During the wet period of the year, an increase in the river water level will cause flooding. When the water level of the river drops and the river recedes into its riverbed, water will still reside in concave micro-relief shapes due to the impermeable substrate. Stagnation causes a lack of oxygen in the soil which lasts from several weeks to several months. The duration of the flood is much shorter in comparison to group 1 (*Pseudostellario-Quercetum roboris*). Water retracts during late spring and summer, leading to the upper part of the soil desiccation. Therefore, the tree layer consists of *Fraxinus angustifolia* and usually *Quercus robur*. Shrub layer is mainly composed of mesophilous and mesohygrophilous species such as *Rubus caesius*, *Amorpha fruticosa*, *Cornus sanguinea*, *Acer tataricum*, etc. The herb layer includes mesohygrophilous species that can withstand the stagnation of the water such as *Carex remota*, *Ranunculus auricomus*, *Lysimachia nummularia*, *Leucojum aestivum* etc. while mesophytes are usually rare.

***Salicetum albae* (group 4)**

Number of relevés: 6.

Site conditions and distribution: banks of the rivers Sava (Greda), Vrbas (Kukulji, Razboj, Petroševci and Laktaši) and of the stream Matura (Bardača).

Diagnostic species: *Salix alba*, *Ulmus laevis*, *Parthenocissus quinquefolia* and *Silene baccifera*.

Constant species: *Acer negundo*, *Salix alba*, *Ulmus laevis*, *U. minor*, *Cornus sanguinea*, *Rubus caesius*, *Galium aparine*, *Iris pseudacorus* and *Lysimachia nummularia*.

Dominant species: *Salix alba* and *Rubus caesius*.

The community is present along the Sava and Vrbas rivers while some degraded and fragmented stands are also present along the Matura stream in Bardača (Fig. 3). As *Salix alba* communities are found in the lowest positions along rivers they are influenced by frequent and long-lasting flooding. During the flood, water currents will mechanically move the soil, uproot poorly rooted and break fragile plants. Due to regular flooding and low position, the soils are nutrient-rich and moist (Fig. 4). Gradual sediment accumulation leads to soil elevation, allowing mesohygrophytes and mesophytes to thrive. *Salix alba* does not persist for a long time on recently elevated soils and is firstly accompanied and then replaced by poplars and/or hardwood riverine species. In the optimal phase, *S. alba* dominates the tree canopy and is occasionally accompanied by *Populus nigra* and/or *Acer negundo* but always with lesser cover. The shrub layer is somewhat more variable than the tree layer, including species of drier habitats such as *Ulmus minor*, *U. laevis*, *Acer negundo*, *Rubus caesius* and others. The herb layer consists of nitrophilous, mesohygrophilous, and hygrophilous plants such as *Galium aparine*, *Lysimachia nummularia* and *Phalaroides arundinacea*. Stands along the Matura River exhibit a slightly swampy character, leading to the presence of tall sedges.

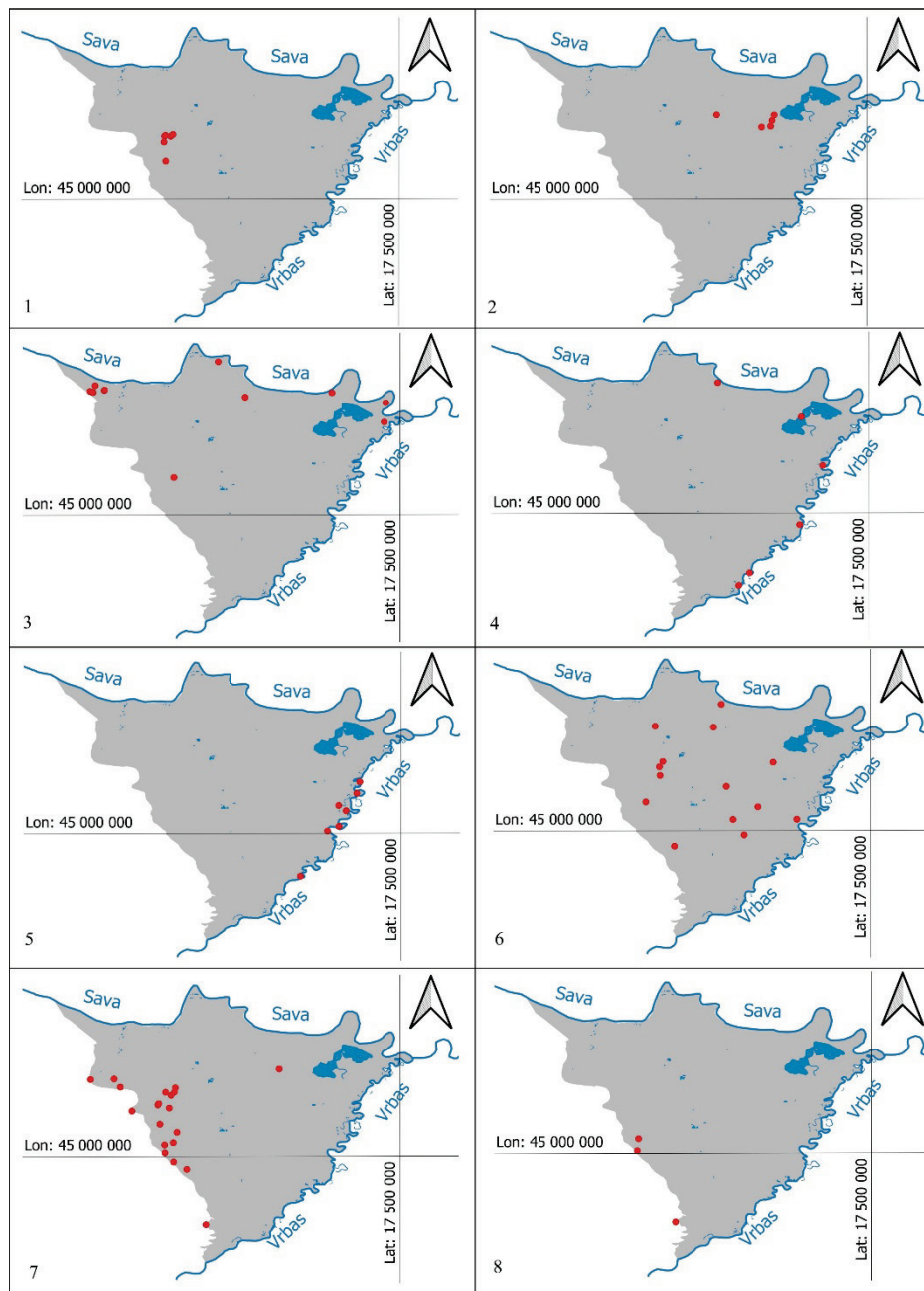


Fig. 3. Distribution maps of each group in the study area. Relevé locations are indicated by red dots. The number in the bottom left corner of each map corresponds to the group numbers used in Table 1, Figures 2 and 4, and in the text.

