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Geographical and ecological differentiation of *Fagus* forest vegetation in SE Europe

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Keywords
Balkans; Beech forest; Chorotypes; Classification; Gradients; Phytogeography; Plant traits; Syntaxonomy

Abbreviations
BF = beech forests; EIV = ecological indicator values; ICPN = International Code of Phytosociological Nomenclature (Weber et al. 2000)

Nomenclature
Flora Europaea (Tutin et al. 1964–1993); International Code of Phytosociological Nomenclature (Weber et al. 2000) .

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Abstract

Questions: What is the main syntaxonomical pattern within beech forests in SE Europe? What macroecological and ecological factors distinguish these forests?

Location: SE Europe: Balkan Peninsula, from the SE Alps in Slovenia, through Croatia, Bosnia and Herzegovina, Serbia, Montenegro and the Republic of Macedonia to N and NE Greece and Bulgaria, covering ca. 400 000 km^2 over a length of 1000 km.

Methods: With a view to differentiating beech and beech–fir forests, a data set of 5952 published and unpublished phytosociological relevés were surveyed. After stratification, 997 relevés remained. Cluster analysis of the data set was used to calculate diagnostic species for each cluster. Ecological indicator values (EIV) were used to estimate ecological conditions. Average EIV, altitude, latitude and longitude for relevés of each cluster were plotted in a detrended correspondence analysis (DCA) diagram for ecological interpretation of clusters and relationships between clusters. Correlations between DCA relevé scores and explanatory variables (EIV, portion of life forms and chorotypes, altitude, latitude and longitude) were subsequently calculated.

Results: Cluster analysis divided mesophilous beech forests of SE Europe into two major clusters. Beech forests can therefore be classified into two alliances, *Aremonio-Fagion* and *Fagion moesiacae*. Further division revealed seven beech and beech–fir forest types, which we interpreted geographically and ecologically. A significant increase in the proportion of chamaephytes, hemicryptophytes and therophytes was detected along the main macroecological gradient towards the S and E. At the same time, the proportion of geophytes and phanerophytes significantly decreased in the same direction. There was also a significant increase in the proportion of Stenomediterranean, Eurymediterranean, Mediterranean-Montane, and Eurasian species, while Boreal species, as expected, decreased toward the southeast. The main differentiation of beech forests in SE Europe is due to macroecological factors (macro-climatic and historical development of vegetation), whereas local ecological factors (particularly temperature and moisture) are reflected in the differentiation of sub-alliances.

Conclusions: Our study confirmed two major groups of beech forests in the research area, which could be classified into two alliances. It also revealed that there is not just an altitudinal distribution of beech forests in the SE part of the research area, but also structural and functional changes of communities as a result of the altitudinal limitation of beech forests and changed macroclimatic factors.

Introduction

Beech forests (BF) make up a remarkably high proportion of the European forest landscape (Bohn et al. 2004). In Central Europe, BF occupy various sites and have a wide altitudinal range, while in S Europe, within their range limit, they can only be found in humid mountain areas (Bergmeier & Dimopoulos 2001; Dierschke & Bohn 2004).

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In general, differences among *Fagus* forests are due to broad scale (historic, phytogeographic, macroclimatic and macroecological) and regional (edaphic, meso-climatic and ecological) factors (Bergmeier & Dimopoulos 2001). Soil ecology is usually considered to be the principal factor on a regional scale (Ellenberg 1996), while on a broader scale macroecological (geography and climate) differentiation has precedence (Dierschke 1990; Dierschke & Bohn 2004). Dierschke & Bohn (2004) proposed a differentiation of European BF into nine regional, geographically based alliances, with subsequent partition towards various sub-alliances, based on the combination and gradual disappearance of several groups of plant species, due to changed ecological factors.

Which factors should be considered more important for classification is an ongoing topic among syntaxonomists dealing with the classification of European *Fagus* forests (Soó 1964; Horvat et al. 1974; Török et al. 1989; Dierschke 1990; Dierschke & Bohn 2004). Willner (2002) and Tzonev et al. (2006) follow an approach based on ecological factors, while Dierschke (1990), Dierschke & Bohn (2004), Dzwonko & Loster (2000) and Bergmeier & Dimopoulos (2001) emphasize geographical differentiation. Various comparative studies suggest that classifications based on both ecological and geographical differentiation are generally more adequate than those that consider ecological or geographical differences alone (e.g. Dzwonko & Loster 2000).

The syntaxonomy of BF of the Balkans is far less clear than that in Central and Western Europe (Dzwonko & Loster 2000). A number of different classifications exist, mostly regional (Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001; Tzonev et al. 2006; Tsiripidis et al. 2007), as well as several check lists (Stefanović 1986; Marinček et al. 1992; Vukelić & Baričević 2002; Redžić 2007; Rexhepi 2007; Trinajstić 2008; Šilc & Čarni 2012), but without a synthesis over the whole area.

In earlier studies, BF of the investigated area were distinguished as regional alliances of *Fagus sylvatica* forests. Horvat (1938) mentioned the possibility of including forests from the SE Alps to Albania and Greece in the special genetic–geographic group called *Fagion sylvaticae illyricum*. Horvat (1950) later classified beech forests from Macedonia and Serbia into the *Fagion illyricum* alliance and pointed out their different floristic composition and smaller number of Illyrian elements in comparison with BF in the N Balkans (Slovenia and Croatia). BF of SE Serbia and Bulgaria were assigned by Soó (1963, 1964) to the *Fagion dacicum* alliance, although many diagnostic species of this alliance are not present in these areas. He designated them Moesian BF, with *Fagus moesiaca* as the differential species. Dafis (1973) used the name *Fagion moesiacae* to comprise Hellenic *Fagus* forests (today it is designated *Geranio versicoloris-Fagion)*, although the alliance *Fagion moesiacae* was considered valid in Blečić & Lakušić (1970) for Montenegro. Horvat et al. (1974) analysed some new data and described and validated the *Fagion moesiacum* alliance, distributed in the C and E Balkans, but they used an illegitimate name, as Fukarek (1969) had invalidly used the same name for the alliance even earlier – for acidophilous BF. They delineated the geographical range of the *Fagion moesiacum* alliance according to the range of the putative taxon *Fagus moesiaca*. This opinion was largely accepted for the region (Jovanović et al. 1986). The illegitimately described name *Fagion illyricum* was replaced (Török et al. 1989) with a new name, *Aremonio-Fagion*. A nomenclatural revision of the associations classified within the alliance *Aremonio-Fagion* was made by Marinček et al. (1992).

During our research, we were faced with difficulties because there was no unified viewpoint concerning the syntaxonomical classification of BF, and we found that these forests have been classified into various alliances. Many authors have examined BF in the C and E part of the Balkans in the last 10 years. The proposed classification of BF of SE Serbia, the Republic of Macedonia and N and C Greece by Dzwonko & Loster (2000) did not consider *Fagion moesiacae* and included BF in the *Aremonio-Fagion* alliance. Bergmeier & Dimopoulos (2001) classified Greek BF into *Fagion sylvaticae*. Rodwell et al. (2002) proposed that beech and fir–beech forests of the area E of the River Drina and on the Rhodope Mountains should be classified into *Doronico orientalis-Fagion moesiacae*. Dierschke & Bohn (2004) placed BF of this area into two alliances: those of the C Balkans (from S Serbia and Macedonia to W Bulgaria) into *Doronico columnae-Fagion moesiacae* and those of NE and C Greece into *Doronico orientalis-Fagion moesiacae*. Tzonev et al. (2006) also did not support the concept of the alliance *Fagion moesiacae* and pointed to the relationship of Bulgarian mesophilous and acidophilous BF to *Doronico columnae-Fagenion moesiacae* and thermophilous BF to *Doronico orientalis-Fagenion moesiacae* but they included Bulgarian BF in three different alliances (*Luzulo-Fagion*, *Asperulo-Fagion* and *Cephalanthero-Fagion*) that were very close to the proposal of Willner (2002) for the S-C European beech forests. The name *Fagion moesiacae* was not considered in the case of BF in Bosnia and Herzegovina and was replaced with a new but invalid name, *Seslerio-Fagion sylvaticae* (Redžić & Barudanović 2010).

Faced with a similar question to that of Bergmeier & Dimopoulos (2001), as to how Greek *Fagus* forest communities syntaxonomically correspond to their Balkan and European counterparts, we tried to answer the question within the framework of SE Europe.

