

# Ecological, floristic and functional analysis of zonal forest vegetation in Bosnia and Herzegovina

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**Abstract** – Zonal vegetation is a large-scale expression of macro-climate and, due to the climatic diversity of the country, there are seven traditionally recognized zonal forest plant communities in Bosnia and Herzegovina. Using data from Bosnia and Herzegovina, this study aimed to reveal whether macro-climate is indeed the most important factor determining the existence of zonal forest plant communities (ZFPC). Detrended correspondence analysis of 398 relevés of seven ZFPCs revealed that the species turnover along the first axis is strongly related to the macro-climatic gradient (annual mean temperature, mean temperature of the coldest quarter and precipitation of the warmest quarter). No correlation was detected between this gradient and topographic factors (slope and aspect) and soil reaction. Floristic analysis revealed clear separation of ZFPCs in terms of diagnostic species. Functional analysis of all layers showed that competitive ecological strategy has the highest proportion, while analysis of the herb layer alone expressed a shift of CSR signatures towards the middle of the C–S axis. Ruderality was overall poorly expressed. Statistically significant differences among communities were discovered along the C–S axis. In terms of life forms, statistically significant differences in the proportions of Phanerophytes, Geophytes and Hemicryptophytes among communities were discovered. Our study confirms that macro-climatic gradient is the most important determinant of the species turnover along ZFPCs. CSR signatures show that zonal forest vegetation is represented by productive communities in a terminal stage of succession. This does not refer to degraded *Quercus ilex* stands (maquis), which are in the middle stage of secondary succession.

**Keywords:** Balkans, climatic gradient, chorotypes, ecological strategies, life forms, ordination, plant functional types, zonal communities

## Introduction

Every plant community is a result of a complex interaction of various ecological factors in a given place and time. In terms of natural vegetation, there are three types of vegetation that generally develop in accordance with the biotic, climatic and soil conditions: zonal, extrazonal and azonal (Dierschke 1994, Ellenberg 2009, Surina 2014). Zonal vegetation is a large-scale expression of climate dominating a particular area, while it is not confined to specific soil conditions, i.e., it most precisely reflects the macroclimatic conditions of particular regions (Kovar-Eder and Kvaček 2007). Zonal vegetation often does not represent a single homogeneous plant association but rather a number of similar communities, which can differ to some extent and, consequently, it is possible to talk of a ‘zonal vegetation group’ (Ellenberg

2009). For example, when different bedrocks and soil series occur within the same climatic zone or there is a species turnover due to minor biogeographical differences, several different, yet similar associations make up the zonal vegetation group. Furthermore, a mountainous relief of a particular climatic zone leads to vertical differentiation of the climatic factors and, accordingly, vertical differentiation of zonal vegetation communities, which are then often called ‘altitudinal belts’.

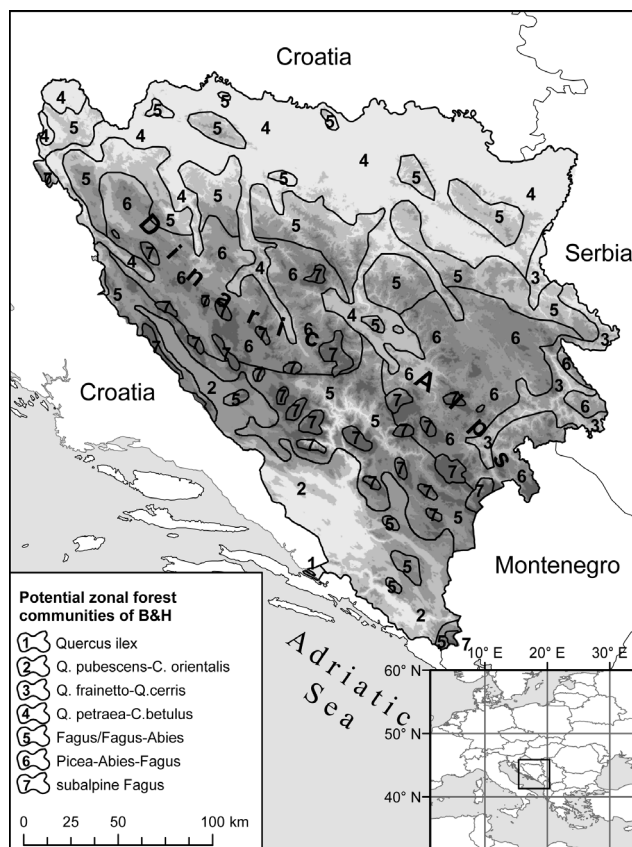
Although in the last several thousand years man has deforested great parts of Europe (Gunia et al. 2012), the potential natural vegetation and, consequently, the zonal vegetation of most of temperate Europe is forest (Bohn and Neuhausl 2004, Ellenberg 2009). The same is valid for Bosnia and Herzegovina (B&H) (Horvat et al. 1974, Stefanović

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et al. 1983). B&H is situated in the western part of the Balkan Peninsula in SE Europe (Fig. 1). Its climate is very diverse, since two major climatic zones overlap here: central European from the north and Mediterranean from the south. The climate of the transitional zone is highly modified by the influence of mountain massifs (Dinaric Alps), while in the eastern part of country the influence of the drier conti-

ental climate can be felt (Milosavljević 1976). While vegetation studies of forests in the neighboring regions have produced synthetic overviews (Borhidi et al. 2012, Vukelić 2012, Chytrý 2013, Tomić and Rakonjac 2013), despite the fairly long tradition of phytosociological studies in B&H (Horvat 1933, 1941, Horvat and Pawlowski 1939, Tregubov 1941) and the considerable number of relevés, the ecology, nomenclature and syntaxonomical position of the majority of B&H forests still remains unsettled (Redžić 2007). With the exception of thermophilous deciduous forest communities (Stupar et al. 2015), this also applies to zonal vegetation, which has only been the subject of a few studies in the past (Horvat et al. 1974, Stefanović et al. 1983, Beus 1984). However, following the macro-climatic diversity, these authors generally agree that seven zonal forest plant communities (ZFPCs) can be distinguished for the territory of B&H (Tab. 1, Fig. 1). Four communities are represented by various oak forests, which occupy the lowlands and hilly region of B&H, while the other three are altitudinal belts (montane, altimontane and subalpine) above the oak forests, mainly built by various types of beech forests (pure and mixed).