Abb. 3. Verbreitungskarten der Vegetationseinheiten im Untersuchungsgebiet. Die Lage der Aufnahmen wird durch rote Punkte angezeigt. Die Zahl in der unteren linken Ecke jeder Karte entspricht den Nummern der Vegetationseinheiten in Tabelle 1, Abbildung 2 und 4 sowie den im Text verwendeten Nummern.

***Fraxino pannonicae-Ulmetum glabrae* (group 5)**

Number of relevés: 7.

Site conditions and distribution: gravelly river terraces along the Vrbas river (Razboj, Lilić, Kukulji, Kosjerovo).

Diagnostic species: *Hedera helix*, *Juglans regia*, *Populus alba*, *P. nigra*, *Aegopodium podagraria*, *Brachypodium sylvaticum*, *Erigeron annuus* and *Poa trivialis*.

Constant species: *Acer negundo*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Hedera helix*, *Juglans regia*, *Ulmus minor*, *Cornus sanguinea*, *Crataegus monogyna*, *Euonymus europaeus*, *Sambucus nigra*, *Dioscorea communis*, *Rubus caesius*, *Aegopodium podagraria*, *Arum maculatum*, *Brachypodium sylvaticum*, *Ficaria verna*, *Galeopsis speciosa*, *Galium aparine*, *Glechoma hederacea*, *Poa trivialis* and *Urtica dioica*.

Dominant species: none.

Those forests are ecologically and spatially positioned between willow dominated forests (group 4) and pedunculate oak and common hornbeam forests (group 6). Soils are formed by river sediment accumulation and are well-elevated above the river level. Therefore, floods are present only during the highest waters. However, even short-lasting floods are sufficient to maintain a high level of nutrients in the soil (Fig. 4). In the summer, after the water level of the river drops, the top layers of soil become dry due to sandy or gravelly texture. On the other hand, the deeper parts of the soil are still under the strong impact of groundwater even in the driest part of the year. Therefore, species highly dependent on groundwater such as *Fraxinus angustifolia*, *Acer negundo*, *Populus nigra* and *P. alba* dominate the tree layer. The tree layer is often polydominant due to the pronounced soil deposition and erosion dynamics that allow species with different ecological niches to germinate and take root in a relatively short time frame in the same place. The heterogeneity of the tree layer is intensified by disturbances such as gravel excavation, the presence of invasive species and wood felling. It should also be noted that the role of *Ulmus minor* and *U. laevis* in these communities is currently unclear since they became rare due to Dutch elm disease. Primarily, those sites were probably dominated by *Fraxinus angustifolia*, *Ulmus laevis*, *U. minor* and also *Quercus robur* in a bit drier habitat. Although this community is highly diverse regarding the tree layer, the habitat conditions of these stands are similar, which is reflected by the relatively homogeneous shrub and herb layer. The shrub layer consists of mesophytes such as *Cornus sanguinea*, *Sambucus nigra*, *Euonymus europaeus*, *Ulmus minor*, etc. Nutrient-demanding, mesophilous and mesohygrophilous species such as *Galium aparine*, *Glechoma hederacea*, *Aegopodium podagraria* dominate the herb layer.

***Stellario nemorum-Alnetum glutinosae* (group 8)**

Number of relevés: 3.

Site conditions and distribution: along small streams in the Kozara foothills (Riječani and Mašići).

Diagnostic species: *Alnus glutinosa*, *Athyrium filix-femina*, *Caltha palustris*, *Carex brizoides*, *Peucedanum palustre*, *Solidago gigantea*, *Stellaria holostea* and *Urtica dioica*.

Constant species: *Acer campestre*, *A. tataricum*, *Alnus glutinosa*, *Carpinus betulus*, *Ulmus minor*, *Cornus sanguinea*, *Corylus avellana*, *Crataegus monogyna*, *Sambucus nigra*, *Rubus caesius*, *Adoxa moschatellina*, *Arum maculatum*, *Athyrium filix-femina*, *Caltha palustris*, *Carex brizoides*, *Ficaria verna*, *Glechoma hederacea*, *Lamium galeobdolon* s. lat., *Peucedanum palustre*, *Solidago gigantea*, *Stellaria holostea*, *S. media*, and *Urtica dioica*.

Dominant species: *Alnus glutinosa* and *Carex brizoides*.

The optimum of this community is on higher elevations and its occurrence in Lijevo is only marginal. Soil is clay fluvisol that gradually transitions into pseudogley. It differs from neighbouring *Quercus robur* and *Carpinus betulus* forests by being slightly hygrophilous (Fig. 4). Nevertheless, it can sometimes be hard to ascertain whether *Alnus glutinosa* stands are permanent stages or a link in the succession chain. The shrub layer is rich in mesophytes such as *Acer tataricum*, *Ulmus minor*, *Sambucus nigra*, *Corylus avellana*, etc. The herb layer is often dominated by *Carex brizoides* and consequently, relatively species-poor. Species such as *Ficaria verna*, *Urtica dioica*, *Stellaria holostea* etc. are commonly present.

***Convallario majalis-Carpinetum betuli* (group 6)**

Number of relevés: 14.

Site conditions and distribution: shallow pseudogley and humofluvisol soils at old river terraces (Romanovci, Elezagići, Berek, Rogolji, Liskovac, Laminci, Kočićevo, Zaton, Lilić, Karazovci, Vakuf, Petrovo Selo, Krajišnik).

Diagnostic species: *Acer campestre*, *Prunus avium*, *Ligustrum vulgare*, *Adoxa moschatellina*, *Anemone ranunculoides*, *Arum maculatum*, *Carex sylvatica*, *Corydalis cava*, *Galium aparine*, *Geranium phaeum*, *Geum urbanum*, *Polygonatum hirtum*, *Primula acaulis*, *Scilla bifolia*, *Smyrniolum perfoliatum*, *Veronica hederifolia*, *Viola odorata* and *V. reichenbachiana*.

Constant species: *Acer campestre*, *A. tataricum*, *Adoxa moschatellina*, *Alliaria petiolata*, *Arum maculatum*, *Carex sylvatica*, *Carpinus betulus*, *Cornus sanguinea*, *Corylus avellana*, *Crataegus monogyna*, *Euonymus europaeus*, *Ficaria verna*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Galium aparine*, *Geum urbanum*, *Hedera helix*, *Ligustrum vulgare*, *Prunus avium*, *Quercus robur*, *Sambucus nigra*, *Ulmus minor*, *Veronica hederifolia* and *Viola reichenbachiana*.

Dominant species: *Quercus robur*.

