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Classification and phytogeographical differentiation of broad-leaved ravine forests in southeastern Europe

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Abstract

Question: How do broad-leaved ravine forests in SE Europe differentiate phytogeographically? Do they differ from analogous European forests? What is their distribution pattern?

Location: southeastern Europe, Apennine-Balkan province.

Methods: The initial data set of 2189 relevés was stratified geographically and phytosociologically; 614 relevés remaining after stratification were classified with a TWINSPAN and cluster analysis, wich resulted in four clusters and eight subclusters. Average Pignatti indicator values for relevés of each subcluster were subjected to PCA to show ecological relationships among the clusters. The spectra of geoelements and sociological species groups of individual subclusters were calculated to show phytogeographical and sociological relationships between them. The diagnostic species combination was calculated by a fidelity measure (ϕ-coefficient) and presented in a synoptic table.

Results: Broad-leaved ravine forests in southeastern Europe form a separate group within the European broad-leaved ravine forests. They are well differentiated by the species with a southeast European distribution, as well as by many other species that reflect their different ecological affinities.

Conclusions: The phytosociological and phytogeographical relationships between the Apennines and the Balkan peninsula that have already been recognized for other vegetation types have been confirmed for broad-leaved ravine forests. According to the numerical analysis, two suballiances of broad-leaved ravine forests in southeastern Europe are proposed, both belonging to the alliance *Tilio-Acerion*: an amphi-Adriatic xerothermophilous suballiance *Ostryo-Tilienion platyphylli* suball. nova and a mesophilous suballiance *Lamio orvalae-Acerenion* suball. nova, the latter appearing only on the Balkan Peninsula.

Keywords: *Acer*; Apennines; Balkan Peninsula; Biogeography; Fidelity; *Fraxinus*; Numerical analysis; Phytosociology; Syntaxonomy; *Tilia*; *Ulmus*.

Abbreviation: BLRF = Broad-leaved ravine forest.

Nomenclature: Tutin et al. (1964-1980); except *Stellaria montana* Pierrat and *Dryopteris affinis* (Lowe) Fraser-Jenkins. *Fagus moesiaca* is included in *Fagus sylvatica*; syntaxonomy follows Mucina et al. (1993), except for the syntaxa under consideration. New names are based on the nomenclature rules in Weber et al. (2000).

Introduction

Broad-leaved ravine forests (BLRFs) grow on spatially restricted sites with specific soil conditions. They occur on slopes, on the foot of slopes, in sinkholes, gorges and hollows with colluvial, skeletal and primarily unstable soil, which allow the broad-leaved trees *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos* and *Ulmus glabra* to replace otherwise competitively stronger tree species, above all *Fagus sylvatica* (Clot 1990; Müller 1992; Mucina et al. 1993; Ellenberg 1996).

BLRFs have already been thoroughly studied in many parts of Europe. In central Europe they are classified into the *Tilio-Acerion* alliance, within which two ecological groups of associations are distinguished, recognized as suballiances by some authors (Müller 1992; Willner 1996): a group of mesophilous *Acer* associations and a group of xerothermophilous associations with *Tilia* and *Corylus* (Mucina et al. 1993; Borhidi 2003). Forests of both groups of associations are found on sites with similar soils, but they differ in temperature and moisture requirements. There have been some locally focused publications on BLRFs in southeastern Europe, but there is still is no synthetic review of these forests in the region available.

We focus on southeastern Europe (Apennine-Balkan province, Fig. 1), the distribution area of zonal *Carpinus* forests of the alliance *Erythronio-Carpinion* and *Fagus* forests of the alliance *Aremonio-Fagion,* both of the order *Fagetalia sylvaticae*, and of thermophilous forests of the alliance *Carpinion orientalis* of the order *Quercetalia pubescentis*. All of these communities are very rich in species and occur on both sides of the Adriatic Sea in the Apennines and the Balkans. They are characterized by numerous relict and endemic species that survived Quaternary glaciations in southern European refugia (Bennet et al. 1991; Trinajstić 1992; Tzedakis 1993; Magri 1998; Petit et al. 2002).

