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PHYTOSOCIOLOGICAL RESEARCH INTO THE ILLYRIAN OAK-HORNBEAM FOREST ON THE LIMESTONE CLIFFS OF KUPA RIVER CANYON (KAMANJE, WEST-CENTRAL CROATIA)

FITOCENOLOŠKO ISTRAŽIVANJE ILIRSKIH HRASTOVO-GRABOVIH ŠUMA S VAPNENAČKIH LITICA KANJONA RIJEKE KUPE (KAMANJE, ZAPADNI DIO SREDIŠNJE HRVATSKE)

Antun JELINČIĆ[1]*, Joso VUKELIĆ[2], Dora PAPKOVIĆ[3]

SUMMARY

In this paper, we present 14 relevés of oak-hornbeam forest from the limestone cliffs of Kupa River canyon in Kamanje, West-Central Croatia. The investigated forest is part of the Natura 2000 ecological network, and it represents one of the rare remnants of climax forest in the area that is not highly influenced by anthropogenic management. Plant community composition was recorded using the six-degree Braun-Blanquet scale, and its relation to similar forests studied by other authors was assessed using agglomerative hierarchical clustering. Because of the abundance of limestone rocks and consequently microhabitats, the forest is very species-rich, with a total of 164 vascular species recorded, ranging from 42 to 80 species per relevé. The Kamanje forest belongs to the association *Epimedio-Carpinetum betuli*, with regard to traditional classification to the subassociation *staphyletosum*, and is rich in species of the Illyrian--Balkan floral geoelement. However, compared to the forests of the same association from other areas, this forest has some distinct floristic features. Among the trees, *Quercus petraea* is replaced by *Q. robur*. The herb layer is abundant with ferns, and geophytes and hemicryptophytes are much more frequent. The most distinct feature of the forest is the high abundance of ferns from the class *Asplenietea trichomanis*, specifically *Asplenium trichomanes* and *Polypodium vulgare*. The cluster analyses separated the Kamanje forest as a unique group in relation to all other traditional subassociations. The Kamanje forest could be considered as a fern-rich subass. *staphyletosum*. However, only after the problems of traditional classification of *Epimedio-Carpinetum betuli* into subassociations are resolved will the exact floristic context of the studied forest be clearer.

KEY WORDS: *Epimedio-Carpinetum betuli*, Illyrian oak forests, semi-natural forests, Natura 2000 forest, peri-Pannonian biogeographic region.

INTRODUCTION
UVOD

Oak-hornbeam forests (alliances *Carpinion betuli* Issler 1931 and *Erythronio-Carpinion betuli* (Horvat 1958) Marinček in Wallnöfer et al. 1993) are among the most phytosociologically researched forests in Croatia; nevertheless, vast areas of these forests have never been investigated.

The syntaxomonical status of the *Erythronio-Carpinion betuli* alliance has not yet been fully resolved (Vukelić 2012). However, Illyrian forests, which are considered to be a part

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of this alliance, are still present in the official classification of higher-rank syntaxa of Croatia (Škvorc et al. 2017) as well as in the Croatian National habitat classification (Topić and Vukelić 2009) and European EUNIS Habitat Classification (Chytrý et al. 2020). In Croatia, within the *Erythronio-Carpinion betuli* alliance, ass. *Epimedio-Carpinetum betuli* (Horvat 1938) Bohridi 1963 is the most studied, and traditionally, six subassociations of this association have been described, namely *caricetosum pilosae*, *erythronietosum*, *asperuletosum*, *staphyletosum*, *castaneetosum*, and *tilietosum tomentosae* (Vukelić 2012). Among them, subass. *staphyletosum* occurs on soils rich in carbonates and without a highly illuviated horizon (Gračanin 2003). However, Vukelić et al. (2015) questioned the division of *Epimedio-Carpinetum betuli* into the traditionally described subassociations and showed that the criteria for this classification are not as solid as considered before.

The ass. *Epimedio-Carpinetum betuli* is present in both the Dinaric and Pannonian parts of Croatia (Horvat 1938, Anić 1940, Horvat et al. 1974, Šegulja 1974, Pelcer 1975, 1979, Vukelić 1991, Baričević 2002, Škvorc 2006, G. Horvat 2011, and others). However, to date, none of the oak-hornbeam forests in the region of Ozalj and along the middle reach of the Kupa River have ever been phytosociologically investigated.

The whole reach of the Kupa River, from its source in the Risnjak National Park to the city of Ozalj, is mostly surrounded by limestone and dolomite canyons, which were deeply carved by the river. When it reaches the city of Ozalj, Kupa leaves the Dinaric ecoregion end enters the Pannonian ecoregion, and this area is the approximate edge of the former Pannonian Sea (see ter Borgh et al. 2013). Some phytosociological research has been carried out on the vegetation along the Croatian side of the Kupa River (Horvat 1951, Vukelić et al. 2012, Vukelić et al. 2018, Kovačić 2019), but only in the upper part of its stretch in the area of Gorski Kotar. However, no phytosociological data exists for the vegetation in the middle stream of the Kupa River. In general, phytosociological research in the whole Ozalj area is scarce, and to date, only one locality has been investigated within a research project on sweet chestnut (*Castanea sativa* Mill.) forests (Medak 2011).

In the present study, phytosociological data on the oak-hornbeam forest inhabiting the limestone cliffs along the Kupa River canyon (Kamanje, W-Central Croatia; Fig. 1.), which are included in the Natura 2000 ecological network, is provided for the first time.