This community is usually found on old river deposits. Those sites are distant from the river (Fig. 3) and therefore not flooded, which is also sometimes intensified by the river embankment. The soils are usually humofluvisol or sometimes shallow to moderately deep pseudogley soil. As those soils are still evolving from gravel deposits, gravel is often present in the soil, making it rich in carbonates. Nutrient levels are also relatively high (Fig. 4). Because of the light texture, the soil is not capable of retaining water on the surface. However, those soils are usually under the impact of groundwater. The tree layer is dense and usually composed of *Quercus robur* and/or *Fraxinus angustifolia* in the upper tree layer and *Carpinus betulus* and/or *Acer campestre* in the lower tree layer. *Quercus robur* can sometimes be absent due to selective logging. The shrub layer is composed of mesophilous species such as *Acer tataricum*, *Ulmus minor*, *Euonymus europaeus*, *Cornus sanguinea* and *Sambucus nigra*. The herb layer is dense and species rich. As this community is light-deprived (Fig. 4), the herb layer is richest in spring when many early-flowering geophytes such as *Corydalis cava*, *Primula acaulis*, *Scilla bifolia*, *Adoxa moschatellina*, *Anemone ranunculoides*, *Galanthus nivalis*, *Crocus heuffelianus* are in bloom. In late spring species such as *Galium aparine*, *Veronica hederifolia*, *Carex sylvatica*, *Polygonatum hirtum*, etc. dominate.

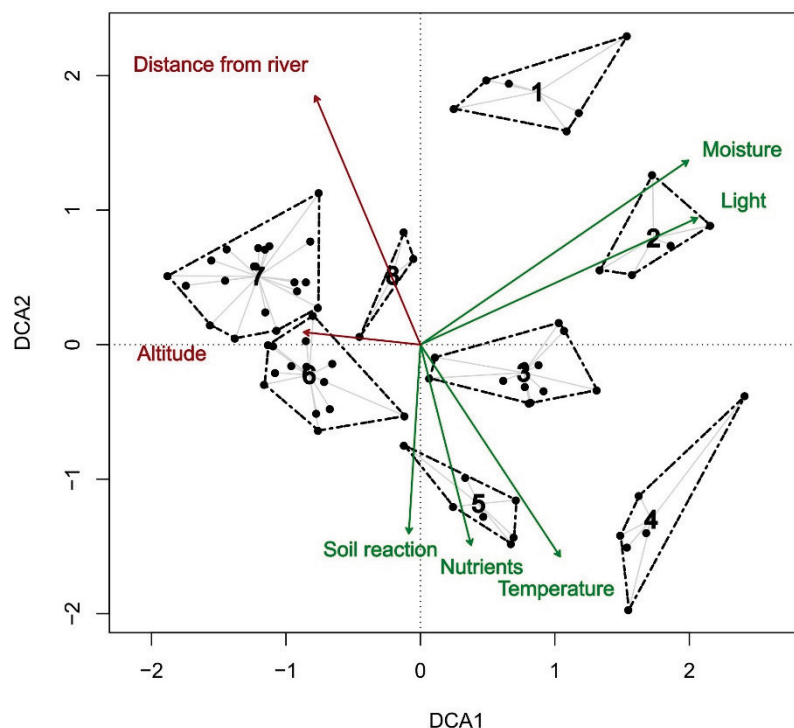


Fig. 4. DCA ordination plot of classified relevés ($n = 73$). Centroids of groups are indicated by numbers of vegetation units corresponding to Table 1, Figures 2–3, and to group numbers used in the text. Statistically significant values for measured data are passively projected as red vectors while statistically significant values for EIV data are passively projected as green vectors.

Abb. 4. DCA-Spinnen-Diagramm der klassifizierten Aufnahmen ($n = 73$). Die Zentren der Gruppen sind durch die Nummern der Vegetationseinheiten gekennzeichnet, die auch in Tabelle 1, Abbildung 2–3 und im Text verwendet werden. Statistisch signifikante Werte für passiv projizierte gemessene Daten sind als rote Vektoren dargestellt, während statistisch signifikante Werte für passiv projizierte EIV-Daten als grüne Vektoren dargestellt werden.

Stellario holosteeae-Carpinetum betuli (group 7)

Number of relevés: 20.

Site conditions and distribution: deep pseudogley soils in Kozara foothills (Rogolji, Elezagići, Mašići, Cerovljani, Lužani, Vilusi and Riječani).

Diagnostic species: *Fagus sylvatica*, *Anemone nemorosa* and *Veratrum album*.

Constant species: *Acer campestre*, *A. tataricum*, *Carpinus betulus*, *Prunus avium*, *Quercus robur*, *Corylus avellana*, *Ajuga reptans*, *Anemone nemorosa*, *Carex brizoides*, *Ficaria verna*, *Polygonatum multiflorum*, *Stellaria holostea* and *Veratrum album*.

Dominant species: none.

This community is developed on deep, highly clayey and dystrophic pseudogley soils. The influence of groundwater is minimal and water stagnation on the surface is rare. However, the soil is saturated in spring by precipitation and water descending from Mount Kozara. The tree layer consists of *Quercus robur* in the upper tree layer and *Carpinus betulus* in the lower tree layer. Occasionally, *Tilia cordata* and *Fagus sylvatica* are present in

the tree layer as well. The shrub layer is composed of mesophilous species capable of withstanding lack of soil moisture in the summer, including *Acer tataricum*, *Euonymus europaeus*, *Sambucus nigra* and *Rubus hirtus*. The herb layer has low cover and is usually composed of mesophilous species such as *Anemone nemorosa*, *Stellaria holostea* and *Polygonatum multiflorum* with the addition of mesohygrophilous species that are dependent on spring waterlogging such as *Ficaria verna*, *Carex brizoides* and *Gagea spathacea*.

3.4 Ecological and floristic comparisons between associations

The TWINSpan classification was supported by the DCA ordination diagram (Fig. 4). The main gradient of species composition along the first axis is correlated with vectors of moisture, light (positively correlated with the first DCA axis), and elevation (negatively correlated with first DCA axis). The elevation serves as an indicator of different parameters such as underground water level, soil type, number of days with frost and similar factors that influence the ecology and floristic composition of the communities. Distance from the river usually dictates the intensity of flooding, impact of underground water and usually accumulation of nitrates. The gradient on the DCA progresses from the driest, most canopy-closed stands occurring on elevated terraces (*Convallario-Carpinetum* and *Stellario-Carpinetum*), through mesohygrophilous and moderately closed forests (*Stellario-Alnetum glutinosae*, *Genisto elatae-Quercetum* and *Fraxino-Ulmetum effusae*), to canopy-open swamp or transitional swamp forests (*Carici elongatae-Alnetum glutinosae* and *Pseudostellario-Quercetum roboris*) and intensively flooded riparian stands (*Salicetum albae*). The main gradient of species composition along the second axis is correlated with vectors of soil reaction, nutrients, and temperature (negatively correlated with the second DCA axis), and distance from the river (positively correlated with the second DCA axis). Therefore, the gradient ranges from forests on dystrophic and base-poor soils (*Pseudostellario-Quercetum roboris*) through mesotrophic forests (*Carici elongatae-Alnetum*, *Genisto elatae-Quercetum*, *Convallario-Carpinetum* and *Stellario nemorum-Alnetum glutinosae*) to forests on eutrophic and base-rich soils along rivers (*Salicetum albae* and *Fraxino pannonicae-Ulmetum*).