The goals of our study were: (1) to establish the main vegetation types of BF communities in SE Europe (excluding acidophilous types) and to discuss the possible syntaxonomical interpretations of the distinguished vegetation

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types; and (2) to detect the major factors that influence BF vegetation in SE Europe.

Taxonomic remarks

At the subspecies level of *Fagus* taxa, the situation in the investigated area is complicated. There are two well-defined subspecies: *Fagus sylvatica* subsp. *sylvatica* and *F. sylvatica* subsp. *orientalis* (Denk 1999) but, in 1933, Czeczott reported *Fagus moesiaca* in the Balkan Peninsula as a species having intermediate morphological characters between these two subspecies. In terms of the latest and most accepted taxonomic classification, it is a species whose taxonomic status is still unclear and it has been the subject of a number of studies (Gömöry et al. 1999; Magri et al. 2006; Gömöry & Paule 2010). Many authors, mainly from Serbia, still distinguish it (Cvjetićanin 2003; Cvjetićanin & Novaković 2004; Čurović et al. 2011) and many authors allow its existence with some reservations (Gömöry et al. 1999; Magri et al. 2006; Brus 2010; Gömöry & Paule 2010). Distinguishing *F. moesiaca* as a separate taxon (whatever the rank) does not seem justified in the opinion of Gömöry & Paule (2010). If such a taxon was to be used for European populations originating from Balkan glacial beech refugia, then it must be reserved for populations in the very southern part of the Balkans, as proposed by Magri et al. (2006).

Methods

Our study comprises forests of *F. sylvatica* subsp. *sylvatica* in the SE part of Europe; from the SE Alps in Slovenia, through Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Bulgaria and Macedonia to N and NE Greece (Fig. 1).

In terms of the long gradient (approximately 1000 km), climatic conditions in the SE are different from those in the NW. Generally, the temperature in the S part is higher and the precipitation is lower. A sub-mediterranean mountainous climate prevails, characterized by high winter precipitation and markedly low summer precipitation (Fig. 2).

Published and unpublished relevés of BF made in this area were taken into consideration for the purpose of the study (Appendix S1). All the relevés were made according to the Braun-Blanquet approach (Braun-Blanquet 1964) and were stored in the TURBOVEG database (Hennekens & Schamineé 2001). From the total number of collected relevés ($n = 5952$), we selected those of BF in which *F. sylvatica* subsp. *sylvatica* had a cover value of at least two in the tree layer according to the Braun-Blanquet scale. We treated *F. moesiaca* as *F. sylvatica* subsp. *sylvatica*, as many authors have also done in previous studies (Dzwonko et al. 1999; Bergmeier & Dimopoulos 2001; Tzonev et al. 2006). *Fagus sylvatica* subsp. *orientalis* forests were not within the focus of our research and were not taken into consideration. We also omitted relevés of the alliances *Luzulo-Fagion* and *Geranio versicolor-Fagion*. The first was omitted because of the acidophilous site characteristics of BF combined in this alliance. The second, BF of the alliance *Geranio versicolor-Fagion*, appear in NW Greece and show a trans-Adriatic distribution pattern with considerable floristic deviation from other *Fagus* forest types in eastern parts of N Greece (Bergmeier & Dimopoulos 2001; Di Pietro 2009). It was first described as *Fagion hellenicum* (Quézel 1967).

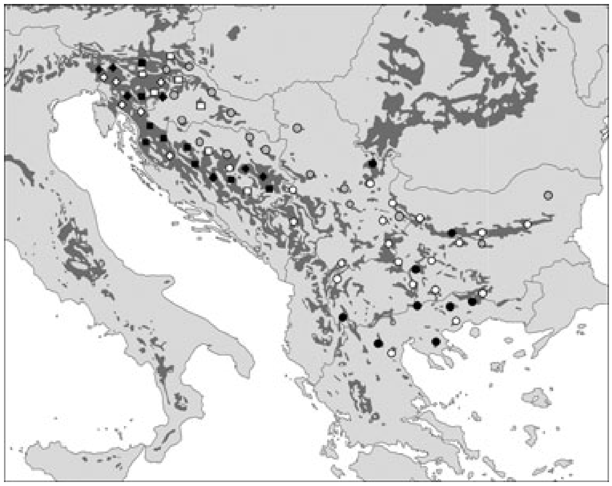

Fig. 1. Study area on a segment of the vegetation map of SE Europe (Bohn et al. 2004) with the distribution of beech forests (dark grey) and symbols that mark positions of each beech forest vegetation type separately. Legend: squares – alliance *Aremonio Fagion*, circles – alliance *Fagion moesiacae*, □ – Cluster 1, ■ – Cluster 2, ◇ – Cluster 3, ♦– Cluster 4, ◎ – Cluster 5, ○ – Cluster 6, ●- Cluster 7. Symbols for clusters are placed subjectively on the map in relation to the highest frequency of occurrence.

In order to avoid an unequal proportion of communities with a high number of samples (oversampling), where possible we chose a maximum ten relevés from each beech forest association, defined by name. Selection was made in such a way that different authors, different publications and different locations within the area were represented (Košir et al. 2008; Čarni et al. 2009). We *a posteriori* georeferenced 997 relevés that remained after this selection. Where the occurrence of individual species was specified for different layers, all strata were amalgamated into one layer, by default function in the JUICE 7.0 program (Tichý 2002). In order to reduce noise in the analysis, taxa occurring in six or fewer relevés were omitted from the analysis (Tsiripidis et al. 2007). Taxa treated at different taxonomic levels (e.g. subspecies, variety) were aggregated to the upper level. Records of species determined to genus level were deleted from the data set. We also excluded moss and lichen species,

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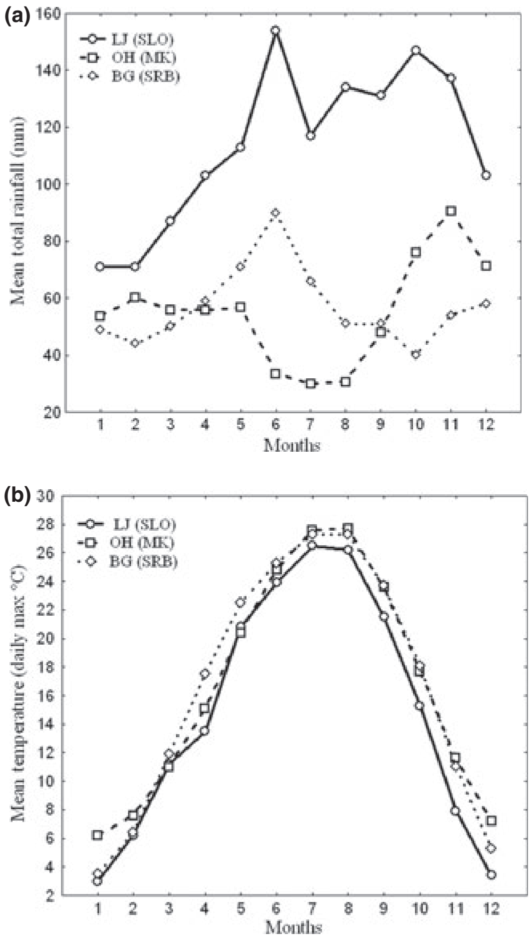

Fig. 2. Mean total rainfall (**a**) and mean monthly temperatures (**b**) in the research area. Climatological information for Ljubljana (Slovenia – SLO) and Ohrid (Republic of Macedonia – MK) is based on monthly averages for the period 1971–2000 and for Belgrade (Serbia – SRB) for the period 1961–1990 according to World Meteorological Organization data (http://www.wmo.int/pages/index_en.html).

since many authors did not record them. In total, 385 species remained in the data set. Species nomenclature is according to Flora Europaea (Tutin et al. 1964–1993).

As beech forest species we selected species with their ecological optima in BF, they are shade-tolerant and adapted to mesic conditions (Ellenberg 1996). For comparison of such species between clusters, we used the beech forest species list from Willner et al. (2009).

For estimation of ecological conditions, we used species ecological indicator values (EIV) for light (L), temperature (T), moisture (M), soil reaction (S), continentality (C) and nutrients (N) (Pignatti et al. 2005). These indicator values have been used in various studies in the Balkans (Bergmeier & Dimopoulos 2008; Šilc et al. 2009; Kavgaci et al. 2010). We were unable to obtain EIV for 25 out of the 385 species; i.e. 6.5% of the total number of species. With up to 20% of taxa excluded from the relevés, environmental indicator values are only weakly affected (Ewald 2003a). We also used chorotypes and life forms (Raunkiaer 1934; Jordanov 1963–1979; Josifović 1970–1977; Pignatti et al. 2005) to support interpretation of the classification.