MATERIALS AND METHODS
MATERIJALI I METODE

Study area – *Područje istraživanja*

The investigated oak-hornbeam forest (Fig. 2) is situated on cliffs composed of biolithitic and bioclastic limestones

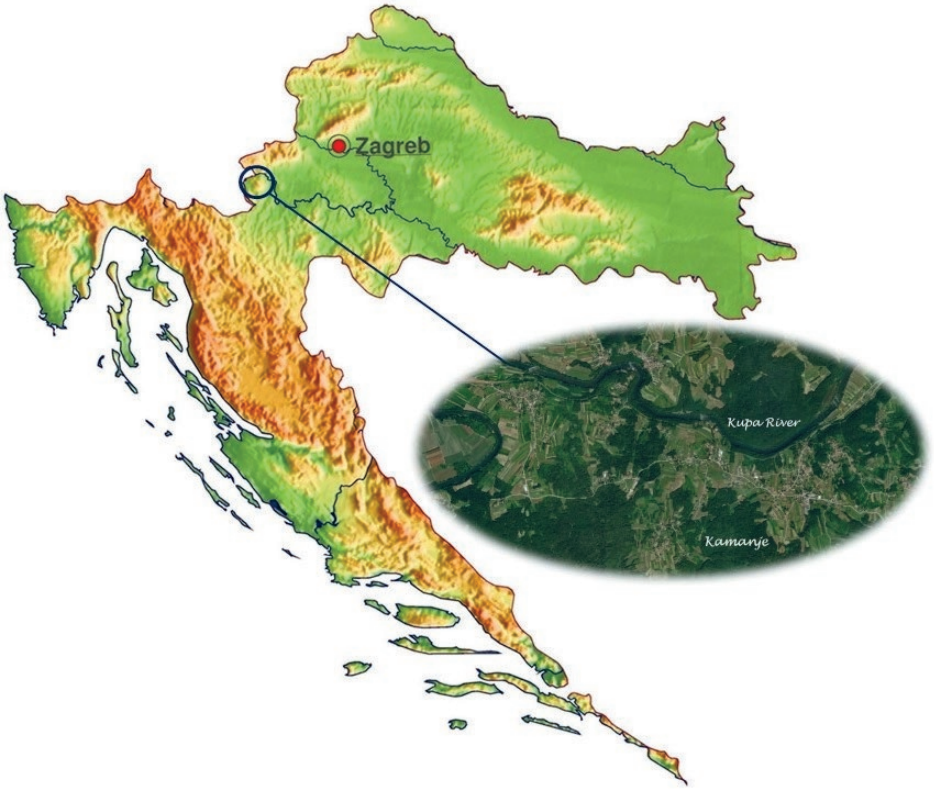

Figure 1. Study area (Kamanje, West-Central Croatia). Map source: www.croatiamap360.com
Slika 1. Istraživano područje (Kamanje, zapadni dio središnje Hrvatske). Izvor karte: www.croatiamap360.com

and carbonate breccias and conglomerates (Bukovac et al. 1984), spanning along the shore of the Kupa River, along a transect that passes through Petrinski kut, Orljakovo, and Kamanje. A detailed geomorphological assessment of the Kamanje landscape is provided in Bregni (2020). In this area, the Kupa River serves as the state border between Croatia and Slovenia. In the present study, we investigated the forest on the Croatian side. The studied forest covers an area of around 15 hectares. The underlying soil is calcocambisol developed from the abovementioned rocks, with many limestone rocks protruding from the soil surface (see Husnjak 2014). According to the World Reference Soil Base (2015), this soil type corresponds to calcic cambisol. In the last century, the forest was rich in nose-horned vipers (*Vipera ammodytes*) and common European viper snakes (*Vipera berus*). However, within the last 20 years, their population greatly decreased, with the reason remaining unknown. In addition, this forest harbors a geomorphological nature monument, the Vrlovka cave.

Field vegetation survey – *Terensko istraživanje vegetacije*

A total of 14 relevés (13 relevés of ~400 m^2 in size and one relevé of ~250 m^2 in size) were surveyed using a classical six-degree Braun-Blanquet scal e (Braun-Blanquet 1964). Some of the relevés were placed on the top of the limestone cliffs with low inclination, while others were placed on their highly inclined edges. The field phytosociological research was conducted partly in 2020 and mainly in 2021. Surveys were conducted during early spring, late spring, and summer. During the surveys, all seedlings were assigned as part of the herb layer.

Data analyses – *Analize podataka*

The relevés obtained in the present study were compared to those of various *Epimedio-Carpinetum betuli* stands from the Dinaric and Pannonian areas. In the analyses, besides our 14 relevés, 97 relevés from other authors were used, including 30 from Horvat (1938), 25 from Vukelić (1991),

Figure 2. Various aspects of the oak-hornbeam forest in the karst canyon of the Kupa River in the study area; a – view of the forest from the river (Slovenian forest on the left side and Croatian forest on the right side of the Kupa River); b – part of the Kamanje forest on the top of the limestone cliffs; c and d – parts of the Kamanje forest on the slopes of limestone cliffs

Slika 2. Različiti aspekti hrastovo-grabove šume u krškom kanjonu Kupe na istraživanom području; a – pogled od rijeke prema šumi (slovenska šuma s lijeve strane i hrvatska s desne strane Kupe); b – dio Kamanjske šume povrh vapnenačkih litica; c i d – dijelovi Kamanjske šume na padinama vapnenačkih litica

26 from Šegulja (1974), and 16 from Pelcer (1975). The main matrix combining all these relevés was made using the Turboveg 2.0 software (Henekens and Schaminée 2001), in which the Braun-Blanquet cover values were converted into mean percentage cover values. Moss species were excluded from the analyses as not all authors recorded them, and different vegetation layers were merged.

Agglomerative hierarchical clustering using complete linkage on the Bray–Curtis species × site dissimilarity matrix was used to assess the relationships between the analyzed forests. This was performed in R with the package 'stats' using the hclust function. Prior to the cluster analysis, species percentage cover values were square-rooted. In addition, non-metric multidimensional scaling (NMDS) set for 2D solution was used to see if the clustering patterns can be confirmed with the ordination method. NMDS was done in the package 'vegan' (Oksanen et al. 2013) using the metaMDS function (ordination plot not shown). The nomenclature of plant taxa follows Kew's Plants of the World Online (POWO 2023).

RESULTS
REZULTATI

Clustering results – *Klasterska analiza*

According to the results of the cluster analysis (Fig. 3), the oak-hornbeam forest analyzed in the present study was separated into a unique cluster. In the other large cluster, two main groups could be recognized. One group contained the subass. *staphyletosum*, *erythronietosum*, and *caricetosum pilosae*, which were grouped into two, mostly author-dependent, clusters. The other group was also composed of two clusters, one containing the subass. *asperuletosum* and *luzuletosum albidae*, and the other containing the subass. *seslerietosum* and *luzuletosum albidae*, the *Veratrum album* variant, as well as four of the *caricetosum pilosae* relevés. NMDS gave a similar clustering pattern of the subassociations with a stress of 22%.