There are two different conceptual frameworks for the study of plant communities. The traditional approach to classification is performed at the species level, while a more recent 'functional' approach is based on plant functional types (Duckworth et al. 2000, Shipley 2010, Škornik et al. 2010). Plant functional types are non-phylogenetic groupings of species that show close similarities in their response to environmental and biotic factors and are derived from plant traits based on species morphology, physiology and/or life history (Pérez-Harguindeguy et al. 2013). Plant functional types can aid in the understanding of ecological processes, such as the assembly and stability of communities and succession, and facilitate the detection and prediction of response to environmental change on a range of scales (Duckworth et al. 2000). With plant functional types, comparisons between communities of widely differing composition can be facilitated (Diaz et al. 2004). There are two main approaches to the classification of functional types



**Fig. 1.** Location of the study area in Bosnia and Herzegovina. The potential zonal forest plant communities (ZFPCs) are indicated (Horvat et al. 1974, modified after Stefanović et al. 1983). Numbers on the map correspond to community numbers in Tab. 1.

**Tab. 1.** Zonal forest plant communities in Bosnia and Herzegovina. Community numbers correspond to those used in Tabs. 3–4, and Figs. 1–4. Asterisk (\*) denotes provisional invalid names still in use in Bosnia and Herzegovina.

Communi- community no.	Forest type	Related syntaxa	No. of relevés	No. of resampled relevés
1	<i>Quercus ilex</i>	<i>Quercon ilicis</i> Br.-Bl. 1931 (1936)	5	5
2	<i>Quercus pubescens</i> - <i>Carpinus orientalis</i>	<i>Querco pubescenti-Carpinetum orientalis</i> Horvatić 1939 ( <i>Carpinion orientalis</i> Horvat 1958)	30	16
3	<i>Quercus frainetto</i>	<i>Quercetum frainetto-cerridis</i> (Rudski 1949) Trinajstić et al. 1996 ( <i>Quercon frainetto</i> Horvat 1954)	38	24
4	<i>Quercus petraea</i> - <i>Carpinus betulus</i>	<i>Querco-Carpinetum illyricum</i> Horvat et al. 1974* ( <i>Erythronio-Carpinion betuli</i> (Horvat 1938) Marinček in Wallnöfer et al. 1993)	43	26
5	pure <i>Fagus</i> / mixed <i>Fagus-Abies</i>	<i>Fagetum montanum illyricum</i> Fukarek et Stefanović 1958*, <i>Abieti-Fagetum dinaricum</i> Tregubov 1957* ( <i>Aremonio-Fagion</i> Török et al. ex Marinček et al. 1993)	231	162
6	mixed <i>Picea</i> - <i>Abies-Fagus</i>	<i>Piceo-Abieti-Fagetum</i> Stefanović et al. 1983* ( <i>Abieti-Piceonion</i> Br.-Bl. in Br.-Bl. et al. 1939)	191	123
7	Subalpine <i>Fagus sylvatica</i>	<i>Fagetum subalpinum</i> s. lato* ( <i>Saxifrago rotundifoliae-Fagenion</i> Marinček et al. 1993)	74	42

(Shipley 2010). The first is used especially by plant geographers, concentrating on the morphological properties of plants, e.g., Raunkiaer's life-forms (Raunkiaer 1934) and how, on average, such morphologies change as a function of major climatic variables. A second approach is based on the notion of ecological 'strategies', for which Grime's model of CSR triangle (Grime 1974, 1977, 2001) is often used (Pugnaire and Valladares 2007). This model is a classification based on how plants deal with two groups of external factors, i.e., stress and disturbance, which results in three primary plant strategies: competitors (C), stress-tolerators (S), and ruderals (R) and four secondary, intermediate ones. The position of each species, as well as each relevé, can be determined in a CSR triangle. The whole community is thus given a functional signature, which can be very useful in comparative studies involving widely differing samples (Hunt et al. 2004).

While the use of ecological strategies is quite common in studies of herbaceous vegetation (Hunt et al. 2004, Zelnik and Čarni 2008, Škornik et al. 2010, Pipenbaher et al. 2013), it has lately also been gaining ground in the study of forest and woodland communities (Kilinç et al. 2010, Paušić and Čarni 2012, Juvan et al. 2013, Košir et al. 2013b, Rozman et al. 2013). Its use is most often related to studies of changes in communities' composition as a response to disturbance, succession, environmental changes or in gradient analysis.

The aim of this study was to test whether zonal vegetation is an expression of macro-climatic conditions or whether there are also other environmental factors involved. The underlying assumptions were (1) that the macro-climatic gradient is the most important for the species and structure turnover along the gradient of ZFPCs in B&H; and (2) that ZFPCs would demonstrate similarities in Grime's ecological strategies, due to the fact that the communities are in terminal stages of succession, with a low level of degradation, occupying habitats on moderately fertile soils.

## Materials and methods

### Data collection and preparation

Seven ZFPCs were identified for B&H (Tab. 1, Fig. 1, Stefanović et al. 1983, Beus 1984): (1) eu-Mediterranean evergreen *Quercus ilex* forests (a very small area of the warmest, southernmost part of B&H; represented by maquis); (2) sub-Mediterranean thermophilous deciduous *Quercus pubescens-Carpinus orientalis* forests (a major part of the lowland and hilly region in southern B&H); (3) Central Balkans thermophilous *Quercus frainetto* forests (relatively narrow lowland and hilly belt of eastern B&H); (4) Illyrian mesophilous *Quercus petraea-Carpinus betulus* forests (major part of northern B&H and marginally in central B&H); (5) montane mesoneutrophilous pure *Fagus* or mixed *Fagus-Abies* forests (altitudinal belt above oak forests in all B&H but mainly in the mountainous region of central B&H (Dinaric Alps); (6) alti-montane, colder and more acidophilous mixed *Picea-Abies-Fagus* forests (altitudinal belt above Community 5, mainly in the Dinaric mountainous region); and (7) subalpine *Fagus sylvatica* forests (uppermost forest altitudinal belt).

Relevés were extracted from the Forest vegetation database of Bosnia and Herzegovina stored in the Global index of vegetation-plot databases (Dengler et al. 2011) with the ID EU-BA-001. This database consists of 2810 published and available unpublished forest vegetation relevés in B&H. We compiled all relevés that were assigned to one of the seven ZFPCs by their authors (Tab. 1), with the exception of two zonal communities of thermophilous deciduous forests (Communities 2 and 3), for which we used the results of formalized classification (Stupar et al. 2015). We did not consider relevés of stands with less than 70% of canopy cover, nor those with edifier tree species cover value less than 3 (25%) on the Braun-Blanquet scale, considering them structurally degraded. Only stands of high, productive forests were thus taken into account, except in the case of Community 1 (*Quercus ilex* stands) because well-established stands do not exist in B&H, and all relevés were made in structurally degraded maquis. All relevés were made using the standard Central European phytosociological method (Braun-Blanquet 1964). Only relevés that could be georeferenced relatively precisely and those that contained complete species records were taken into consideration. In all 612 relevés were compiled in the Turboveg database (Hennekens and Schaminée 2001) and exported to JUICE 7 software (Tichý 2002) for further analysis.