It has already been established that mesophilous deciduous forests of southeastern Europe differ from forests in central Europe, and vicariant alliances have been described. The southeastern European alliances *Aremonio-Fagion* and *Erythronio-Carpinion* are vicariant to the central European alliances *Fagion sylvaticae* and *Carpinion betuli* within the order *Fagetalia sylvaticae*. In that respect, the question of phytogeographic differentiation within European BLRFs is raised. Should southeastern European BLRFs be classified like zonal vegetation of *Fagus*- and *Carpinus* forests in a vicariant alliance regarding central European forests? This paper addresses this question by reviewing and discussing BLRFs in southeastern Europe, above all their floristic composition, chorology, syntaxonomy and phytogeographical differentiation in comparison with the central European BLRFs.

Methods

Forest vegetation relevés made by applying the Braun-Blanquet approach (Braun-Blanquet 1964), classified by their authors as broad-leaved ravine forests and/or dominated by broad-leaved species, and originating from SE and C Europe (Fig. 1), were collected from the literature (*n* = 2636). Relevés were entered into the TURBOVEG (Hennekens & Schaminée 2001) database. The relevés with an incomplete list of herb species indicated by the authors were not included into the analyses. With regard to the definition of BLRFs by Clot (1989), we excluded the relevés whose dominant tree species (cover value 4 and 5) are species of climazonal and other forest types (*Abies alba*, *Alnus glutinosa*, *A. incana*, *Carpinus betulus*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus ornus*, *Ostrya carpinifolia*, *Picea abies*, *Quercus cerris*, *Q. ilex*, *Q. petraea*, *Q. pubescens* and *Q. robur*), as well as those where none of the tree species characteristic of BLRFs (*Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata, T. platyphyllos* and *Ulmus glabra*) had a cover value of at least 2 (Chytrý et al. 2002a). There were 2189 BLRF relevés remaining after this selection.

This data set of 2189 relevés was then stratified. Stratified resampling was made by combining the geographical stratification with stratification by phytosociological association (Knollová et al. 2005). This means up to ten relevés of one association in one area were selected in such a way that different authors, different publications and different locations within the area were represented. We took the biogeographic map of Europe (Rivas-Martínez et al. 2004) as the basis of geographical stratification, where sectors were used as geographical strata. The associations were defined according to synthetic works (Clot 1990; Mucina et al. 1993; Willner 1996) or expert assignments in case they were not treated in any of those synthetic works. Syntaxa described in older publications under the names *Aceri-Fraxinetum*, *Aceri-Tilietum* and *Tilio-Fraxinetum* were considered separately according to the author and publication. After stratification, 614 relevés remained (App. 1), originating from 87 combined geographic-habitat strata.

As many authors did not record mosses, we excluded them from our analysis before numerical processing. For the purpose of numerical analysis and in the synoptic table we unified the system of layer division, which differs from author to author. All sublayers of the tree layer were incorporated into one, whereas the herb and scrub layers, where scrub species, tree saplings, seedlings and lianas occur, were united into one scrub layer.