We carried out cluster analysis of the data set in the program PC-ORD 5 (MjM Software Design; Gleneden Beach, OR, USA), using relative Sörensen (Rel. Manh.) as a distance measure and Ward's algorithm for dendrogram construction.

Diagnostic species of each of the clusters were calculated in JUICE 7.0 (Tichý 2002) by calculating the fidelity of each species to each cluster using the phi-coefficient as a fidelity measure (Bruelheide 2000; Chytrý et al. 2002). In our calculations, each cluster was compared with the other relevés in the data set, which were taken as a single, undivided group. The threshold phi-value for the species to be considered diagnostic was set at 0.20. Fidelity calculation was made using presence/absence data. Clusters consisted of unequal numbers of relevés and higher phi-values for larger clusters were therefore expected. In order to avoid this, each of the n clusters was virtually equalized to $1/n$ of the size of the entire data set (Tichý & Chytrý 2006). The statistical significance of the concentration of each species in each cluster was measured with Fisher's exact test ($P < 0.001$) (Chytrý et al. 2002). A data set divided into two main clusters was used for estimation of diagnostic species of the alliances. The same procedure was used as for the individual clusters. The results of the classification are presented in a synoptic table, in which both percentage species frequencies and phi-values higher than 0.20 are indicated. The description of the new syntaxon was done according to the ICPN.

Detrended correspondence analysis (DCA) was performed using JUICE 7.0 (Tichý 2002) in the environment of R software (R Development Core Team 2008; R Foundation for Statistical Computing, Vienna, AT, USA), using the *vegan* package. For better ecological interpretation and the relationships between these clusters, average EIV and the altitude of each relevé were used in a diagram as supplementary environmental data. Original releves were plotted as centroids. Correlations between DCA relevé scores and explanatory variables (EIV, life forms, chorotypes, altitude, latitude and longitude) were calculated, using the non-parametric Kendall-Tau coefficient in the program Statistica 7.0 (2004; http://www.statsoft.com).

It is accepted (Čarni et al. 2009) that the main macroecological gradient goes along the Dinaric Alps in a direction from NW to SE. We therefore projected the longitude and latitude of a single relevé onto this gradient. We obtained the distance along the major gradient for all the relevés, to be used as an explanatory variable for vegetation patterns.

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The Mann–Whitney *U*-test was used to test differences between the two separated groups of clusters (northern group = clusters 1–4, southern group = clusters 5–7).

Results

Classification of the selected 997 phytosociological relevés is presented in the dendrogram (Fig. 3) and in the synoptic table (Table 1). The first division of the clusters is at the level of two major groups of BF, and reveals BF of the NW part of the investigated area, traditionally classified in the alliance *Aremonio-Fagion* (northern group) and BF of the central and eastern part in the alliance *Fagion moesiacae* (southern group). Further division continues into seven clusters – units that can be best interpreted ecologically and geographically. Diagnostic species for each of the accepted clusters are presented in Table 1. The distribution of the vegetation units is presented in Fig. 1.

Cluster 1 combines relevés that represent montane BF of the NW part of the investigated area and are traditionally treated as *Lamio orvalae-Fagenion*, a central suballiance of the *Aremonio-Fagion* alliance. Such BF mostly occur in Slovenia and along the Dinaric Alps to Bosnia and Herzegovina, at an average of 840 m a.s.l. (Figs 1, 3 and 5). Diagnostic species are *Corydalis cava*, *Isopyrum thalictroides, Paris quadrifolia, Arum maculatum* and others (Table 1).

Cluster 2 incorporates mostly relevés of beech–fir forests. These forests are part of the *Lamio orvalae-Fagenion* suballiance. The area of distribution of such forests is very similar to that of Cluster 1, with an average altitude of 1086 m. Diagnostic species are *Abies alba, Rubus fruticosus, Oxalis acetosella, Rhamnus alpinus* subsp. *fallax*, etc. (Table 1).

Cluster 3 consists of thermophilous BF of the NW part and syntaxonomically corresponds to the suballiance *Ostryo-Fagenion*. The vegetation of this type can be found on southern, dry and warm slopes, with an average altitude of 612 m a.s.l, mostly in Slovenia. *Fraxinus ornus, Cyclamen purpurascens, Tanacetum corymbosum, Carex flacca, Solidago virgaurea* and others are diagnostic species for this vegetation unit (Table 1).

Cluster 4 mainly includes relevés of altimontane and subalpine BF, as well as relevés of a community of lower altitudes thriving on northern slopes (*Arunco-Fagetum*). It syntaxonomically corresponds to the suballiance *Saxifrago rotundifoliae-Fagenion*. It represents BF vegetation of the highest altitudes, mostly from Slovenia to the central part of Bosnia and Herzegovina (average altitude 1256 m a.s.l). Diagnostic species are *Asplenium viride, Rubus saxatilis, Rosa pendulina, Clematis alpina, Lonicera alpigena,* etc. (Table 1).

Cluster 5 represents communities that are situated in the lowlands on the southern edge of the Pannonian plain and on the plains of NE Bulgaria (Danubian plain). It combines BF that grow mainly in the rare solitary mountains in the Pannonian region in the NE part of the research area and lowland BF, mainly from Serbia and C and E Bulgaria (average altitude 662 m a.s.l). These are not the most favourable habitats for BFs. Due to high temperatures and low precipitation they are more suitable for oak forests. Only a limited number of species characteristic of BF appear in this cluster and the phytogeographic pattern is thus not clear. We suggest *Tilio tomentosae-Fagenion sylvaticae* as the name of this new suballiance, with *Tilia cordata*, *Glechoma hirsuta* and *T. tomentosa** (see Appendix 1) as diagnostic species (Table 1).

Cluster 6 incorporates relevés of montane BF that thrive in the Republic of Macedonia, SE Serbia, W Bulgaria and N Greece; at the highest altitudes, at an average of 1262 m a.s.l. (Figs 1, 3 and 5). It is traditionally treated as *Doronico columnae-Fagenion moesiacae*. Diagnostic species are *Lapsana communis, Moehringia trinervia, Melica uniflora*, *Poa chaixii*, *Pulmonaria rubra, Helleborus cyclophyllus* and others (Table 1).

Cluster 7 consists of BF under the influence of the mediterranean climate. They thrive in N Greece, Bulgaria and the Republic of Macedonia, at an average altitude of 1220 m a.s.l. (Figs 1, 3 and 5) and correspond to *Doronico orientalis-Fagenion sylvaticae*. Diagnostic species are *Abies borisii-regis, Orthilia secunda, Lathyrus alpestris, Silene multicaulis, Monotropa hypopitys, Doronicum orientale* and others (Table 1).

The results of cluster analysis were used in ordination, using DCA with passively projected EIV and geographic indicators (altitude, latitude and longitude; Fig. 4). Axis 1 is highly correlated with latitude and longitude, while Axis 2 shows a higher correlation with altitude. It can be seen that temperature and moisture correlate with both Axis 1 and 2. They change in a NW–SE direction, as shown in Table 2, although they also change on a local scale

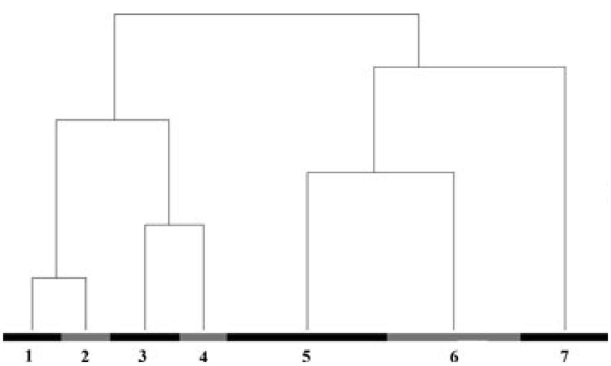

Fig. 3. Classification of seven relevé groups of beech forest vegetation of SE Europe. Two large groups of clusters, revealing two alliances (*Aremonio-Fagion* and *Fagion moesiacae*), are distinguished. Numbers refer to Table 1.

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Table 1. Synoptic table of SE European beech forests. Species values are percentage frequencies. Diagnostic species of individual suballiances are shaded and ranked by decreasing fidelity. Only species with $\phi > 0.20$ are included among diagnostic species. Diagnostic species of alliances are indicated in the first column.