Mosses, as well as taxa determined only to the genus level, were removed from the data set prior to numerical analysis. All vegetation layers were merged into one layer. Taxonomy and nomenclature followed Flora Europaea (Tutin et al. 1968–1993) unless a more modern taxon concept or circumscription suggested otherwise. These taxa, as well as those from taxonomically critical groups that were combined into aggregates (agg.) or species that included several subspecies that were not always recorded or recognized by authors and were combined under the abbreviation 's.l.' (*sensu lato*), were listed in On-line Suppl. Tab. 1. The dubious taxon *Quercus dalechampii* was treated as part of *Quercus petraea* agg., following Di Pietro et al. (2012). Records of *Fagus moesiaca* were treated as *F. sylvatica* (Marinšek et al. 2013).

To avoid geographic overrepresentation of some vegetation types due to oversampling of certain regions, we performed geographical stratification and resampling of the initial data set (Knollová et al. 2005), a frequent strategy in recent national and regional level vegetation studies (Chytrý 2013, Košir et al. 2013a, Rodríguez-Rojo et al. 2014). Stratification was performed in a geographical grid with 1 km<sup>2</sup> size. If two or more relevés assigned to the same community fell in the same grid cell, only one of them was selected. Stratification was not performed on Community 1 since it consisted of only five relevés. The resulting stratified data set contained 398 relevés and 669 species.

### Data analysis

The data set was then subjected to detrended correspondence analysis (DCA) in R software, version 2.10.1 (R Development Core Team 2009) using the vegan package (<http://cc.oulu.fi/~jarioksa/softhelp/vegan.html>) on presence-absence data. To extract the main gradients in species composition,

398 relevés, together with the selected ecological variables were projected onto the two-dimensional ordination space of DCA. Unweighted average species ecological indicator values (EIVs) for soil reaction (Pignatti et al. 2005) and selected climatic variables available from the WorldClim database (Hijmans et al. 2005) were used as explanatory ecological variables. The significance of EIVs correlation with the DCA relevé scores was tested using the modified permutation test proposed by Zelený and Schaffers (2012). Climate variables best explaining variation in species composition were selected through forward selection in canonical correspondence analysis (CCA) in CANOCO 4.5 software (Microcomputer Power, Ithaca, NY, US). Other explanatory variables (altitude, inclination of slope, aspect, chorotypes, latitude and longitude, life forms and ecological strategies) were selected and projected based on the strength of correlation with the first and second DCA axis. The significances of correlations between these explanatory variables and DCA relevé scores were calculated using the Kendall tau coefficient in Statistica software (StatSoft, Inc.; v 7.0, <http://www.statsoft.com>). Chorological spectra of the zonal forest communities (Gajić 1980, Pignatti et al. 2005) were calculated for each relevé using presence-absence data. Endemic Illyrian species were separated from southeast European species in a broader sense.

In order to reveal the floristic differences among the seven ZFPCs, we calculated their diagnostic species in the resampled data set using phi coefficient in the JUICE 7 program (Chytrý et al. 2002), after standardization to a relevé group size equal to a seventh of the total data set size (Tichý and Chytrý 2006). Fisher's exact test was calculated giving a zero fidelity value to species whose phi values were not statistically significant ( $P > 0.001$ ). The threshold phi value for a species to be considered diagnostic was set at 0.25.

The functional study of zonal forest communities was performed using data of plant functional traits, i.e., life forms (Raunkiaer 1934) and ecological strategies (Grime 1977). Plants were classified according to Grime's primary

and secondary strategies into seven functional types using data from the BIOLFLOR database (Klotz et al. 2002). We thus obtained data for about 80% of species. Ecological strategies for the remaining species were calculated using the dichotomous key suggested by Vela (2002). Averages of each strategy type weighted by cover-percentage were calculated and standardized for each relevé as suggested by Hunt et al. (2004). Ecological strategy scores for each group of relevés were then calculated with the CSR Signature Calculator 1.2 program (Hunt et al. 2004) and represented on a CSR ternary plot. We did a separate analysis for all layers and for the herb layer alone because herb functional signatures respond more quickly to environmental changes in the course of late succession (Paušič and Čarni 2012). Plant life forms obtained from Pignatti et al. (2005) and supplemented by our expert knowledge were used for the calculation of life forms spectra for each relevé using presence-absence data, and mean proportions were compared between ZFPCs. The occurrence of an individual functional trait in each of the ZFPCs was compared using the Scheffé post hoc test for normal distributions and Kruskal-Wallis test by ranks and median for non-normal distributions using Statistica software. A normality check was performed using Lilliefors test.

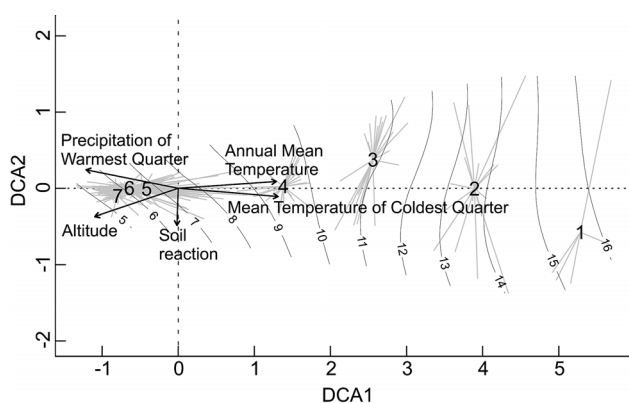
## Results

### Gradient analysis within ZFPCs in Bosnia and Herzegovina

Forward selection suggested that the climatic variables with the highest explanatory value of the variation in species composition are annual mean temperature (BIO1), mean temperature of the coldest quarter (BIO11) and precipitation of the warmest quarter (BIO18). The first DCA axis represents the main gradient in the data set, and all three climatic variables are significantly related to the first DCA axis at  $P < 0.001$  (Tab. 2, Fig. 2). It runs from the cold-

**Tab. 2.** Correlations (Kendall-Tau coefficient) between detrended correspondence analysis (DCA) relevé scores and explanatory variables. BIO1 – annual mean temperature; BIO11 – mean temperature of the coldest quarter; BIO18 – precipitation of the warmest quarter; Eur – European and Eurasian; SEur – south and southeast European; EuriMed – Euri-Mediterranean; StMed – Steno-Mediterranean; Illyr – Endemic Illyrian; Bor – Boreal; SEOro – South European orophytes; Cosm – Widespread species; P – Phanerophytes; NP – Nano-phanerophytes; Ch – Chamaephytes; H – Hemicryptophytes; G – Geophytes; T – Terophytes; C – Competitors; S – Stress-tolerators; R – Ruderals. Asterisk (\*) denotes significant correlation at  $P < 0.001$ .