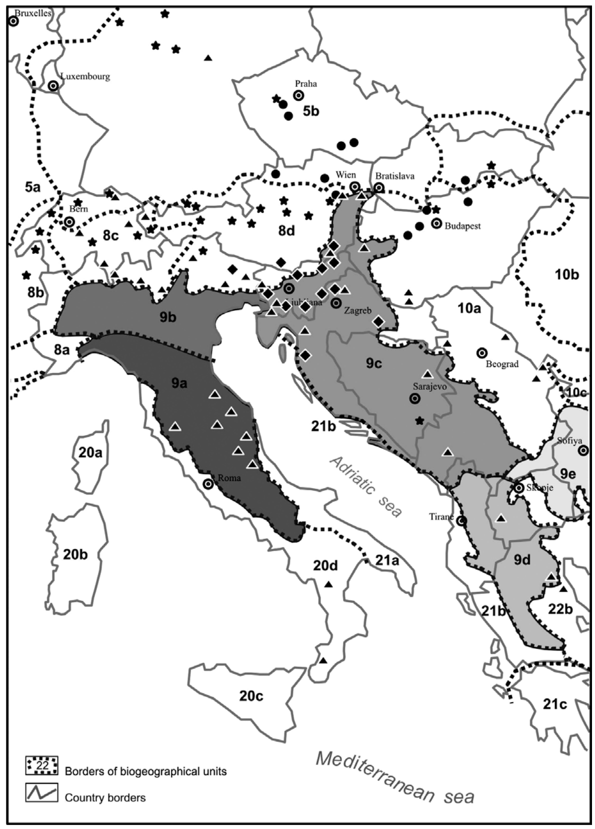

Fig. 1. The study area on the Biogeographical map of Europe (Rivas-Martínez et al. 2004). Legend: The Apennine-Balkan province (9; shaded) is divided into the Apennine (9a), Padanian (9b), Illyrian (9c), Pindan (9d) and Bulgarian (9e) sectors. Neighbouring provinces and sectors include the central European province (5) with the middle European sector (5b), Alpine province (8) with the western Alpine (8b), central Alpine (8c) and Eastern Alpine (8d) sectors, Pannonio-Carpathian province (10) with the Pannonian (10a) and Carpathian (10b) sectors, Italo-Thyrrhenian (20), Adriatic (21) and Graeco-Aegean (22) province. Broad-leaved ravine forest suballiances distinguished in this paper: ▲ *Ostryo-Tilienion,* ◆ *Lamio orvalae-Acerenion,* ● *Tilienion*, ✱ *Lunario-Acerenion*.

When processing and analysing the BLRF relevés of SE and C Europe we carried out a TWINSPAN classification (Hill 1979), run under the JUICE 6.4 program (Tichý 2002). TWINSPAN pseudospecies cut levels for species abundances were set to 0 -2 -5 -10 -20% scale units as proposed by McCune & Grace (2002). Initially, six division levels were chosen and the minimum group size for division was set to five relevés. As we were investigating classification of BLRFs on the level of superior syntaxa, the level of division was raised until groups of relevés still interpretable regarding ecology and phytogeography were obtained. Three levels of division were accepted, resulting in eight groups of relevés.

As TWINSPAN cannot perform a fully hierarchically organized classification tree (it does not consider cluster heterogeneity), the relationships between the resulting eight TWINSPAN groups were further investigated by cluster analysis, using the SYN-TAX program (Podani 2001). Percentage frequencies of species occurrences (constancies) in the eight TWINSPAN groups were used as input data for cluster analysis. We used several methods: β-flexible with parameter $\beta = -0.25$, group average (UPGMA), complete link (farthest neighbour) method with similarity ratio as the resemblance measure, all leading to similar results. Only the result of the complete link method is presented in this paper. One TWINSPAN group with a small number of relevés, set apart on the first level of cluster analysis, was not interpreted (see explanation later in the text).

According to the result of cluster analysis of seven TWINSPAN groups (subclusters), four clusters were obtained, since several authors suggested that there are four groups based on the main ecological and phytogeographical gradient of these forests in the area. Further, these four main clusters were also supported by the spectra of geo-elements and sociological species groups (see below).

Diagnostic species of each of the seven subclusters and four clusters were determined in the JUICE 6.4 program (Tichý 2002) by calculating the fidelity of each species to each cluster and subcluster (Bruelheide 1995, 2000; Chytrý et al. 2002b; Havlová et al. 2004), using the ϕ-coefficient as fidelity measure and presented in Table 1. In these calculations, each cluster was compared with the other relevés in the data set, which were taken as a single, undivided group. Each of the seven subclusters and four clusters was virtually adjusted to 1/7 or 1/4 of the size of the entire data set, respectively, while holding the percentage occurrences of a species within and outside a target cluster the same as in the original data set (Tichý & Chytrý 2006). Species diagnostic for the BLRFs of SE Europe (calculated after merging subclusters 2.1, 2.2 and 4.1, whose relevés geographically belong to this area) are also indicated in Table 1. For this analysis, fidelity was calculated based on the merged clusters and after adjusting the number of relevés to 1/2 of the size of the entire data set. We also calculated Fisher´s exact test and gave zero fidelity value to the species with significance $P < 0.001$. The range of the ϕ-coefficient is –1 to 1, but the values were multiplied by 100 in Table 1. The threshold ϕ-value for the species to be considered as diagnostic was set at 30.0.

