Botanica SERBICA 42 (1): (2018) 91-107

Original Scientific Paper

Beech forests (order *Fagetalia sylvaticae* Pawlowski 1928) in Serbia

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ABSTRACT: Beech forests occupy considerable areas in Serbia. The principal aims of this research were to detect variability patterns and determine biodiversity components in Serbian beech forests. The K-means clustering of a data set comprising 270 relevés and more than 500 species revealed seven ecologically interpretable groups of beech forests in Serbia. The groups are presented in a synoptic table, with calculation of diagnostic species. Canonical correspondence analysis indicates that the altitudinal gradient is the main factor affecting diversification of the investigated forests. Species richness and alpha diversity are greatest in beech forests of ravine habitats.

Keywords: altitudinal gradient, alpha diversity, beech (*Fagus sylvatica*) forests, canonical correspondence analysis, K-means clustering, species richness

Received: 25 May 2017 Revision accepted: 27 September 2017

UDC: 497.11:630.228(633.872)
DOI: 10.5281/zenodo.1173560

INTRODUCTION

Fagus sylvatica L. (beech) is the most abundant broadleaved tree in Central Europe and in mountain regions of Southern Europe. Beech is a species adapted to humid climate. It thrives well in regions with mild winters and humid summers without a pronounced dry season (Matevski *et al.* 2011). Due to dense foliage and specific shape of the tree crowns, *Fagus sylvatica* L. significantly reduces the amount of light reaching the interior of mesic forests. Such dysphotic (light shortage) conditions represent strong selective pressure for many plants. Plants adapted to disphotic stress can be divided into two categories: *shade-evaders* (vernal ephemeroides) and *shade-tolerant* species (Walter & Breckle 1985; Popović *et al.* 2005, 2006, 2016).

The taxonomic status of beech on the Balkan Peninsula is a controversial and still unresolved problem (Mišić 1957; Gömöry *et al.* 1995, 1999; Hazler *et al.* 1997; Sijačić-Nikolić *et al.* 2013). Some authors treat the east-Balkan population of beech as a separate species, *Fagus moesiaca* (K. Maly) Czeczott, that is distinct from European beech (*Fagus sylvatica* L.) and oriental beech (*Fagus orientalis* Lypski). Other authors assume that the Balkan beech is a subspecies of European beech (*Fagus sylvatica* L. ssp. *moesiaca* (K. Maly) Hjelmquist). Mišić (1957) noticed a gradual change in traits of leaves, flowers, and fruits from northwestern to southeastern Europe. Gömöry *et al.* (1999) observed a similar trend of genetic differentiation (a clinal spatial distribution of allozyme frequencies). Due to clinal variation of both morphological traits and allozyme frequencies, it is hard to discriminate European, Balkan, and oriental beech.

Beech forests have a broad, almost pan-European, distribution (Meusel *et al.* 1965, 1978; Meusel & Jäger 1992). Numerous investigations in the Nordic countries (Diekmann *et al.* 1999), central and western parts of Europe (Ellenberg 1986; Dierschke 1990, 1997; Müller 1992; Matuszkiewicz 1993), the Apennines (Pignatti 1998), and the Balkans (Soó 1964; Horvat *et al.* 1974; Török *et al.* 1989; Dzwonko *et al.* 1999; Dzwonko & Loster 2000) have resulted in accumulation of knowledge for a detailed syntaxonomy of European beech forests. These forests are traditionally grouped into the following geographic alliances: *Scillo lilio hyacinthae-Fagion* Br.-Bl. 1967 (beech forests of the Pyrenees and northern Spain); *Endymio non scriptae-Fagion* Dierschke 1989 (Atlantic beech forests of northwestern France and England);

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Aremonio-Fagion (Horvat 1938) Török, Podani *et* Borhidi 1989 (Illyrian beech forests of Southeast Europe); *Symphyto cordatae-Fagion* (Vida 1963) Täuber 1982 (beech forests of the Carpathians); *Lonicero alpigenae-Fagion* Oberd. et Müller 1984 (pre-Alpine beech forests of southern Germany and adjacent areas); *Galio (Asperulo) odorati Fagion* Tx.1955 (beech forests of Central Europe); *Geranio striati-Fagion* Gentile 1969 (beech forests of southern Italy); and *Doronico orientalis-Fagion moesiacae* Raus 1980 (beech forests of southern Serbia, Macedonia, Albania, and Greece). The species-poor beech forests in habitats with acid and nutrient-poor soil belong to the alliance *Luzulo luzuloidis-Fagion sylvaticae* W. Lohmeyer & Tüxen in Tüxen 1954.

Serbian beech forests were investigated by the authors of numerous articles (complete references of the articles are given in Kojić *et al.* 1998; Lakušić 2005; and Tomić 2006). The principal aims of the present research were to detect variability patterns and biodiversity components in the shady deciduous forests of Serbia.

MATERIAL AND METHODS

Relevés of beech forests were collected from all regions of Serbia. Combined cover-abundance values of Braun-Blanquet's (Braun-Blanquet 1965) alpha-numeric scale were replaced by nine-degree numeric values (Westhoff & van der Maarel 1973). The taxonomic nomenclature was harmonised with the Plant List Database, which gives the accepted Latin name for vascular plants and bryophytes (http://www.theplantlist.org).

The K-means (MacQueen 1967) clustering procedure was used to obtain maximally homogeneous clusters of relevés. Diagnostic species of each cluster were determined by calculating the fidelity of each species to each cluster, using the f coefficient of association (Chytrý *et al.* 2002). The phi coefficient is closely related to the chi square statistic and to the Pearson correlation coefficient (Sokal & Rohlf 1995; Karadžić & Marinković 2009).

The ecological response of diagnostic species to environmental gradients was assessed using the Gaussian logistic regression (Ter Braak 1985; James *et al.* 2013).

Differentiation of communities with respect to environmental variables was assessed using canonical correspondence analysis (Ter Braak 1986). Environmental variables included directly measured topographic paremeters and a set of variables (temperature, moisture, light intensity, soil acidity) that were assessed indirecly, using the weighted average of ecological indicator values (Kojić *et al.* 1997). Topographic parameters included altitude, slope, and aspect. A simple procedure was applied for conversion of nominal to numerical aspect values (Fig. 1). To detect the statistical significance of explanatory variables, forward selection of environmental variables was performed. At each partial regression step, the variable that adds most to the explained variance in data is selected and statistical significance of the hypothesis that the selected variable is unrelated to vegetation was tested by means of the Monte Carlo permutation test using 5000 permutations.

Alpha diversity was assessed using two parameters, viz., species richness and Shannon's index

$$H_{(p)} = -\sum_{i=1}^{N} p_i \log p_i,$$

where p_i is the proportion of species *i* within a particular site, and N denotes the number of species within the site.

All statistical analyses were performed using the "FLORA" software package (Karadžić 2013). The newest version of this package is the culmination of a programming project that has been running continuously since 1998 (Karadžić *et al.* 1998, 1999, 2003; Karadžić & Marinković 2009).

Nomenclatural revision of particular vegetation units was done according to the rules of the International Code of Phytosociological Nomenclature (ICPN; Weber *et al.* 2000).

RESULTS AND DISCUSSION

Distribution of shady deciduous forests in Serbia. Zonal vegetation in Serbia reflects regional climatic conditions. The lowlands (the Pannonian plain and the Danube, Morava, and Sava valleys) have a (semi)arid climate (either a 'Csa"or a 'Cfa" climate, *sensu* Kottek *et al.* 2006). Besides heterogeneous agricultural areas, this region is covered by forests of the alliance *Aceri tatarici-Quercion* Zólyomi et Jakucs 1957 (Čarni *et al.* 2009), by riparian forests along the large rivers (Karadžić *et al.* 2015), and by fragments of halophytic vegetation (*Thero-Salicornietea* Pignatti 1953 *emend.* R. Tx. 1955), steppe vegetation (*Festuco-Puccinellietea* Soó 1968), and psammophytic vegetation (*Festucetea vaginatae* Soó 1968 *emend.* Vicherek 1972).