	Ecological factors						Geographical factors		
	Altitude	Aspect	Slope	BIO1	BIO11	BIO18	Latitude	Longitude	
DCA 1	-0.521*	0.046	0.050	0.569*	0.566*	-0.451*	-0.200*	0.367*	
DCA 2	-0.151*	-0.034	-0.103	0.118*	0.103	-0.011	0.028	-0.041	
	Chorotypes								
	Eur	SEur	EuriMed	StMed	Illyr	Bor	SEOro	Cosm	
DCA 1	0.088	0.203*	0.445*	0.309*	-0.172*	-0.313*	-0.510*	-0.155*	
DCA 2	0.077	-0.034	0.035	-0.004	-0.066	-0.009	-0.138*	0.077	
	Life forms				Ecological strategies				
	P	NP	Ch	H	G	T	C	S	R
DCA 1	0.182*	0.020	0.045	0.080	-0.317*	0.109	0.045	-0.048	0.014
DCA 2	0.010	-0.059	0.110	0.057	-0.121*	0.126*	-0.049	-0.067	0.109



**Fig. 2.** Detrended correspondence analysis (DCA) spider plot of 398 relevés of zonal forest plant communities with climatic variables, ecological indicator values (EIVs) for soil reaction and altitude passively projected. The surface variable is annual mean temperature. The length of the first DCA axis is 7.02 SD units, the length of the second axis is 2.85 SD units. Centroids of clusters are indicated by numbers that refer to Tab. 1.

est and most mesophilous subalpine beech forests (Community 7) on the left side of the diagram to the most xerothermophilous *Quercus ilex* maquis (Community 1) on the far right side of diagram. It is positively correlated with annual mean temperature and mean temperature of the coldest quarter, and negatively with the precipitation of the warmest quarter (Fig. 2, Tab. 2). These are strong indicators that the first DCA axis represents a macro-climatic gradient that runs from wet summers, cold winters and lower annual

temperatures to dry summers but warmer winters and higher overall annual temperatures. There is also a high negative correlation with altitude, which is again related to macro-climatic factors. The positive correlation with longitude and negative correlation with latitude reflects the fact that south and east parts of B&H are warmer and dryer than the north and west. Correlations between the first axis and slope and aspect are not statistically significant (Tab. 2). A modified permutation test also showed that the correlation between DCA 1 and EIVs for soil reaction was not statistically significant ( $R^2=0.125$ ,  $P=0.195$ ). In terms of chorotypes, DCA axis 1 shows a positive correlation with the proportions of south- and southeast European, Euri-Mediterranean and Steno-Mediterranean chorotypes, and a negative correlation with Boreal and south European orophytic chorotypes, while the correlation with the most abundant European and Eurasian chorotypes is not statistically significant. Correlations between the first axis and life forms are significant only for the proportions of phanerophytes (positive) and geophytes (negative). There is no significant correlation between ecological strategies and DCA axes (Tab. 2).

### Floristic differentiation

Analysis revealed differences in the floristic composition among the seven ZFPCs. Tab. 3 shows a simplified frequency-fidelity synoptic table of the ZFPCs of B&H based on a data set of 398 resampled relevés (full version is given in On-line Suppl. Tab. 2).

**Tab. 3.** Frequency-fidelity table of zonal forest plant communities (ZFPCs) in Bosnia and Herzegovina. Frequencies of species are presented as percentages with phi values multiplied by 100 shown in superscript. Diagnostic species (phi values higher than 0.25) for each community are shaded (only ten species with the highest phi value for every community are presented). Proportions of chorotypes and altitudinal ranges of each community are also shown. Community numbers correspond to those used in Tab. 1 and Fig. 1.

Community number	1	2	3	4	5	6	7
No. of relevés	5	16	24	26	162	123	42
Altitudinal range (m)	0–150	100–650	150–700	200–900	700–1400	800–1600	1400–1800
<b>Chorotype (% of all species in a community)</b>							
Widespread species	3	1	3	5	7	7	4
European and Eurasian	13	29	56	67	59	55	49
south and southeast European	21	30	21	16	13	10	12
Eurimediterranean	29	29	13	5	1	1	0
Stenomediterranean	33	7	0	0	0	0	0
Endemic Illyrian	1	3	1	0	1	2	3
Boreal	0	1	6	6	10	13	13
South European orophytes	0	0	0	1	9	12	19
<b>ZFPC 1</b>							
<i>Quercus ilex</i>	100 <sup>96.5</sup>	6 <sup>-</sup>	.	.	.	.	.
<i>Arbutus unedo</i>	80 <sup>88</sup>	.	.	.	.	.	.
<i>Teucrium polium</i> ssp. <i>capitatum</i>	80 <sup>84.1</sup>	6 <sup>-</sup>	.	.	.	.	.
<i>Centaureum erythraea</i>	80 <sup>83.2</sup>	.	.	8 <sup>-</sup>	.	.	.
<i>Pistacia terebinthus</i>	100 <sup>82.6</sup>	38 <sup>18.3</sup>	.	.	.	.	.
<i>Juniperus phoenicea</i>	60 <sup>75</sup>	.	.	.	.	.	.
<i>Pistacia lentiscus</i>	60 <sup>75</sup>	.	.	.	.	.	.
<i>Juniperus oxycedrus</i> ssp. <i>macrocarpa</i>	40 <sup>60.3</sup>	.	.	.	.	.	.