4. Discussion

One group was classified into class *Alnetea glutinosae* (swamp alder forests) and its alliance *Alnion glutinosae*. This class is rare in Bosnia and Herzegovina and poorly researched. It was mentioned in the past (Koljanin et al. 2023), but never investigated in detail. However, this vegetation has been well-researched in Croatia. According to Vukelić et al. (2012) two associations are commonly noted: *Frangulo-Alnetum glutinosae* Rauš (1971) 1973 and *Carici elongatae-Alnetum glutinosae*. In newer studies (Vukelić et al. 2019, 2023) the association *Carici acutiformis-Alnetum glutinosae* was noted and used for *Alnus glutinosa* forests at higher altitudes. Besides that, two other associations were mentioned exclusively by Rauš (1971b) including *Sparganio-Alnetum glutinosae* Rauš 1971 prov. and *Glycerio maximae-Alnetum glutinosae* Rauš 1971 prov. but were never after that compared to already described associations. Recent research did not support the recognition of the *Frangulo-Alnetum glutinosae* (Douda et al. 2016). Having in mind all previously said, the community from Lijevo should be classified as a widely accepted Central European association – *Carici elongatae-Alnetum glutinosae*.

There are many issues and disagreements in the number and definition of alliances in the order *Alno-Fraxinetales excelsioris* (class *Alno glutinosae-Populetea albae*). While the

alliance *Alnion incanae* is widely accepted and distributed throughout Europe, the alliances *Alno-Quercion roboris* and *Fraxino-Quercion roboris* are still subjects of contradictory understanding among phytosociologists. In some recent publications, these units have not been considered as separate alliances but rather as parts of the *Alnion incanae* (Vukelić 2012, Chytrý 2013, Douda et al. 2016). Rudski (1949) considered *Fraxino-Quercion roboris* a synonym of *Alno-Quercion*. On the other hand, *Alno-Quercion roboris* and *Fraxino-Quercion roboris* are sometimes defined as ecologically distinct from *Alnion incanae* but geographically separated whereas the former is confined to the Balkans and parts of southern Europe while the latter is distributed in the nemoral zone of Europe (Mucina et al. 2016, Preislerová et al. 2022). However, it was noted in a recent study that those two alliances might be ecologically differentiated in the Balkan peninsula and ecological and floristical differences of those two units were discussed (Koljanin et al. 2023). Four groups are recognized as associations belonging to the *Alno-Fraxinetalia excelsioris*. Group 1 and group 3 are classified into *Alno-Quercion*, group 5 in *Fraxino-Quercion* and group 8 in *Alnion incanae*.

Group 1 includes monodominant *Quercus robur* stands with pronounced swamp character. Several associations of hygrophilous monodominant *Q. robur* forests are described in Europe, but those are generally overlooked and are often neglected vegetation types. Sokołowski (1972) described monodominant *Q. robur* forests from the northeastern part of Poland under the name *Carici elongatae-Quercetum roboris* Sokołowski 1972. The author noted as characteristic species *Deschampsia caespitosa* and *Juncus effusus*, which also occur in the analyzed stands from Lijevče, but also other cold-climate species such as *Picea abies*, *Betula pendula*, *Carex canescens*, *C. nigra*, and *Molinia coerulea*. In Slovenia, Accetto (1974) described *Pseudostellario-Quercetum roboris*, encompassing a gradient from slightly moist to swamp monodominant *Quercus robur* forests. Although the species *Pseudostellaria europaea* does not occur in Lijevče Polje, analyzed stands are likely more similar to those in Slovenia. It should be noted that they particularly correspond to the subassociation *Pseudostellario-Quercetum roboris deschampietosum caespitosae* Accetto 1974, characterized by the presence of elements from the alliance *Alnion glutinosae* (Accetto 1974). Molnár (2010) later described a similar association present in Hungary, Romania, and Serbia under the name *Cardamino parviflorae-Quercetum roboris* Molnár 2010 which is, in our opinion, similar to the *Pseudostellario-Quercetum roboris*. Those stands contain several species that are absent in the stands found in Lijevče (*Calamagrostis epigeios*, *Ranunculus polyphyllus*, and *Cardamine parviflora*). Moreover, the *Pseudostellario-Quercetum roboris* was first to be described between those two associations and therefore we decided to classify the analysed stands as *Pseudostellario-Quercetum roboris*. It should also be pointed out that Douda et al. (2016) consider the association *Pseudostellario-Quercetum roboris* as a synonym of the association *Ficario vernaе-Ulmetum campestris* Knapp ex Medwecka-Kornaš 1952. In our opinion, the difference in floristic composition and ecology of the *Pseudostellario-Quercetum roboris* compared to the *Ficario vernaе-Ulmetum campestris* is pronounced. For instance, the *Ficario vernaе-Ulmetum campestris* usually contains a set of mesophilous species such as *Gagea lutea*, *Brachypodium sylvaticum*, *Pulmonaria officinalis* agg., *Stachys sylvatica*, *Anemone nemorosa* etc. (Douda et al. 2016), which were not recorded in stands occurring in Lijevče Polje. On the other hand, hygrophilous species are well established in the analysed stands. Therefore, the *Pseudostellario-Quercetum roboris* is considered an association on its own and the stands from Lijevče Polje were attributed to it.

Group 3 encompasses regularly flooded stands of *Fraxinus angustifolia* and *Quercus robur* mostly on pseudogley developed on hard clays. In our opinion, this group can be attributed to the *Genisto elatae-Quercetum roboris* which was commonly noted and well-documented in the Balkan Peninsula (Horvat 1938, Stefanović 1989, Tomić & Rakonjac 2011, Vukelić 2012, Šilc & Čarni 2012). This association was recently considered as a synonym of the *Fraxino pannonicae-Ulmetum glabrae* (Douda et al. 2016). However, later analyses (Koljanin et al. 2023) revealed a high level of floristic differences between the transitional swamp on impermeable substrate and riverine forests on a water-permeable substrate in the western Balkan Peninsula. Following this concept, we recognized the *Genisto elatae-Quercetum* as a distinct entity encompassing swamp forests of *Fraxinus angustifolia* and *Quercus robur* and placed it into the *Alno-Quercion roboris* while the name *Fraxino pannonicae-Ulmetum glabrae* was used for riverine forests occurring on water-permeable substrates (Group 5). It should also be pointed out that some relevés from group 3 lack *Quercus robur* in the tree layer. Instead, *Fraxinus angustifolia* dominates. Traditionally, monodominant *Fraxinus angustifolia* forests have been classified as *Leucojo aestivi-Fraxinetum angustifoliae* Glavač 1959. In the original description provided by Glavač (1959) characteristic species of the *Leucojo-Fraxinetum* are *Cardamine pratensis*, *Alisma lanceolatum*, *Roripa amphibia*, *Carex vesicaria*, *Sium latifolium* etc. which are also characteristic for wet meadows and other open habitats. These species are nearly absent in the analyzed relevés. The absence of *Quercus robur* is likely the result of selective logging in many locations. It should also be mentioned that *Q. robur* is close to extinction in some localities and could not occupy habitats that are in the process of succession simply due to a lack of mature seed-producing individuals. In such scenarios, *Fraxinus angustifolia* is at an advantage because it has light seeds that can be more easily carried over longer distances. Having all this in mind, we considered the whole group 3 as one association – *Genisto elatae-Quercetum*. The lack of the *Leucojo-Fraxinetum* in the studied area could be due to extensive hydrological melioration that happened in the past. It is also possible that this community has slow pace during establishment which is often interrupted by wood harvesting.