The hilly regions (between 300 and 500 m) are more humid, but also very dry, especially in eastern Serbia. This climate zone is covered by oak forests (the xeric alliance *Quercion confertae* Horvat 1954 and more mesic alliance *Quercion petraeae-cerris* Čarni *et al.* 2009). The mountain region (between 500 and 1000 m) is characterised by a humid period during all seasons, with at least four months averaging above 10°C (moderate 'Cfb" climate). Mesic beech forests on moist soil dominate within this climate zone. Coniferous forests dominate in the altimontane habitats (between 1000 and 1500 m) with microthermal boreal climate (Köppen's 'Dfb", 'Dfc", and 'Dsb" climates). Finally, herbaceous vegetation (classes *Juncetea trifidi* Hadač 1944, *Elyno-Seslerietea* BR.-BL. 1948 = *Festuco-Seslerietea* Barbero *et* Bonim 1969 and *Betulo-Adenostyletea* Br.-Bl. et R. Tx. 1943) dominates within the (sub)alpine zone with tundra climate (Köppen's "ET climate"). The upper limits of vegetation zones increase with decreasing latitude (Pianka 1983; Stupar & Čarni 2016).

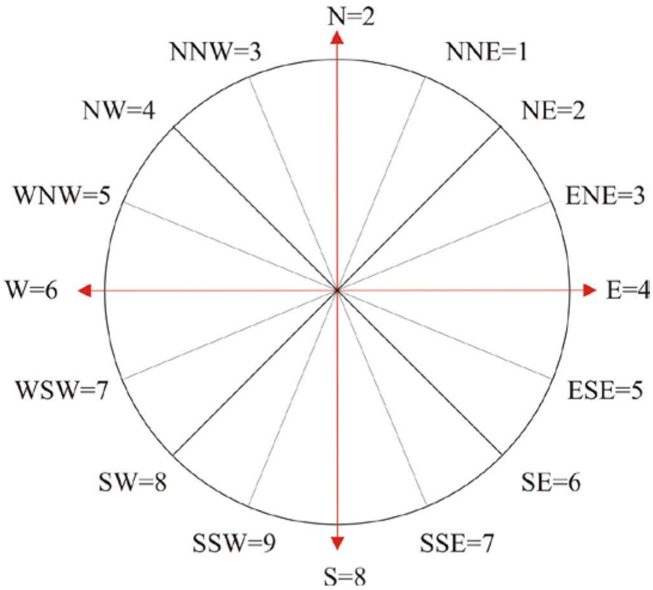

Fig. 1. Conversion of nominal to numerical aspect values was performed using a modified version of the Goldsmith insolation index (1973).

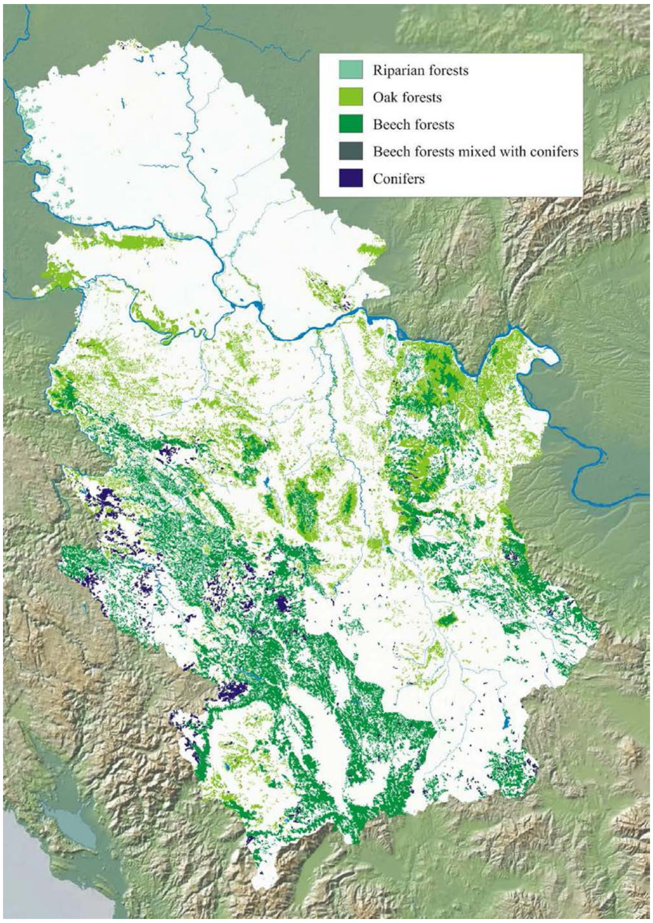

Fig. 2. Forest vegetation in Serbia.

A detailed map of the distribution of forest vegetation in Serbia is presented in Fig. 2. The map was obtained using both the CORINE (coordination of information on the environment) LandCover database and additional information sources. The LandCover Project was part of the CORINE programme, implemented by the European Commission from 1985 onwards (Moss *et al.* 1996). The processing of satellite imagery assures that the CORINE LandCover database exactly and very precisely detects the main land cover classes (artificial surface, agricultural areas, forests and semi-natural areas, wetlands, and water bodies). These five land cover classes are divided into subclasses. For example, forest vegetation is divided into three main groups, viz., broadleaved forests, coniferous forests, and mixed forests. However, such categorisation of forest ecosystems is too rough. To overcome this problem, the CORINE LandCover database was combined with other sources of information from vegetation maps of Serbia (Jovanović *et al.* 1986; Matvejev & Puncer 1989). The combined map indicates that beech frests dominate in mountainous regions. At higher altitudes, *Fagus sylvatica* L. codominates in mixed forests with the conifers *Abies alba* Mill. and/or *Picea abies* (L.) H.Karst., as well with the endemo-relic pines *Pinus heldreichii* H. Christ. and *Pinus peuce* Griseb. in Kosovo.

Numerical classification. The K-means clustering of beech forests in Serbia resulted in seven clusters. For each cluster a set of diagnostic species was detected using the phi coefficient (Table 1). The first cluster is defined by the diagnostic species *Tilia tomentosa* Moench, *Tilia cordata* Mill., *Quercus pubescens* Willd., *Ulmus glabra* Huds., *Ligustrum vulgare* L., and *Lonicera caprifolium* L. (in the tree and scrub layers); and *Ruscus hypoglossum* L., *Asperula taurina* L., *Carex pilosa* Scop., *Galanthus nivalis* L., *Asarum europaeum* L., *Lathyrus niger* (L.) Bernh., *Festuca drymeja* Mert. & W.D.J.Koch, and *Alliaria petiolata* (M.Bieb.) Cavara & Grande (in the herbaceous layer). The relevés from this group appear on the edge of the Panonnian basin. Submontane beech forests are widely distributed in the peri-Panonnian low mountains. Tomić (2006) assumed that these forests belong to the suballiance *Helleboro odori Fagenion moesiacae* Borhidi 1960. Such nomenclature is questionable, however, since *Heleborus odorus* L. is not a diagnostic species for these forests (Table 1). Marinšek *et al.* (2013) included the peri-Panonnian beech forests in the suballiance *Tilio tomentose-Fagenion sylvaticae* of the alliance *Aremonio-Fagion* (Horvat 1950) Borhidi in Török *et al.* 1989 (formerly *Fagion illyricum*). Since the range of peri-Panonnian lime-beech forests extends significantly into the Illyrian province, it is proper to extract these forests into a separate alliance, namely *Tilio tomentose Fagion sylvaticae* (Marinšek, Čarni et Šilc 2013) al. nova.

The dominant trees and shrubs in the second cluster are *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Rhamnus catharticus* L., *Rhamnus fallax* Boiss., *Euonymus verru-*

cosus Scop., *Quercus pubescens* Willd., *Tilia platyphyllos* Scop., *Juglans regia* L., and *Quercus frainetto* Ten. Diagnostic species in the layer of herbaceous plants are *Galium pseudoaristatum* Schur, *Teucrium chamaedrys* L., *Primula vulgaris* Huds., *Juniperus communis* L., *Asplenium scolopendrium* L., *Arabis turrita* L., *Carex pairae* F.W.Schultz, *Galium pumilum* Murray, *Clinopodium nepeta* (L.) Kuntze, *Melitis mellissophyllum* L., *Euphorbia fragifera* Jan., *Asplenium adiantum-nigrum* L., *Cephalanthera damasonium* (Mill.) Druce, *Ceterach officinarum* Willd., *Viola alba* Besser, *Silene nutans* L., *Sesleria varia* Jacq., *Viola hirta* L., *Carex flacca* Schreb., *Digitalis laevigata* Waldst. & Kit., and *Arabis procurrens* Waldst. & Kit. Ravine beech and black hornbeam communities are distributed in canyons and gorges of western Serbia, where they occur on shallow skeletal soil of colluvial deposits and screes (Pavlović *et al.* 2017). These forests belong to the alliance *Ostryo carpinifoliae Fagion sylvaticae* Borhidi, 1963.