Tab. 3. – continued

Community number	1	2	3	4	5	6	7
No. of relevés	5	16	24	26	162	123	42
Altitudinal range (m)	0–150	100–650	150–700	200–900	700–1400	800–1600	1400–1800
<i>Crepis sancta</i>	40 <sup>60.3</sup>	.	.	.	.	.	.
<i>Cistus salvifolius</i>	40 <sup>60.3</sup>	.	.	.	.	.	.
<b>ZFPC 2</b>							
<i>Quercus pubescens</i>	20 <sup>-</sup>	100 <sup>84.5</sup>	12 <sup>-</sup>	.	.	.	.
<i>Cornus mas</i>	.	88 <sup>83.6</sup>	8 <sup>-</sup>	8 <sup>-</sup>	.	.	.
<i>Acer monspessulanum</i>	.	62 <sup>76.7</sup>	.	.	.	.	.
<i>Sesleria autumnalis</i>	20 <sup>-</sup>	81 <sup>76.5</sup>	.	.	1 <sup>-</sup>	1 <sup>-</sup>	.
<i>Frangula rupestris</i>	.	56 <sup>72.4</sup>	.	.	.	.	.
<i>Viola hirta</i>	.	75 <sup>69.4</sup>	17 <sup>-</sup>	12 <sup>-</sup>	.	.	.
<i>Rubus ulmifolius</i>	.	50 <sup>67.9</sup>	.	.	.	.	.
<i>Carex halleriana</i>	20 <sup>-</sup>	62 <sup>64.2</sup>	.	.	.	.	.
<i>Brachypodium sylvaticum</i>	.	75 <sup>61.1</sup>	12 <sup>-</sup>	19 <sup>-</sup>	5 <sup>-</sup>	6 <sup>-</sup>	7 <sup>-</sup>
<i>Juniperus oxycedrus</i>	40 <sup>-</sup>	69 <sup>60</sup>	.	.	.	.	.
<b>ZFPC 3</b>							
<i>Quercus frainetto</i>	.	19 <sup>-</sup>	100 <sup>90.3</sup>	.	.	.	.
<i>Chamaecytisus hirsutus</i> agg.	.	.	58 <sup>70.4</sup>	4 <sup>-</sup>	.	1 <sup>-</sup>	.
<i>Quercus cerris</i>	.	50 <sup>23</sup>	100 <sup>69.8</sup>	27 <sup>-</sup>	1 <sup>-</sup>	1 <sup>-</sup>	.
<i>Thymus pulegioides</i>	.	.	54 <sup>65.7</sup>	.	4 <sup>-</sup>	1 <sup>-</sup>	2 <sup>-</sup>
<i>Lychnis coronaria</i>	.	.	46 <sup>64.8</sup>	.	.	.	.
<i>Lathyrus niger</i>	.	12 <sup>-</sup>	58 <sup>63</sup>	4 <sup>-</sup>	.	.	.
<i>Euphorbia cyparissias</i>	.	19 <sup>-</sup>	58 <sup>61.7</sup>	.	.	.	.
<i>Dianthus armeria</i>	.	.	42 <sup>61.6</sup>	.	.	.	.
<i>Carex caryophylla</i>	.	19 <sup>-</sup>	58 <sup>57.8</sup>	8 <sup>-</sup>	.	.	.
<i>Silene viridiflora</i>	.	12 <sup>-</sup>	46 <sup>55.4</sup>	.	.	.	.
<b>ZFPC 4</b>							
<i>Carpinus betulus</i>	.	.	42 <sup>19.6</sup>	100 <sup>77.3</sup>	11 <sup>-</sup>	.	.
<i>Cruciata glabra</i>	.	.	4 <sup>-</sup>	69 <sup>67.5</sup>	11 <sup>-</sup>	8 <sup>-</sup>	.
<i>Prunus avium</i>	.	.	25 <sup>-</sup>	65 <sup>60.7</sup>	6 <sup>-</sup>	1 <sup>-</sup>	.
<i>Luzula luzuloides</i>	.	.	.	58 <sup>59.9</sup>	1 <sup>-</sup>	8 <sup>-</sup>	12 <sup>-</sup>
<i>Pteridium aquilinum</i>	.	.	38 <sup>-</sup>	77 <sup>57.7</sup>	12 <sup>-</sup>	15 <sup>-</sup>	.
<i>Stellaria holostea</i>	.	.	8 <sup>-</sup>	50 <sup>36.6</sup>	1 <sup>-</sup>	.	7 <sup>-</sup>
<i>Melampyrum pratense</i>	.	.	17 <sup>-</sup>	50 <sup>54.5</sup>	.	1 <sup>-</sup>	2 <sup>-</sup>
<i>Erythronium dens-canis</i>	.	.	.	27 <sup>49</sup>	.	.	.
<i>Crataegus monogyna</i>	.	44 <sup>-</sup>	29 <sup>-</sup>	69 <sup>45.3</sup>	15 <sup>-</sup>	2 <sup>-</sup>	.
<i>Hieracium racemosum</i>	.	.	.	23 <sup>45.2</sup>	.	.	.
<b>ZFPC 5</b>							
<i>Galium odoratum</i>	.	.	.	12 <sup>-</sup>	76 <sup>46.5</sup>	59 <sup>-</sup>	36 <sup>-</sup>
<i>Acer pseudoplatanus</i>	.	.	.	12 <sup>-</sup>	81 <sup>44.6</sup>	69 <sup>-</sup>	52 <sup>-</sup>
<i>Cardamine bulbifera</i>	.	.	.	12 <sup>-</sup>	67 <sup>42.3</sup>	30 <sup>-</sup>	55 <sup>-</sup>
<i>Lonicera xylosteum</i>	.	.	.	.	31 <sup>38.9</sup>	15 <sup>-</sup>	2 <sup>-</sup>
<i>Cardamine enneaphyllos</i>	.	.	.	.	62 <sup>38.1</sup>	35 <sup>-</sup>	62 <sup>-</sup>
<i>Daphne mezereum</i>	.	.	.	.	51 <sup>35.1</sup>	37 <sup>-</sup>	38 <sup>-</sup>
<i>Salvia glutinosa</i>	.	.	4 <sup>-</sup>	4 <sup>-</sup>	31 <sup>34.9</sup>	14 <sup>-</sup>	2 <sup>-</sup>
<i>Glechoma hirsuta</i>	.	.	17 <sup>-</sup>	19 <sup>-</sup>	50 <sup>34.6</sup>	26 <sup>-</sup>	12 <sup>-</sup>
<i>Rubus hirtus</i>	.	.	12 <sup>-</sup>	42 <sup>-</sup>	57 <sup>33.1</sup>	36 <sup>-</sup>	14 <sup>-</sup>
<i>Cardamine trifolia</i>	.	.	.	.	28 <sup>32.9</sup>	20 <sup>-</sup>	2 <sup>-</sup>
<b>ZFPC 6</b>							
<i>Picea abies</i>	.	.	.	.	51 <sup>-</sup>	100 <sup>59.7</sup>	69 <sup>-</sup>

