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Floristic and ecological diversity of stands dominated by *Carpinus orientalis* in gorges and canyons of eastern Serbia (SE Europe)

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ABSTRACT

We investigated stands dominated by *Carpinus orientalis* Mill. in five gorges and canyons across eastern Serbia. Floristic and ecological analyses were conducted on a dataset of 102 phytosociological relevés collected in the field and 33 relevés from the existing literature. Hierarchical classification distinguished four groups of phytosociological relevés within the dataset. Floristic composition, diversity and phytogeographical characteristics of the groups were determined. These groups occur in ecologically different habitats and differ with respect to ecological gradients. Non-metric multidimensional scaling revealed that the main gradients that influence the variation in the floristic composition were moisture, nutrients, temperature and light. The results obtained in our analyses allowed us to describe the new association *Seslerio filifoliae–Carpinetum orientalis* ass. nova hoc loco, that occupies very steep and stony slopes, and is developing at altitudes between 80 and 550 m a.s.l. in all aspects.

ARTICLE HISTORY

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Oriental hornbeam; classification; diversity; phytosociology; ravine habitats; Seslerio filifoliae–Carpinetum orientalis; syntaxonomic scheme

Introduction

Carpinus orientalis Mill. (Oriental hornbeam) is a small tree or shrub that is found mainly on sunny slopes on shallow or rocky soils and prefers calcareous substrates (Chiarucci et al. 1996). The Oriental hornbeam is a xerothermophilous pioneer plant species that can easily colonize open and degraded habitats (Popović et al. 1997). It has a wide distribution from the Apennines and the Balkan Peninsula, through the Pontic region, Turkey, Syria, and Iran, to the Caucasus region (Sikkema and Caudullo 2016). In southeastern Europe, C. orientalis is a typical element of the zonal belt of sub-Mediterranean forest vegetation. It dominates in thermophilous amphiadriatic low-altitude calcareous (Carpinion orientalis Horvat 1958) and sub-Mediterranean thermophilous forests of the central and southern Balkans (Syringo-Carpinion orientalis Jakucs (1959) 1960) of the class Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959 (Mucina et al. 2016). Outside the sub-Mediterranean zone, C. orientalis forms extrazonal communities in the inland areas of its range with some continental influences, mainly in river gorges and canyons (Čarni et al. 2009; Stupar et al. 2015, 2016; Čarni 2016).

Stands dominated by *C. orientalis* are floristically diverse and occur in different regions with different ecological conditions.

Until recently, they were poorly studied and included into only a few associations, but recent research has shown that they are much more diverse and that more associations exist (Tzonev 2013; Stupar et al. 2020). Communities dominated by *C. orientalis* in the ravine habitats of eastern Serbia form stands that may be low or high, open or closed, in all stand combinations, and are most common on limestone, steep slopes and skeletal soils of varying depths (Mišić et al. 1978; Kojić et al. 1998; Lakušić et al. 2005). They are all classified in the *Syringo-Carpininon orientalis* alliance, which includes the following associations: *Carpino orientalis—Quercetum mixtum* Mišić 1967, *Querco-Carpinetum orientalis* B. Jovanović 1953 (1979), and *Syringo-Carpinetum orientalis* Jakucs 1959 (Lakušić et al. 2005).

Despite numerous studies conducted in ravine habitats of eastern Serbia, the available information on the diversity of stands dominated by Oriental hornbeam is incomplete. In view of this, we performed field investigations in five gorges and canyons in eastern Serbia to: (1) classify *C. orientalis*-dominated stands; (2) determine the floristic composition, diversity, and phytogeographical characteristics of the identified groups; (3) identify the main ecological factors influencing the variation in the floristic composition of the groups; and (4) propose a syntaxonomic scheme of the obtained groups.

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Materials and methods

Study area

The research was carried out in eastern Serbia, which is biogeographically located in the Moesian floristic province (Janković 1984; Stevanović 1995). This region is located in the transition zone from temperate-continental to continental climate. The climate in this area is characterized by a severe and cold winter with strong and frequent winds, snow drifts, and a long, pronounced dry period in the middle of the growing season. To determine the specific climate conditions in each investigated gorge, we extracted bioclimatic parameters from the WorldClim set of global climate layers. We used BIO1 (average annual temperature) and BIO12 (annual precipitation) to characterize the specific climate types. Bioclimatic parameters were extracted using the software DIVA-GIS 7.5 (Fick and Hijmans 2017).

The investigated gorges and canyons are located in the Carpathian-Balkan Mountains, which extend from the Danube and Timok valleys in the north to Mt. Stara Planina in the southeast and further east to Bulgaria (Figure 1). The area of eastern Serbia is characterized by various geological substrates, which change over relatively short distances (Pavlović et al. 2017). All the investigated sites were found on limestone bedrock.

We analyzed stands dominated by *C. orientalis* in five gorges and canyons: (1) Đerdap Gorge, (2) Lazar's Canyon, (3) Sićevo Gorge, (4) Jelašnica Gorge and (5) Jerma River Canyon (Figure 1).

The Đerdap Gorge is located in eastern Serbia on the border with Romania. It is 100 km long, extends from Golubac to Sip, and cuts through the Carpathians in a west–east direction. Downstream of the Danube are arranged gorges and valleys, alternating in the following order: Golubačka gorge, Ljupkovska valley, Gospođin Vir gorge, Donjomilanovačka valley, Kazani gorges, Oršavska valley and Sipska gorge. The Đerdap Gorge has been protected as the Đerdap National Park since 1974. The sampled sites were recorded at altitudes between 88 and 445 m a.s.l., on limestone bedrock and on different soil types: Leptosols, calcaric Leptosols and dystric Cambisols. The average annual temperature at the investigated sites in the Đerdap Gorge is 10.3 °C, while the annual precipitation is 664 mm.

The Lazar's Canyon is a natural monument located on the eastern slopes of the Kučaj Mountains. The Lazar's River, which cut an imposing canyon at the foot of the Malinik ridge, flows into the Zlotska River. Lazar's Canyon runs in a southwest-northeast direction and has a total length of about 5 km. The valley sides of the canyon are very steep, almost vertical limestone cliffs, which exceed a height of 300m in the central part. At the narrowest point it is only 3–4m wide. The sampled sites were recorded at altitudes between 294 and 350m a.s.l., with calcaric Leptosols on limestones. At the investigated localities in the Lazar's canyon, the average annual temperature is 9.3 °C and the annual precipitation is 698 mm.