For further interpretation of the seven subclusters and four clusters, unweighted average indicator values for relevé groups (Pignatti 2005), calculated in the JUICE program, were passively projected onto a Principal Components Analysis biplot (PCA from CANOCO 4.5; ter Braak & Šmilauer 2002) to show ecological relationships among these clusters and to explain environmental gradients underlying the main ordination axes. Square-root transformed percentage frequencies were used as the input data.

We also calculated the spectra of geo-elements and sociological species group composition of individual subclusters. Spectra of geo-elements were calculated according to Poldini (1991) and Pignatti (2005). Five sociological species groups – diagnostic species of the class *Querco-Fagetea*, orders *Fagetalia sylvaticae* and *Quercetalia pubescentis*, and alliances *Carpinion orientalis* and *Aremonio-Fagion* – were taken from various literature sources (Poldini 1988; Marinček et al. 1993; Mucina et al. 1993; Oberdorfer 1994; Dzwonko & Loster 2000; Marinček & Čarni 2000; Blasi et al. 2001, 2004, 2005; Biondi et al. 2002). In general, the categories of geo-elements proposed by Pignatti (2005) were taken into consideration but some adjustments were made, such as Eurymediterranean (incorporating Stenomediterranean), Mediterranean-montane, Eurasian (incorporating montane European, montane central European, montane south European), separately elaborating SE European (incorporating montane SE European) and Pontic, Atlantic (incorporating montane SW-European), Endemic, Cosmopolitan, Palaeotropic and Adventive.

In the calculations, we considered only the species occurring in at least three relevés within individual subclusters (Dzwonko et al. 1999). The spectra of geo-elements and sociological species groups of individual subclusters are presented as proportions (percentage) of the entire species composition of individual subclusters. The proportions of geoelements in individual subclusters are plotted (similarly as average indicator values) as supplementary data on the PCA ordination diagram of seven subclusters to show phytogeographical relationships. The sociological species group spectra are indicated at the head of the synoptic table to show sociological relationships between subclusters.

Table 1. Synoptic table of the classification results (Fig. 2). Species values are percentage frequencies. Diagnostic species for the clusters and subclusters (defined as those with $\phi \geq 30.0$) are shown, ranked by decreasing value of the ϕ-coefficient, indicated by asterisks (for subclusters) and shading (for clusters and subclusters). t = tree layer, s = shrub layer, h = herb layer. Some of the species diagnostic for BLFs of southeastern Europe are, at the same time, diagnostic for only one cluster (cluster 2 or 4) and therefore appear twice in the table: they are indicated with r.