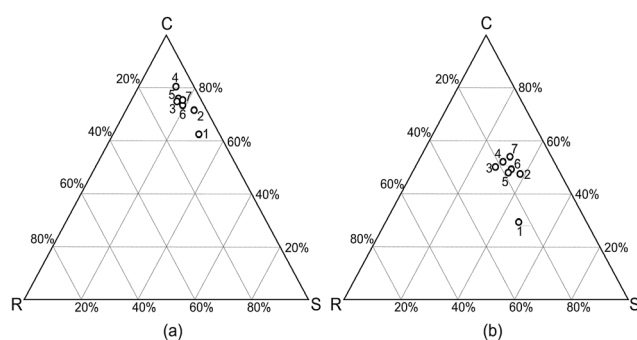
Tab. 3. – continued

Community number	1	2	3	4	5	6	7
No. of relevés	5	16	24	26	162	123	42
Altitudinal range (m)	0–150	100–650	150–700	200–900	700–1400	800–1600	1400–1800
<i>Abies alba</i>	.	.	.	8 <sup>-</sup>	73 <sup>-</sup>	98 <sup>52.5</sup>	76 <sup>-</sup>
<i>Athyrium filix-femina</i>	.	.	.	8 <sup>-</sup>	38 <sup>-</sup>	63 <sup>49</sup>	14 <sup>-</sup>
<i>Galium rotundifolium</i>	.	.	.	.	9 <sup>-</sup>	41 <sup>46.5</sup>	12 <sup>-</sup>
<i>Oxalis acetosella</i>	.	.	.	.	64 <sup>-</sup>	83 <sup>46.1</sup>	69 <sup>-</sup>
<i>Lonicera nigra</i>	.	.	.	.	19 <sup>-</sup>	46 <sup>43.9</sup>	17 <sup>-</sup>
<i>Sorbus aucuparia</i>	.	.	.	.	33 <sup>-</sup>	63 <sup>42.1</sup>	50 <sup>-</sup>
<i>Senecio nemorensis</i> s.l.	.	.	.	.	38 <sup>-</sup>	59 <sup>40.8</sup>	38 <sup>-</sup>
<i>Prenanthes purpurea</i>	.	.	.	4 <sup>-</sup>	46 <sup>-</sup>	68 <sup>38.9</sup>	67 <sup>-</sup>
<i>Lamiastrum galeobdolon</i>	.	.	.	27 <sup>-</sup>	56 <sup>-</sup>	73 <sup>38.8</sup>	52 <sup>-</sup>
<b>ZFPC 7</b>							
<i>Saxifraga rotundifolia</i>	.	.	.	.	12 <sup>-</sup>	24 <sup>-</sup>	76 <sup>66.7</sup>
<i>Luzula sylvatica</i>	.	.	.	.	3 <sup>-</sup>	20 <sup>-</sup>	67 <sup>65.6</sup>
<i>Adenostyles alliariae</i>	.	.	.	.	5 <sup>-</sup>	23 <sup>-</sup>	64 <sup>61.8</sup>
<i>Valeriana montana</i>	.	.	.	.	4 <sup>-</sup>	8 <sup>-</sup>	45 <sup>55.3</sup>
<i>Cicerbita alpina</i>	.	.	.	.	1 <sup>-</sup>	10 <sup>-</sup>	43 <sup>53.9</sup>
<i>Veronica urticifolia</i>	.	.	.	.	4 <sup>-</sup>	23 <sup>-</sup>	52 <sup>52.8</sup>
<i>Ranunculus platanifolius</i>	.	.	.	.	2 <sup>-</sup>	5 <sup>-</sup>	38 <sup>52.4</sup>
<i>Astrantia major</i>	.	.	.	.	.	1 <sup>-</sup>	31 <sup>51.8</sup>
<i>Homogyne alpina</i>	.	.	.	.	.	.	29 <sup>50.5</sup>
<i>Veratrum lobelianum</i>	.	.	.	.	.	.	24 <sup>46</sup>
<b>Species diagnostic for more than one community</b>							
<i>Phillyrea latifolia</i>	100 <sup>78.2</sup>	50 <sup>28.4</sup>	.	.	.	.	.
<i>Clematis flammula</i>	80 <sup>64.5</sup>	50 <sup>33</sup>	.	.	.	.	.
<i>Asparagus acutifolius</i>	60 <sup>40.5</sup>	81 <sup>62.1</sup>	.	.	.	.	.
<i>Carpinus orientalis</i>	.	88 <sup>68.3</sup>	54 <sup>34.5</sup>	.	.	.	.
<i>Fraxinus ornus</i>	60 <sup>-</sup>	100 <sup>50.4</sup>	83 <sup>36.5</sup>	31 <sup>-</sup>	2 <sup>-</sup>	1 <sup>-</sup>	.
<i>Genista tinctoria</i>	.	.	54 <sup>50.6</sup>	35 <sup>26.7</sup>	1 <sup>-</sup>	.	.
<i>Quercus petraea</i>	.	.	71 <sup>43.7</sup>	100 <sup>71.3</sup>	1 <sup>-</sup>	1 <sup>-</sup>	.
<i>Acer campestre</i>	.	12 <sup>-</sup>	42 <sup>27.5</sup>	58 <sup>45.1</sup>	4 <sup>-</sup>	.	.
<i>Fagus sylvatica</i>	.	.	12 <sup>-</sup>	46 <sup>-</sup>	100 <sup>39.8</sup>	100 <sup>39.8</sup>	100 <sup>-</sup>
<i>Vaccinium myrtillus</i>	.	.	.	4 <sup>-</sup>	12 <sup>-</sup>	57 <sup>40.3</sup>	57 <sup>40.6</sup>

**Analysis of functional traits**

In the standard CSR triangle plot, communities are positioned in the upper right part of the diagram (Fig. 3a). This means that zonal forest plant communities are dominated by species with considerable competitive capacity. However, there is apparent divergence of Communities 1, 2 and 4 from the main cluster along the C–S axis, whereby statistically significant differences were discovered (Tab. 4). The highest ratio of stress tolerant-species occurs in Community 1, much less in Community 2, while the most competitive ability is expressed by Community 4. CSR signatures of the herb layer are shifted to the middle of the C–S axis (Fig. 3b).

The most significant differences in functional traits of a life form were detected for Phanerophytes and Geophytes between Communities 1–4 and Communities 5–7, and for Hemicryptophytes between Communities 1 and 5 and the rest of the data set (Tab. 4). The highest ratios of Phanero-

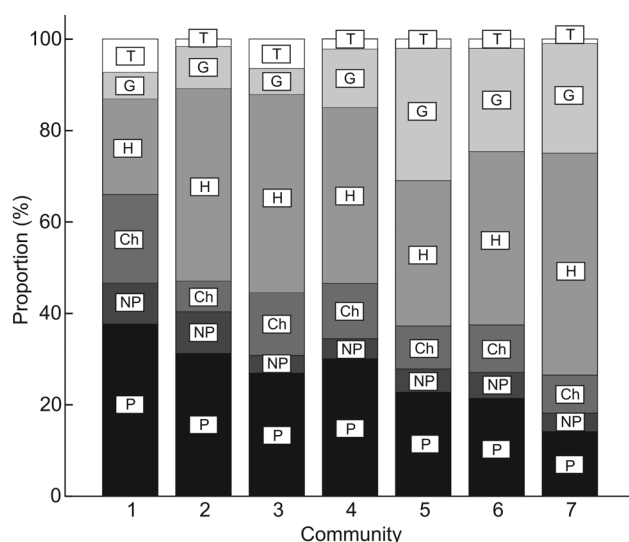


**Fig. 3.** CSR triangle of the ordination of zonal forest plant communities in Bosnia and Herzegovina according to ecological strategy scores (proportion of competitors – C, stress-tolerators – S and ruderals – R components in each community). Community numbers correspond to those used in Tab. 1 and Fig. 1. (a) All layers together; (b) Herb layer.