Plant community composition and structure of the studied forest – *Florni sastav i struktura istraživane šume*

The oak-hornbeam forest investigated in the present study comprised a total of 164 vascular plant species (Table 1). The number of species in a relevé ranged from 42 to 80, with a mean ± standard error of 63 ± 3.

According to the traditional classification of sessile oak and common hornbeam forest subassociations in Croatia, this oak-hornbeam forest of Kamanje can be classified as ass. *Epimedio-Carpinetum betuli* subass. *staphyletosum*. Among the diagnostic species of this subassociation, *Staphylea pinnata* occurred in 78% of the relevés in the shrub layer and in 65% of the relevés in the herb layer. *Hacquetia epipactis* occurred in 78% of the relevés, followed by *Carex digitata* occurring in 71% of the relevés.

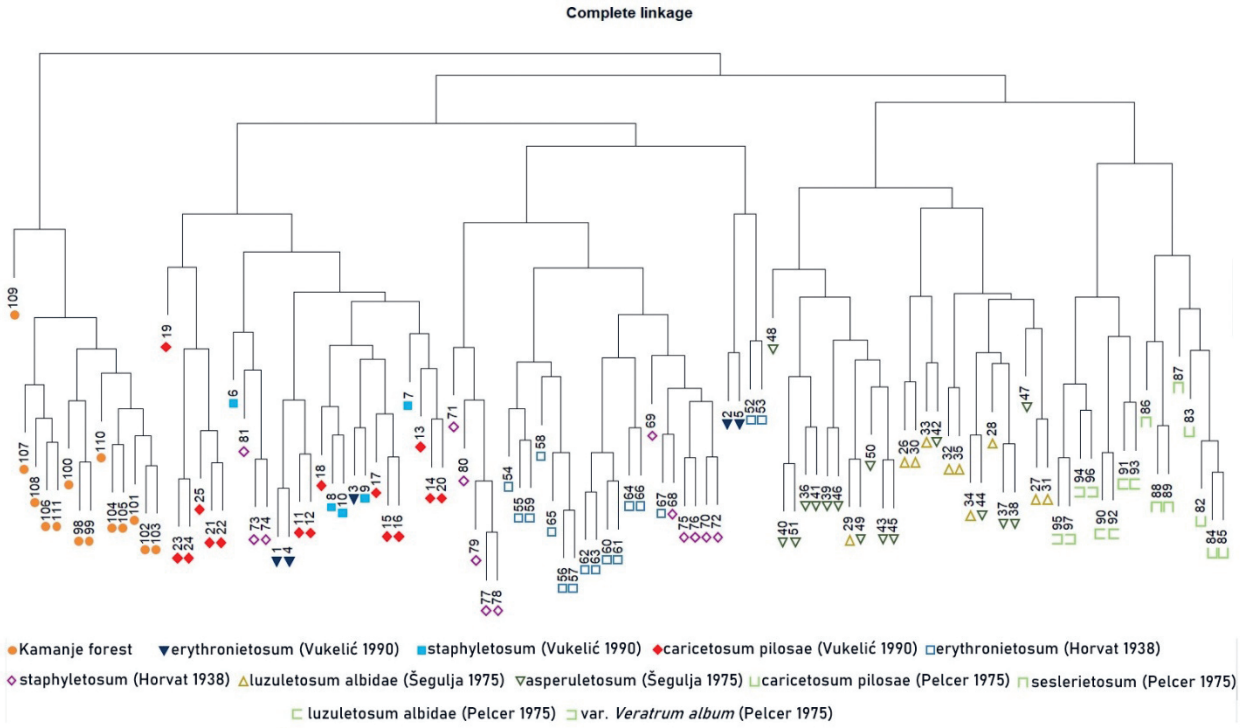

Figure 3. Dendrogram produced by hierarchical clustering using complete linkage
Slika 3. Dendrogram dobiven hierarhijskom klasterskom analizom koristeći complete linkage metod

Table 1. Relevés of the studied oak-hornbeam forest (Kamanje, West-Central Croatia)
Tablica 1. Fitocenološki snimci istraživane hrastovo-grabove šume (Kamanje, zapadni dio središnje Hrvatske)