Cluster 3 is comprised of species-poor relevés. The dominant plants in these communities are *Fagus sylvatica* L., *Carpinus betulus* L., *Quercus petraea* (Matt.) Liebl, *Luzula luzuloides* (Lam.) Dandy & Wilmott, *Hieracium murorum* L., *Veronica officinalis* L., *Hieracium pilosella* L., *Luzula campestris* (L.) DC., and the mosses *Leucobryum glaucum* (Hedw.) Ångström and *Polytrichum commune* Hedw. Floristically impoverished acidophilous beech forests (*Luzulo luzuloidis-Fagion sylvaticae* Lohmeyer et Tx. in Tx. 1954) occur in Serbia on silicate acidic soils, from the montane belt to the altimontane belt.

The alliance *Galio (Asperulo) odorati Fagion* Tx. 1955 consists of Central European beech forests on neutral (or weakly acidic) and nutrient-rich soils. In Serbia, these forests occupy mountainous areas. Diagnostic species of these forests are *Scilla bifolia* L., *Corydalis cava* (L.) Koerte, *Corydalis solida* (L.) Clairv., *Cardamine bulbifera* (L.) Crantz, *Allium ursinum* L., *Arum maculatum* L., *Anemone nemorosa* L., *Anemone ranunculoides* L., *Circaea lutetiana* L., *Carex sylvatica* Huds., *Galium odoratum* (L.) Scop. (=*Asperula odorata* L.), *Athyrium filix femina* (L,) Roth., *Carex pendula* Huds., *Viola reichenbachiana* Jord. ex Boreau, *Lamium galeobdolon* (L.) Crantz, *Impatiens noli tangere* L., *Mycelis muralis* (L.) Rchb., *Salvia glutinosa* L., *Scrophularia nodosa* L., etc.

Forests of *Corylus colurna* L. and *Fagus sylvatica* L. occupy ravine habitats in eastern Serbia, from 700 to 1200 m a.s.l. These forests are included in the alliance *Fago-Colurnion colurnae* Borhidi 1964. Diagnostic species of the alliance are *Corylus colurna* L., *Fraxinus excelsior* L., *Sorbus aucuparia* L., *Spiraea chamaedryfolia* L., *Rosa arvensis* Huds., *Prunus spinosa* L., *Acer hyrcanum* Fisch. et C. A. Mey. subsp. *intermedium* (Pančić) Palam., *Rubus idaeus* L., *Euonymus europaeus* L., and *Acer heldreichii* Orph. ex Boiss. Syntaxonomic relationships of these forests with the ravine forests in Macedonia, dominated by *Corylus colurna* (Matevski *et al.* 2011), should be analysed. The alliances *Fago-Colurnion colurnae* Borhidi 1964 and *Ostryo carpinifoliae-Fagion sylvaticae* are geographically vicariant.

Mixed forests of beech and conifers (alliance *Abieto albae Fagion sylvaticae* Moor, 1952) occur in altimontane regions. The dominant species of these forests are *Fagus sylvatica* L., *Abies alba* Mill., *Sorbus aucuparia* L., *Rosa pendulina, Sorbus austriaca* (Beck) Hedl., *Picea abies* (L.) H.Karst., *Daphne blagayana* Freyer, *Symphytum tuberosum* L., *Senecio jackobaea*, *Trifolium pignantii* Fauche & Chaub., *Asplenium serpentini* Tausch, *Rubus idaeus* L., *Sambucus racemosa* L., *Laserpitium krapffii* Crantz, *Oxalis acetosella* L., *Vaccinium myrtillus* L., *Galium rotundifolium* L., *Senecio ovatus* Willd., *Aruncus dioicus* (Walter) Fernald, *Campanula patula* L., *Inula conyza* (Griess) DC., *Thymus praecox* subsp. *jankae* (Celak.) Jalas, *Luzula sylvatica* (Huds.) Gaudin, *Polygonatum verticillatum* (L.) All., *Asplenium adulterinum* Milde, *Alyssum markgrafii* O. E. Schulz, *Senecio squalidus* L., *Prenanthes purpurea* L., *Silene dioica* (L.) Clairv., and *Gentiana asclepiadea* L. Although mixed forests of beech and conifers occupy significant area in Central and Southern Europe, only a few authors extracted these forests into separate alliances (Moor 1952; Ellenberg & Klötzli 1972; Jovanović & Jovanović-Dunjić 1976).

The uppermost beech forests form a transitional zone with vegetation above the tree line. These forests have a large proportion of species that belong to subalpine tall herbaceous and deciduous shrub communities (the vegetation class *Mulgedio Acconitetea* Hadač et Klika *in* Klika et Hadač 1944). Diagnostic species of this cluster are *Sorbus mougeotii* Soy.-Will. & Godr., *Salix silesiaca* Willd., *Lonicera alpigena* L., *Actaea spicata* L., *Galium intermedium* Schult., *Rosa alpina* Ledeb., *Daphne mezereum* L., *Chaerophyllum aureum* L., *Calamagrostis arundinacea* (L.) Roth, *Festuca varia* Haenke, *Senecio procerus* (Griseb.) Vel., *Aquilegia vulgaris* L., *Hypericum umbellatum* A. Kern., *Campanula rotundifolia* L., *Valeriana montana* L., *Rubus saxatilis* L., *Primula veris* L., *Doronicum columnae* Ten., *Aconitum lycoctonum* L., *Thalictrum aquilegifolium* L., *Erysimum sylvestre* (Crantz) Scop., *Seseli rigidum* W. et K., and *Cytisus hirsutus* L. On the basis of its diagnostic species and according to the International Code of Phytosociological Nomenclature, communities of the cluster are included in the alliance *Calamagrostio arundinaceae Fagion sylvaticae* all. nova.

Results of logistic regression (Fig. 3) indicate that key diagnostic species of the alliances are well separated along the elevation gradient.

Environmental conditions. The altitudinal gradient creates varied climates, promoting diversification of plant communities (Whittaker 1972; Pianka 1983). Different alliances gradually replace each other along the altitudinal gradient (Fig. 4). The lowermost communities belong to the alliance *Tilio tomentosae-Fagion sylvaticae*, while the uppermost ones belong to the subalpine alliance *Calamagostrio arundi-*

Table 1. Synoptic table of Serbian beech forests.

Trees and shrubs	Alliances						
	1	2	3	4	5	6	7
Tilia tomentosa Moench	61	-	-	-	-	-	-
Acer campestre L.	33	9	-	-	-	-	-
Tilia cordata Mill.	32	-	-	-	-	-	-
Ulmus glabra Huds.	25	13	-	-	9	-	-
Ligustrum vulgare L.	17	-	-	-	-	-	-
Lonicera carpinifolia L.	12	-	-	-	-	-	-
Ostrya carpinifolia Scop.	6	83	-	-	9	-	-
Fraxinus ornus L.	-	52	-	1	20	-	-
Rhamnus catharticus L.	-	52	-	-	-	-	-
Rhamnus fallax Boiss.	-	26	-	-	-	-	-
Euonymus verrucosus Scop.	-	25	-	-	-	-	-
Quercus pubescens Willd.	-	25	-	-	-	-	-
Tilia platyphyllos Scop.	8	28	-	-	-	-	-
Juglans regia L.	9	21	-	-	18		
Quercus frainetto Ten.	-	25					
Carpinus betulus L.	6	-	26	-	25	-	-
Quercus petraea (Matt.) Liebl.	-	-	23	8	20		
Ulmus minor Mill.	-	-	-	34	-	-	-
Acer pseudoplatanus L.	9	-	-	43	9	-	21
Salix caprea L.	-	-	-	52	-	-	-
Corylus avellana L.	-	-	3	22	26	-	-
Prunus avium (L.) L.	18	-	-	31	-	-	-
Crataegus monogyna Jacq.	-	19	-	28	10	-	-
Acer platanoides L.	12	14	-	30	-	-	-
Sorbus aria (L.) Crantz	-	8	-	-	50	-	-
Corylus colurna L.	-	-	-	-	80	-	-
Fraxinus excelsior L.	24	-	-	-	56	-	-
Sorbus aucuparia L.	-	-	-	-	26	-	25
Spiraea chamaedryfolia L.	-	-	-	-	70	-	-
Rosa arvensis Huds.	-	-	-	-	62	-	-
Prunus spinosa L.	-	-	-	-	44	-	-
Acer hyrcanum subsp. *intermedium* (Pančić) Palam.	-	-	3	-	81	-	-
Rubus idaeus L	-	-	-	-	40	10	-
Euonymus europaeus L.	-	-	-	1	46	-	-
Syringa vulgaris L.	-	-	-	-	31	-	-
Abies alba Mill.	-	-	-	15	-	78	-