Group 5 encompasses polydominant riverine stands on elevated, water-permeable, humofluvisol along the Vrbas river (Fig. 3). Slavnić (1952) described stands of ash and elms on riverbanks under the name *Fraxino angustifoliae-Ulmetum effusae* Slavnić 1952. Later, several authors accepted this association (Vukelić & Baričević 2004, Juvan et al. 2013) attributing hardwood riverine stands on water-permeable substrates to it. However, the association described by Slavnić (1952) has a significant share of swamp species. Therefore, it is likely very similar to the earlier described *Genisto elatae-Quercetum*. In Central Europe, riverine hardwood forests were often classified under the name *Fraxino pannonicae-Ulmetum glabrae* (Willner & Grabherr 2007, Kevey 2007, Borhidi et al. 2012, Chytrý 2013, Valachovič et al. 2021). Analyzed stands correspond well to the described stands from Hungary (Kevey 2007) but also to the subassociation *Fraxino pannonicae-Ulmetum glabrae populetosum* (Jurko 1958) Džatko 1972 (Petrášová & Jarolímek 2012, Valachovič et al. 2021) from Slovakia. Following the same principle of separation of association in different alliances used for Group 3, this group does not belong to transitional swamps from the alliance *Alno-Quercion* but rather to the *Fraxino-Quercion*. One more problem with the riverine type of vegetation is that invasive species largely floristically change those forests, and their classification remains problematic as it is hard to draw the border between *Robinietaea* and *Alno glutinosae-Populetea albae*. The classification of this vegetation type is

not sufficiently studied, and the small number of relevés was a limiting factor. However, our analyses did not support the division of *Acer negundo* dominated stands from native tree dominated communities. Therefore, we considered this group as *Fraxino pannonicae-Ulmetum glabrae*.

Group 4 was classified in the class *Salicetea purpureae* and its subordinate alliance *Salicion albae*. Group 4 encompasses *Salix alba* dominated stands developed in stripes close to the rivers. European authors usually classify all white willow communities into one association – *Salicetum albae* (Chytrý 2013, Valachovič et al. 2021). However, alongside this association, some authors recognised other associations such as: *Salici-Populetum nigrae* (Tx. 1931) Meyer Drees 1936 (Rauš 1976, Tomić & Rakonjac 2011, Vukelić 2012), *Galio palustri-Salicetum albae* Rauš 1973 (Rauš 1976, Poldini et al. 2011), *Leucojo aestivi-Salicetum albae* Kevey in Borhidi & Kevey 1996 (Borhidi et al. 2012), *Carici elatae-Salicetum albae* Kevey 2008 (Borhidi et al. 2012), etc. A comprehensive analysis of this vegetation type across a broader area is necessary for an objective assessment of the number of associations and could not be determined at this point. However, it should be noted that this group has a good resemblance with *Salicetum albae* s. lat.

There is a disagreement over the number of alliances within the order *Carpinetalia betuli*. Most authors in the Balkans and parts of Southern Europe recognize the *Erythronio-Carpinion* (Borhidi et al. 2012, Košir et al. 2013, Biondi et al. 2014, Mucina et al. 2016, Škvorc et al. 2017, Stupar & Čarni 2017, Preislerová et al. 2022). However, Novák et al. (2023) argue against this, considering the *Erythronio-Carpinion* only as part of the *Carpinion betuli*. There were also proposals to place azonal hornbeam forests into the *Fraxino pannonicae-Carpinion betuli* (Accetto 2006), but this has not been widely accepted. Groups 6 and 7 are classified in associations belonging to the *Carpinion betuli*.

Group 6 includes mesophilous and mesohygrophilous stands (Fig. 4) of *Quercus robur* and *Carpinus betulus* with frequent occurrence of *Fraxinus angustifolia* and *Acer campestre* in the tree layer. Most authors classified all *Quercus robur* and *Carpinus betulus* stands from the Sava river confluence into the association *Carpino betuli-Quercetum roboris* Anić (1959) Rauš 1975 (Rauš 1971a, Stefanović 1989, Tomić & Rakonjac 2011, Vukelić 2012) and usually placed it into the *Carpinion betuli*. Exceptions from this were Slovenian lowland oak-hornbeam stands that were classified as *Pseudostellario-Carpinetum betuli* (Accetto 1974) Novák 2020 and placed in the Illyrian *Erythronio-Carpinion* alliance (Accetto 1974, Šilc & Čarni 2012, Novák et al. 2020). Marinček (1994) found the name *Carpino betuli-Quercetum roboris* invalid, replaced it with the name *Lonicero caprifolii-Quercetum* (Rauš 1979) Marinček 1994 and placed it into the alliance *Erythronio-Carpinion*. The problems with this name were in detail described by Vukelić (2012) while the problems of affiliation to alliances were later also elaborated by Vukelić et al. (2018) who proposed a concept in which stands that contain species of the Illyrian geo-element should be classified within the alliance *Erythronio-Carpinion*, and those in which these species are not present in the alliance *Carpinion betuli*. As the analyzed oak-hornbeam communities lack the Illyrian floristic geo-element while at the same time demonstrating a substantial resemblance to the Central European or Pannonian associations, we decided to follow the concept that was provided by Novák et al. (2020). Therefore, this group can be considered as a part of the Pannonian lowland oak-hornbeam association developed in floodplains along lowland rivers – *Convallario majalis-Carpinetum betuli* Kevey 2008. In the traditional view, this community could be regarded as *Carpino betuli-Quercetum roboris typicum* Rauš 1975 sensu Vukelić (2012).

Group 7 encompasses mesophilous stands (Fig. 4) of *Quercus robur* and *Carpinus betulus* with *Fagus sylvatica*, developed at the foothills of Mount Kozara (Fig. 3). By the traditional concept (Vukelić 2012), this community of *Quercus robur* and *Carpinus betulus* with *Fagus sylvatica* could be regarded as *Carpino betuli-Quercetum roboris fagetosum* Rauš 1975. Similarly to the previous group, this group also lacks the Illyrian floristic element. It is linked to the previous community, but it occupies higher positions, thus represents a transitional community between floodplain forests and the upland forests of *Quercus petraea* and *Carpinus betulus*. In comparison with the previous group, it is differentiated by the absence of typical riverine mesophytes and mesohygrophytes and by the presence of species confined to mesophilous habitats (*Fagus sylvatica* or *Quercus petraea*-*Carpinus betulus* forests) such as *Fagus sylvatica*, *Prunus avium*, *Rubus hirtus*, *Corylus avellana*. This is characteristic for the *Stellario-Carpinetum* (Novák et al. 2020). Therefore, we are inclined to the opinion that this group should be considered *Stellario holostaeae-Carpinetum betuli*.