Relevé number *Broj snimka*		1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Relevé size (~m²) *Površina snimka* (~m²)		400	400	400	400	400	400	400	400	400	400	400	250	400	400	
Elevation (~m a.s.l.) *Nadmorska visina (~m)*		155	145	142	148	144	143	141	145	136	138	138	138	133	143	
Exposition (sh = sinkhole) *Ekspozicija (sh = vrtača)*		sh	sh	NNE	N	sh	sh	NE	N	NE	NW	N	N	N	E	
Average inclination (°) *Prosječni nagib (°)*		5	15	15	3	12	15	10	15	35	45	55	60	50	50	Frequency *Učestalost*
Char. sp. ass. Epimedio-Carpinetum betuli																
Epimedium alpinum*	C	3	4	3	4	5	5	5	5	1	1	+	+	1	2	100
Primula vulgaris*		+	+	.	.	+	+	+	.	.	.	.	.	+	+	50
Diff. sp. subass. staphyletosum																
Staphylea pinnata*	B	.	1	+	.	1	1	.	1	2	2	2	1	2	+	79
Staphylea pinnata*	C	.	1	+	+	.	.	.	1	1	+	1	1	+	.	64
Hacquetia epipactis*		+	+	.	.	+	+	+	.	+	+	+	+	+	+	79
Carex digitata		.	+	.	.	+	+	+	+	.	+	+	+	+	+	71
Erythronio-Carpinion betuli																
Lonicera caprifolium*	B	.	.	.	.	.	+	.	.	.	.	.	.	.	.	7
Lonicera caprifolium*	C	1	1	+	1	1	+	.	+	.	.	.	.	1	.	57
Galanthus nivalis*		.	+	+	+	+	+	+	+	1	1	1	1	1	+	93
Cyclamen purpurascens*		+	+	+	.	+	+	.	+	+	+	+	.	+	+	79
Lamium orvala*		+	+	+	+	+	.	.	.	.	.	+	1	1	+	64
Helleborus dumetorum*		.	.	.	+	.	+	.	+	+	.	+	+	+	+	57
Aposeris foetida*		.	+	.	+	+	.	+	.	.	.	.	.	+	+	43
Erythronium dens-canis*		.	.	.	+	.	+	+	+	.	.	.	.	+	+	43
Crocus vernus*		.	.	+	.	.	.	1	1	.	.	.	.	.	.	21
Knautia drymeia*		.	.	.	+	.	.	.	.	.	.	.	.	+	+	21
Carpinion betuli																
Carpinus betulus	A	5	4	3	4	3	4	5	5	4	3	5	.	4	5	93
Tilia cordata		.	2	2	1	1	2	.	.	2	2	2	3	1	2	79
Acer campestre		.	1	.	1	.	.	.	.	1	+	.	3	1	.	43
Prunus avium		.	.	+	.	1	1	.	.	.	.	.	.	.	.	21
Carpinus betulus	B	+	1	.	+	+	+	+	.	.	.	.	.	1	.	50
Acer campestre		+	.	+	+	+	1	+	1	.	+	.	.	+	2	71
Tilia cordata		.	.	1	.	.	1	.	.	+	1	+	.	.	+	43
Prunus avium		.	.	.	.	+	+	1	.	.	.	.	.	.	+	29
Stellaria holostea	C	1	1	+	+	1	+	+	1	3	+	.	.	+	+	86
Carex pilosa		+	1	3	+	1	1	.	1	2	1	.	.	+	+	79
Carpinus betulus		+	.	+	+	+	+	+	.	+	.	.	.	+	.	57
Acer campestre		1	+	+	+	+	+	+	1	+	+	.	+	+	+	93
Prunus avium		+	+	+	+	+	+	+	.	+	+	+	.	.	+	79
Melampyrum nemorosum		+	+	+	+	+	.	.	+	+	+	.	.	.	1	64
Tilia cordata		.	+	+	+	.	+	.	.	+	.	.	+	.	.	43
Vinca minor		.	.	.	.	.	.	.	.	4	.	.	.	3	.	14
Aremonio-Fagion																
Cardamine enneaphyllos*	C	+	+	+	.	+	+	+	+	+	+	+	+	+	+	93
Omphalodes verna*		+	+	+	+	+	+	.	+	+	+	+	.	+	+	86
Isopyrum thalictroides*		3	+	+	.	+	.	+	+	1	+	+	+	.	.	71
Cardamine trifolia*		.	.	.	.	.	.	.	+	.	+	+	+	.	+	36
Aremonia agrimonoides*		.	.	.	+	.	.	.	+	.	.	.	.	.	+	21

Relevé number *Broj snimka*		1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Relevé size (~m²) *Površina snimka* (~m²)		400	400	400	400	400	400	400	400	400	400	400	250	400	400	
Elevation (~m a.s.l.) *Nadmorska visina (~m)*		155	145	142	148	144	143	141	145	136	138	138	138	133	143	Frequency *Učestalost*
Exposition (sh = sinkhole) *Ekspozicija (sh = vrtača)*		sh	sh	NNE	N	sh	sh	NE	N	NE	NW	N	N	N	E	
Average inclination (°) *Prosječni nagib (°)*		5	15	15	3	12	15	10	15	35	45	55	60	50	50	
Tilio-Acerion																
Acer pseudoplatanus	A	.	.	.	.	.	1	1	.	.	2	.	3	2	.	36
Acer platanoides		.	.	.	.	.	.	.	.	.	2	.	.	.	.	7
Tilia platyphyllos		.	.	.	.	.	.	.	.	1	.	.	.	.	.	7
Acer pseudoplatanus	B	.	.	+	+	+	+	+	2	.	.	.	+	.	+	57
Tilia platyphyllos		.	.	.	.	.	.	.	+	.	.	.	.	.	.	7
Euonymus latifolius*		.	.	.	.	+	.	.	.	.	.	.	.	.	.	7
Acer pseudoplatanus	C	.	+	+	+	+	+	+	+	+	+	+	.	+	.	79
Glechoma hirsuta		+	1	.	+	+	.	+	.	+	+	.	.	.	+	57
Polystichum setiferum*		+	.	1	.	.	+	+	.	.	.	1	1	+	+	57
Polystichum aculeatum		.	.	.	.	+	.	+	+	.	.	1	1	1	.	43
Geranium robertianum		+	.	.	+	.	.	.	.	+	+	+	.	.	.	36
Euonymus latifolius*		.	.	.	+	.	+	.	.	.	.	.	.	.	.	14
Arum maculatum		.	.	.	.	.	.	.	.	+	+	.	.	.	.	14
Acer platanoides		.	.	.	.	.	.	.	.	.	+	.	.	.	.	7
Alnion incanae																
Quercus robur	A	1	3	3	2	3	1	1	3	2	3	.	.	2	2	86
Ulmus minor		.	1	.	.	.	1	.	.	.	.	.	.	.	1	21
Ulmus minor	B	.	+	1	.	+	1	1	+	.	.	.	.	.	.	43
Quercus robur	C	+	+	+	+	+	+	+	+	+	+	+	.	+	+	93
Ulmus minor		.	+	+	.	+	.	.	.	.	.	.	.	+	.	29
Glechoma hederacea		.	.	.	+	.	.	.	+	.	.	.	.	+	.	21
Cerastium sylvaticum		.	.	.	.	.	.	.	.	.	.	.	.	+	+	14
Fagetalia sylvaticae																
Fagus sylvatica	A	.	.	.	.	.	.	.	2	.	.	.	.	.	.	7
Fraxinus excelsior		.	.	.	+	.	.	.	.	.	.	1	.	.	.	14
Sambucus nigra	B	.	.	.	+	.	+	+	.	.	+	1	+	+	1	57
Fagus sylvatica		.	.	.	.	.	.	1	2	+	.	.	+	.	+	36
Fraxinus excelsior		.	.	.	.	.	.	+	.	1	.	.	.	.	.	14
Dryopteris filix-mas	C	+	+	+	+	+	+	1	+	+	+	1	1	1	1	100
Asplenium scolopendrium		+	1	+	+	+	+	.	+	1	1	1	1	+	1	93
Pulmonaria officinalis		+	+	+	+	.	+	+	+	+	+	+	+	+	+	93
Asarum europaeum		+	+	+	+	+	.	+	+	+	.	+	+	+	+	86
Lamium galeobdolon		+	+	+	+	+	+	+	+	+	+	+	.	+	+	93
Euphorbia dulcis		.	+	+	+	+	+	+	+	+	+	+	.	+	+	86
Carex sylvatica		+	1	+	+	1	+	+	.	+	+	+	.	+	+	86
Polygonatum multiflorum		.	+	.	.	.	.	+	+	.	+	.	.	+	.	36
Sanicula europaea		.	+	.	.	+	+	+	.	+	+	+	.	+	+	64
Mercurialis perennis		.	+	.	.	.	.	.	+	+	+	+	1	+	+	57
Fraxinus excelsior		.	.	.	+	+	.	.	.	+	.	+	.	.	+	36
Viola reichenbachiana		.	.	.	+	.	.	.	.	+	.	+	.	1	+	36
Cardamine bulbifera		.	+	.	.	.	+	.	.	+	+	+	.	.	.	36
Campanula trachelium		.	+	+	.	+	.	.	.	.	+	.	+	.	.	36
Mycelis muralis		.	+	.	.	.	.	.	.	.	+	+	+	.	.	29
Fagus sylvatica		.	.	.	.	.	.	.	.	+	+	.	.	.	+	21
Sambucus nigra		+	.	.	.	.	.	+	.	.	.	.	.	.	+	21