Diagnostic spec. for alliances	Alliance	AF				Fm		
	Group No. (Clusters)	1	2	3	4	5	6	7
	No. of relevés	97	80	78	114	263	219	146
	Average number of species	36	35	37	37	24	27	13
	Average number of beech forest species	18	17	11	13	1	9	3
Montane BF (*Lamio orvalae-Fagenion*)								
AF	*Corydalis cava*	36	–	–	–	3	2	–
	Isopyrum thalictroides	36	1	–	2	3	2	–
	Paris quadrifolia	72	40	14	25	7	13	–
	Arum maculatum	42	9	3	–	11	9	1
	Galanthus nivalis	25	1	4	1	2	1	–
	Leucojum vernum	19	2	–	1	–	1	–
	Cardamine waldsteinii	26	9	–	3	1	2	–
	Sambucus nigra	42	18	6	3	18	8	1
	Cardamine bulbifera	80	39	15	29	40	64	19
	Cardamine kitaibelli	19	5	1	–	1	1	–
	Lunaria rediviva	20	8	–	–	2	1	–
	Adoxa moschatellina	20	4	1	4	1	4	–
	Asplenium scolopendrium	26	16	5	–	5	1	–
	Dryopteris filix-mas	84	72	28	46	38	58	20
AF	*Acer pseudoplatanus*	86	69	72	61	52	20	10
	Stellaria nemorum subsp. *glochidisperma*	8	–	–	–	–	–	–
	Allium ursinum	22	5	3	3	2	9	–
	Polygonatum multiflorum	43	20	37	8	19	1	–
	Vicia oroboides	22	–	5	12	4	–	1
AF	*Lamium orvala*	36	28	21	12	3	3	1
AF	*Ranunculus lanuginosus*	18	6	–	12	1	–	–
	Anemone ranunculoides	14	1	–	2	1	9	–
	Corydalis solida	9	–	–	–	2	2	1
	Anemone nemorosa	55	42	21	44	20	32	1
AF	*Senecio nemorensis* subsp. *fuchsii*	32	12	27	24	4	–	–
	Ranunculus ficaria	9	–	–	–	4	1	–
	Ulmus glabra	32	25	21	4	14	3	1
AF	*Actaea spicata*	43	38	24	28	7	14	2
	Veratrum album	23	5	3	21	2	7	–
AF	*Aconitum vulparia*	16	5	6	10	–	–	–
Beech-fir forests (*Lamio orvalae-Fagenion*)								
AF	*Abies alba*	25	99	15	43	24	11	3
	Rubus fruticosus	1	35	–	3	3	1	–
AF	*Oxalis acetosella*	49	82	10	39	14	35	5
AF	*Rhamnus alpinus* subsp. *fallax*	11	44	5	19	3	4	–
	Senecio nemorensis agg.	14	45	8	11	6	16	1
	Ajuga reptans	5	44	8	14	21	10	2
	Sambucus racemosa	2	20	3	–	5	1	–
	Sanicula europaea	44	71	23	26	37	36	9
	Hordelymus europaeus	10	28	–	1	3	15	–
	Athyrium filix-femina	51	64	14	23	31	25	8
	Carex sylvatica	38	51	18	11	27	3	5
AF	*Cardamine trifolia*	22	36	8	24	2	–	–
AF	*Lonicera nigra*	3	21	–	14	1	–	–
	Dryopteris dilatata	4	19	1	5	1	5	–
	Polystichum aculeatum	27	49	10	32	17	19	4
	Viola reichenbachiana	34	65	26	33	41	46	15
	Rubus idaeus	11	38	4	24	5	23	15
AF	*Festuca altissima*	11	22	3	15	3	1	–
	Adenostyles alliariae	9	20	–	13	1	5	1
	Solanum dulcamara	3	10	1	–	2	–	–
	Euphorbia amygdaloides	39	68	37	55	32	48	18
	Myosotis sylvatica	12	20	–	4	3	9	3

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Table 1. *(Continued).*

Thermophilous BF (*Ostryo-Fagenion*)								
AF	*Fraxinus ornus*	11	1	76	10	19	7	5
	Cyclamen purpurascens	42	21	91	42	6	1	–
	Tanacetum corymbosum	3	–	36	1	4	1	–
	Carex flacca	–	–	28	–	2	–	–
AF	*Solidago virgaurea*	9	5	62	28	12	1	2
	Ostrya carpinifolia	4	2	47	10	5	7	4
AF	*Sorbus aria*	8	8	55	31	3	1	2
	Melittis melissophyllum	4	–	44	8	15	2	3
	Primula vulgaris	7	–	45	11	10	7	3
	Clematis vitalba	16	5	47	3	15	5	1
	Convallaria majalis	9	–	40	11	3	6	1
	Rosa arvensis	12	–	41	–	14	5	4
	Campanula trachelium	7	4	38	3	9	7	2
	Peucedanum oreoselinum	–	–	17	1	–	–	–
	Laserpitium latifolium	1	1	19	4	1	–	–
	Vincetoxicum hirundinaria	–	–	19	4	2	1	–
	Sesleria autumnalis	1	1	23	4	6	2	–
	Tamus communis	13	–	33	4	15	4	1
	Acer campestre	13	–	36	1	25	5	1
	Berberis vulgaris	1	–	12	–	–	–	–
	Sorbus torminalis	–	–	21	–	8	4	1
	Cornus sanguinea	9	–	22	4	3	1	–
	Asarum europaeum subsp. *caucasicum*	2	–	13	1	–	–	–
AF	*Aposeris foetida*	27	2	40	25	6	2	–
	Euphorbia dulcis	19	2	28	2	8	–	–
	Viburnum lantana	7	–	23	4	6	4	–
AF	*Carex digitata*	18	9	40	28	8	7	1
	Centaurea montana	–	–	10	2	–	–	–
	Cornus mas	3	–	23	–	13	7	1
AF	*Buphthalmum salicifolium*	–	–	15	9	–	–	–
	Cruciata glabra	2	1	18	1	7	1	1
	Crataegus monogyna	3	2	28	7	19	5	–
AF	*Helleborus niger*	10	8	28	19	–	1	–
	Anthericum ramosum	–	–	9	1	–	–	–
AF	*Erica herbacea*	–	–	15	10	–	–	–
AF	*Anemone trifolia*	–	1	19	15	1	1	–
	Ligustrum vulgare	2	–	14	–	5	1	–
	Galium sylvaticum agg.	12	5	36	28	14	4	1
	Crataegus laevigata	–	–	10	–	3	–	–
	Melampyrum sylvaticum	2	1	14	4	2	1	–
	Salvia glutinosa	29	34	49	15	25	11	1
	Campanula persicifolia	–	–	14	1	2	5	2
	Peucedanum austriacum	2	–	13	3	2	–	1
AF	*Hacquetia epipactis*	21	9	27	11	2	–	–
AF	*Lonicera xylosteum*	18	18	36	21	3	12	1
	Rhamnus cathartica	1	–	8	–	1	–	–
AF	*Galium laevigatum*	2	–	17	14	1	–	–
	Brachypodium sylvaticum	18	9	36	6	25	12	4
	Acer obtusatum	3	2	21	3	8	8	2
	Staphylea pinnata	8	4	14	–	1	–	–
	Viburnum opulus	2	–	9	2	1	–	–
	Serratula tinctoria	2	–	8	–	1	1	–
	Mercurialis ovata	–	–	9	–	2	1	2
Altimontane and subalpine BF (*Saxifrago rotundifoliae-Fagenion*)								
AF	*Asplenium viride*	1	1	–	39	–	1	–
AF	*Rubus saxatilis*	–	2	3	33	–	1	–
AF	*Rosa pendulina*	8	10	8	51	4	4	–
AF	*Clematis alpina*	–	–	1	26	–	–	–
AF	*Lonicera alpigena*	29	36	6	66	2	6	1
AF	*Valeriana tripteris*	1	1	17	37	–	1	1
	Sorbus mougeotii	–	–	–	20	1	1	–
AF	*Sorbus aucuparia*	12	36	5	57	2	13	5