The Sićevo Gorge has been placed under protection as a natural asset of great importance and classified as a nature park. It

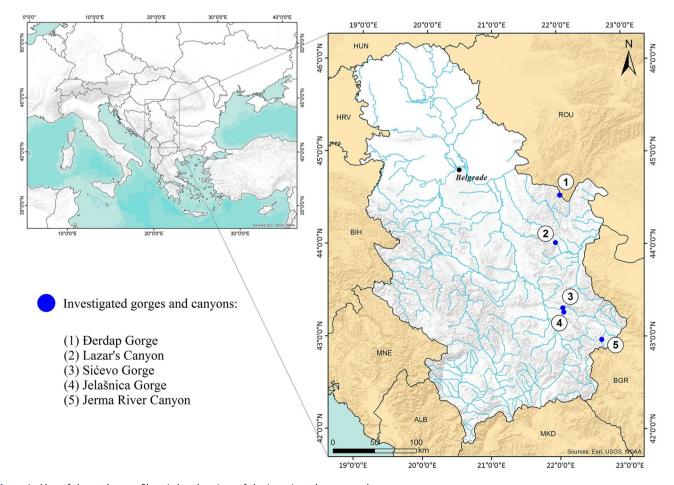


Figure 1. Map of the study area. Blue circle – locations of the investigated gorges and canyons.

is located in southeastern Serbia and stretches for about 16km. The gorge is surrounded on all sides by high mountain ridges, with the ridge of the Svrljiške Mountains standing out in the north. The course of the Nišava River runs in an east-west direction, changing direction in several places. The sampled sites are located at altitudes between 334 and 379m a.s.l. on limestone bedrock, on which eutric Cambisols have developed. The average annual temperature at the studied sites of the Sićevo Gorge is 10.7°C, while the annual precipitation is 613 mm.

The special nature reserve Jelašnica Gorge is located 15 km southeast of the city of Niš, surrounded by the great massif of Mt. Suva Planina. Most of the gorge is situated at lower altitudes and is exposed to the influence of continental and southern climate. The Jelašnica gorge has a southeast-northwest orientation. The analyzed stands were found at an altitude of 340 m a.s.l. on calcaric Leptosols on limestone bedrock. At the studied sites in the Jelašnica Gorge, the average annual temperature is 9.9°C, while the annual precipitation is 628 mm.

Jerma River Canvon is a special nature reserve in southeastern Serbia, near the town of Dimitrovgrad. The Jerma River is a left tributary of the Nišava River and flows in the narrow canyon part in a south-southeast direction through the massifs of the Vlaška and Greben Mountains. The studied communities in this canyon were registered at altitudes between 498 and 550 m a.s.l. on limestone bedrock, on calcaric Leptosols and eutric Cambisols. The average annual temperature at the investigated sites in Jerma River Canyon is 9.0°C, while the annual precipitation is 600 mm.

Data collection and analyses

During the field survey, which was conducted seasonally from spring to autumn between 2020 and 2021, we recorded 102 phytosociological relevés. The relevés were sampled according to the standard methodology of the Zürich-Montpellier School (Braun-Blanquet 1964). The size of the sampling sites ranged from 100 to 400 m². For each relevé, the geographic position and topographic variables (altitude, aspect and slope) were directly measured in the field using a portable GPS device. The combined cover-abundance values were transformed into numeric scale values (van der Maarel 1979). In addition, 33 previously recorded phytosociological relevés from stands dominated by C. orientalis in gorges and canyons of eastern Serbia were added from the literature and included in the analyses (Jovanović 1977; Mišić 1981, 1982). All newly collected relevés were entered into the FLORA database (Karadžić 2013) and exported into JUICE 7.0 software (Tichý 2002) for further analysis.

The nomenclature and taxonomy of plant taxa follow the Euro+Med PlantBase (2006+). The life forms of the plants were determined according to Mueller-Dombois and Ellenberg (1974), adapted by Stevanović (1992b) for the flora of Serbia. The chorotypes were determined following the classification proposed by Meusel et al. (1965, 1978) and Meusel and Jäger (1992), which were modified for the territory of Serbia by Stevanović (1992a).

The hierarchical classification of the dataset was performed using PC-ORD 6.08 software (McCune and Mefford 2011) integrated with JUICE 7.1 software (Tichý 2002). We performed various cluster analyses of the analytical data

using different combinations of distance measures and group linkage methods. The cluster analysis using Flexible beta algorithm ($\beta = -0.25$) for group linkage and the Relative Sørensen index as a distance measure gave the most ecologically interpretable result. The floristic data were extracted from each obtained vegetation group to analyze the floristic characteristics using phytogeographical and life form analyses. The average number of species per plot was calculated for each vegetation group in JUICE 7.1 software (Tichý 2002). The same software was used to calculate the indices of species diversity for each group: the Shannon-Wiener diversity index (H') and Shannon's equitability (evenness; EH).

The diagnostic species of each cluster were determined using the Phi-coefficient as a fidelity measure in the JUICE program. All groups were standardized to an equal size, and species with a phi coefficient value ≥0.30 were considered diagnostic. This threshold was chosen subjectively after examining results with higher and lower thresholds. Species with frequency ≥50% were listed as constant species in a group. The dominant species were considered to have a cover of ≥35% for species present in at least 5% of the relevés. A combined synoptic table with the frequency and fidelity values of the species within the groups was prepared using JUICE 7.1 software. In addition to the use of diagnostic, dominant, and constant species, all groups were characterized by the presence of endemic, relict, or taxa important for conservation at the national level. The taxa important for conservation at the national level were identified in accordance with the Rulebook on declaration and protection of strictly protected and protected wild species of plants, animals, and fungi (Official Gazette of RS 2010-2016), while endemic and relict plant species were determined based on previously published data for the investigated territory (Mišić 1981; Gajić 1984; Stevanović 1999; Tomović et al. 2014).

Using the JUICE software, Ellenberg's indicator values (EIV) (Pignatti et al. 2005) were obtained for almost all species in the dataset and average unweighted EIV values for light, temperature, moisture, continentality, nutrients and soil reaction were calculated for each plot. To perform a better ecological characterization of the groups, non-metric multidimensional scaling (NMDS) with passively projected indicator values was applied using Juice software. We used Bray-Curtis distance measure and square-root transformation of cover data. All relevés along with unweighted ecological indicator values (EIVs) of species for temperature, light, moisture, continentality, soil reaction and nutrients, were passively projected onto an NMDS plot to reveal main ecological factors influencing variation in floristic composition within the dataset.

Results

Cluster analysis and characteristics of the identified groups

Based on the hierarchical classification of the analyzed stands four groups of phytosociological relevés can be distinguished within the dataset (Figure 2).