Trees and shrubs	Alliances						
	1	2	3	4	5	6	7
Sorbus aucuparia L.	-	-	-	-	-	57	25
Rosa pendulina	-	-	-	-	-	49	-
Sorbus austriaca (Beck) Hedl.	-	-	-	-	-	31	-
Picea abies (L.) H.Karst.	-	-	-	-	-	37	19
Sorbus mougeotii Soy.-Will. & Godr.	-	-	-	-	-	-	70
Salix silesiaca Willd.	-	-	-	-	-	-	45
Lonicera alpigena L.	-	-	-	-	-	-	49
Herbaceous plants							
Ruscus hypoglossum L.	54	-	-	4	-	-	-
Carex pilosa Scop.	46	-	-	-	-	-	-
Festuca drymeja Mert. & W.D.J.Koch	31	-	-	-	-	15	-
Lathyrus vernus (L.) Bernh.	21	35	-	-	4	-	-
Alliaria petiolata (M.Bieb.) Cavara & Grande	21	9	-	-	-	-	-
Galanthus nivalis L.	27	-	-	-	-	-	-
Lathyrus niger (L.) Bernh.	17	-	-	-	-	-	-
Galium pseudoaristatum Schur	-	42	-	-	-	-	-
Teucrium chamaedrys L.	-	45	-	-	-	-	-
Primula vulgaris Huds.	-	47	-	-	-	-	-
Juniperus communis L.	-	42	-	-	-	-	-
Asplenium scolopendrium L.	-	42	-	-	-	-	4
Arabis turrita L.	-	30	-	-	-	-	11
Carex pairae F.W.Schultz	-	14	-	-	-	-	-
Galium pumilum Murray	-	14	-	-	-	-	-
Clinopodium nepeta (L.) Kuntze	-	25	-	-	-	-	-
Melitis mellissophyllum L.	9	32	-	-	-	-	-
Asplenium adiantum-nigrum L.	-	26	17	-	-	-	-
Cephalanthera damasonium (Mill.) Druce	-	25					
Ceterach officinarum Willd.	-	33					
Viola alba Besser	-	21					
Silene nutans L.	-	14					
Sesleria varia Jacq.	-	14					
Viola hirta L.	-	36					
Carex flacca Schreb.	-	25					
Digitalis laevigata Waldst. & Kit.	-	29					
Arabis procurrens W. et K.	-	25					
Luzula luzuloides (Lam.) Dandy & Wilmott	-	-	37	-	-	21	-
Hieracium murorum L.	-	-	37	1	-	-	-

Trees and shrubs	Alliances						
	1	2	3	4	5	6	7
Leucobryum glaucum (Hedw.) Ångström	-	-	17	-	-	-	-
Hieracium pilosella L.	-	-	18	17	-	-	-
Polytrichum commune Hedw.	-	-	32	20	-	-	-
Veronica officinalis L.	-	-	28	11	6	-	-
Luzula campestris (L.) DC.	-	-	17	-	-	-	-
Lamium galeobdolon (L.) Crantz	5	-	-	48	-	13	-
Arum maculatum L.	-	-	-	40	-	-	5
Carex sylvatica Huds.	4	-	-	46	-	-	-
Galium rotundifolium L.	-	-	0	48	-	-	-
Cardamine bulbifera (L.) Crantz	-	-	-	53	-	-	5
Neottia nidus-avis (L.) Rich.	-	-	-	43	-	4	-
Stellaria nemorum L.	-	-	-	42	-	-	-
Galium odoratum (L.) Scop.	14	-	-	33	-	12	9
Anemone nemorosa L.	-	19	-	23	-	26	-
Carex pendula Huds.	-	-	-	39	-	-	-
Viola reichenbachiana Jord. ex Boreau	5	-	-	34	10	-	-
Impatiens noli tangere L.	-	-	-	33	-	-	-
Eupatorium cannabinum L.	-	-	-	34	-	-	-
Digitalis ferruginea L.	-	-	-	29	-	-	-
Allium ursinum L.	-	-	-	34	-	-	6
Corydalis solida (L.) Clairv.	-	5	-	36	-	-	-
Geranium sanguineum L.	-	-	-	-	54	-	-
Galium mollugo L.	-	-	-	-	54	-	-
Solidago virgaurea L.	-	8	-	-	50	-	-
Potentilla argentea L.	-	-	-	-	54	-	-
Torilis anthriscus (L.) C.C. Gmelin	-	-	-	-	76	-	-
Spiraea chamaedryfolia L.	-	-	-	-	54	-	-
Bromus sterilis L.	-	-	-	-	44	-	-
Astragalus glycyphyllos L.	-	3	-	-	46	-	-
Heracleum spondylium L.	-	-	-	-	54	-	-
Geranium macrorrhizum L.	-	-	-	-	33	-	32
Daphne blagayana Freyer	-	-	-	-	-	49	-
Symphytum tuberosum L.	-	-	-	-	8	45	21
Senecio jackobaea L.	-	-	-	-	-	54	-
Trifolium pignantii Fauche & Chaub.	-	-	-	-	-	49	-
Asplenium serpentini Tausch	-	-	-	-	-	54	-
Rubus idaeus L.	-	-	-	-	16	50	28

Trees and shrubs	Alliances						
	1	2	3	4	5	6	7
Sambucus racemose L.	-	-	-	-	-	54	-
Laserpitium krapffii Crantz	-	-	-	-	-	44	-
Oxalis acetosella L.	-	-	-	3	-	61	-
Vaccinium myrtillus L.	-	-	12	-	-	48	10
Galium rotundifolium L.	-	-	-	-	-	38	-
Senecio ovatus Willd.	-	-	-	-	-	31	-
Aruncus dioicus (Walter) Fernald	-	-	-	-	-	31	-
Campanula patula L.	-	-	7	-	-	23	6
Inula conyza (Griess) DC.	-	-	-	-	-	31	-
Thymus praecox subsp. *jankae* (Celak.) Jalas	-	-	-	-	-	31	-
Polygonatum verticillatum (L.) All.	-	-	-	-	8	28	19
Asplenium adulterinum Milde	-	-	-	-	-	38	-
Alyssum markgrafii O. E. Schulz	-	-	-	-	-	31	-
Senecio squalidus L.	-	-	11	-	-	16	-
Prenanthes purpurea L.	-	-	4	-	12	33	4
Silene dioica (L.) Clairv.	-	-	-	-	-	31	-
Gentiana asclepiadea L.	-	-	-	-	-	35	22
Actaea spicata L.	-	-	-	-	-	-	61
Galium intermedium Schult.	-	13	2	-	-	-	42
Daphne mezereum L.	-	-	-	-	13	5	46
Chaerophyllum aureum L.	-	-	-	-	-	-	53
Calamagrostis arundinacea (L.) Roth	-	-	-	-	-	-	40
Festuca varia Haenke	-	-	-	-	-	-	45
Senecio procerus (Griseb.) Vel.	-	-	-	-	-	-	40
Aquilegia vulgaris L.	-	-	-	-	-	-	57
Hypericum umbellatum A. Kern.	-	-	-	-	-	-	64
Campanula rotundifolia L.	-	-	-	-	-	-	40
Valeriana montana L.	-	-	-	-	-	-	40
Rubus saxatilis L.	-	-	-	-	-	-	60
Primula veris L.	-	-	-	-	-	-	45
Doronicum columnae Ten.	-	-	-	-	-	-	49
Aconitum lycoctonum L.	-	-	-	-	-	-	28
Thalictrum aquilegifolium L.	-	-	-	-	-	-	34
Erysimum sylvestre (Crantz) Scop.	-	-	-	-	-	-	19
Seseli rigidum W. et K.	-	5	-	-	-	-	22
Cytisus hirsutus L.	-	2	-	-	-	-	25