Table 1. *(Continued).*

AF	*Adenostyles alpina*	5	4	1	27	–	–	–
AF	*Phyteuma ovatum*	–	–	3	18	–	–	–
	Vaccinium myrtillus	–	26	4	45	3	11	7
	Valeriana montana	–	–	–	17	1	1	–
AF	*Thalictrum aquilegiifolium*	2	4	1	22	1	1	–
	Sesleria albicans	–	–	–	13	–	–	–
AF	*Polygonatum verticillatum*	20	25	–	45	4	14	1
	Polystichum lonchitis	6	9	1	32	2	8	6
AF	*Gentiana asclepiadea*	21	18	33	52	11	5	1
	Hypericum umbellatum	–	–	–	11	–	–	–
AF	*Laserpitium krapfii*	–	–	6	18	1	–	–
	Laburnum alpinum	–	–	5	17	1	1	–
AF	*Homogyne sylvestris*	4	11	23	33	1	–	–
AF	*Calamagrostis varia*	–	9	13	26	2	–	–
	Gymnocarpium dryopteris	4	1	–	17	–	1	–
	Rhododendron hirsutum	–	–	1	12	–	–	–
	Saxifraga cuneifolia	–	–	–	10	–	–	–
	Luzula sylvatica	4	18	1	42	6	25	20
	Carex ferruginea	–	–	–	9	–	–	–
	Ranunculus platanifolius	7	5	–	19	1	2	–
	Salix appendiculata	1	–	–	10	–	–	–
	Saxifraga rotundifolia	12	16	–	37	2	22	8
	Homogyne alpina	–	–	–	9	–	1	–
	Asplenium ruta-muraria	1	1	6	18	1	1	3
	Aster bellidiastrum	–	–	–	8	–	–	–
	Thymus serpyllum	–	–	–	9	1	–	–
	Aquilegia vulgaris	1	–	1	11	1	–	–
AF	*Aconitum lycoctonum* subsp. *vulparia*	3	–	3	12	–	–	–
	Calamagrostis arundinacea	1	1	18	26	1	5	10
	Carex brachystachys	–	–	–	7	–	–	–
	Melica nutans	5	1	13	23	7	3	–
AF	*Maianthemum bifolium*	5	14	10	24	3	–	–
	Larix decidua	–	–	–	6	–	1	–
	Cicerbita alpina	3	5	–	13	1	3	–
	Gymnocarpium robertianum	1	4	3	11	1	–	–
Lowland BF (*Tilio tomentosae-Fagenion sylvaticae*)								
	Carpinus betulus	19	1	15	4	54	3	6
	Quercus petraea	18	–	19	–	33	1	5
	Circaea lutetiana	24	9	–	–	29	10	1
	Festuca drymeja	9	16	3	7	37	19	16
	Rubus hirtus agg.	23	30	18	12	54	42	16
	Tilia cordata	1	1	12	1	16	–	–
	Stellaria holostea	3	–	–	3	14	5	–
	Galeopsis tetrahit	3	–	–	–	11	4	–
	Glechoma hirsuta	9	15	–	11	25	5	1
	Viola odorata	–	–	1	–	9	4	–
Montane BF of the central and south-eastern part (*Doronico columnae-Fagenion moesiacae*)								
Fm	*Lapsana communis*	–	–	–	1	2	15	1
Fm	*Moehringia trinervia*	3	2	1	2	8	26	10
	Melica uniflora	5	2	18	1	22	32	4
	Poa chaixii	–	–	–	1	–	8	–
	Pulmonaria rubra	–	–	–	1	1	9	1
	Helleborus cyclophyllus	–	–	–	–	1	8	–
Fm	*Potentilla micrantha*	4	1	6	1	7	28	24
Fm	*Geum urbanum*	1	1	–	3	15	21	5
	Epilobium montanum	8	35	–	18	15	40	20
	Campanula sparsa	–	–	–	–	1	10	5
	Luzula luzulina	–	2	–	1	–	8	–
Fm	*Lathyrus laxiflorus*	–	–	–	–	7	18	17
	Digitalis viridiflora	–	–	–	–	–	5	–
	Veronica officinalis	–	8	–	4	8	20	10

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Table 1. *(Continued).*

		1	2	3	4	5	6	7
BF of the SE part, under the influence of a Mediterranean climate (*Doronico orientalis-Fagenion sylvaticae*)								
Fm	*Abies borisii-regis*	–	–	–	–	–	9	30
	Orthilia secunda	–	2	1	16	2	12	35
Fm	*Lathyrus alpestris*	–	–	–	–	–	6	18
	Silene multicaulis	–	–	–	–	–	–	10
	Monotropa hypopitys	1	–	–	–	–	1	12
	Viscum album s.lat.	–	1	–	1	–	–	9
Fm	*Luzula forsteri*	1	–	1	–	2	12	16
	Doronicum orientale	–	–	–	–	–	6	10
Species diagnostic for more than one suballiance								
AF	*Cardamine enneaphyllos*	64	22	19	52	5	5	–
	Galium odoratum	88	72	18	22	62	78	30
	Hedera helix	43	1	55	6	33	10	4
AF	*Mercurialis perennis*	59	30	63	54	23	14	4
AF	*Picea abies*	32	81	22	56	8	8	3
	Galium rotundifolium	2	45	–	2	6	15	39
AF	*Prenanthes purpurea*	36	69	33	63	18	32	12
AF	*Veronica urticifolia*	2	31	12	42	5	7	1
AF	*Daphne mezereum*	54	45	68	85	10	15	–
AF	*Cirsium erisithales*	2	9	29	37	–	–	–
AF	*Hepatica nobilis*	9	–	37	35	5	3	–
AF	*Carex alba*	–	2	19	18	–	–	–
Fm	*Poa nemoralis*	2	4	3	18	16	47	55
Other species diagnostic for alliance *Aremonio-Fagion*								
	Symphytum tuberosum agg.	43	35	21	39	14	31	1
	Lilium martagon	33	14	26	28	7	12	4
	Omphalodes verna	10	14	10	8	1	–	–
	Phyteuma spicatum	14	11	18	18	2	1	–
Other species diagnostic for alliance *Fagion moesiacae*								
	Veronica chamaedrys	10	11	3	15	17	37	36
	Galium aparine	1	1	–	1	10	11	5
	Physospermum cornubiense	–	–	–	–	2	10	7
Other species with high frequncy								
	Fagus sylvatica	100	100	100	100	100	100	100
	Lamiastrum galeobdolon agg.	56	54	31	24	44	46	9
	Mycelis muralis	41	72	24	53	48	71	51
	Acer platanoides	35	14	33	4	28	15	4
	Pulmonaria officinalis	34	16	40	11	24	15	1
	Asarum europaeum	32	29	37	14	28	8	1
	Geranium robertianum	30	41	5	21	27	44	7
	Aremonia agrimonoides	29	60	18	42	19	57	30
	Heracleum sphondylium	28	5	14	18	7	4	8
	Prunus avium	25	2	26	3	30	10	1
	Fragaria vesca	25	46	27	38	32	29	13
	Lathyrus vernus	25	16	29	16	25	4	2
	Euonymus latifolius	22	8	12	9	4	8	1
	Corylus avellana	22	18	27	9	29	11	3
	Aegopodium podagraria	21	4	8	9	8	14	–
	Urtica dioica	18	2	–	3	6	13	5
	Doronicum austriacum	16	8	1	8	2	8	–
	Ruscus hypoglossum	16	10	12	3	21	2	3
	Luzula luzuloides	15	10	10	11	22	24	23
	Milium effusum	15	10	–	2	3	8	1
	Fraxinus excelsior	13	6	13	4	14	4	2
	Daphne laureola	11	16	3	1	3	5	1
	Aruncus dioicus	11	6	8	10	6	1	–
	Scilla bifolia	11	1	1	1	–	7	1

AF = alliance *Aremonio-Fagion*; Fm = alliance *Fagion moesiacae*; 1 = montane beech forests of *Lamio orvalae-Fagenion*; 2 = beech–fir forests of *Lamio orvalae-Fagenion*; 3 = *Ostryo-Fagenion*; 4 = *Saxifrago rotundifoliae-Fagenion*; 5 = *Tilio tomentosae -Fagenion sylvaticae*; 6 = *Doronico columnae-Fagenion moesiacae*; 7 = *Doronico orientalis-Fagenion sylvaticae*.