The group sizes varied, with Group 4 being represented with the lowest number of relevés (6), while Group 1 had the highest

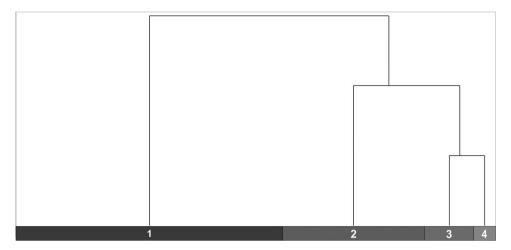


Figure 2. Dendrogram of relevés of analyzed stands dominated by *Carpinus orientalis* in gorges and canyons of eastern Serbia. Identified groups (clusters) are labeled with numbers (1, 2, 3, 4).

Table 1. Parameters of floristic diversity for the four vegetation groups.

						J 1
Group	Number of relevés	Number of species	Average number of species per plot	Shannon-Wiener index (<i>H</i> ₁)	Evenness (EH)	Number of taxa important for conservation
1	75	210	23.89	2.13	0.67	47
2	40	186	30.55	2.75	0.81	39
3	14	121	22.29	2.43	0.80	33
4	6	62	29.33	3.04	0.90	15

number (75) (Table 1, column 2). The Shannon–Wiener diversity index (H') ranged from 2.13 to 3.04 (Table 1, column 5), whereas Shannon's equitability (evenness; EH) varied from 0.67 to 0.90 (Table 1, column 6). Group 4 had the highest average Shannon–Wiener diversity index and the highest average values of species evenness. Group 1 had the lowest mean scores for both diversity index and species evenness. The highest average number of species per plot had Group 4, while the lowest average number of species per plot had Group 1.

Based on the phytogeographical analysis, all registered taxa were classified into 10 area types: Arctic-Alpine (AA), Adventive (ADV), Boreal (BOR), Central European (CE), Eurasian Mountain (EAM), Eurasian (EURAS), Holarctic Cosmopolitan (COSM), Mediterranean-sub-Mediterranean (MED-SMED) and Pontic (PONT). Taxa belonging to the AA area type were the least represented, occurring only in Group 3 (Figure 3). Taxa belonging to ADV area type were registered only in Group 1, while BOR in Groups 1 and 3. The Eurasian area type (EURAS) was the most represented in all groups, followed by CE. The EAM type had the highest percentage in Group 3. In general, Groups 1, 2 and 3 were characterized by a significant percentage of the flora belonging to the Eurasian and Central European area type, while the Mediterranean-sub-Mediterranean type was most represented in Group 4 together with the Eurasian type (Figure 3).

The flora of the investigated stands in canyons and gorges in eastern Serbia was classified into seven plant life forms. Hemicryptophytes dominated in all obtained groups, whereas scandentophytes and nanophanerophytes were the least represented, the second being completely absent in Group 4 (Figure 4). Chamaephytes were the most represented in

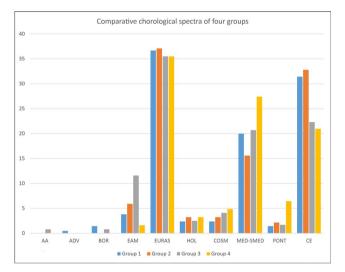


Figure 3. Comparative Chorological spectra of the identified groups. Eurasian area type (EA), Mediterranean-sub-Mediterranean area type (MED-SMED), Cosmopolitan area type (COSM), Holarctic area type (HOL), Adventive area type (ADV), Central European area type (CE), Pontic area type (PONT), and Eurasian Mountain area type (EAM).

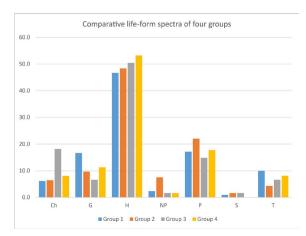


Figure 4. Comparative life form spectra of the identified groups. Life forms: Ch - Chamaephytes, G - Geophytes, H - Hemicryptophytes, NP - Nanophanerophytes, P - Phanerophytes, S - Scandentophytes, T - Therophytes.

Group 3, while in Group 1 geophytes had the higher percentage compared to other groups.

From the total of 330 registered taxa, 84 (25.5%) were designated as important for conservation, being either strictly protected (Daphne laureola L.) or protected (Anacamptis pyramidalis (L.) Rich., Staphylea pinnata L.) by national legislation, relict (Juglans regia L., Syringa vulgaris L.) and endemic (Ramonda serbica Pančić), or protected by national legislation so as to restrict their trade for commercial purposes. The number of taxa important for conservation varied among groups. Group 1 had the highest number of strictly protected, protected, relict, and endemic taxa (47), while Group 4 had the lowest number of taxa important for conservation (15) (Table 1, column 7).

Ordination analysis

The NMDS analysis revealed that the ecological factors that distinguish the four groups are moisture and nutrients, which are negatively correlated with the first axis, and light and temperature positively correlated with the first axis (Figure 5). These results indicated that habitat humidity largely determined the floristic composition of the analyzed groups. A light-moisture gradient separated the shady and mesophilous variants (Group 1 and Group 2) from the xerophilous and more open variants (Group 3 and Group 4).

Syntaxonomic scheme and description of the associations

Based on our results, we propose a syntaxonomic scheme of the identified groups. The three groups distinguished in the cluster analysis could be assigned to already described associations (Groups 1, 2 and 4), while Group 3 is described as a new association. A synoptic table with fidelity and frequency values of taxa within each association is given in Table 2.

Quercetea pubescentis Doing-Kraft ex Scamoni Passarge 1959

Quercetalia pubescenti-petraeae Klika 1933

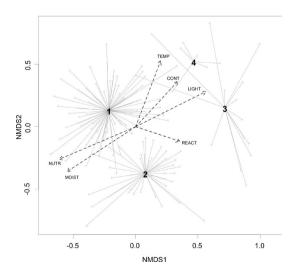


Figure 5. NDMS Spider plot of analyzed relevés with EIVs passively projected. Centroids of clusters are indicated by numbers corresponding to Table 1, Figure 2, and to group numbers used in the text.

Syringo-Carpinion orientalis Jakucs (1959) 1960

Arabio turritae-Carpinetum orientalis Tzonev 2013 (Group 1) Carpino orientalis-Quercetum mixtum Mišić 1967 (Group 2) Seslerio filifoliae-Carpinetum orientalis Sekulić ass. nova hoc loco (Group 3)

Syringo-Carpinetum orientalis (Greb. 1950.) Mišić 1967 (Group 4)

Group 1 (Arabio turritae-Carpinetum orientalis Tzonev 2013) is heterogeneous, being characterized by numerous species characteristic of mesophilous deciduous forests, e.g. Brachypodium sylvaticum (Huds.) P.Beauv., Drymochloa drymeja (Mert. & W.D.J.Koch) Holub, Hedera helix L., Melica uniflora Retz., Polypodium vulgare L., Stellaria holostea L., etc. (Table 2, column 1). This was the largest group, consisting of 75 relevés in which 210 species were recorded (Table 1, column 3). These stands were found on gentle to very steep slopes (5°-60°), but also on flat terrains where deeper soils occurred. The phytosociological relevés were recorded at altitudes between 90 and 550 m a.s.l., and in all aspects (predominantly south and north).