**Tab. 4.** Comparison of differences in functional traits occurrences between each pair of zonal forest plant communities (ZFPCs). Statistical significance established using Kruskal-Wallis test by ranks and median, except for R, H and G, for which the Scheffé post hoc test for a normal distribution was used. Community numbers correspond to those used in Tab. 1 and Fig. 1. FT – Functional type; C – Competitors; S – Stress tolerators; R – Ruderals; P – Phanerophytes; NP – Nanophanerophytes; Ch – Chamaephytes; H – Hemicryptophytes; G – Geophytes; T – Therophytes. \*\*\* p<0.001; \*\* p<0.01; \* p<0.05.

FT	Compared pairs of ZFPCs																				
	1-2	1-3	1-4	1-5	1-6	1-7	2-3	2-4	2-5	2-6	2-7	3-4	3-5	3-6	3-7	4-5	4-6	4-7	5-6	5-7	6-7
C			***	*				**				*				**	***	*			
S		**	***	**		*	**	***	***							*	***	**	***		
R							**		***	**											
P					*	***			*	**	***				***	**	***	***		***	***
NP							***	***	***	*	***										
Ch	**			*		**	***	*					*		**						
H	***	***	**		**	***			**				***		*		***	***	***	***	***
G				***	**	***			***	***	***		***	***	***	***	***	***	***	*	
T						*	**						***	**	***						

phytes and Nanophanerophytes are found in the first two communities, with a decline in Phanerophytes towards Community 7 (Fig. 4). Beech-dominated forests (Communities 5–7) have twice the ratio of Geophytes compared to oak-dominated forests (Communities 1–4). There is the highest proportion of Chamaephytes in Community 1, while the biggest share of Therophytes is found in Communities 1 and 3.



**Fig. 4.** Proportions of life forms in zonal forest plant communities in Bosnia and Herzegovina. Community numbers correspond to those used in Tab. 1 and Fig. 1. P – Phanerophytes; NP – Nanophanerophytes; Ch – Chamaephytes; H – Hemicryptophytes; G – Geophytes; T – Therophytes.

## Discussion

Our study strongly suggests macro-climatically based differentiation of ZFPCs in B&H. While gradient analysis revealed a major influence of climatic factors on the species turnover, there is little or no impact of topographic (slope and aspect) or edaphic conditions (Fig. 2, Tab. 2), which is

congruent with the traditional understanding of zonal vegetation (Dierschke 1994, Ellenberg 2009, Surina 2014). Macro-climatic gradient is supported by the significant correlation with the geographic factors (altitude, longitude and latitude), which are all determinants of climate on a larger scale (Ellenberg 2009, Adams 2010). A recent study of zonal forests of Korean Peninsula similarly showed that the main factor discriminating individual forest types was temperature (annual mean temperature, as well as temperature extremes) followed by precipitation, altitude and aridity (Černý et al. 2015). While chorotypes indicate units that describe distribution patterns shared by several species, explaining origins and history of development of particular floras (Pignatti and Pignatti 2014, Passalacqua 2015), some studies suggest that there is a correlation between chorotypes and climatic conditions (Ferrer-Castán and Vetaas 2003, Abbate et al. 2012). In the case of our study, the proportion of ‘warmer’ (Euri-Mediterranean and Steno-Mediterranean) chorotypes increases in a direction of the main gradient, while the proportion of ‘colder’ (Boreal and Orophytic) chorotypes decreases (Tab. 3), which again suggests the macro-climatic gradient.

Floristic analysis showed a clear separation of seven ZFPCs in B&H. **Community 1** (*Quercus ilex* maquis, Tab. 3, col. 1) occupies only a small area (about 20 km<sup>2</sup>) in the extreme south of B&H. It is represented by the secondary succession stage of the eastern Adriatic eu-Mediterranean zonal association *Fraxino orni-Quercetum ilicis* (Kutleša and Lakušić 1964). Mean annual temperatures are above 15 °C (Fig. 2) and elevations 0–150 m. Diagnostic species are mainly of Steno-Mediterranean, Euri-Mediterranean and south and southeast European chorotypes. Diagnostic herb species are mainly indicators of rocky habitats due to structural degradation. Although in the last 50 years this community has expanded its distribution area in B&H, due to the abandonment of coppicing, burning and goat breeding, there are still no high stands (Drešković et al. 2011). The situation is similar, though a little better, in neighboring Croatia (Vukelić 2012). **Community 2** (*Quercus pubes-*



*cens-Carpinus orientalis* forests, Tab. 3, col. 2) is represented by high, not degraded stands of zonal thermophilous deciduous forest of the association *Quercus pubescenti-Carpinetum orientalis* (Stupar et al. 2015) found in the lowlands and hilly area of sub-Mediterranean B&H. However, due to the negative human impact, they have mainly been replaced by the secondary scrub community *Rusco aculeati-Carpinetum orientalis* (Muratspahić et al. 1991), while their present distribution area is restricted to small patches of mainly private old groves (Stupar et al. 2015). Mean annual temperatures are between 12 and 15 °C (Fig. 2), occupying elevations between 100 and 650 m. Diagnostic species are thermophilous and xerophilous plants of mainly S/SE European or Euri-Mediterranean distribution, although some widespread nemoral herbs and shrubs appear with high frequency, e.g.: *Brachypodium sylvaticum*, *Dactylis glomerata*, *Veronica chamaedrys*, *Crataegus monogyna*, *Hedera helix* etc., indicating more mesophilous microclimatic conditions under the closed canopy. **Community 3** (*Quercus frainetto* forests, Tab. 3, col. 3) is found in the eastern parts of B&H, where the influence of the continental drier climate increases. This is a zonal community of Central Balkans lowlands and hilly areas (Horvat et al. 1974) and is represented by the fairly heterogeneous association *Quercetum frainetto-cerridis* (Tomić and Rakonjac 2013, Stupar et al. 2015). Although we included in the analysis only stands with 70% and more canopy cover, these forests are mainly found in the proximity of human settlements, so they are frequently degraded by grazing and browsing, as well as occasional fires. Mean annual temperatures are between 10 and 12 °C (Fig. 2), and elevations are between 150 and 700 m. They are dominated by a mixture of thermophilous, acid tolerant and widespread nemoral species, as well as some more light-demanding herbs, indicating wood pasture and cutting. **Community 4** is represented by sessile oak-common hornbeam forests, which are considered a zonal forest vegetation community for the area of NW Balkans (*Quercus petraea-Carpinus betulus* forests, Tab. 3, col. 4). In B&H they are found mainly in the hilly area of northern parts of the country but can also penetrate deeper into the south (e.g., Central Bosnian basin, Fig. 1). Habitats of these forests have been under intensive anthropogenic influence since the Neolithic (Horvat et al. 1974), so it is hard to find stands of high, productive forests with *Quercus petraea* cover value in the tree layer more than 3 on the Braun-Blanquet scale (25–50% of cover) and more than 70% of overall canopy cover. They are often, due to bad management, structurally degraded to *Carpinus betulus* coppice. Mean annual temperatures are between 9 and 10 °C (Fig. 2) and they occupy elevations between 200 and 900 m. Several types of these forests occur in B&H but neither the syntaxonomy nor nomenclature has been settled (Lakušić et al. 1978, Redžić 2007). In addition, there is disagreement about the taxonomical position of these forests on the regional level. While Croatian and Slovenian authors assign these forest to the Illyrian alliance *Erythronio-Carpinion betuli* (Vukelić 2012, Košir et al. 2013a), some other authors question this view, arguing that the group is weakly characterized by diagnostic species (Will-