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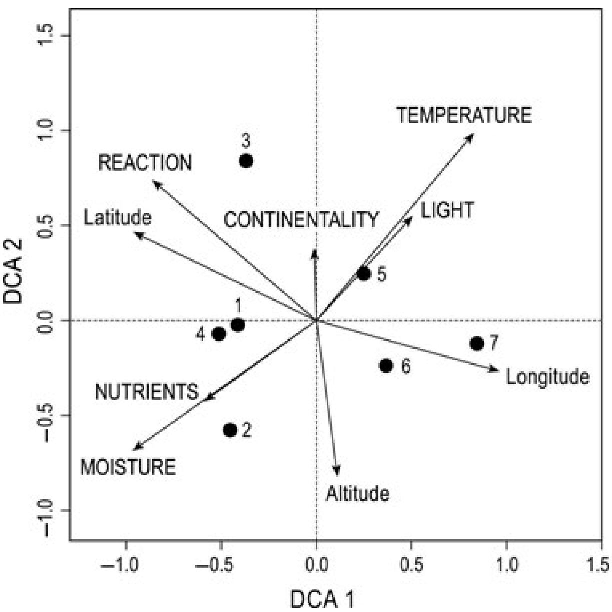

Fig. 4. Detrended correspondence analysis (DCA) of seven relevé clusters, with passively projected explanatory variables. The numbering of the clusters is the same as in Table 1.

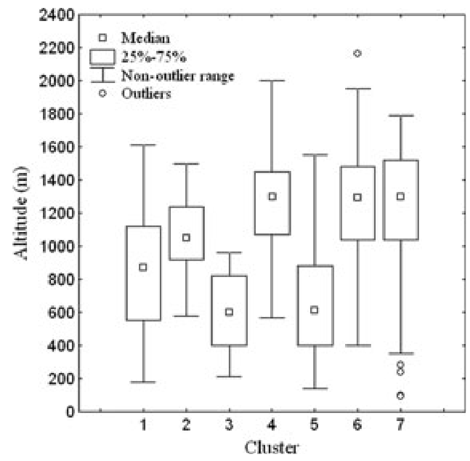

Fig. 5. Box-whiskers graph presents altitudes and altitudinal range for each cluster individually.

according to altitudinal gradient. We therefore consider Axis 1 to be the generally accepted macroecological gradient in the Balkans, which runs along the Dinaric Alps in a NW–SE direction. As expected, the correlation between Axis 1 and altitude is not significant (Table 2), because a wide altitudinal range is characteristic of the study area (Fig. 5) and BF are found along the whole altitudinal gradient in northern and southern regions. The distribution and range of altitudes among clusters is shown in Fig. 5.

The correlation between DCA relevé scores of Axis 1 and 2 and the mean EIV, tested with Kendall's coefficient, showed some significant differentiation along both axes (Table 2). EIV for light and temperature show a significant increase along the geographical gradient toward the SE (Axis 1), while indicators for moisture, reaction and nutrients show a significant decrease. All correlations between Axis 2 and EIV are significant. Altitude and EIV for moisture and nutrients significantly decrease, while indicator values for light, temperature, continentality and reaction significantly increase (Table 2).

Along Axis 1, there is a significant increase in the proportion of chamaephytes, hemicryptophytes and therophytes toward the SE. At the same time, the proportion of geophytes and phanerophytes significantly decreases in the same direction (Table 2) and reflects changed ecological conditions.

We also found correlations between Axis 1 and the proportion of chorotypes differed significantly different. Stenomediterranean, Eurymediterranean, Mediterranean-Montane, Eurasian and Montane S European species show an increasing trend toward the SE, while Boreal species decrease in the same direction. These results confirm our assumptions of geographically or macroecologically based differentiation of BF vegetation.

The highest number of species can be observed in the BF of the N group (Fig. 6), especially in thermophilous BF (Cluster 3 – *Ostryo-Fagenion*) and in altimontane and subalpine BF (Cluster 4 – *Saxifrago-Fagenion*). Species numbers in clusters of the SE group (5, 6, 7) are in general lower. The lowest number of species and BF species is observed in BF of the SE part under the influence of a mediterranean climate (Cluster 7 – *Doronico orientalis-Fagenion sylvaticae*). In general, species richness decreases along the geographical gradient. Comparing Clusters 4, 6 and 7 in Figs 5 and 6, it is obvious that altitude does not affect species richness. Both types of BF thrive at the high altitudes, but Cluster 4 contains the highest number of species and Cluster 7 the lowest.

Since the analysis shows two main groups of BF in the investigated area (Fig. 3), we attempted to determine significant differences between them. We therefore compared the vegetation characteristics of the northern group (alliance *Aremonio-Fagion*) and the southern group (alliance *Fagion moesiacae*). The results of the Mann–Whitney *U*-test in Table 3 show statistically significant differences in the proportions of all life forms between the groups, except for hemicryptophytes and phanerophytes. Table 2 also indicates a higher proportion of geophytes and phanerophytes in the northern group, while other life forms have a higher proportion in forests of the alliance *Fagion moesiacae*.

All EIV are significantly different between the two groups (Table 3). The table shows that BF of the alliance *Fagion moesiacae* thrive in conditions with higher temperatures, lower rainfall and are lower nutrients than stands of the alliance *Aremonio-Fagion*.

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Table 2. Correlations (Kendall-Tau coefficient) between DCA relevé scores and explanatory variables (latitude, longitude, altitude, life forms, EIV and chorotypes).

Axis	Geogr. fact		Ecological factors									
	Latit.	Longit.	Gradient	Altitude	Light	Temp.	Cont.	Moist.	React.	Nutr.	Axis 1	Axis 2
1	−0.554*	0.568*	0.606*	0.067	0.142*	0.310*	−0.06	−0.370*	−0.416*	−0.196*	1	0.032
2	0.160*	−0.077*	−0.094*	−0.467*	0.206*	0.494*	0.117*	−0.303*	0.222*	−0.154*	0.032	1
	Life forms											
	P	N	C	H	G	T						
1	−0.098*	0.081	0.230*	0.144*	−0.195*	0.412*					1	0.032
2	0.335*	−0.106*	−0.039	−0.116*	−0.190*	−0.013					0.032	1
	Chorotypes											
	End	StM	EuM	MeM	EuA	Atl	MSE	Bor	WiS			
1	0.032	0.322*	0.365*	0.320*	0.119*	0.047	0.272*	−0.082*	−0.06		1	0.032
2	−0.208	−0.027	0.153*	−0.033	0.364*	0.069	−0.292*	−0.287*	−0.223*		0.032	1

C = chamaephytes; G = geophytes; H = hemicryptophytes; N = nanophanerophytes; P = phanerophytes; T = therophytes; End. = Endemic; StM = Stenomediterranean; EuM = Eurymediterranean; MeM = Mediterranean-Montane; EuA = Eurasian; Atl. = Atlantic; MSE = Montane S European; Bor = boreal; WiS = widespread species.

*Correlations significant at 0.001 level.

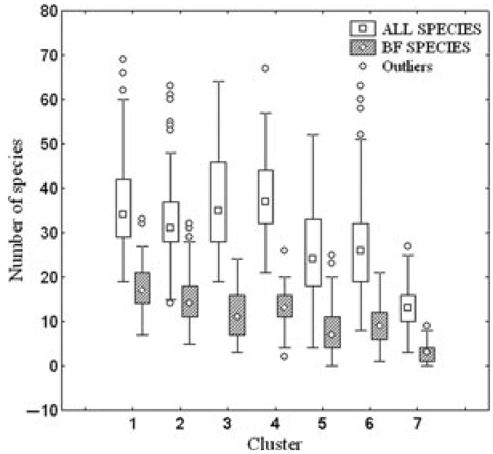

Fig. 6. Box-whiskers graph presents the average number of species and average number of BF species defined in individual clusters. Beech forest species were defined according to Willner et al. (2009).

In terms of the proportion of chorotypes in the species composition of the two groups, there are significantly increased numbers of endemic, Stenomediterranean, Eurymediterranean, Eurasian, Atlantic, Montane S European and widespread species in the BF of alliance *Fagion moesiacae*.

All of those indices highlight not only the different ecological factors in each of the two groups but also a different structure of species traits composition.