Group 2 (Carpino orientalis-Quercetum mixtum Mišić 1967) is characterized by the presence of different species of the genus Quercus (Quercus cerris L., Quercus frainetto Ten., Quercus petraea (Matt.) Liebl., Quercus pubescens Willd) (Table 2, column 2). This group included 40 relevés with 186 species recorded (Table 1, column 3). The stands of this association were recorded on gentle to steep slopes (15°-40°), at altitudes between 80 and 600 m a.s.l., and in all aspects (predominantly S and N). NMDS analysis confirmed that Group 2 is also mesophilous, but not to the same extent as Group 1.

The stands belonging to Group 4 (Syringo-Carpinetum orientalis (Greb. 1950.) Mišić 1967) were recorded on steep slopes (30°-50°) at altitudes between 240 and 330 m a.s.l., on eastern and southeastern aspects. It is a xerophilous association, where light was the main ecological factor influencing the separation of this group of relevés from other groups. The total number of recorded taxa was 62 in six relevés (Table 1, column 3).

Group 3 consisted of 14 relevés with 121 species recorded (Table 1, column 3) and is described here as a new association named Seslerio filifoliae-Carpinetum orientalis Sekulić ass. nova hoc loco (Figure 6).

Seslerio filifoliae-Carpinetum orientalis Sekulić ass. nova hoc loco (Table 2, column 3)

Holotypus: Table 3, rel. 12

Locus classicus: Serbia, Jerma River Canyon; 42.97548N,

Diagnostic taxa: Achillea ageratifolia (Sm.) Benth. & Hook.f., Achnatherum calamagrostis (L.) P.Beauv., Allium flavum L., Arabis hirsuta (L.) Scop., Arabis procurrens Waldst. & Kit., Asperula cynanchica L., Asplenium ruta-muraria L., Bupleurum praealtum L., Clinopodium nepeta (L.) Kuntze, Campanula sibirica L., Cardamine graeca L., Cicerbita muralis Wallr., Clematis vitalba L., Dianthus petraeus Waldst. & Kit., Draba lasiocarpa Rochel, Erysimum comatum Pančić, Euphorbia cyparissias L., Festuca xanthina Roem. & Schult., Galium verum L., Helianthemum nummularium Mill., Hieracium waldsteinii Tausch, Jurinea mollis (L.) Rchb., Minuartia verna (L.) Hiern, Rosa canina L., Satureja montana L., Scabiosa ochroleuca L., Sedum hispanicum L., Sedum rupestre L., Sesleria filifolia Hoppe, Sorbus austriaca (Beck) Prain, Stachys recta L., Stipa pennata L., Taxus baccata L., Verbascum lychnitis L., and Viola tricolor L.

Table 2. Frequency-fidelity combined synoptic table of Carpinus orientalis-dominated stands (fidelity value in superscript multiplied by 100).

Group number		1	2	2	3		4
No. of releves		75	4	0	14		6
Arabio turritae-Carpinetum orientalis Tzonev 2013							
Viola odorata L.	45	61.9					
Ficaria verna Huds.	29	48.7					
Arum maculatum L.	37	45.6	10				
Corydalis cava (L.) Schweigg. & Körte	20	39.7					
Alliaria petiolata (M.Bieb.) Cavara & Grande	25	38.7	5				
Geranium lucidum L.	23	35.8	5				
Isopyrum thalictroides L.*	29	35.6	13				
Galium aparine L.	45	34.6	8		14		17
Carex halleriana Asso	15	33.8					
Polypodium vulgare L.	15	33.8					
Scilla bifolia L.	15	33.8					
Cardamine bulbifera Crantz	20	32.8	5				
Glechoma hederacea L.	32	31.2	15		7		
Cornus sanguinea L.	33	30.9	18		7		
Carpino orientalis-Quercetum mixtum Mišić 1967					•		
Cornus mas L.*	11		93	83.9	7		
Viburnum lantana L.	33		83	68.2	•		·
Sorbus torminalis (L.) Crantz	20		60	57.7			
Corylus avellana L.	3		43	56.9			
Rosa arvensis Huds.			45 35	53.6			
Quercus petraea (Matt.) Liebl.	16		35 45	47.8			
	5		45 33	45.5			
Drymochloa drymeja (Mert. & W.D.J.Koch) Holub	5 17		33 43	44.6			
Euonymus verrucosus Scop.				43.5			
Quercus cerris L.	47		60 33	42.3			
Festuca valesiaca Gaudin*	•		23	42.3			
Fraxinus excelsior L.			23	42.5			
Euphorbia amygdaloides L.	27		58		21		
Pyrus communis subsp. pyraster (L.) Ehrh.	15		35	39.5			
Hedera helix L.	63		78	39	36		
Carpinus betulus L.	12		38	38.6	7		
Festuca heterophylla Lam.			18	37			
Galium sylvaticum L.	3		20	35.8			
Crataegus monogyna Jacq.	69		85	35.2	14		50
Rubus canescens DC.			15	34.2			
Lathyrus vernus (L.) Bernh.	19		33	34.1			
Prunus mahaleb L.*	7		23	33.8			
Veronica chamaedrys L.*	13		28	33			
Ramonda serbica Pančić*	3		18	32.9			
Juglans regia L.*	11		25	32.6			
Tilia cordata Mill.	11		35	32.4	14		
Hylotelephium telephium (L.) H.Ohba			13	31.1			
Asperula purpurea (L.) Ehrend.			13	31.1			
Vincetoxicum hirundinaria Medik.	7		20	30.9			
Seslerio filifoliae-Carpinetum orientalis ass. nova hoc. loco							
Dianthus petraeus Waldst. & Kit.					50	65.5	
Achnatherum calamagrostis (L.) P.Beauv.					50	65.5	
Sesleria filifolia Hoppe					50	65.5	
Festuca xanthina Roem. & Schult.					43	60	
Satureja montana L.*					36	54.2	
Galium verum L.					29	48	
Sorbus austriaca (Beck) Prain*					29	48	
Erysimum comatum Pančić*					29	48	
Bupleurum praealtum L.	5		5		36	43.8	
Arabis hirsuta (L.) Scop.	,		3		21	41.2	
Arabis procurrens Waldst. & Kit.*					21	41.2	
Euphorbia cyparissias L.			8		29	39.4	
Sedum hispanicum L.	1		U		21	39.2	
Stachys recta L.	1				21	39.2	
Stacrys recta L. Cardamine graeca L.	16				21 36	39.2	
Allium flavum L.	8				36 29	38.9	
Rosa canina L.*	8 9		0			38.6	
			8		36 21	37.4	
Asplenium ruta-muraria L.	3		10		21	35.6	
Cicerbita muralis Wallr.	15		18		43	33.3	
Asperula cynanchica L.*					14	33.3	
Achillea ageratifolia (Sm.) Benth. & Hook.f.*					14		
Jurinea mollis (L.) Rchb.*					14	33.3	
Verbascum lychnitis L.*					14	33.3	
Sedum rupestre L.					14	33.3	
Taxus baccata L.*					14	33.3	
Helianthemum nummularium Mill.					14	33.3	
Minuartia verna (L.) Hiern					14	33.3	
					14	33.3	