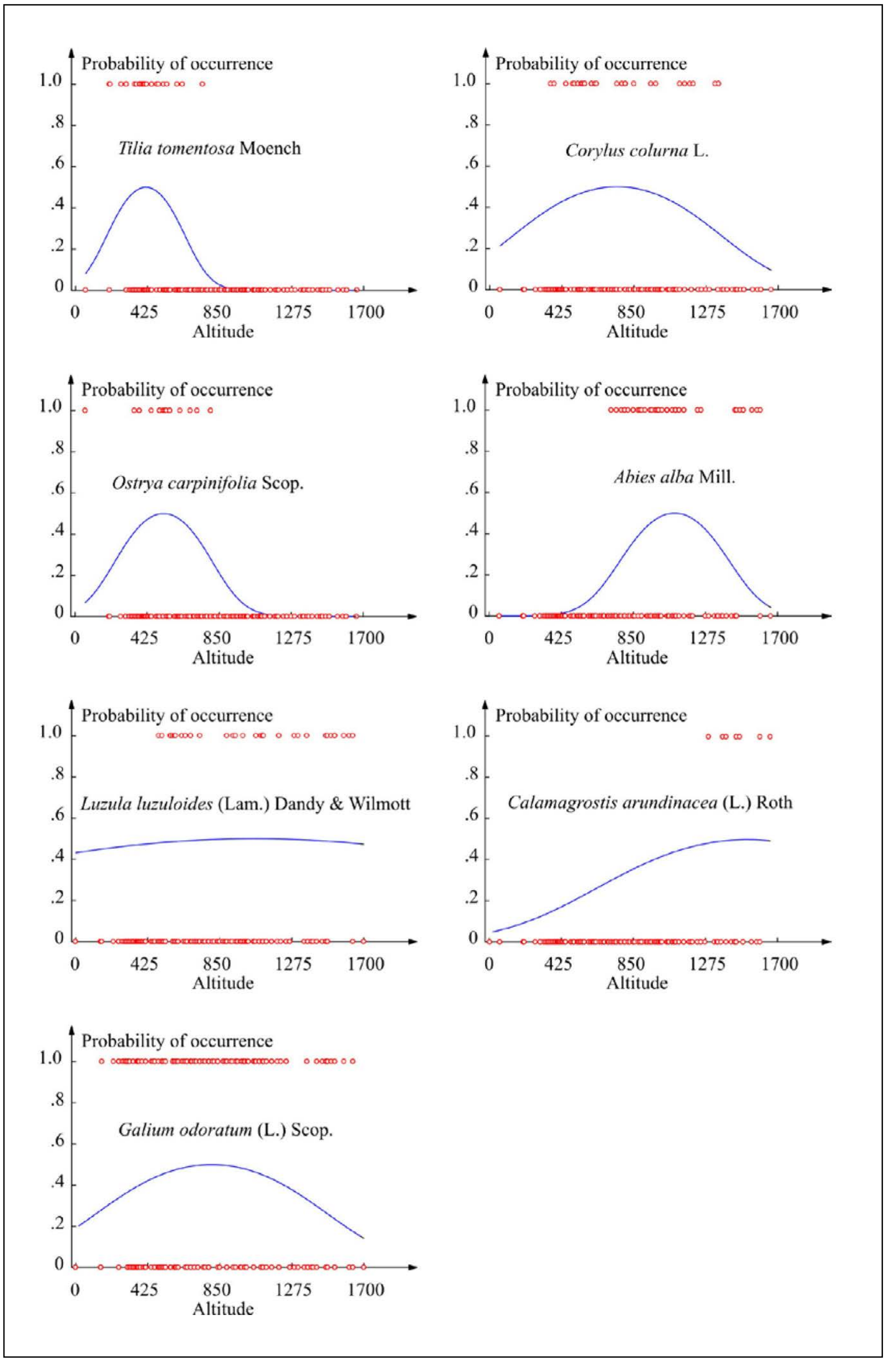

Fig. 3. Ecological response of diagnostic species for different alliances of beech forests in Serbia along the altitudinal gradient. Circles denote either the presence (1) or absence (0) of a species at a particular site. Response functions specify the probability of occurrence of taxa along the gradient.

naceae-Fagion sylvaticae. Communities belonging to the alliance *Luzulo luzuloidis-Fagion sylvaticae* have the widest altitudinal range and are distributed from the lowermost to the uppermost sites. Ravine communities of the alliances *Fago sylvaticae-Columnion colurnae* and *Ostryo carpinifoliae-Fagion sylvaticae* occupy the steepest habitats.

The altitudinal gradient is the main factor affecting diversification of the investigated forests. This is an expected result, since several environmental factors change predictably with increasing altitude. Changes of environmental variables in beech communities along the altitudinal gradient are presented in Fig. 5.

Temperature is the factor most closely associated with altitude. The thermal lapse (decrease in temperature with increase of altitude) in Serbia is approximately 0.53°C per 100 m (Milovanović 2010). Light intensity sharply decreases in beech forests mixed with spruce (*Picea abies* (L.) H.Karst.). Other factors (moisture, the soil reaction, and availability of soil nitrogen) are poorly correlated with altitude.

Effects of environmental variables on floristic differentiation of the analysed forests were detected using canonical correspondence analysis (CCA). The canonical ordination axes correspond to the directions of greatest

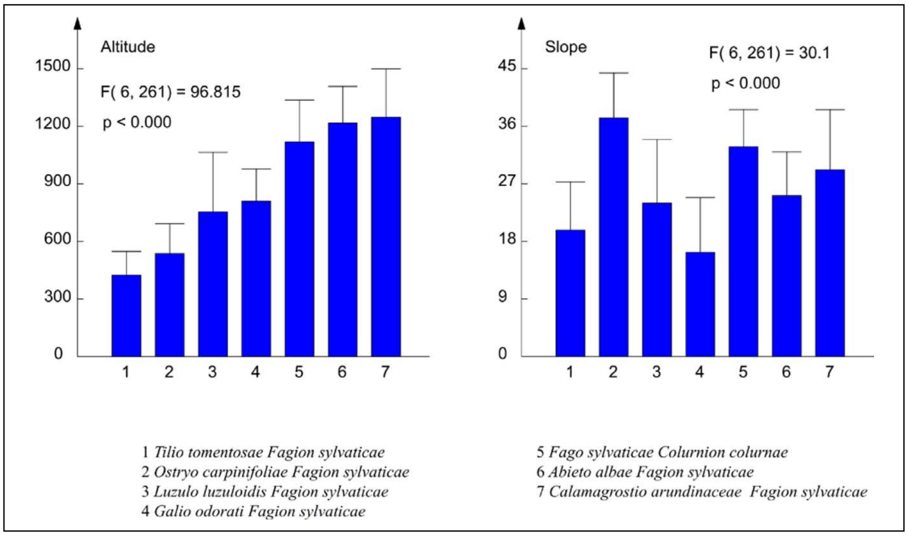

Fig. 4. Differentiation of beech alliances with respect to topographic variables.

variability of the data set that can be explained by environmental variables. The altitudinal gradient clearly separates the thermophilous alliances *Tilio tomentosae-Fagion sylvaticae* and *Ostryo carpinifoliae-Fagion sylvaticae* from the altimontane and subalpine alliances *Abieto albae-Fagion sylvaticae* and *Calamagrostio arundinaceae-Fagion sylvaticae*. The temperature gradient is inversely correlated with altitude (Fig. 6). As was indicated above, moisture, the soil reaction (soil acidity), and availability of soil nitrogen are poorly correlated with altitude. However, these factors are well correlated with slope. Moisture decreases with increasing inclination of the slope. Due to the sparse distribution of *Fagus sylvatica* (and other trees), steep slope habitats are much drier than planar habitats, where the presence of a dense tree canopy forms conditions of a moist microclimate. Contrary to steep slope habitats, where skeletal soil is poorly developed on scree and coluvial deposits, the soil in planar habitats has rich litter and horizons of humus accumulation. The availability of soil nitrogen is therefore much greater in planar than in steep slope habitats.

Canonical ordinations are explanatory techniques that make it possible to investigate species-environment relationships. The null hypothesis of species-environment independence was tested using the Monte Carlo permutation test. Results of the test indicate that the set of analysed environmental variables significantly affects floristic differentiation of Sebian beech forests ($F=3.63$, $p<0.000$). The partial effect of each of the analysed variables on the given forests is also statistically significant (Table 2).

Diversity of beech forests. Besides clear environmental distinctions, particular types of beech forests in Serbia differ with respect to diversity. Alpha diversity (within-community diversity) depends on species richness and equality of species abundances in a community (Whittaker 1972; Karadžić & Marinković 2009).

Compared to Central European forests, the beech forests in Serbia are more complex and more diverse. More than 50 different species were detected in tree and schrub strata of the analysed forests. Calculated for entire communities, both species richness and entropy are greatest in the ravine alliances *Ostryo carpinifoliae-Fagion sylvaticae* and *Fago sylvaticae-Colurnion colurnae*. Calculated for trees and shrubs only, species richness and entropy in these two alliances are significantly greater than in other alliances (Fig. 7). The lowest species richness and entropy were detected in acidophilous forests on nutrient-poor soils (communities of the alliance *Luzulo luzuloidis-Fagetalia sylvaticae* Scamoni et Passarge 1959).