Relevé number *Broj snimka*		1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Relevé size (~m²) *Površina snimka* (~m²)		400	400	400	400	400	400	400	400	400	400	400	250	400	400	
Elevation (~m a.s.l.) *Nadmorska visina (~m)*		155	145	142	148	144	143	141	145	136	138	138	138	133	143	
Exposition (sh = sinkhole) *Ekspozicija (sh = vrtača)*		sh	sh	NNE	N	sh	sh	NE	N	NE	NW	N	N	N	E	
Average inclination (°) *Prosječni nagib (°)*		5	15	15	3	12	15	10	15	35	45	55	60	50	50	Frequency *Učestalost*
Melica nutans		.	.	.	+	+	.	.	.	.	+	.	.	.	.	21
Ranunculus lanuginosus		.	+	.	.	.	.	.	.	.	+	.	.	+	.	21
Heracleum sphondylium		.	.	.	.	.	.	.	.	.	.	.	.	+	+	14
Quercetalia pubescentis																
Fraxinus ornus	A	1	.	1	.	1	1	.	.	1	.	.	.	+	.	43
Quercus cerris		.	.	.	2	2	2	.	.	.	.	.	.	.	.	21
Sorbus torminalis		.	.	.	.	1	.	.	.	.	.	.	.	.	.	7
Euonymus verrucosa	B	1	1	.	+	1	1	1	1	2	1	1	1	1	1	93
Cornus mas		1	1	+	+	1	1	1	1	2	1	1	+	.	.	86
Fraxinus ornus		+	1	+	.	1	+	+	1	1	+	.	.	+	.	71
Euonymus verrucosa	C	+	+	+	.	+	+	+	.	.	+	+	+	+	+	79
Fraxinus ornus		+	1	+	+	+	+	.	1	1	+	.	.	.	+	71
Cornus mas		+	+	.	.	+	.	.	.	+	+	.	.	.	+	43
Lathyrus niger		.	+	+	+	.	.	.	.	.	.	.	.	.	.	21
Viola alba		+	+	.	.	.	+	.	.	.	.	.	.	.	.	21
Viola hirta		.	.	.	+	.	+	.	.	.	.	+	.	.	.	21
Sorbus torminalis		.	.	+	.	.	.	.	.	.	.	.	.	+	.	14
Convallaria majalis		.	.	.	.	+	.	.	.	.	.	.	+	.	.	14
Sedum sp.		.	+	.	.	+	.	.	.	.	.	.	.	.	.	14
Quercus cerris		.	.	.	.	+	.	.	.	.	.	.	.	.	.	7
Quercetalia robori-petraeae																
Pteridium aquilinum	C	+	+	+	+	+	+	+	+	.	.	.	.	.	.	57
Serratula tinctoria		.	+	.	.	+	+	.	.	.	.	.	.	.	.	21
Betula pendula		.	+	.	.	+	.	.	.	.	+	.	.	.	.	21
Sedum telephium		.	.	.	.	+	+	.	.	.	+	.	.	.	.	21
Querco-Fagetea																
Hedera helix	A	1	+	.	.	.	.	.	.	+	1	+	+	.	2	50
Quercus petraea		.	.	1	1	.	2	.	1	.	.	.	.	.	.	29
Corylus avellana	B	1	1	+	+	1	1	1	1	1	2	+	3	2	1	100
Quercus petraea		.	.	.	.	.	.	+	.	.	.	.	.	.	.	7
Anemone nemorosa	C	+	+	1	+	3	4	1	2	1	1	1	2	3	1	100
Hepatica nobilis		+	+	+	+	+	+	+	.	+	+	+	+	+	+	93
Hedera helix		2	2	+	1	1	1	1	1	3	.	2	1	1	1	93
Corylus avellana		+	+	.	+	+	.	+	.	+	+	+	+	+	+	79
Melica uniflora		+	+	+	+	.	+	+	.	.	.	+	.	+	+	64
Rosa arvensis		+	.	.	+	+	1	+	.	+	.	.	.	+	+	57
Cruciata glabra		1	+	.	.	.	+	.	.	.	+	.	.	+	.	36
Galium sylvaticum		.	+	.	.	.	+	+	.	.	+	.	.	.	+	36
Scilla bifolia		.	.	.	.	.	.	+	.	.	.	+	+	+	.	29
Quercus petraea		.	+	.	.	.	.	.	.	.	.	.	.	.	.	7
Crataego-Prunetea (syn. Rhamno-Prunetea)																
Crataegus monogyna	A	.	.	.	.	1	.	.	.	.	.	.	.	.	.	7
Cornus sanguinea	B	1	1	1	.	+	.	1	.	.	+	.	.	+	1	57