Subcluster number		1.1	2.1	2.2	3.1	3.2	3.3	4.1
No. of relevés		59	141	126	116	49	44	62
Cluster number		1	2		3			4
Sociological type (% of all species in the subcluster)								
Carpinion orientalis		0.5	7.1	4.5	0.5	0.6	0.7	0.6
Aremonio-Fagion		1.6	8.5	9.1	4.8	1.3	2	15.6
Quercetalia pubescentis		15.9	13.3	12.9	2.7	5	0.7	0.6
Fagetalia sylvaticae		34.9	30.9	32.7	51.3	48.4	52.7	55.7
Querco-Fagetea		19.6	17.7	17.8	17.6	12.6	9.6	10.8
Character species of *Tilio-Acerion*								
Fraxinus excelsior	t	51	71	60	78	67	25	42
Fraxinus excelsior	s	42	35	52	64	63	20	26
Ulmus glabra	t	39	48	40	63	47	25	40
Ulmus glabra	s	36	37	32	34	45	16	42
Tilia cordata	t	**42**	**11**	**44**	5	10	11	2
Tilia cordata	s	**29**	**4**	**38** *	3	10	2	3
Acer platanoides	t	**58**	**40**	**29**	11	2	2	10
Acer platanoides	s	**49**	**33**	**25**	16	8	2	8
Tilia platyphyllos	t	**76**	**55**	**56**	25	6	14	8
Tilia platyphyllos	s	**39**	**31**	**27**	9	6	14	5
Acer pseudoplatanus	t	46	70	67	**89**	**98**	**98**	**95**
Acer pseudoplatanus	s	37	38	54	**67**	**55**	**59**	**82**
Species diagnostic for one cluster								
Cluster 1								
Poa nemoralis	h	81 *	14	32	23	47	41	2
Sedum telephium	h	44 *	6	15	5	.	2	.
Quercus petraea	t	42 *	15	11	.	.	.	.
Quercus petraea	s	17	5	8	.	.	.	.
Campanula persicifolia	h	34 *	8	6	.	.	.	.
Carpinus betulus	t	63 *	40	23	3	.	.	24
Carpinus betulus	s	39	20	14	4	.	.	15
Cardaminopsis arenosa	h	29 *	2	6	.	4	.	6
Galium aparine	h	42 *	24	3	7	2	.	3
Euonymus verrucosus	s	31 *	11	11	.	.	.	.
Rosa canina agg.	s	27 *	5	9	3	.	.	.
Impatiens parviflora	h	25 *	4	2	8	4	2	.
Chelidonium majus	h	32	15	2	12	.	.	.
Cluster 2								
Primula vulgaris	h	.	29	25	2	.	.	3
Ostrya carpinifolia	t	.	16	34 *	1	.	.	2
Ostrya carpinifolia	s	.	2	5	.	.	.	.
Hedera helix	s	22	64 *	48	25	2	2	10
Fraxinus ornus	t	8	27	28	.	.	.	.
Fraxinus ornus	h	7	17	17	.	.	.	.
Acer campestre	t	17	51 *	22	3	.	.	11
Acer campestre	s	29	35	22	3	2	.	11
Crataegus monogyna	t	.	1	.	.	.	.	.
Crataegus monogyna	s	8	33	21	3	.	.	.
Rosa arvensis	s	2	18	22	.	.	.	.
Melica uniflora	h	12	47 *	18	6	.	2	2
Cyclamen purpurascens	h	2	10	56 *	4	.	.	13
Tamus communis	s	2	27	21	4	.	.	3
Helleborus odorus	h	7	30	16	1	.	.	5
Festuca heterophylla	h	2	17	20	1	2	.	.
Daphne laureola	h	3	24	13	1	.	.	2
Hepatica nobilis	h	25	30	51	10	6	2	6
Euonymus latifolius	s	.	13	26	.	.	2	6
Ligustrum vulgare	h	3	18	12	.	.	.	.
Melittis melissophyllum	h	5	13	19	.	.	.	.
Clematis vitalba	s	20	34	32	9	10	.	.
Cluster 3								
Impatiens noli-tangere	h	20	4	5	55 *	47	36	42
Viola biflora	h	.	.	.	2	16	45 *	.
Polygonatum verticillatum	h	.	.	6	10	37	55	16
Chaerophyllum hirsutum	h	2	2	2	10	22	59	13