ner and Grabherr 2007, Borhidi et al. 2012). This is sustained by our results, in the sense that this ZFPC is the only one in B&H that completely lacks endemic Illyrian species (Tab. 3). Diagnostic species are mainly represented by mesophilous European and Eurasian elements. **Community 5** (pure *Fagus* / mixed *Fagus-Abies* forests, Tab. 3, col. 5) represents the first altitudinal belt above oak forests and is made up of mesoneutrophilous montane pure beech, as well as mixed fir-beech forests. The syntaxonomy and nomenclature of these forests have not yet been the subject of thorough analysis but two main types, or widely understood associations, are included: *Fagetum montanum illyricum* and *Abieti-Fagetum dinaricum* (Beus 1984). They belong to the alliance *Aremonio-Fagion* (Marinšek et al. 2013). Mean annual temperatures are between 6 and 8 °C (Fig. 2) and they are mainly found at elevations between 700 and 1400 m. Floristically and ecologically similar to this type is **Community 6** (mixed *Picea-Abies-Fagus* forests Tab. 3, col. 6), which also has a considerable amount of Boreal and south European orophytic elements, while annual mean temperatures are between 5 and 7 °C (Fig. 2). In the view of Beus (1984), which is supported by our results, the main difference between Community 6 and the previous community is that Community 6 has a higher proportion of spruce (100% frequency) and acidophilous *Vaccinio-Piceetea* species, while the proportion of mesoneutrophilous *Aremonio-Fagion* species is remarkably lower. In addition, it comes as an altitudinal belt above Community 5 (elevations between 800 and 1600 m) and can be found exclusively in the central range of Dinaric Alps, while Community 5 extends more to the north and south (Fig. 1). This is explained by the fact that the hot dry summers of the northern and southern chains of Dinaric Alps do not favor spruce (Beus 1984). The syntaxonomy and nomenclature of Community 6 have also not been settled, so in B&H this complex type is identified under the invalid provisional name *Piceo-Abieti-Fagetum*. **Community 7** is the highest altitudinal belt, represented by subalpine *Fagus sylvatica* forests (Tab. 3, col. 7). This is yet another group the syntaxonomy and nomenclature of which in B&H has not been analyzed and it is known by the generic name of *Fagetum subalpinum* s. lato. These forests belong to the suballiance *Saxifrago rotundifoliae-Fagenion* of the alliance *Aremonio-Fagion* (Marinšek et al. 2013). These are mainly mesoneutrophilous pure beech forests found mainly on the mountains of the central and southern chains of the Dinaric Alps (Fig. 1). Mean annual temperatures are between 5 and 6 °C (Fig. 2), with elevations between 1400 and 1800 m. This community harbors the highest proportion (32%) of Boreal and south European orophytic elements.

Functional analysis of ecological strategies showed small overall differences among ZFPCs. Based on the communities' locations on the CSR triangle, competitive strategy (C) is dominant in all seven communities, followed by CSR and SC strategies (Fig. 3). Considering the course of succession (Fig. 3a), site production is high (Grime 1974), while the importance of ruderality is insignificant, which indicates late stages of succession, as pointed out by Prévost et al. (2011). The terminal stage of zonal communi-

ties is supported by the position of the communities on the CSR plot when only the herb layer was analyzed (Fig. 3b). In this plot, stress tolerance becomes more important since shading and lack of nutrients in the herb layer coincide with the development of large long-lived forest trees (Grime 1977, 1988). Only Community 1 (*Quercus ilex* maquis), which has the largest share of ruderals, expresses conditions of moderate productivity and middle to late stage of secondary succession (maquis). The increased proportion of stress-tolerators in Community 1 and also, to a much lesser extent, in Community 2 is related to drought stress during the summer season in the Mediterranean limestone region of B&H. On the other hand, Community 4 (*Quercus petraea-Carpinus betulus* forests) has an increased proportion of competitors, which indicates higher productive capacities. Also, this community lies in the middle of the macro-climatic gradient (Fig. 2), which altogether suggests the most favorable conditions for forest vegetation development in B&H.

Changes in the life form proportions of different communities are expressed in the greater share of woody species in the more thermophilous vegetation types, which corresponds with the statement that 'the Phanerophyte is the plant type that belongs to warm regions' (Raunkiaer 1934). Similar results were obtained in the study of the gradient from warm to mesic temperate forests on the Galičica mountain range in Macedonia (Čarni et al. 2016). The proportion of Geophytes is higher in Communities 5–7 (beech dominated forests), which have spring ephemerals (mainly bulbous Geophytes), also abundant in oak communities (Popović et al. 2016), in addition to harboring a considerable number of non-ephemeral rhizomatous ferns and species from the family Liliaceae. This is congruent with the notion that rhizomatous Geophytes are adapted to life in regions with a severe unfavorable period (e.g., hard winters), but have at the same time a long period of vegetation (Raunkiaer 1934). The proportion of Therophytes is insignificant except in Communities 1 and 3, which can be explained by water shortage in the conditions of harsher Med-

iterranean and continental climates (Kavgaci et al. 2012, Raju et al. 2014). The same can be said for the proportion of Chamaephytes in Community 1. On the other hand, according to Bloch-Petersen et al. (2006) plant life forms differentiate not only due to climatic variations, but seem also to relate to humane disturbance and management. Prasad (1995) studied the effects of grazing on the plant species and life form composition and found that the percentage of Therophytes was higher on grazed areas than on protected areas, which reflects the disturbance through grazing in Communities 1 and 3.

To conclude, the results of our analysis support the hypothesis that zonal forest vegetation in B&H is an expression of macro-climatic conditions and that there are no remarkable differences in CSR plant strategies among the ZFPCs in B&H (excluding Community 1). However, having in mind that the currently protected forest area in B&H is very small and covers only a few types of ZFPCs (Stupar 2011), in order to facilitate further research into the ecological, floristic and functional characteristics of ZFPCs there is a need for establishment of a national network of protected areas which would cover all ZFPC types, thus preserving the representative stands in as natural conditions as possible (Milanović et al. 2015). Particular emphasis should be given to thermophilous forests, especially to Community 1 (stands of *Quercus ilex*) which should be converted from maquis to high forests.

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