Table 2 Continued

Table 2. Continued.					
Group number	1	2	3	4	
Draba lasiocarpa Rochel			14 33.3		
Viola tricolor L.			14 33.3		
Hieracium waldsteinii Tausch			14 ^{33.3}		
Stipa pennata L.*			14 ^{33.3}		
Doronicum columnae Ten.	8		21 31.1		
Campanula sibirica L.*	1		14 30.9		
Asplenium trichomanes L.	27	30	50 30.5		
Clinopodium nepeta (L.) Kuntze	1	8	21 30.3		
Syringo-Carpinetum orientalis (Greb. 1950.) Mišić 1967					
Turritis glabra L.				100	100
Achillea nobilis L.				83	88.9
Digitalis laevigata Waldst. & Kit.*				83	88.9
Verbascum phoeniceum L.*				83	88.9
Paliurus spina-christi Mill.		5		83	85.3
Hippocrepis emerus subsp. emeroides (Boiss. & Spruner) Greuter	8	8	43	100	71.3
& Burdet ex Lassen					
Dictamnus albus L.*	1		7	67	70.8
Clinopodium vulgare L.	·	13	•	67	67.9
Cleistogenes serotina (L.) Keng		.5		50	65.5
Trifolium hirtum All.*				50	65.5
Quercus pubescens Willd.	29	38	21	100	61.2
Teucrium chamaedrys L.*	3	18	14	67	55
Erysimum diffusum Ehrh.*	J	10	14	50	53.3
Cota tinctoria (L.) J.Gay*			17	33	52.2
Trifolium alpestre L.*				33	52.2
Ajuga laxmannii (L.) Benth.*				33	52.2
Euphorbia carniolica Jacq.*				33	52.2
Arum italicum Mill.				33	52.2
Veronica spicata L.*				33	52.2
Phleum phleoides (L.) H.Karst.*				33	52.2
				33 33	52.2
Hypericum umbellatum A.Kern.*					52.2
Crataegus pentagyna Willd.*				33	52.2
Althaea cannabina L.				33	52.2
Achnatherum bromoides (L.) P.Beauv.*	21	25	1.4	33	49.9
Acer monspessulanum L.	31	35	14	83	48
Ulmus minor Mill.	4	15	7	50 22	47.6
Clinopodium acinos Kuntze	4		-	33	45.7
Dactylis glomerata L.	17	30	7	67	45.7
Helleborus odorus Willd.	60	35		83	42.2
Glechoma hirsuta Waldst. & Kit.	28	35	-	67	41.5
Hylotelephium maximum (L.) Holub	19	8	7	50	40.1
Clinopodium menthifolium (Host) Stace	1	28	7	50	
Syringa vulgaris L.*	27	50	43	83	37.7
Berberis vulgaris L.		15		33	37.6
Medicago polymorpha L.		•		17	36.1
Allium rotundum L.		•		17	36.1
Silene italica (L.) Pers.		•		17	36.1
Tordylium maximum L.				17	36.1
Aegonychon purpurocaeruleum (L.) Holub	15	28	7	50	33.6
Poa nemoralis L.	4	18		33	32.9
Convolvulus cantabrica L.	1		21	33	32.1
Viola hirta L.	8	15		33	32
Lathyrus venetus (Mill.) Wohlf.	19	5		33	31.5
Cyclamen hederifolium Aiton*	16	10		33	30.1
Other species with high frequency					
Carpinus orientalis Mill.	100	100	100	100	
Fraxinus ornus L.	93	100	93	100	
Melica uniflora Retz.	77	73	7	67	
Asplenium ceterach L.	25	25	14	33	
Piptatherum virescens Boiss.	13	3	14	17	
Potentilla micrantha DC.	37	10	21	50	
Brachypodium sylvaticum (Huds.) P.Beauv.	41	63	14	67	
Acer campestre L.	56	55	29	33	
Di	<u></u>			1	

Diagnostic species (phi values higher than 0.30 given in superscript) for each group-community are printed in bold. Group numbers correspond to those used in the text.

Constant taxa: Carpinus orientalis Mill., Clematis vitalba L., and Fraxinus ornus L.

Dominant taxa: Achnatherum calamagrostis (L.) P.Beauv., Bothriochloa ischaemum (L.) Keng, Brachypodium sylvaticum (Huds.) P.Beauv., Campanula lingulata Waldst. & Kit., Carpinus orientalis Mill., Hippocrepis emerus subsp. emeroides (Boiss. & Spruner) Greuter & Burdet ex Lassen, Festuca xanthina Roem. & Schult., Galium verum L., Sesleria filifolia Hoppe, and Sorbus austriaca (Beck) Prain.

Diagnosis: The Seslerio filifoliae-Carpinetum orientalis ass. nova hoc loco is developed on limestone bedrock, over

^{*}Species important for conservation (including endemics and relicts).



Figure 6. Stand of the newly described association Seslerio filifoliae-Carpinetum orientalis Sekulić ass. nova hoc loco.

which skeletal soil types occur, classified into calcaric Leptosols. These stands occupy very steep (20°-50°) and stony slopes (50°-80°) and occur at altitudes between 80 and 550 m a.s.l. and all aspects. The total number of taxa recorded in 14 relevés was 121. The rocky cliffs were covered by sparsely distributed individuals of Oriental hornbeam and other xerophilous tree (Fraxinus ornus L.) and shrub species. The tree species do not reach great heights, the average canopy height is about 5 m, and they are not very dense. The average canopy cover is 70%. Among the diagnostic and constant species, many chasmophytic species and species that inhabit steep slopes were registered: Achnatherum calamagrostis (L.) P.Beauv., Dianthus petraeus Waldst. & Kit., Festuca xanthina Roem. & Schult., Sesleria filifolia Hoppe, etc.