Discussion

The first level of division in the dendrogram (Fig. 3) revealed the main geographic division and reflects the geographic differentiation of BF in SE Europe. The northern group (including Clusters 1–4) was classified into the alliance *Aremonio-Fagion* and the second, the southern group (including Clusters 5–7), into the alliance *Fagion moesiacae*. In the nomenclature revision of Illyrian BF of Slovenia, Croatia, SW Hungary, S Austria and NE Italy, Marinček et al. (1992) differentiated four suballiances within the *Aremonio-Fagion* alliance. Our analysis revealed three of them in our study: Cluster 1 as mesophilous *Lamio orvalae-Fagenion*, Cluster 2, which incorporates mostly fir–beech forests, according to Marinček et al. (1992) is also classified into the *Lamio orvalae-Fagenion* suballiance, Cluster 3 as thermophilous *Ostryo-Fagenion*, while Cluster 4 was altimontane *Saxifrago rotundifoliae-Fagenion.* Cluster 4 includes not only altimontane to subalpine BF but also lower montane ones (e.g. *Arunco-Fagetum*). This is confirmation of Willner (2002), who pointed out the close floristic relationship between *Arunco-Fagetum* and *Anemono trifoliae-Fagetum*.

Table 3. Mann–Whitney *U*-test of differences in life forms, indicator values and chorotypes between the northern group (AF: alliance *Aremonio-Fagion*) and southern group (Fm: alliance *Fagion moesiacae*) of BF vegetation types.

Variable	*z*	*P*-level	Valid *N* AF	Valid *N* Fm
% *C*	−7.9606	0.0000*	324	526
% *G*	5.8837	0.0000*	368	611
% H	−1.7326	0.0832	367	622
% N	−3.8153	0.0001*	318	385
% P	1.6052	0.1084	369	628
% T	−10.7364	0.0000*	132	311
Altitude	−1.3653	0.1722	369	628
Light	−4.3717	0.0000*	369	628
Temperature	−11.8139	0.0000*	369	628
Continentality	4.1931	0.0000*	369	628
Moisture	12.8679	0.0000*	369	628
Soil reaction	14.4035	0.0000*	369	628
Nutrients	4.4918	0.0000*	369	628
End.	−4.6764	0.0000*	37	28
StM	−10.0349	0.0000*	170	264
EuM	−8.4353	0.0000*	180	335
MeM	−2.7316	0.0063	321	250
EuA	−5.4226	0.0000*	369	628
Atl	−5.211	0.0000*	84	80
MSE	3.8103	0.0001*	345	409
Bor	2.65	0.008	368	597
Wis	−8.8218	0.0000*	293	465

End.= Endemic; StM = Stenomediterranean; EuM = Eurymediterranean; MeM = Mediterranean-Montane; EuA = Eurasian; Atl. = Atlantic; MSE = Montane south European; Bor = Boreal; WiS = widespread species.
*Significant at $P < 0.001$.

The suballiance *Epimedio-Fagenion,* which is not clearly separated, is found in Cluster 3. The similarity between *Ostryo-Fagenion* and *Epimedio-Fagenion* was already emphasized by Willner (2002), but these two suballiances are ecologically different, since *Ostryo-Fagenion* appears on steep southern slopes over shallow rendzinas and *Epimedio-Fagenion* in lowlands on deeper soils. They have many common thermophilous species. Their exact syntaxonomical position therefore needs further research.

The southern group of BF includes Clusters 5–7. BF of Cluster 5 thrive in the marginal regions of BF in the investigated area (Fig. 1) but over a wide geographical range. These marginal regions extend from Austria to the Black Sea region, and it is usually difficult to classify such communities on the edge of an area of distribution. In sub-optimal conditions, species of BF become weak competitors and gradually disappear. These are common features of such lowland BF types (Cluster 5). Possible reasons for a different species composition in Cluster 5 in relation to other beech forest vegetation types are also:

- sub-optimal growing conditions (lower precipitation and higher temperature),
- growing in solitary montane islands of the sub-Pannonian region, mostly surrounded by *Quercus* and *Carpinus* forest types,
- the longest distance from the nearest glacial refuge area (Magri et al. 2006; Willner et al. 2009) and possible delayed post-glacial dispersal of European BF understorey species. In the opinion of Magri et al. (2006), the post-glacial expansion of *Fagus* appears to have been limited by large plains with a continental climate and by important river valleys, such as the Hungarian plain and the lower Danube valley, while Willner et al. (2009) observed the highest species richness in areas close to potential glacial refuge areas,
- all of the above.

A difficulty that occurs in the classification of vegetation in Cluster 5 is that many species appear that are also characteristic of *Quercus* and *Carpinus* forests (Marinček & Čarni 2000) and, in the SE part, species of *Quercion frainetto* (Čarni et al. 2009; Kavgaci et al. 2010; Lyubenova et al. 2011). There are actually three possibilities for solving this situation:

1. Split Cluster 5 arbitrarily into a northern and southern part and include each part into the alliances of those areas; northern lowland BF (including those from Bosnia and Herzegovina, Croatia and SE Slovenia) to alliance *Aremonio-Fagion*, and those from Serbia and Bulgaria lowland to alliance *Fagion moesiacae*. This division is geographically founded. It results from a lack of beech forest species and presence of lowland and thermophilous species that unify all BF from E Slovenia to the Black Sea region into one group.
2. Include them in the species-poor C European *Fagion sylvaticae* alliance,
3. Describe a new (sub)alliance of the marginal communities, extending from the Black Sea region to outcrops of the S Alps.

An aspiration for a new suballiance, which would comprise BF and beech–fir forests from the Pannonian region in Croatia, already appeared when Vukelić & Baričević (2007), while investigating beech–fir forests, pointed out the need for a new suballiance into which these forests would fit. They merely proposed a potential name, *Festuco drymeiae-Fagenion sylvaticae,* which could be classified into the alliance *Aremonio-Fagion*.

In terms of our investigations, BF of the alliance *Fagion moesiacae* unexpectedly also extend over the whole SW edge of the Pannonian plain (Fig. 1). This finding is in agreement with Rivas-Martínez et al. (2011), who designated the border between the oceanic and continental bioclimate in the Balkan Peninsula. This confirms that optimal ecological conditions for BF are linked to an oceanic bioclimate. In any case, the alliance comprises three clusters, which represent the following groups of forests:

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1 Lowland BF (Cluster 5), comprising beech forest communities from the lowest altitudes, mainly occurring on the sub-Pannonian plain from SE Slovenia to the N and E Bulgaria. In relation to the aforementioned three possible solutions for these forests, we suggest a new suballiance *Tilio tomentosae-Fagenion sylvaticae* (typified in Appendix S1) for such lowland forests.
2 Montane BF of the continental part of the C Balkans (Cluster 6), which have been traditionally treated as the suballiance *Doronico columnae-Fagenion moesiacae*. Such BF, mainly from SE Serbia, the Republic of Macedonia and N Greece and high altitudes southward to E-C Greece, were already classified in the same suballiance (Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001).
3 Montane BF influenced by a mediterranean climate (Cluster 7), included in the suballiance *Doronico orientalis-Fagenion sylvaticae*. BF of N and C Greece were already classified by Dzwonko & Loster (2000) and Bergmeier & Dimopoulos (2001) into the suballiance *Doronico orientalis-Fagenion moesiacae* (invalid name – see Appendix 1).

The syntaxonomic classification of these three southern suballiances on the level of higher rank syntaxa has not yet been unified. The separation of suballiances *Doronico columnae-Fagenion moesiacae* and *Doronico orientalis-Fagenion sylvaticae* was based on the altitudinally and the strongly geographically distinct groups of diagnostic species. Dzwonko & Loster (2000) placed them as separate suballiances of *Aremonio-Fagion*, while Bergmeier & Dimopoulos (2001) and Tzonev et al. (2006) classified them into *Fagion sylvaticae*. The reason is probably a lack of comparable data from the intermediate area between the SE part of the researched area and C European *Fagion sylvaticae* forests.

These forests were classified to different alliances, as already proposed in the past but not validly described, according to ICPN, by Quézel (1967), Dafis (1973) and Horvat et al. (1974). Because we are taking a larger area into consideration, we suggest that both of them, together with suballiance *Tilio tomentosae-Fagenion sylvaticae*, should be classified into the alliance *Fagion moesiacae*, although Cluster 7 is rather isolated from the rest of the data set and indicates a somewhat unique floristic composition.

According to our results, the number of species significantly decreases towards the southeast and BF of that area are relatively species-poor, especially those belonging to *Doronico orientalis-Fagenion sylvaticae*, mainly located in NE Greece, on the edge of the alliance area. The area's centre lies in SW Serbia and in W and C Bulgaria (Fig. 1). It is therefore hard to find appropriate diagnostic and differential species for the alliance.