Relevé number *Broj snimka*		1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Relevé size (~m²) *Površina snimka* (~m²)		400	400	400	400	400	400	400	400	400	400	400	250	400	400	
Elevation (~m a.s.l.) *Nadmorska visina (~m)*		155	145	142	148	144	143	141	145	136	138	138	138	133	143	Frequency *Učestalost*
Exposition (sh = sinkhole) *Ekspozicija (sh = vrtača)*		sh	sh	NNE	N	sh	sh	NE	N	NE	NW	N	N	N	E	
Average inclination (°) *Prosječni nagib (°)*		5	15	15	3	12	15	10	15	35	45	55	60	50	50	
Ligustrum vulgare		.	+	.	+	+	.	+	1	.	.	.	.	+	+	50
Crataegus monogyna		.	.	+	+	+	1	+	.	1	.	.	.	.	.	43
Euonymus europaea		.	.	1	.	.	.	.	+	.	+	+	.	.	.	29
Viburnum lantana		.	.	.	.	.	.	.	.	+	+	.	.	.	+	21
Berberis vulgaris		.	.	.	.	.	+	.	+	.	.	.	.	.	.	14
Prunus spinosa		.	.	+	.	.	.	.	.	.	.	.	.	.	.	7
Crataegus laevigata		.	.	.	+	.	.	.	.	.	.	.	.	.	.	7
Crataegus monogyna	C	+	+	+	+	+	+	.	+	.	+	.	.	+	+	71
Ligustrum vulgare		+	+	.	+	+	+	.	1	+	.	.	.	+	.	57
Berberis vulgaris		.	.	.	.	+	+	+	.	.	.	.	.	+	.	29
Cornus sanguinea		.	+	+	+	.	.	.	.	.	.	.	.	.	.	21
Euonymus europaea		.	.	+	+	.	.	.	+	.	.	.	.	.	.	21
Viburnum lantana		+	+	.	.	.	.	.	.	+	.	.	.	.	.	21
Clematis vitalba		.	.	.	+	.	+	.	.	.	.	.	.	+	.	21
Prunus spinosa		+	.	+	.	.	.	.	.	.	.	.	.	.	.	14
Crataegus laevigata		+	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Vaccinio-Picetea																
Picea abies	A	.	.	.	1	.	1	1	1	.	.	.	.	.	.	29
Picea abies	B	.	.	.	.	1	1	1	1	.	.	.	.	.	.	29
Luzula pilosa	C	+	+	.	+	.	+	+	.	.	.	.	.	.	.	36
Picea abies		.	.	.	+	.	.	+	.	.	.	.	.	+	.	21
Asplenietea trichomanis																
Asplenium trichomanes	C	+	+	+	+	+	+	+	+	+	+	+	+	+	+	100
Polypodium vulgare		+	1	+	1	+	+	.	+	1	1	+	1	1	+	93
Saxifraga cuneifolia		.	.	.	.	.	.	.	.	+	+	+	+	.	.	29
Moehringia muscosa		.	.	.	.	.	+	.	.	.	.	+	+	.	.	21
Cardaminopsis arenosa		.	+	.	.	.	+	.	.	.	+	.	.	.	.	21
Other species																
Robinia pseudoacacia	A	.	.	1	2	.	.	.	.	.	.	.	.	.	.	14
Robinia pseudoacacia	B	.	.	+	.	.	.	.	.	.	.	.	+	.	.	14
Geranium phaeum	C	+	+	.	.	.	.	.	.	.	+	+	.	+	+	43
Aegopodium podagraria		.	.	.	.	.	.	.	.	.	+	.	+	+	1	29
Geum urbanum		+	+	.	+	.	+	.	.	.	.	.	.	.	.	29
Urtica dioica		.	.	.	.	.	.	.	.	.	+	.	+	.	.	14
Ajuga reptans		.	+	+	+	.	.	.	.	.	.	.	.	+	+	36
Knautia arvensis		.	.	.	.	.	+	.	.	.	+	.	.	.	.	14
Athyrium filix-femina		.	+	.	.	.	+	.	.	.	.	+	+	+	+	43
Milium effusum		.	+	.	.	.	.	+	.	.	+	+	.	.	.	29
Senecio cf. ovatus		.	.	.	+	.	+	.	.	.	.	.	.	.	.	14
Juglans regia		.	.	+	.	.	.	+	.	.	.	.	.	.	.	14
Rubus hirtus		+	1	1	+	+	+	1	+	+	.	+	+	+	1	93
Corydalis solida		+	+	.	.	.	.	.	.	+	+	.	.	.	+	36
Juglans regia		.	.	.	.	+	+	.	+	+	.	.	.	.	+	36

Relevé number *Broj snimka*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Relevé size (~m²) *Površina snimka* (~m²)	400	400	400	400	400	400	400	400	400	400	400	250	400	400	
Elevation (~m a.s.l.) *Nadmorska visina (~m)*	155	145	142	148	144	143	141	145	136	138	138	138	133	143	
Exposition (sh = sinkhole) *Ekspozicija (sh = vrtača)*	sh	sh	NNE	N	sh	sh	NE	N	NE	NW	N	N	N	E	Frequency *Učestalost*
Average inclination (°) *Prosječni nagib (°)*	5	15	15	3	12	15	10	15	35	45	55	60	50	50	
Fragaria vesca	+	+	.	.	.	.	.	+	.	+	.	.	+	.	36
Ranunculus auricomus	+	+	.	.	.	.	.	.	.	.	.	.	+	+	29
Galeopsis speciosa	.	+	.	+	.	.	.	.	+	.	.	.	+	.	29
Lamium purpureum	+	.	.	.	.	.	.	.	+	.	+	.	.	+	29
Polystichum x illyricum	.	.	.	.	.	+	.	.	+	.	.	.	.	+	21
Rubus caesius	.	.	.	.	.	.	.	+	.	+	.	.	+	.	21
Festuca sp.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	14
Cirsium oleraceum	.	.	.	.	.	.	.	.	.	+	.	.	+	.	14
Oxalis corniculata	.	.	.	.	.	.	.	.	.	.	+	.	.	+	14
Robinia pseudoacacia	.	.	.	.	.	.	.	.	.	.	.	.	+	.	7