Discussion

Communities dominated by C. orientalis are widely distributed on the Balkan Peninsula, not only in the zonal sub-Mediterranean area, but also in the continental region (Arsene et al. 2006; Bergmeier and Dimopoulos 2008; Čarni et al. 2009; Stupar et al. 2016; Tzonev et al. 2019; Kavgacı et al. 2021). Due to their heterogeneous structure and broad distribution range, they are challenging to differentiate. The results of our study, in which three distinguished groups were assigned to previously described associations, but one was described as a new association, confirm that much higher diversity exists within C. orientalis dominated communities (Stupar et al. 2020).

The high number of identified taxa in the investigated communities confirms the fact that thermophilous communities, especially those occurring in ravine habitats, are characterized by great species richness and diversity (Košir et al. 2008; Hrivnák et al. 2019; Karadžić et al. 2020; Sekulić et al. 2021). The Arabio turritae-Carpinetum orientalis association contained the highest total number of taxa and the highest number of relevés but had the lowest average number of species per plot and the lowest average Shannon index values, indicating its unevenness. In contrast, Syringo-Carpinetum orientalis being present with only six relevés and 62 taxa had

the highest average values of Shannon diversity index and equitability, indicating greater evenness.

The phytogeographical analysis showed that the Eurasian area type is absolutely dominant in all groups, followed by the Central European, indicating the continental character of the studied localities. However, the relatively high representation of the Mediterranean-sub-Mediterranean area type is not surprising (second place in the Syringo-Carpinetum orientalis). Mediterranean influences are expressed from the direction of the Aegean, reaching the valley of the Vardar and the southern Morava, in a highly modified form, northward to eastern and southeastern Serbia. The spread of Mediterranean elements deep into the continent is conditioned not only by climatic influences, but also by the nature of the geological substrate (more abundant on limestone). Thus, Mediterranean species taking advantage of the Mediterranean climate along river valleys and gorges can reach continental limestone areas as far as the Sićevo Gorge, but even such remote places as some areas in northeastern Serbia (Stevanović and Stevanović 1995).

Hemicryptophytes predominate in the studied stands, which is understandable since they represent the most numerous life form in temperate zones (Diklić 1984). Considering that the gorges and canyons on the Balkan Peninsula are specific for the different forms of forest and shrub vegetation (polydominant relict forest communities, thickets) (Blečić 1958; Janković 1984; Košir et al. 2008; Lakušić 1972; Mišić 1981, 1982; Redžić et al. 1992; Stefanović 1977), the presence of a large number of phanerophytes, nanophanerophytes and chamaephytes is valid. The relatively high proportion of geophytes is explained primarily by their ability to develop under unfavourable developmental conditions with extreme fluctuations in climatic parameters and to survive underground, where these fluctuations are less pronounced. Although the habitat conditions in which the investigated communities occur are not conducive to the development of this life form (shallow soil, low soil moisture), nevertheless, therophytes represent a significant part of the biological spectrum of these stands. The increased occurrence of therophytes may indicate the increasing degradation of habitats and developing communities (Ranđelović et al. 2007).

The specific topography in gorges and canyons creates a strong light-moisture gradient that separates the sunny and xeric variants (Groups 3 and 4) from the more mesophilous ones (Groups 1 and 2). The chasmophytic stands of Group 3 occur on stones and rocks, so when it comes to soil humidity, they are in the most unfavorable position. As a result, a large number of xerophytes appear in these stands. Edaphic conditions in the stands of Groups 1 and 2 are significantly more favourable, so the degree of mesophility increases successively. A strong light gradient is also a consequence of the different densities of tree and shrub layers in the investigated stands (Karadžić et al. 2020). All groups occur on habitats that differ in terms of soil development. The differences between Groups 1 and 2 lie in the soil reaction gradient. Phytosociological relevés from Group 2 occur on more shallow soils, so the geological substrate significantly influences their differentiation (Čarni et al. 2022). We noticed that the content of soil nutrients is one of the main ecological factors determining the floristic differentiation of the analyzed stands,

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		Jelašnica	Gorge	
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lable 3. Continued.			Locality	

Partial pounda Part																	
	Locality	Đerdap Gorge	Đerdap Gorge	Đerdap Gorge	Đerdap Gorge	Đerdap Gorge	Jelašnica Gorge		Jerma River Canyon	Jerma River Canyon	Jerma River Canyon			Jerma River Canyon	Jerma River Canyon		
	Sorbus austriaca								+		æ	m	+			29	=
	(Beck) Prain <i>Viola reichenbachiana</i>				+				+	-		+				29	=
	Jord. ex Boreau															č	=
	Arabis hirsuta (L.) Scop.											+	+	+		1.7	=
	Arabis procurrens								-	-			+			21	=
	waldst. & Nit. Asplenium								2	+			+			21	=
	ruta-muraria L.																
	Bothriochloa ischaemum (L.)					2	2	m								21	=
	Keng															,	:
	Clinopodium nepeta (I) Kuntze			+	+			+								21	=
	Convolvulus				+	+		+								21	=
	cantabrica L.								4	4		4				1,0	=
	Doronicum columnae Ten.								+	+		+				17	=
	Euphorbia								+			+	+			21	=
	arnygaalolaes L. Muscari neglectum			-	-		+									21	=
	Ten.										•					ć	=
	Potentilla micrantna DC.				+						+	+				17	=
	Quercus pubescens				2		+	+								21	=
	VVIIIG. Sedum hispanicum L.			+	+			2								21	=
	Stachys recta L.				+		+	+								21	=
	Acer monspessulanum				+		+									14	_
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	Achillea ageratifolia (Sm.) Benth &												+	+		4	_
+ - + + + + + + + + + + + + + + + + + +	Hook.f.																
	Asperula cynanchica						+						+			14	-
	L: Brachvoodium				m							-				14	_
	sylvaticum (Huds.)																
	P.Beauv.	-	-													5	-
+ + + + + + + + + + + + + + + + + + + +	Asplenium ceterach L.	+	+ -										-			<u>†</u> 4	
+ + + + + + + + + + + + + + + + + + +	Cytisus hirsutus L.					+							+			14	-
+ + + + + +	Crataegus monogyna				+		+									14	_
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+ + + +	Erysimum diffusum Fhrh	+	+													4	_
+ + + +	Galium aparine L.				-				+							14	_
+ + +	Galium mollugo L.												+	+		14	_
+ +	Helianthemum						+	+								14	_
(VIII) Soják	Pilosella piloselloides						+	+								14	-
	(Vill.) Soják																