Group 8 represents *Alnus glutinosa* communities distributed along small and fast streams at the foothills of Mount Kozara (Fig. 3). Horvat (1938) described an *Alnus glutinosa* association on marshy soils under the name *Carici brizoidis-Alnetum glutinosae* Horvat 1938 and defined several characteristic species including *Carex elongata*, *Solanum dulcamara*, *Lycopus europaeus* and *Rumex sanguineus*. This association was later recorded in Bosnia and Herzegovina (Fabijanić et al. 1963) as well as in other Balkan countries, where much drier stands were attributed to this association (Čarni et al. 2008, Vukelić 2012). However, the stands in Lijevče have pronounced mesophilous character and thus significantly differ from the original description of the *Carici brizoidis-Alnetum* provided by Horvat (1938). On the other hand, most Central European authors classify mesophilous black alder stands at lower and middle elevations near streams into the association *Stellario nemorum-Alnetum glutinosae* (Douda 2008, Slezák et al. 2014, Douda et al. 2016) which is the concept that was adopted here. It is worth mentioning that a similar association, *Lamio orvalae-Alnetum glutinosae* Dakskobler 2016, was described in Slovenia (Dakskobler 2016) with differential species such as *Ornithogalum pyrenaicum* and *Lamium orvala* which are not present in this community in the study area Lijevče.

5. Conclusion

The study brings the first detailed overview of the lowland forest vegetation from the peri-Pannonian Bosnia. 73 relevés were classified into 8 ecologically and floristically homogeneous groups that correspond to the level of association. Those groups varied from driest, *Carpinus betulus* and *Quercus robur* dominated stands on elevated terraces to swamp forests in microdepressions with open canopies. The riverine forests had higher values of nutrients and bases in the soil because of frequent sedimentation while the swamps have lower values because of pedological processes induced by the lack of oxygen. Ellenberg indicator values for moisture, light, soil reaction, nutrients, and temperature as well as elevation and distance from the nearest river proved to be good parameters which can to some extent explain the turnover in the species composition and the forming of different communities. The most widespread communities are those dominated by *Carpinus betulus* and *Quercus robur* which is probably due to extensive hydromelioration. Riparian forests are most common along riverbanks with a natural regime of flooding. On the other hand, swamp forests are confined to microdepressions in only several localities that were not hydromeliorated.

Erweiterte deutsche Zusammenfassung

Einleitung – Zu den Tieflandwäldern im peri-pannonischen Bosnien (nördliches Bosnien-Herzegowina) gehören verschiedene azonale Vegetationseinheiten, die von *Quercus robur*, *Carpinus betulus*, *Fraxinus angustifolia*, *Populus alba*, *P. nigra*, *Alnus glutinosa*, *Salix euxina* und *S. alba* dominiert werden. Die Waldstandorte sind essenziell für die Artenvielfalt und bieten wichtige Ökosystemleistungen, die Bestände sind aber fragmentiert und degradiert als Folge eines negativen menschlichen Einflusses seit mehr als 200 Jahren (Begović 1960, Mrgić 2007). Trotz ihrer ökologischen Bedeutung sind die Wälder wissenschaftlich noch kaum erforscht, und es wurden bisher nur wenige pflanzensoziologische Aufnahmen aus diesem Raum veröffentlicht (Fukarek 1975). Das Untersuchungsgebiet ist die Region der Lijevče Polje im peri-pannonischen Bosnien. Unsere Untersuchung hat zum Ziel, die floristische Zusammensetzung und die ökologischen Faktoren der Tieflandwälder zu verdeutlichen sowie einen Überblick ihrer Vegetationseinheiten zu geben. Gleichzeitig schließen wir eine Datenlücke über Wälder in dieser Region.

Methoden – Zwischen 2016 und 2023 wurden 73 Vegetationsaufnahmen nach der pflanzensoziologischen Methode (Braun-Blanquet 1964) in ungestörten Waldbeständen in der Lijevče Polje angefertigt. Auf allen Aufnahmeflächen wurden Daten erhoben zur Artenzusammensetzung, zur Deckung der einzelnen Arten und der Vegetationsschichten, zum Boden und zur Höhenlage. Die Aufnahmen und Daten wurden im Datenbankprogramm Turboveg gespeichert (Hennekens & Schaminée 2001). Die Aufnahmen (Anhang E1 und E2) wurden anschließend mittels der Software Juice (Tichý 2002) analysiert. Die Taxonomie folgt Euro+Med (2006–), die Syntaxonomie Mucina et al. (2016). Um das Rauschen bei der statistischen Analyse zu reduzieren, wurden Arten, die nur in einer oder zwei Aufnahmen vorkommen, entfernt. Für die hierarchische Klassifikation wurde der TWINSpan-Algorithmus eingesetzt. Bei der Transformation der Daten in TWINSpan wurden die *pseudospecies*-Schnittwerte 0, 5, 10, 25 und 50 % gesetzt. Die zunächst damit ermittelten Gruppen wurden zu floristisch und ökologisch homogenen Einheiten vereinigt, die Assoziationen entsprechen. Diagnostische Arten wurden aufgrund ihrer Treue ($\Phi \geq 0,40$) ermittelt. Um die hauptsächlichen ökologischen Faktoren für die Unterscheidung der Einheiten zu erkennen, wurden die Ellenberg-Zeigerwerte (EIV) der benachbarten Gruppen verglichen.

Die statistische Signifikanz ($p < 0,05$) von Unterschieden bei den Messdaten (Höhenlage und Entfernung zum nächsten Fluss) zwischen den Einheiten wurde mittels des Mann-Whitney-U-Tests in der Software Statistica Version 14.0 (TIBCO Software Inc.) bestimmt. Eine Varianzanalyse (ANOVA) der ermittelten EIV wurde in Juice durch einen modifizierten Permutationstest (Zelený & Schaffers 2012) berechnet. Um die Ergebnisse der Klassifikation und die Beziehungen zwischen den Gruppen im Datensatz zu veranschaulichen, wurden die Aufnahmen in ein Ordinationsdiagramm (DCA) gesetzt. Messwerte und errechnete Werte, die sich bezüglich der ersten beiden Ordinationsachsen per Spearmans Korrelationskoeffizient in Statistica als signifikant erwiesen, gingen passiv projiziert in das DCA-Diagramm ein.