Herb layer species occurring in only one relevé (number in the parentheses represents relevé number): *Neottia nidus-avis* (1), *Luzula forsteri* (1), *Veronica chamaedrys* (2), *Eupatorium cannabinum* (2), *Erigeron annuus* (2), *Acer obtusatum* (3), *Poa pratensis* (4), *Orobanche* sp. (4), *Corydalis bulbosa* (5), *Pilosella officinarum* (5), *Melittis melissophyllum* (6), *Helleborus atrorubens*² (6), *Asplenium ruta-muraria* (6), *Juniperus communis* (6), *Daphne mezereum* (7), *Gentiana asclepiadea* (7), *Cardamine waldsteinii* (9), *Viburnum opulus* 10), *Cardamine impatiens* (10), *Euphorbia verrucosa* (10), *Chelidonium majus* (10), *Stellaria nemorum* (10), *Paris quadrifolia* (10), *Doronicum cf. austriacum* (10), *Hieracium* sp (10), *Allium ursinum* (11), *Galinsoga ciliata* (11), *Aconitum lycoctonum* (11), *Polystichum lonchitis* (12), *Viscum album* (13), *Taraxacum officinale* (13), *Impatiens glandulifera* (13), *Lycopus europaeus* (13), *Dryopteris carthusiana* (13), *Cystopteris fragilis* (13), *Centaurea jacea* (13), *Symphytum tuberosum* (13), *Salvia glutinosa* (14), *Ranunculus ficaria* (14), *Lathraea squamaria* (14), *Anemone ranunculoides* (14), *Alnus glutinosa* (14)

Legend: A – tree layer, B – shrub layer, C – herb layer (including the seedlings)
* Species of the Illyrian-Balkan floral geoelement (according to Vukelić 2012)

Among the diagnostic species of the ass. *Epimedio-Carpinetum betuli*, *Epimedium alpinum* was present in all relevés, whereas *Lonicera caprifolium* and *Primula vulgaris* were present in 57% and 50% of relevés, respectively. Many Illyrian species characteristic for the *Erythronio-Carpinion betuli* and *Aremonio-Fagion* alliances were also frequent, especially *Staphylea pinnata*, *Galanthus nivalis, Cardamine enneaphyllos, Cyclamen purpurascens*, *Lamium orvala*, *Helleborus dumetorum*, *Erythronium dens-canis, Omphalodes verna, Isopyrum thalictroides* and *Hacquetia epipactis*.

In the tree layer, *Carpinus betulus* was the most abundant and most frequent tree species, followed by *Quercus robur* and *Tilia cordata*. In terms of frequency, these species were followed by *Fraxinus ornus*, *Acer campestre*, and *A. pseudoplatanus*. In the tree layer, *Q. petraea* appeared in only 29% of the relevés. Here, we must emphasize that many of the recorded *Q. petraea* individuals highly resembled the intermediates between *Q. robur* and *Q. petraea*. However, for the purpose of our phytosociological survey, the possible hybrids having similar morphological features to that of *Q. petraea* were recorded as *Q. petraea*. In the shrub layer, *Corylus avellana* was the most abundant and frequent species, followed by *Euonymus verrucosa*, *Staphyllea pinnata*, *Cornus mas*, *Fraxinus ornus*, and *Acer campestre*. In the herb layer, *Epimedium alpinum* was the dominant species in more than half of the relevés. Moreover, many spring-flowering geophytes and hemicryptophytes appeared in all or almost all relevés, including *Galanthus nivalis*, *Cyclamen purpurascens*, *Cardamine enneaphyllos*, *Anemone nemorosa*, *Hepatica nobilis*, *Asarum europaeum*, *Lamium galeobdolon*, *Pulmonaria officinalis*, *Omphalodes verna*, and *Stellaria holostea*, among others. Some ferns also appeared in more than 90% of relevés in the herb layer, including *Asplenium trichomanes*, *A. scolopendrium*, *Polypodium vulgare*, and *Dryopteris filix-mas*. Among the seedlings, the most frequent were those of *Q. robur*, *A. campestre*, *A. pseudoplatanus*, and *E. verrucosa*.

DISCUSSION AND CONCLUSIONS
RASPRAVA I ZAKLJUČCI

The oak-hornbeam forest investigated in the present study belongs to ass. *Epimedio-Carpinetum betuli* (all. *Erythronio-Carpinion*). At the traditional subassociation level, this forest is edaphically and floristically the closest to *staphyletosum* (Gračanin 2003, Horvat 1938); however, the current classification of *Epimedio-Carpinetum betuli* into various subassociations still needs to be resolved (Vukelić et al. 2015).

Our findings showed many differences between the studied forest from Kamanje and those of the same association researched by other authors. Firstly, one very peculiar difference is the high frequency of species characteristic for the *Asplenietea trichomanis* class in the Kamanje forest, which was related to the high abundance of stony microhabitats

favorable for their growth. This especially refers to the ferns *Asplenium trichomanes* and *Polypodium vulgare*, appearing in 100% and 93% of the relevés, respectively. In addition, other species characteristics for this class were present in this forest, such as *Saxifraga cuneifolia*, *Moehringia mucosa*, and *Cardaminopsis arenosa*. These three species were not highly frequent in our relevés; however, they grow on extremely inclined stony microhabitats within the forest, and parts of these microhabitats were not accessible in this phytosociological survey.

Secondly, an interesting feature of this forest is that *Q. robur* replaces *Q. petraea*. Even though the limestone cliffs on which the forest occurs are 15–25 meters higher than the fluvisols in which the *Q. robur* usually grows near the Kupa River, it is still the dominant oak species in the tree layer. It seems that it is able to protrude its roots through the limestone crevices and reach the groundwater favorable for its growth while also taking advantage of the seepage water intruding from the upper hills. Mixed *Q. robur* and *Q. petraea* stands are not as rare in Croatia as it could be interpreted from the literature. They are very common in northern parts of Croatia on gentle slopes and transitional areas from colline to planar belts. Examples include the areas of Bjelovarska Bilogora, Kalnik, lower slopes of Slavonian hills, Medvednica Mountain, and others.