At the same time, the question is raised of the low number of species, including BF species (Willner et al. 2009), in that region. It is clear from Fig. 6, which shows the average number of species in different clusters, that the highest number can be found in the group of clusters belonging to *Aremonio-Fagion* and the lowest number of species in both cases can be found in Clusters 5 and 7. There are various reasons for the lower number of species in the SE part of the investigated area. One possible reason is that BF form the timber line in the SE (Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001), in contrast to the NW part of the researched area (SE Alps, Dinarids), where the timber line consists almost entirely of coniferous forests (*Pinus mugo, Larix decidua, Picea abies*). There are therefore no other forest communities above them in the SE and the rare species exchange is restricted to grassland communities above and to forests in contact with lower belts. The species pool is consequently limited.

Another reason could be the acidophilous character of the substrate in the southern part (Tsiripidis et al. 2007). Ewald (2003b) claims that the pool of C European flora consists of a majority of vascular plant taxa that are restricted to very base-rich and calcareous soils and offers the hypothesis that Pleistocene range contractions caused the extinction of more acidophilous than calciphilous species, because acid soils were much rarer when refugial areas were at their minimum. Willner et al. (2009) also found that acidic BF contributed little to the number of beech forest species and that soil type diversity is a weak predictor of the number of beech forest species. They found distance to the nearest potential refuge area to be the strongest predictor of beech forest species richness. On the basis of our analysis, we found forests of Cluster 6 had the highest species richness in the SE part of the region (Fig. 6). On the basis of their and our own findings, we can corroborate one of the potential refuge areas in SW Bulgaria, proposed by Magri et al. (2006).

Syntaxonomy should reflect the main factors that cause the differentiation of vegetation types. Regionally defined units reflect macroclimatic patterns, while locally defined vegetation units usually reflect patterns connected with local ecological factors, such as soil properties or altitude (Knollová & Chytrý 2004). We found the influence of different climatic types in the Balkan Peninsula were very important for distinguishing these two forest types (alliances).

Our study also confirmed ecological factors as the basis for the second level of division (Fig. 3), which reflect regionally defined units. We found that soil reaction was an insignificant factor for differentiation, which is in agreement with Di Pietro (2009), who claimed that the role of soil pH, which serves to distinguish basiphilous BF (*Fagion* s. l., *Fagetalia*) and acidophillous BF (*Luzulo-Fagion*, *Querce-*

talia robori-petraeae), appears not to be applicable to the Apennines.

The question of the prevailing impact of ecological as opposed to macroecological and phytogeographical gradients on vegetation, and vice versa, arises in many studies (Willner 2002; Tzonev et al. 2006; Tsiripidis et al. 2007). Unfortunately, these studies were done on the northern and southern edges of the distribution area and did not comprise the whole diversity of Balkan BF. A quick glance at the vegetation units distinguished in the past, at separate local levels, shows the delimitation of vegetation on the basis of various criteria. Marinček et al. (1992) classified BF based on ecological conditions within the framework of the geographically distinguished *Aremonio-Fagion* alliance. Tzonev et al. (2006) established that Bulgarian *F. sylvatica* communities do not show any distinct pattern of geographical differentiation but follow edaphic and local topoclimatic gradients. The reason for such results is the relatively small investigation area. Strong phytogeographical differentiation along a N–S gradient is suggested for BF in S Serbia, Macedonia and N and C Greece (Dzwonko et al. 1999; Dzwonko & Loster 2000). This is in accordance with the results of our study, although Dzwonko & Loster (2000) neglected refugia in the S Balkans and classified all BF communities (except acidophilous BF) into the alliance *Aremonio-Fagion*.

Together with a significantly increased proportion of life forms (chamaephytes, therophytes) and chorotypes (above all Stenomediterranean, Eurymediterranean, Mediterranean-Montane species) toward the SE, the results show that beech forest communities are differentiated on the basis of (phyto)geographical and macroclimatic conditions, while ecological factors have a stronger influence on vegetation on a smaller scale. There is not only narrower altitudinal distribution of BF in the SE part of the research area, but also structural, functional and geo-elemental changes of BF as a result of changed macroclimatic factors and their development in the post-glacial period.

Conclusions

Our investigation confirmed the division of BF into two alliances in the region (Rodwell et al. 2002). Classification to lower units and the status of some forests, especially lowland BF on the edge of the area, extending from the Pannonian lowland (mainly Croatia and Serbia) to NE Bulgaria, is not very clear and needs further investigation. The findings of Tsiripidis et al. (2007) that the S Balkan Peninsula is a place in which views and hypotheses on the role of ecological and geographical factors in the differentiation of beech forest vegetation are partly complementary and partly contradictory, can be generalized for the whole of SE Europe.

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Appendix 1: Nomenclature of *Fagus sylvatica* forest syntaxa in Southeast Europe

Querco-Fagetea Braun-Blanquet et Vlieger in Vlieger 1937

Fagetalia sylvaticae Walas 1933

Aremonio-Fagion Török, Podani et Borhidi ex Marinček, Mucina, Zupančič, Poldini, Dakskobler et Accetto 1993

Lamio orvalae-Fagenion Borhidi ex Marinček, Mucina, Zupančič, Poldini, Dakskobler et Accetto 1993

Saxifrago-Fagenion Marinček, Mucina, Zupančič, Poldini, Dakskobler et Accetto 1993

Ostryo-Fagenion Borhidi ex Soó 1964 (incl. ***Epimedio-Fagenion*** Marinček et al. 1993)

Fagion moesiacae Blečić et Lakušić 1970

(Syn.: *Fagion moesiacum Fukarek* 1969 nom. inval. [art. 2b], *Fagion moesiacum* Horvat, Glavać et Ellenberg 1974 nom. illeg. [art. 34], *Fagion moesiacae* Török, Podani et Borhidi 1989 nom. illeg. [art 31], *Doronico orientalis-Fagion moesiacae* Dierschke 1998 nom. inval. [art. 2b], Doronico columnae-Fagion moesiacae (Dzwonko, Loster, Dubiel et Drenkovski 1999) Dierschke 2004 [syntax. syn.])

Doronico orientalis-Fagenion sylvaticae Marinšek, Čarni et Šilc suball. nov.

(Syn.: *Doronico orientalis-Fagenion moesiacae* Raus 1977 nom. inval. [art. 1], *Doronico orientalis-Fagenion moesiacae* Raus 1980 nom. inval. [art. 2b], *Doronico orientalis-Fagenion moesiacae* Raus ex Raus 1980 nom. inval. [art. 2b], *Doronico orientalis-Fagenion moesiacae* Raus ex Bergmeier 1990 nom. inval. [art. 5], *Doronico orientalis-Fagenion moesiacae* Raus ex Bergmeier et Dimopoulos 2001 nom. inval. [art. 3f])

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Doronico columnae-Fagenion moesiacae Dzwonko, Loster, Dubiel et Drenkovski 1999
Tilio tomentosae-Fagenion sylvaticae Marinšek, Čarni et Šilc suball. nov.

New syntaxa and lectotypifications

Fagion moesiacae Blečić et Lakušić 1970:
Lectotypus hoc loco: *Elymo-Fagetum moesiacae* Blečić et Lakušić 1970 (Nomenclatural type, lectotypus: relevé no. 2, table 4 in Blečič et Lakušić (1970))

Doronico orientalis-Fagenion sylvaticae Raus ex Marinšek, Čarni et Šilc suball. nov. hoc loco:
Nomenclature type –holotypus: *Lathyro alpestris-Fagetum sylvaticae* Bergmeier 1990
Diagnostic species: *Abies borisii-regis, Lathyrus alpestris, Luzula forsterii, Silene multicaulis, Monotropa hypopitys, Doronicum orientale.*
Ecological circumstances: thermophilous beech forests of continental part of the southern Balkan, nder the influence of the Mediterranean climate.

Tilio tomentosae-Fagenion sylvaticae Marinšek, Čarni et Šilc suball. nov. hoc loco:
Nomenclature type –holotypus: *Tilio tomentosae-Fagetum sylvaticae* Tzonev, Dimitrov, Chytrý, Roussakova, Dimova, Gussev, Pavlov, Vulchev, Vitkova, Gogoushev, Nikolov, Borisova et Ganeva 2006.
Diagnostic species: *Tilia cordata*, *Glechoma hirsuta* and *Tilia tomentosa**.
*taxon *Tilia tomentosa* has phi-value 17.5 but its geographical distribution corresponds to the areal of the the suballiance. Therefore we decided to select it as a diagnostic species. Ecological circumstances: lowland thermophilous beech forests under continental climate.

Supporting Information

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

Appendix S1. Bibliography of relevé data Set.

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