Ergebnisse und Diskussion – Die TWINSpan-Gruppierung des Datensatzes ergab zunächst 15 Gruppen (Fig. 1). Auf der ersten Hierarchiestufe der Klassifikation wurden regelmäßig überflutete lichte Wälder getrennt von seltener überfluteten schattigen Wäldern. Auf der zweiten Hierarchiestufe wurden vier Gruppen getrennt, die sich hauptsächlich durch Überflutungshäufigkeit und Bodeneigenschaften unterscheiden. Zur ersten Aufnahmegruppe gehörten länger überflutete Wälder auf nährstoffarmen Böden, zur zweiten weniger lange überflutete Wälder auf nährstoffreichen Böden. Die dritte Gruppe umfasst selten überflutete Wälder auf Pseudogley-Böden mit hoher Nährstoffverfügbarkeit auf Mittel- und Niederterrassen. Die vierte Gruppe schließlich umfasst Aufnahmen vom Vorland des Kozara-Gebirges, wo die nur selten überfluteten Böden mit Nährstoffen schlecht versorgt sind. Durch die Kombination von 15 Gruppen, die sich auf der vierten TWINSpan-Hierarchiestufe unterscheiden ließen, wurden 8 Einheiten erzeugt. Die Einheit 1 (Gruppen 1 und 2) umfasst *Quercus robur*-Bestände mit einer Krautschicht aus Arten sumpfiger Wälder. Die Einheit 2 (Gruppen 3 und 4) umfasst *Alnus glutinosa*-Sumpfwälder in kleinen Geländemulden. Die Einheit 3 (Gruppen 5 und 6)

besteht aus Wäldern aus *Fraxinus angustifolia* und/oder *Quercus robur* mit einer Mischung aus meso-hygrophilen Arten. Einheit 4 (Gruppe 7) besteht aus *Salix alba*-Beständen auf Niederterrassen der großen Flüsse. Einheit 5 (Gruppe 8) enthält Hartholz- und Weichholz-Mischbestände auf etwas erhöhten, wasserdurchlässigen Terrassen entlang der großen Flüsse. Die Einheit 6 (Gruppen 9, 10, 11 und 12) umfasst mesophile bis meso-hygrophile artenreiche Eichen-Hainbuchen-Wälder mit *Quercus robur* und *Carpinus betulus* sowie häufigen Vorkommen von *Fraxinus angustifolia* auf den höchsten Alluvialterrassen, gewöhnlich außerhalb der Überflutungsbereichs. Die Einheit 7 (Gruppen 13 und 14) umfasst Stieleichen-Hainbuchen-Wälder mit häufigen Vorkommen von *Fagus sylvatica* auf diluvialen Terrassen des Kozara-Vorlandes. Einheit 8 (Gruppe 15) umfasst bachbegleitende *Alnus glutinosa*-Wälder.

Die Ergebnisse der TWINSPAN-Klassifikation wurden unterstützt durch die Aussage des DCA-Ordinationsdiagramms (Fig. 4). Der Gradient der Artenzusammensetzung entlang der ersten Achse ist positiv mit den Vektoren Feuchtigkeit und Licht korreliert und negativ mit der Höhenlage. Der Gradient erstreckt sich von den trockensten dichtesten Beständen auf den erhöhten Terrassen (Einheiten 6, 7 und 8) über mäßig dichtkronige meso-hygrophile Bestände (Einheiten 3 und 5) bis zu offenkronigen Sumpfwäldern (Einheiten 1 und 2) sowie Wäldern mit langer Überflutungsdauer (Einheit 4). Die Vektoren der Bodenreaktion, Nährstoffe und Temperatur sind signifikant mit der zweiten DCA-Achse korreliert. So reicht der Gradient entlang der zweiten Achse von Wäldern auf nährstoff- und basenarmen Böden (Einheit 1) über mesotrophe Wälder (Einheiten 2, 3, 6 und 8) bis zu Wäldern auf eutrophen und basenreichen Böden entlang der Flüsse (Einheiten 4 und 5).

Die hier vorgeschlagene syntaxonomische Interpretation der Vegetationseinheiten ist wie folgt:

- K: *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946
 - O: *Alnetalia glutinosae* Tx. 1937
 - V: *Alnion glutinosae* Malcuit 1929
 - A: *Carici elongatae-Alnetum glutinosae* Tüxen 1931 (Einheit 2)
- K: *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968
 - O: *Alno-Fraxinetalia excelsioris* PAarge 1968
 - V: *Alno-Quercion roboris* Horvat 1950
 - A: *Pseudostellario-Quercetum roboris* Accetto 1973 (Einheit 1)
 - A: *Genisto elatae-Quercetum roboris* Horvat 1938 (Einheit 3)
 - V: *Fraxino-Quercion roboris* PAarge 1968
 - A: *Fraxino pannonicarum-Ulmetum glabrae* Aszod 1935 corr. Soo 1963 (Einheit 5)
 - V: *Alnion incanae* Pawłowski et al. 1928
 - A: *Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957 (Einheit 8)
- K: *Salicetea purpureae* Moor 1958
 - O: *Salicetalia purpureae* Moor 1958
 - V: *Salicion albae* Soó 1951
 - A: *Salicetum albae* Issler 1926, (Einheit 4)
- K: *Carpino-Fagetea sylvaticae* Jakucs ex PAarge 1968
 - O: *Carpinetalia betuli* P. Fukarek 1968
 - V: *Carpinion betuli* Issler 1931
 - A: *Convallario majalis-Carpinetum betuli* Kevey 2008 (Einheit 6)
 - A: *Stellario holostearum-Carpinetum betuli* Oberdorfer 1957 (Einheit 7)

Authors contributions

DK, VS, ĐM, TŠ and JB conceived and designed the research, DK, VS, ĐM and JB carried out the data collecting, DK performed all analysis and data processing, JB supervised the research and helped to draft the manuscript, DK, VS, ĐM, TŠ and JB wrote the manuscript.

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Supplements

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

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

Supplement E1. Relevés of the original dataset

Anhang E1. Vegetationsaufnahmen des originalen Datensatzes.

Supplement E2. Header data (location, elevation, distance from the nearest river, covers per layers, EIVe values and date) for the original relevés of Supplement E1.

Anhang E2. Kopfdaten (Lage, Höhe, Entfernung vom nächsten Fluss, Deckungsgrad pro Schicht, EIVe-Werte und Datum) für die Originalaufnahmen von Anhang E1.

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Supplement E2. Header data (location, elevation, distance from the nearest river, covers per layers, EIVe values and date) for the original relevés of Supplement E1.

Anhang E2. Kopfdaten (Lage, Höhe, Entfernung vom nächsten Fluss, Deckungsgrad pro Schicht, EIVE-Werte und Datum) für die Originalaufnahmen von Ergänzung E1.