Syntaxonomy. Beech-dominated forests on the Balkan Peninsula have traditionally been grouped into the regional alliances *Fagion illyricum* Horvat 1950, *Fagion moesiacum* Blečić et Lakušić 1970, *Fagion dacicum* Soó 1960, and *Fagion orientalis* Soó 1964. The names of these groups of forests were taken from former names of the ancient Roman provinces. *Fagion illyricum* (nomen invalidum) covers the beech forests in Slovenia, Croatia, Bosnia and Hezegovina, Montenegro, Albania, and Greece (Soó 1964; Horvat *et al.* 1974; Bergmeier & Dimopoulos 2001). *Fagion dacicum* (nomen invalidum) applies to beech forests in the Carpathian Mountains of Romania, southeastern Serbia, Bulgaria, and northern Greece (Borhidi 1964; Soó 1964). Moesian beech forests (*Fagion moesiacum* Fukarek 1969) are distributed in the area with a more continental climate in the eastern Balkans (eastern Serbia, Bulgaria). Finally, the alliance *Fagion orientalis* Soó 1964, which includes communities of *Fagus orientalis* Lipsky, occurs in southeastern Bulgaria, eastern Greece, the European part of Turkey, the Pontic mountains, and the Caucasus (Quézel *et al.* 1980, 1992; Tzonev *et al.* 2006; Kavgaci *et al.* 2012).

A relatively small number of *Fagetalia* species differentiate regional alliances. For example, *Cardamine waldsteinii* Dyer = *Dentaria trifolia* Waldst. et Kit. is characteristic

Table 2. The fact of selection of the listed explanatory variables indicates that the partial effect of each variable on floristic differentiation of the analysed forests is statistically significant.

Variable	Eigenvalue	F statistic	Probability
Temperature	.4408	9.047	.001
Moisture	.3382	6.887	.001
Soil acidity	.2511	5.079	.001
Altitude	.1948	3.924	.001
Soil nitrogen	.1628	3.271	.001
Light	.1500	3.011	.001
Slope	.1469	2.948	.001
Aspect	.0798	1.595	.001

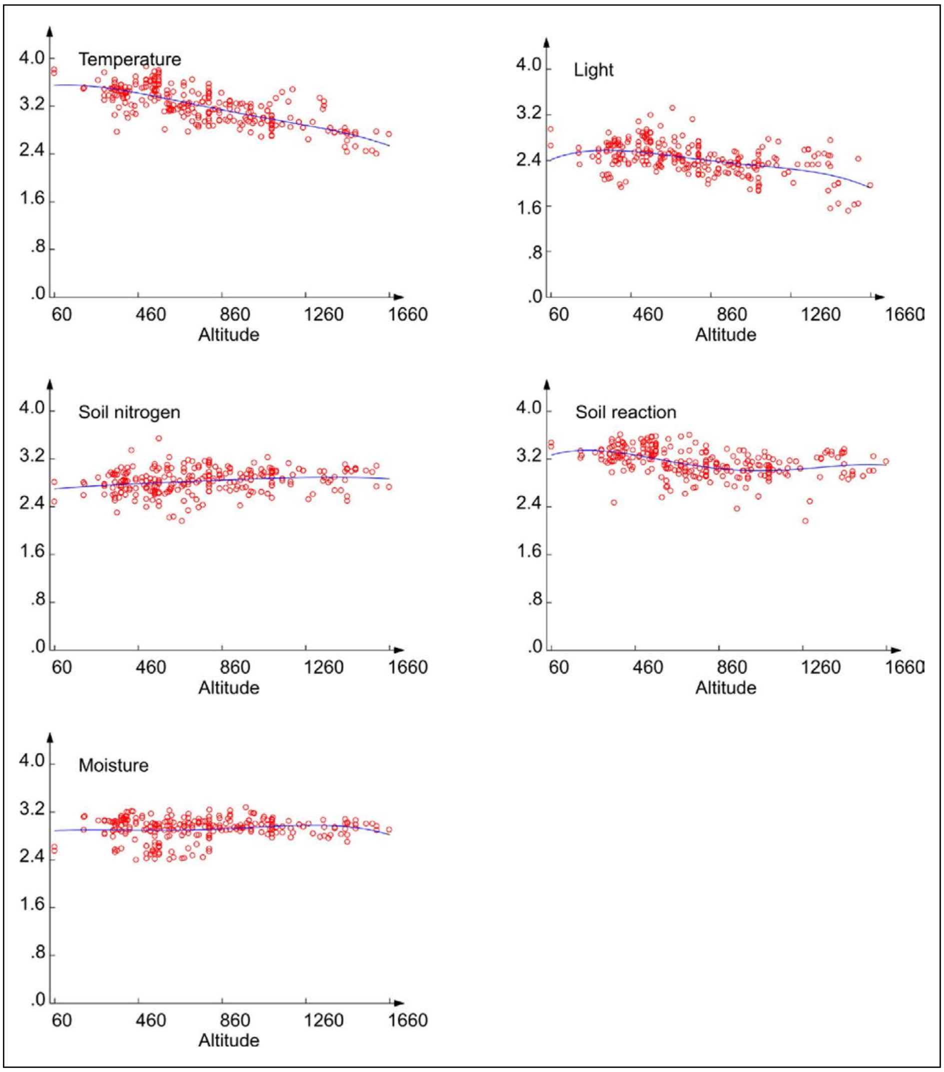

Fig. 5. Relationship between altitude and environmental conditions in beech forests.

of montane beech woods in the west-Balkan countries. The vicariant Dacio-Carpathian species *Cardamine glanduligera* O.Schwarz = *Dentaria glandulosa* Waldst. et Kit. is characteristic of eastern parts of Serbia, Romania, and Bulgaria (Fig. 8). However, due to similar environmental conditions (mesic habitats, disphotic stress), geographical variants of beech communities have similar and broadly overlapping floristic composition. The boundaries of regionally defined alliances of Balkan beech forests are arbitrary. Therefore, the validity of geographically based no-

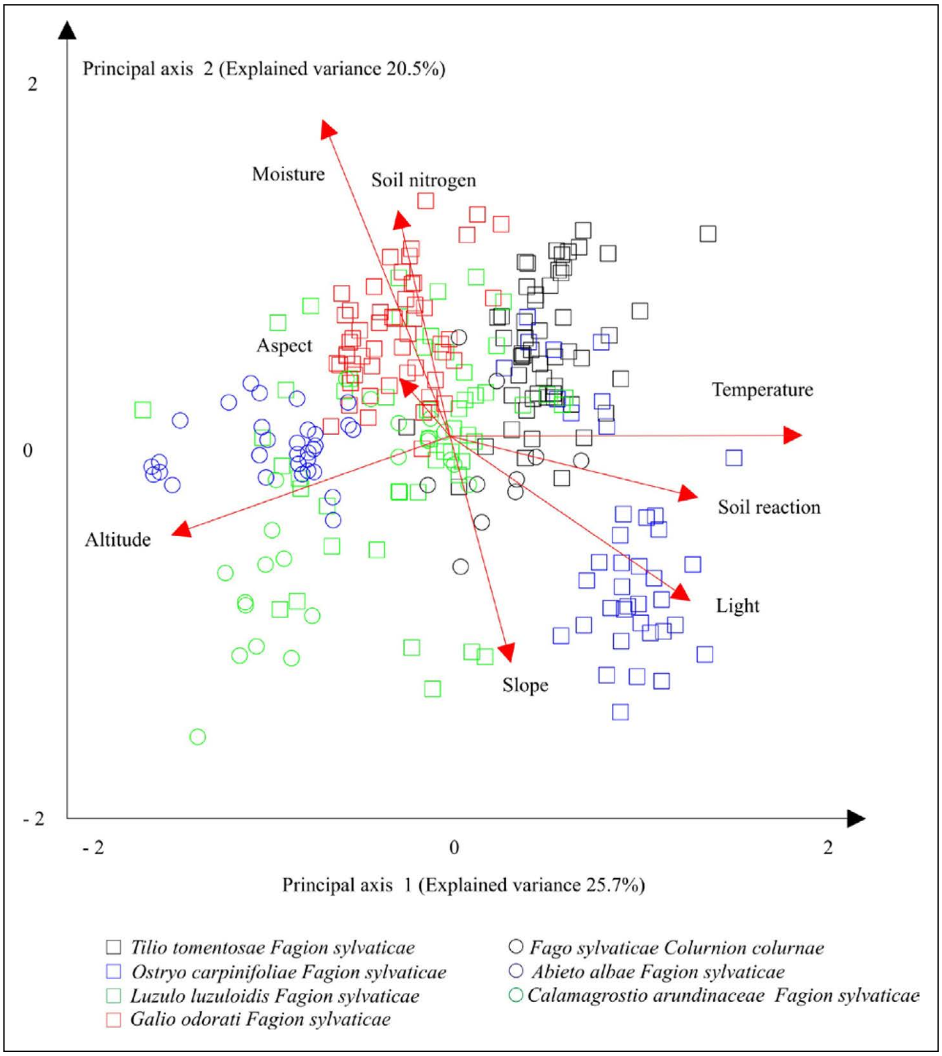

Fig. 6. Canonical correspondence analysis of beech foerests in Serbia.

menclature of these forests is questionable. Moreover, according to the ICPN (Weber *et al.* 2000), any geographical nomenclature of vegetation types is explicitly forbidden, since geographical epithets used for syntaxonomic names (if they do not belong to a name-giving taxon) contain no floristic information. Despite the fact that the nomenclature of regional alliances of Balkan beech forests is erroneous, the name of the alliance *Fagion moesiacae* is accepted by some authors, since the epithet *moesiacae* refers not to a geographical distribution, but rather to the name of Balkan beech [*Fagus moesiaca* (K. Maly) Czeczott].