Furthermore, a specific floristic feature of the studied forest is the high abundance of certain ferns that were not recorded in the forests studied by other authors. These include *Asplenium scolopendrium*, which appeared in 93% of the relevés, followed by *Polystichum setiferum* and *P. aculeatum* appearing in 57% and 43% of the relevés, respectively. Other species occurring in more than half of the relevés that were also recorded only in the Kamanje forest were *Omphalodes verna* and *Ulmus minor.*

In addition, many species that were also present in the forests investigated by other authors were much more frequent in the Kamanje forest. In the herb layer, these include *Hepatica nobilis*, *Galanthus nivalis*, and *Isopyrum thalictroides*. Among the shrubs, these include *Cornus mas* and *Euonymus verrucosa*, and among the tree species *Tilia cordata*. Indeed, *E. verrucosa* appeared in all the relevés of the forest studied by Pelcer (1975), which he assigned to the *seslerietosum* subbasociation. However, his study included only four relevés per subassociation; thus, his observations cannot be used for floristic generalization about the *Epimedio-Carpinetum betuli* forests in the whole Lika plateau, where his research was conducted.

Another interesting feature of the Kamanje forest is the high frequency of *Carex pilosa*, *H. nobilis*, and *E. dens-canis*. The first two are traditionally considered as diagnostic for subass. *caricetosum pilosae*, and *E. dens-canis* is considered as diagnostic for subass. *erythronietosum*. The high occurrence of these species in the Kamanje forest, despite it being most similar to the subass. *staphyletosum*, supports the discussion of Vukelić et al. (2015), who questioned the traditional classification of these subassociations.

As mentioned before, if we followed the trend of classifying the *Epimedio-Carpinetum betuli* association into the traditional subassociations, the Kamanje forest investigated here would be classified as subass. *staphyletosum*. In addition, because of the high occurrence of ferns, which were not present in any of the previously studied forests, the Kamanje forest could be considered as a fern-rich *staphyletosum* subassociation. Because of the high limestone abundance and frequently high inclination, there are many rock crevices serving as microhabitats for these species. Thus, *A. trichomanes* and *P. vulgare* are the species that best reflect the stony habitat conditions in the Kamanje forest in contrast to other *Epimedio-Carpinetum betuli* forests. In addition, high air and soil moisture because of the proximity of the Kupa River, abscence of wood cutting, and high canopy closure also favor the growth and reproduction of other ferns, such as *D. filix-mas*, *A. scolopendrium*, *Athyrium filix-femina*, *P. setiferum*, and *P. aculeatum*.

We also want to note that the oak-hornbeam forests along the Kupa River canyon span farther than the area of our research, and these other areas should also be phytosociologically studied (including those on the Slovenian side of the river). This includes the canyon parts stretching further from Kamanje to the city of Ozalj, as well as the oak-hornbeam forests in the broad area of Vodenica hill. Most parts of these forests are not as preserved as the one in Kamanje because they are used for wood extraction, but research on these forests would still provide valuable insights about the oak-hornbeam forests on the south-west edge of the Pannonian basin, which are highly understudied.

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SAŽETAK

U ovome radu fitocenološki smo istražili hrastovo-grabovu šumu s vapnenačkih litica kanjona rijeke Kupe u mjestu Kamanje (zapadni dio središnje Hrvatske). Istraživana šuma zauzima površinu od ~15 ha, bogata je biljnim vrstama i dio je ekološke mreže Natura 2000. Relativno je dobro sačuvana, jer u posljednjih pedesetak godina nije bilo jačih zahvata koji bi znatnije utjecali na florni sastav i strukturu. U istraživanjima smo koristili klasičnu metodu srednjoeuropske fitocenološke škole (Braun-Blanquet 1964) koja u fitocenološkim snimanjima koristi šeststupanjsku skalu. Na 14 snimaka površine 250 do 400 m^2 zabilježene su 164 vaskularne biljne vrste, od 42 do 80 po snimku. Položaj istraženih sastojina u odnosu na ostale šume sveze *Erythronio-Carpinion* u Hrvatskoj utvrđen je aglomerativnom hierarijskom klasterskom analizom.

Hrastovo-grabova šuma iz Kamanja pripada asocijaciji *Epimedio-Carpinetum betuli* (Horvat 1938) Bohridi 1963. i po tradicionalnoj tipološkoj raščlanjenosti najbliža je njenoj subasocijaciji *staphyletosum* Horvat 1938. Međutim, u odnosu na ostale do sada istražene sastojine te asocijacije u Hrvatskoj, odlikuje se nekim posebnostima. To se ponajprije odnosi na sloj drveća, u kojemu zbog blizine rijeke Kupe i specifičnog hidrološkog režima obalnih padina hrast lužnjak dominira u odnosu na kitnjak. Nadalje, u prizemnom sloju na istoj površini prisutne su razlikovne vrste iz više subasocijacija prema dosadašnjoj tradicionalnoj podjeli, čime se dovodi u pitanje njena opravdanost i nameće potreba daljnjih istraživanja i širih analiza. U prizemnom sloju u odnosu na ostale hrastovo-grabove sastojine uočljiva je velika prisutnost paprati, što je posljedica ponajprije visoke vlage u zraku i tlu. Relativno velik broj vrsta razreda *Asplenietea trichomanis* posljedica je velike stjenovitosti kanjonskih obala i rubova. Među tim vrstama posebice se ističe *Saxifraga cuneifolia* – relativno rijetka vrsta u šumama Hrvatske.

Na specifičnost istraživanih sastojina ukazuju i rezultati klasterske analize uz korištenje metode complete linkage; one su svrstane u jedinstveni zasebni klaster, dok je drugi veliki klaster sadržavao sve ostale sastojine asocijacije *Epimedio-Carpinetum*. To nalaže potrebu detaljnijeg istraživanja sličnih sastojina na prijelazu dinarskog i panonskog područja, odnosno na opsežnu analizu *Carpinetum* zajednica u Hrvatskoj i susjednim područjima.

KLJUČNE RIJEČI: *Epimedio-Carpinetum betuli*, ilirske hrastove šume, poluprirodne šume, šume Natura 2000, peripanonska biogeografska regija