Table number	Group number	Locality	WGS84		Elevation (m)	Distance from the nearest river (m)	Area (m ²)	Position	Soil	Number of woody species	Number of herb species	Cover (%)					Ellenberg indicator values						Date (YYYY-MM-DD)	
			N (°)	E (°)								A1 - higher tree layer (more than 20 m)	A2 - lower tree layer (10-20 m)	B1 - tall shrub layer (5-10 m)	B2 - medium-tall shrub layer (1-5 m)	B3 - low shrub layer (less than 1 m)	C - herb layer	Light	Temperature	Continentality	Moisture	Soil reaction		Nutrients
1	1	Elezagići	45,068918	17,241189	96	15739	400	Diluvial terrace	Gleyosol	6	21	90	0	0	60	5	90	6,46	5,62	5,09	7,55	6,18	5,71	2021-06-16
2	1	Elezagići	45,069739	17,242257	101	15704	400	Diluvial terrace	Gleyosol	4	15	30	20	20	40	15	60	6,11	5,67	5	7,22	5,92	5,5	2023-05-07
3	1	Berek	45,041194	17,242484	105	14540	400	Diluvial terrace	Gleyosol	5	10	90	20	0	40	5	90	6	5,5	5,19	7,2	5,5	5,33	2021-06-26
4	1	Elezagići	45,062384	17,240599	101	15474	400	Diluvial terrace	Gleyosol	3	11	30	20	15	30	10	50	6,19	5,87	5,31	7,8	6,25	6,17	2021-07-03
5	1	Elezagići	45,070727	17,250356	98	15189	400	Diluvial terrace	Gleyosol	2	8	90	10	25	15	10	40	5,92	5,7	4,92	7,7	5,56	4,64	2023-07-09
6	1	Elezagići	45,068767	17,247924	97	15257	400	Diluvial terrace	Gleyosol	3	16	30	15	50	5	2	85	6,68	5,31	5,06	8,16	5,57	4,82	2021-06-17
7	2	Kočićevo	45,078864	17,383162	92	5606	400	Alluvial terrace	Gleyosol	8	21	80	10	5	5	20	90	6,14	5,73	4,75	7,14	5,88	6,39	2021-07-08
8	2	Laminci	45,092415	17,333602	90	9787	400	Alluvial terrace	Gleyosol	4	18	70	0	10	10	0	95	6,55	5,56	4,8	8,05	6,07	6,56	2021-06-18
9	2	Kočićevo	45,086101	17,394671	90	5196	400	Alluvial terrace	Gleyosol	9	19	90	10	15	10	45	85	6,21	5,54	4,92	6,76	6	6,15	2021-07-10
10	2	Kočićevo	45,079838	17,393078	92	4944	400	Alluvial terrace	Gleyosol	9	12	90	20	25	10	5	90	6,14	5,45	4,8	7,29	5,71	6,26	2021-07-10
11	2	Bardača	45,092282	17,397036	91	5477	400	Alluvial terrace	Gleyosol	11	29	40	75	20	25	10	85	6,34	5,55	4,86	7,25	5,8	6,32	2021-07-18
12	3	Milava	45,130425	17,329068	91	1773	400	Alluvial terrace	Gleyosol	10	15	100	30	30	25	60	50	5,73	6	4,92	6,83	6,19	6,29	2021-06-18
13	3	Vrbaška	45,136124	17,160399	92	1687	400	Alluvial terrace	Gleyosol	13	12	70	0	20	50	80	40	6	5,95	5,05	6,36	6,06	5,28	2017-06-28
14	3	Bajinci	45,10263	17,48248	90	501	900	Alluvial terrace	Gleyosol	8	17	90	25	5	15	20	80	6,04	6,12	4,91	6,54	6,32	6,09	2016-05-29
15	3	Bardača	45,12412	17,48419	90	544	900	Alluvial terrace	Gleyosol	9	13	80	30	70	40	50	30	5,96	6,09	5	6,27	6,39	6	2016-05-29
16	3	Milava	45,13591	17,161216	92	1684	400	Alluvial terrace	Gleyosol	6	17	70	30	70	25	25	90	5,96	5,78	4,91	6,83	6,32	5,9	2022-05-08
17	3	Poljanska	45,1355	17,42463	89	291	400	Alluvial terrace	Gleyosol	10	9	70	30	25	70	30	50	5,83	6,27	5,14	5,91	6,68	6,35	2016-05-29
18	3	Milava	45,13811	17,17347	92	1102	625	Alluvial terrace	Gleyosol	13	14	75	10	10	60	10	55	5,9	5,96	4,8	6,29	6,48	5,83	2016-05-28
19	3	Mačkovac	45,16999	17,29904	91	631	100	Alluvial terrace	Gleyosol	10	15	75	30	25	30	30	60	5,76	6	4,76	6,16	6,6	6,27	2016-05-29
20	3	Berek	45,040862	17,250064	100	13956	400	Alluvial terrace	Gleyosol	12	20	85	15	80	20	30	60	5,39	5,66	4,83	5,73	6,52	6,35	2023-05-09
21	3	Dubrave	45,13703	17,15777	92	1686	900	Alluvial terrace	Gleyosol	9	17	80	20	10	50	15	70	5,67	6	4,79	6,04	6,5	5,78	2016-05-28
22	3	Milava	45,143302	17,163341	92	867	225	Alluvial terrace	Gleyosol	8	8	80	10	40	30	35	60	5,26	6	4,84	5,65	6,5	5,94	2023-04-16
23	3	Milava	45,138487	17,173807	92	1053	400	Alluvial terrace	Gleyosol	11	23	60	40	80	50	60	100	5,91	5,9	4,87	6,18	6,2	6,29	2021-06-12
24	4	Bardača	45,106405	17,42531	90	4213	225	Alluvial terrace	Fluvisol	5	11	40	30	20	20	60	50	6,4	5,86	4,92	7,8	6,25	6,42	2021-07-08
25	4	Kukulji	44,986361	17,423511	100	208	400	Alluvial terrace	Fluvisol	5	12	75	40	20	5	2	100	6,13	6,21	5,14	6,12	5,71	5,93	2021-06-27
26	4	Laktaši	44,917974	17,356395	119	207	200	Alluvial terrace	Fluvisol	13	10	70	0	10	40	90	10	5,57	6,05	4,81	6,32	6,5	6,35	2022-05-29
27	4	Greda	45,144617	17,333239	90	366	400	Alluvial terrace	Fluvisol	5	6	0	70	100	10	30	5	5,82	5,82	5	6,27	6,9	7,2	2021-06-18
28	4	Petroševci	44,931908	17,368311	115	175	100	Alluvial terrace	Fluvisol & deposol	10	6	0	100	5	30	90	10	5,19	5,86	4,88	6,47	6,46	6,58	2023-05-12
29	4	Razboj	45,052222	17,448828	92	175	75	Alluvial terrace	Fluvisol	11	13	0	95	20	10	70	60	6,36	6	4,91	6,82	6,42	6,56	2021-06-30
30	5	Razboj	45,044022	17,451037	96	243	200	Alluvial terrace	Humofluvisol	10	11	95	10	15	30	90	25	5,57	5,86	4,91	5,44	6,16	6,71	2023-05-08
31	5	Lilić	45,030428	17,430896	96	1065	225	Alluvial terrace	Humofluvisol	13	9	50	55	30	30	50	25	5,2	5,91	5,04	5,39	6,74	6,5	2023-05-08
32	5	Lilić	45,024548	17,439106	100	241	100	Alluvial terrace	Fluvisol	7	9	30	90	10	25	80	60	5,69	5,64	4,69	5,56	6,07	6,29	2023-05-08
33	5	Kukulji	45,002037	17,418616	103	145	400	Alluvial terrace	Fluvisol	12	12	90	50	10	45	90	25	5,5	6,09	4,88	5,44	6,04	6,16	2023-05-12
34	5	Razboj	45,05681	17,454205	95	158	400	Alluvial terrace	Fluvisol	8	10	20	95	30	10	10	95	5,91	6,19	4,95	5,79	6,5	5,94	2021-06-30
35	5	Kukulji	45,0071756																					