Besides the problem with wrong use of nomenclature for regional alliances, another issue in coherent syntaxonomy of beech forests is linked with the nomenclature of higher syntaxa (vegetation orders and classes). Traditionally, these forests were included in the class *Querco-Fagetea* Br.-Bl. *et* Vlieg. 1937. More recent classification systems (Quézel *et al.* 1980; Chytrý 1997; Sanda *et al.* 2008, Mucina *et al.* 2016) divide oak and beech forests into two separate vegetation classes: the *xerothermic* woods of Southeast Europe (the class *Quercetea pubescentis* Doing-Kraft *ex* Scamoni & Passarge 1959); and forests that occupy *temperate* and *moist* habitats (the class *Carpino betuli-Fagetea sylvaticae* Passarge in Passarge and Hofmann 1968). In the present article, syntaxonomy of the analysed forests is harmonised with the most comprehensive description of European vegetation, namely that proposed by Mucina *et al.* (2016). Syntaxonomic relations of the analysed forests can be represented by the following system:

Vegetation class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968

- Vegetation order *Luzulo-Fagetalia sylvaticae* Scamoni et Passarge 1959
  - Alliance *Luzulo-Fagion sylvaticae* Lohmeyer et Tx. in Tx. 1954
- Vegetation order *Fagetalia sylvaticae* Pawłowski 1928
  - All. *Tilio tomentose-Fagion sylvaticae* (Marinšek, Čarni et Šilc 2013.) all. nova
  - All. *Ostryo carpinifoliae-Fagion sylvaticae* Borhidi, 1963
  - All. *Galio (Asperulo) odorati-Fagion* Tx.1955.
  - All. *Fago-Colurnion colurnae* Borhidi 1964

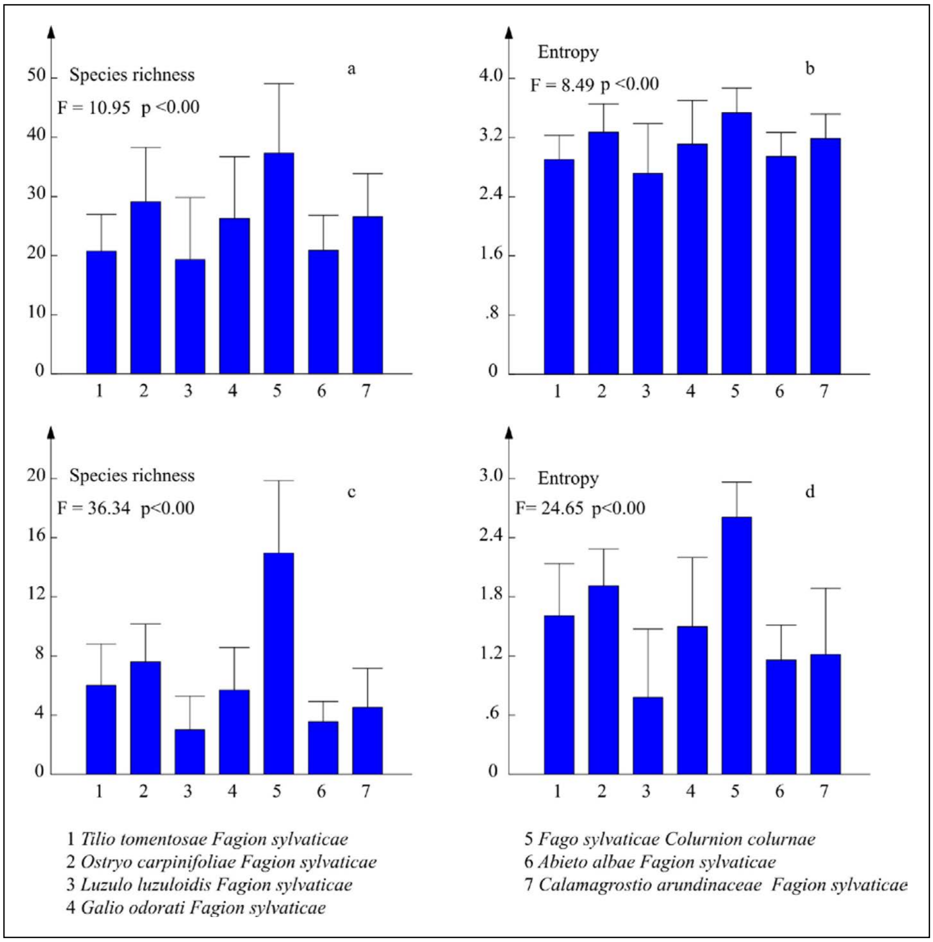

Fig. 7. Diversity components of beech forests in Serbia. Species richness and entropy are calculated for entire communities (a, b), as well for trees and shrub strata (c, d).

All. *Abieto albae-Fagion sylvaticae* Moor, 1952
All. *Calamagrostio arundinaceae-Fagion sylvaticae* all. nova

Mucina *et al.* (2016) included the basiphilous beech and mixed fir-beech forests in only three alliances: *Aremonio-Fagion* (Horvat 1950) Borhidi in Török *et al.* 1989 (refugial basiphilous beech and mixed fir-beech forests of the northwestern Balkans and eastern Alps); *Fagion sylvaticae* Luquet 1926 (partly refugial post-glacial basiphilous beech and mixed fir-beech forests of the temperate region of Europe); and *Geranio striati-Fagion* Gentile 1970 (refugial basiphilous beech and mixed fir-beech forests of southern Italy and the southwestern Balkans). Such a syntaxonomy, however, is open to question.

Peri-Panonnian submontane lime-beech forests are not solely confined to the Illyrian floristic province, but have a much wider distribution instead (Tzonev *et al.* 2006, 2009, this article). These forests should therefore not be included in the alliance *Aremonio-Fagion* (Horvat 1950) Borhidi in Török *et al.* 1989. It is more appropriate to extract these forests into a separate alliance, viz., *Tilio tomentose-Fagion sylvaticae* (Marinšek, Čarni et Šilc 2013) al. nova.

Mucina *et al.* (2016) included mixed forests of beech and European hop hornbeam (*Ostrya carpinifolia* Scop.) in the (non-ravine) suballiance *Ostryo-Fagenion* of the alliance *Aremonio-Fagion* (Horvat 1950) Borhidi in Török *et al.* 1989. The syntaxonomy of the ravine alliances *Ostryo carpinifoliae Fagion sylvaticae* Borhidi, 1963 and *Fago-Colurnion colurnae* Borhidi 1964 is a complex and yet unresolved issue, due to the ambiguous relationship of these forests with several ecologically different syntaxa (e.g., *Fagetalia sylvaticae* Pawłowski 1928, *Quercetalia pubescentis* Klika 1933, *Aceretalia pseudoplatani* Moor 1976, *Asplenietea trichomanis* Br.-Bl. in Meyer & Br.-Bl. 1934, and *Thlaspietea rotundifoliae* Br.-Bl. 1948). Some authors (Košir *et al.* 2008; Matevski *et al.* 2011; Mucina *et al.* 2016) include the Balkan ravine forests in the alliance *Tilio platyphylli-Acerion pseudoplatani* Klika 1955 of the order *Aceretalia pseudoplatani* Moor 1976. The high frequency, and in some cases almost exclusive dominance, of *Fagus sylvatica* and other "*Fagetalia*" species on bottoms and northern slopes of numerous canyons and gorges in central Balkan regions (Bosnia and Herzegovina, Montenegro, Serbia) cannot be ignored. These ravine forests should therefore be included in the order *Fagetalia sylvaticae* Pawłowski 1928 instead of the order *Aceretalia pseudoplatani* Moor 1976. Further syntaxonomic analyses of these forests are needed.