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	Đerdap	Đerdap	Đerdap	Đerdap	Đerdap	Jelašnica	Jelašnica	Jerma River	Jerma River Jerma River Jerma River	Jerma River	Jerma River	Holotypus Jerma River	Jerma River	Jerma River Jerma River		
Locality	Gorge	Gorge	Gorge	Gorge	Gorge	Gorge	Gorge	Canyon	Canyon	Canyon	Canyon	Canyon	Canyon	Canyon		
Hieracium waldsteinii									+	+					14	-
Jurinea mollis (L.)						+	+								14	-
Rchb.										-	-				7	-
Minuartia verna (L.)						-	+			+	+				4 7	
Hiern						-	+								<u>t</u>	-
Ornithogalum			-	2											14	-
umbellatum L.															;	
Piptatherum virescens Roiss				+	+										4	-
Scabiosa ochroleuca						-	+								14	-
Sedum rupestre L.												+	-		14	-
Stipa pennata L.						+	2								14	-
Taxus baccata L.								-						+	14	-
Teucrium chamaedrys				1			+								14	-
· ·															;	
Iilia cordata Mill.								+			+				14	-
Verbascum lychnitis L.			+	+											14	-
Viola tricolor L.												-	+		14	-
Clinopodium alpinum					+										7	-
(L.) Kuntze																
Aethionema saxatile							+								7	_
(L.) W.T.Aiton				,											,	•
Ajuga genevensis L.				_											_ 1	
Allium					+										`	-
spnaerocepnaion I																
Aurinia saxatilis Desv.			+												7	-
Anthriscus sylvestris			+													_
(L.) Hoffm.																
Astragalus							+								7	-
glycyphyllos L.																
Aegonychon					+										7	-
purpurocaeruleum																
(L.) Holub		-													7	-
menthifolium		ŀ														-
(Host) Stage																
Campanula lingulata						m									7	-
Waldst. & Kit.																
Carpinus betulus L.										+					7	-
Cornus mas L.					+										7	-
Cornus sanguinea L.						2									7	-
Cystopteris fragilis (L.)								+							7	-
Bernh.																
Dactylis glomerata L.				+											7	-
Dictamnus albus L.		+													7	_
Digitalis grandiflora											+				7	-
Fruthronium										+					7	-
dens-canis L.										-						-

Table 3. Continued.

Section Sect	Locality	Đerdap													ċ		
+ + + + + + + + + + + + + + + + + + +		Gorge	Đerdap Gorge	Đerdap Gorge	Đerdap Gorge	Đerdap Gorge	Jelašnica Gorge	Jelašnica Gorge				Jerma River Canyon	Jerma Kiver Canyon	Jerma Kiver Canyon	Jerma Kiver Canyon		
+ + + + + + + + + + + + + + + + + + +	Euonymus europaeus												+			7	_
	Euphorbia							+								7	-
+ + + + + + + + + + + + + + + + + + +	epithymoides L.															ı	-
	Festuca ovina L.				+ (۱ /	
	Glechoma hederacea				7											^	_
+ + + + + + + + + + + + + + + + + + +	Hieracium murorum L.											2				7	_
+ + + + + + + + + + + + + + + + + + +	Inula conyzae (Griess.)			+												7	_
+ + + + + + + + + + + + + + + + + + +	Muscari comosum					+										7	-
+ + + + + + + + + + + + + + + + + + +	Will.																
+ + + + + + + + + + + + + + + + + + +	Linaria genistifolia (L.) Mill						+									7	_
+ + + + + + + + + + + + + + + + + + +	Lycopus europaeus L.		+													7	-
+ + + + + + + + + + + + + + + + + + +	Melica ciliata L.	+														7	_
+ + + + + + + + + + + + + + + + + + +	Melica uniflora Retz.				7											7	
+ + + + + + + + + + + + + + + + + + +	Melilotus officinalis					+										_	_
+ + + + + + + + + + + + + + + + + + +	Mentha longifolia (L.)		+													7	-
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+ + + + + + + + + + + + + + + + + + +	Mercurialis perennis L.								-	+						\ r	
+ + + + + + + + + + + + + + + + + + +	Moentingia bavanca (L.) Gren.								+							,	-
+ + + + + + + + + + + + + + + + + + +	Pinus nigra J.F.Arnold														+	7	-
+ + + + + + + + + + + + + + + + + + +	Potentilla erecta (L.)			+												7	_
+ + + + + + + + + + + + + + + + + + +	Primula acaulis (L.) L.				+											7	-
+ + + + + + + + + + + + + + + + + + +	Primula veris L.													+		7	_
+ + + + + + + + + + + + + + + + + + +	Pulmonaria officinalis				+											7	-
+ + + + + + + + + + + + + + + + + + +	L. Rubus caesius L.			+												7	-
+ + + + + + + + + + + + + + + + + + +	Salvia glutinosa L.								+							7	-
+ + + + + + + + + + + + + + + + + + +	Saxifraga tridactylites							+								7	-
+ + + + + + + + + + + + + + + + + + +	L. Scabiosa columbaria												+			7	_
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+ + + + + + + + + + + + + + + + + + +	Sedum acre L.							+								7 1	
+ + + + + + + + + + + + + + + + + + +	Sedum dibum L. Sedum dasynhyllum I						+		+							, ,	
14 19 20 38 23 28 27 25 18 20 23 28 21 8	Sedum magellense								-					2		7	
+ + + + + + + + + + + + + + + + + + +	Ten.															1	,
+ + + + + + + + + + + + + + + + + + +	Hylotelephium				+											7	_
+ + + + + + + + + + + + + + + + + + +	Holub																
+ + + + + 14 19 20 38 23 28 27 25 18 20 23 28 21 8	Sideritis montana L.					+										7	_
+ + + + + + + + + + + + + + + + + + +	Taraxacum officinale				+											7	-
14 19 20 38 23 28 27 25 18 20 23 28 21 8	F.n.wigg. Teucrium montanum							+								7	_
+ 14 19 20 38 23 28 27 25 18 20 23 28 21 8																ı	-
14 19 20 38 23 28 27 25 18 20 23 28 21 8	Varonica austriaca I										+					, ,	
	Number of species per	14	19	20	38	23	28	27	25	18	20	23	28	21	80		-

especially for Group 1. Due to the presence of colluvial soil layer that can be rich in humus, several nitrophilous species are present in this group's phytosociological relevés. Continentality as a gradient separates Groups 3 and 4 from the others in our results. Gradients on the Balkan Peninsula are complex, especially in the eastern parts, where continentality also represents an important gradient (Košir et al. 2013).