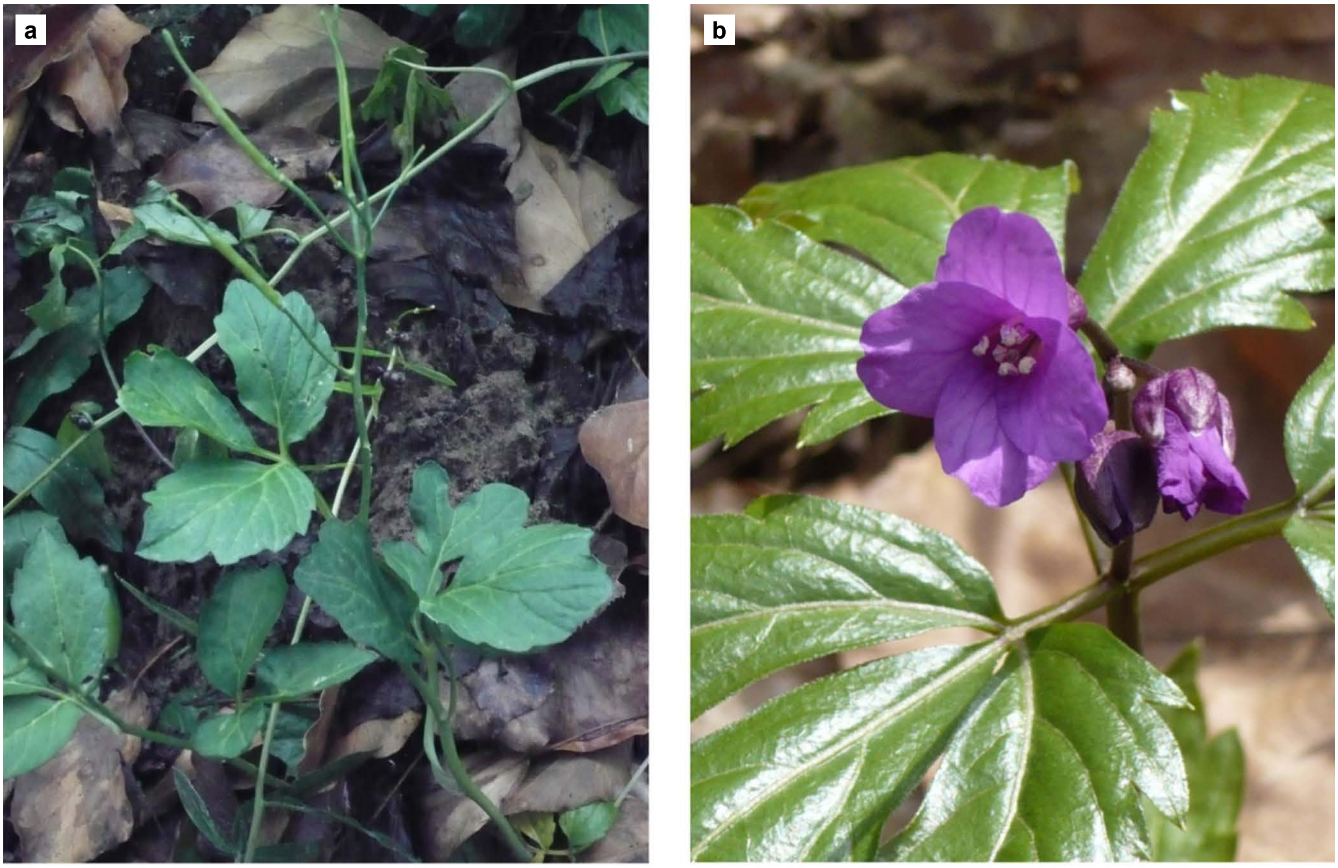

Fig. 8. The vicariant species *Cardamine waldsteinii* Dyer = *Dentaria trifolia* Waldst. & Kit. (a) and *Cardamine glanduligera* O. Schwarz = *Dentaria glandulosa* Waldst. & Kit. (b) differentiate west-Balkan and east-Balkan beech forests.

The alliance *Galio (Asperulo) odorati-Fagion* Tx. 1955 includes Central European beech forests on neutral (or weakly acidic) and nutrient-rich soils. This alliance corresponds to the alliance *Fagion sylvaticae* Luquet 1926 in Mucina *et al.* (2016).

Many authors disregard the alliance *Abieto albae-Fagion sylvaticae* Moor, 1952, and include mixed beech-fir forests in the alliance *Fagion sylvaticae* Luquet 1926. Such an approach is erroneous, since mixed beech-fir forests have a specific floristic composition that includes both *Fagetalia* and acidophylic *Vaccinio-Piceetalia* species. Serbian mixed beech-fir forests grow on silicate, carbonate, and serpentine soils (Pavlović *et al.* 2017). Diagnostic species of serpentinic variants of these forests (*Alyssum markgrafii* O. E. Schulz, *Daphne blagayana* Freyer, etc.) clearly separate Serbian from Central European beech-fir communities. The alliance *Abieto albae-Fagion sylvaticae* Moor, 1952, although ignored by many authors, should be accepted, since mixed beech-fir forests are ecologically and floristically clearly distinct from other types of beech-dominated forests.

Tomić (2006) included subalpine beech forests in the suballiance *Acero heldreichii - Fagenion = Fagion subalpinum* Jovanović 1976. The endemorelic species *Acer heldreichii* Orph. ex Boiss. codominates with beech in the subalpine forests *Aceri heldreichii–Fagetum* Jovanović 1957. In addition, it is a member of diverse mixed broadleaf–coniferous forest communities mainly dominated by beech and fir, beech, fir and spruce, spruce, Scots pine, and Balkan pine. Due to its ambiguous relationship with different vegetation types, *Acer heldreichii* is a poor diagnostic species. As fidelity coefficients indicate (Table 1), a more appropriate name for subalpine beech forests is *Calamagrostio arundinaceae-Fagion sylvaticae*. *Calamagrostis arundinacea* (L.) Roth with other taxa of the subalpine class *Mulgedio-Acconitetea* Hadač et Klika in Klika et Hadač 1944 dominate in herb-rich fir forests on limestone and dolomite boulder screes in subalpine belts of the maritime Dinaric mountains (*Calamagrostio-Abietion* Horvat 1962).

CONCLUSIONS

Detailed numerical analyses revealed seven ecologically interpretable alliances of beech forests in Serbia. The alliances gradually replace each other along the altitudinal gradient. The lowermost communities belong to the alliance *Tilio tomentosae-Fagion sylvaticae*. The uppermost communities belong to the subalpine alliance *Calamagrostio arundinacea-Fagion sylvaticae*.

Compared to Central European shady forests, beech forests in Serbia are more complex and more diverse. More than 50 different species have been detected in the tree and shrub strata of the analysed forests. Both species richness and entropy are greatest in the ravine alliances *Ostryo carpinifoliae - Fagion sylvaticae* and *Fago sylvaticae-Colurnion colurnae*.

Acknowledgements — This work was supported by the Ministry of Education, Science, and Technological Development of the Republic of Serbia (Grant No. 173018). I would like to thank two anonymous referees for valuable comments on the syntaxonomy of European beech forests.

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REZIME

Bukove šume (red *Fagetalia sylvaticae* Pawlowski 1928) u Srbiji

Branko Karadžić

U ovom radu su analizirane komponente biodiverziteta, kao i faktori koji utiču na varijabilnost bukovih šuma u Srbiji. Klasifikaciona analiza, koja je uradjena metodom K-proseka na setu podataka od 270 fitocenoloških snimaka i više od 500 vrsta, pokazala je da se bukove šime u Srbiji mogu grupisati u sedam ekološki i floristički jasno razgraničenih, varijanti. U radu je data sintaksonomska tabela sa dijagnostičkim vrstama svih sedam grupa bukovih zajednica. Rezultati kanonske korespondentne analize ukazuju da je visinski gradijent osnovni faktor diverzifikacije istraživanih zajednica. Bogatstvo vrstama i alfa diverzitet su najveći u bukovim zajednicama koje naseljavaju kanjonska staništa.

Ključne reči: Visinski gradijent, alfa diverzitet, kanonska korespondentna analiza, K-proseci, bogatstvo vrstama