Phytosociological relevés belonging to Group 1 (Arabio turritae-Carpinetum orientalis) occur in habitats with more favorable conditions for mesic tree species to form a dense and closed tree canopy. Of the diagnostic, dominant and constant species of this group, thermophilous species are the most abundant. However, many species that are diagnostic for mesic deciduous and mixed forests (Carpino-Fagetea sylvaticae Jakucs ex Passarge 1968) according to Mucina et al. (2016) are present in comparison to the other three groups (e.g. Ficaria verna Huds., Arum maculatum L., Melica uniflora Retz., Corydalis cava (L.) Schweigg. & Körte, and Isopyrum thalictroides L.). A mixture of mesophilous and thermophilous species in stands dominated by C. orientalis has also been reported in other regions, not only in the Balkans (Stupar et al. 2020), but also in Italy (Blasi 2001) and Georgia (Novák et al. 2021).

Carpino orientalis-Quercetum mixtum (Group 2) belongs to a polydominant forest association occurring in gorges and canyons, generally occupying smaller areas. The stands of this association are found on various slope gradients and at varying altitudes and aspects. Among the diagnostic, dominant and constant species, a large proportion of characteristic thermophilous species of trees, shrubs and herbaceous plant species were recorded, such as Cornus sanguinea L., Corylus avellana L., Quercus cerris L., Rosa arvensis Huds., Viburnum lantana L. and Euonymus verrucosus Scop. These species are characteristic of the class of scrub vegetation seral or marginal to broad-leaved forests in the nemoral zone and the sub-Mediterranean regions of Europe (Crataego-Prunetea Tx. 1962 nom. conserv. propos.) according to Mucina et al. (2016). Thermophilous species enrich the tree and shrub layers, closing the canopy of these stands. Regarding the structural characteristics, we found similarities between the stands of Group 1 and Group 2. The average canopy height is about 10 m, while the average canopy cover of the stands in both groups is about 90%. The process of progressive succession can take a very long time when vegetation degradation is advanced and Oriental hornbeam is well established on the habitats, especially on exposed steep slopes with shallow soils. Intensive and frequent logging, as well as occasional clearing of the forest, resulted in the dominance of certain species that did not play a significant role as edifying species in the original community. Thus, the Oriental hornbeam formed low and high thickets which, due to their density and cover, prevented the recovery of the edifying species of the original potential community (Mišić 1994). Following this logic, the stands of Group 1 (Arabio turritae-Carpinetum orientalis) can be considered as a successional stage of the stands of Group 2 (Carpino orientalis-Quercetum mixtum).

Syringo-Carpinetum orientalis represents mostly low forests and coppices with a dense canopy and is the main forest type of limestone areas on steep slopes in canyons and gorges in eastern Serbia (Mišić 1981). It represents a

relatively stable degradation stage. Due to its development on steep slopes and degraded soils, it is very difficult for an old potential forest to develop.

The stands of the newly described association Seslerio filifoliae-Carpinetum orientalis Sekulić ass. nova hoc loco develop on screes, rocky crevices and cliffs, on the steepest slopes with a very thin soil layer. Among the diagnostic and constant species, many chasmophytic species and species that inhabit steep slopes were registered: Achnatherum calamagrostis (L.) P.Beauv., Dianthus petraeus Waldst. & Kit., Festuca xanthina Roem. & Schult., Sesleria filifolia Hoppe, etc. Sparsely distributed individuals of Oriental hornbeam and other xeric tree and shrub species were also present in this group. Species characteristic for the class Thlaspietea rotundifolii Br.-Bl. 1948 are well established in habitats in which succession development has gradually led to stands dominated by C. orientalis (Achnatherum calamagrostis (L.) P.Beauv., Aethionema saxatile (L.) W.T.Aiton, Hylotelephium maximum (L.) Holub, Melica ciliata L., Pilosella piloselloides (Vill.) Soják, Sedum magellense Ten.). Rocky habitats with steep slopes are suitable for species occurring in rock crevices (class Asplenietea trichomanis [Br.-Bl. In Meier & Br.-Bl. 1934] Oberdorfer 1977), namely Achillea ageratifolia (Sm.) Benth. & Hook.f., Asplenium ceterach L., Asplenium ruta-muraria L., Asplenium trichomanes L., Campanula lingulata Waldst. & Kit., Cystopteris fragilis (L.) Bernh., Erysimum comatum Pančić, Hypericum umbellatum A.Kern., Moehringia bavarica (L.) Gren., Sedum dasyphyllum L., and Sedum hispanicum L. (Kojić et al. 1998). In addition, a large percentage of species are from the class of dry grassland and steppe vegetation (Festuco-Brometea Br.-Bl. et Tx. ex Soo 1947) (Mucina et al. 2016). A similar community was registered on vertical limestone rocks in the area of the Đerdap Gorge - Seslerio-Syringetum Vukićević 1968, that was classified in Pruno tenellae-Syringion Jovanović ex Čarni et Mucina 2013 (Lakušić et al. 2005). However, this community is characterized by the underdevelopment of the tree layer, which is one of the main features of the shibliak vegetation. Additional sites of the association Seslerio filifoliae-Carpinetum orientalis ass. nova hoc loco could possibly be found in eastern Serbia and western Bulgaria, especially in habitats suitable for its development within gorges and canyons.

The role of forests in providing a wide range of ecosystem services is increasingly recognized, especially in the context of climate change. According to climate change scenarios, the climate in the region will become hotter and drier in the near future. The strongest negative impacts are expected for forests at altitudes between 0 and 800m a.s.l. Therefore, Oriental hornbeam, as one of the most drought-resistant and adaptable tree species, could be considered a key species for mitigating climate change impacts in the driest areas, ensuring forest survival and providing ecosystem services (Dodev et al. 2020).

The results of this work show the great complexity and importance of the stands dominated by C. orientalis at the investigated sites, and the importance of ravine habitats has been shown in previous studies (Lakušić 1972; Hewitt 2011). The studied stands are characterized by a diverse and rich floristic composition and a large number of taxa of conservation importance, such as relict and endemic species that survived Quaternary glaciations in refugia on the Balkan Peninsula (Petit et al. 2002). The importance of forests developing in ravine habitats has been recognized at the European scale - Tilio-Acerion forests are



included in the list of priority habitat types in Annex I of the Habitats Directive. The studied C. orientalis stands represent a successional stage of turkey oak-sessile oak forests (91M0 Pannonian-Balkanic turkey oak-sessile oak forests) and are therefore not included in the Annex I of the Habitats Directive as a separate habitat type.

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