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Quercetalia pubescentis		15.9	13.3	12.9	2.7	5	0.7	0.6
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Querco-Fagetea		19.6	17.7	17.8	17.6	12.6	9.6	10.8
Cluster 4								
Stellaria montana	h	.	4	8	1	.	.	55 *
Symphytum tuberosum	h	5	21	22	5	.	.	66 *
Cardamine bulbifera	h	10	39	13	7	.	.	71 *
Doronicum austriacum	h	.	.	3	.	.	.	35 *
Chrysosplenium alternifolium	h	8	9	2	24	2	16	60 *
Lamium orvala	h	.	13	25	2	.	.	56 *
Cardamine trifolia	h	.	1	9	8	.	5	44 *
Adoxa moschatellina	h	7	16	13	9	2	30	58 *
Anemone nemorosa	h	3	21	6	9	4	9	53 *
Cardamine enneaphyllos	h	7	28	27	5	2	9	63 *
Cardamine waldsteinii	h	.	1	.	.	.	.	24 *
Leucojum vernum	h	.	4	2	7	4	2	34 *
Scopolia carniolica	h	.	1	2	2	.	.	24 *
Dryopteris carthusiana agg.	h	3	2	5	9	8	27	39 *
Oxalis acetosella	h	19	16	33	53	37	64	77 *
Omphalodes verna	h	.	1	2	.	.	.	21 *
Polystichum braunii	h	.	1	4	3	.	.	24 *
Anthriscus nitida	h	5	1	.	7	2	5	27 *
Dryopteris affinis	h	.	1	6	6	.	2	27 *
Gentiana asclepiadea	h	.	1	10	5	10	7	31 *
Corydalis solida	h	5	13	1	.	.	.	27 *
Lunaria rediviva	h	15	8	5	33	14	25	48
Veratrum album	h	.	.	3	.	4	23	24 *
Sambucus nigra	t	2	2	1	.	.	.	.
Sambucus nigra	s	24	53	29	48	14	9	73
Polystichum x *illyricum*	h	.	.	4	.	.	2	16
Species diagnostic for one subcluster								
Acer obtusatum	t	.	19 *	1	.	.	.	.
Acer obtusatum	s	.	1	.	.	.	.	.
Lathyrus venetus	h	7	23 *	1	.	.	.	.
Galanthus nivalis	h	7	35 *	7	2	4	.	6
Ruscus hypoglossum	s	2	18 *	.	.	.	.	2
Tilia tomentosa	t	3	18 *	.	.	.	.	.
Tilia tomentosa	s	2	16 *	.	.	.	.	.
Crataegus laevigata	s	5	28 *	6	2	2	.	.
Anemone ranunculoides	h	12	34 *	2	6	.	2	8
Viola alba	h	.	17 *	1	1	.	.	.
Quercus cerris	t	3	16 *	.	.	.	.	.
Quercus cerris	s	2	4	.	.	.	.	.
Ornithogalum umbellatum	h	.	12 *	.	.	.	.	.
Ranunculus ficaria	h	10	28 *	1	3	.	.	15
Carex digitata	h	12	15	63 *	11	12	16	6
Luzula nivea	h	.	.	24 *	3	.	2	.
Lonicera xylosteum	s	15	10	72 *	39	31	23	21
Asplenium ruta-muraria	h	2	1	18 *	.	2	.	.
Solidago virgaurea	h	3	4	50 *	10	49	34	2
Galium laevigatum	h	.	.	17 *	.	.	2	3
Sorbus aria agg.	t	7	7	28	3	4	9	.
Sorbus aria agg.	s	2	3	23 *	.	6	5	.
Anemone trifolia	h	.	3	19 *	1	.	.	5
Knautia dipsacifolia	h	.	.	5	2	45 *	23	.
Phyteuma spicatum	h	.	4	16	14	63 *	27	8
Silene vulgaris	h	8	1	.	1	31 *	5	.
Crepis pyrenaica	h	.	.	.	.	22 *	5	.
Adenostyles glabra	h	.	.	6	7	37 *	18	2
Vicia sylvatica	h	2	.	1	.	20 *	2	.
Calamagrostis varia	h	.	1	19	1	41 *	16	2
Bromus ramosus agg.	h	15	10	18	9	51 *	5	2
Valeriana officinalis	h	7	6	6	2	41 *	36	.
Hordelymus europaeus	h	7	8	1	7	35 *	7	.
Cirsium oleraceum	h	.	4	.	8	35 *	23	6
Pimpinella major	h	3	1	3	.	22 *	2	.
Vicia sepium	h	2	5	4	3	27 *	7	.
Rubus saxatilis	s	.	.	3	1	20 *	11	.

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Querco-Fagetea		19.6	17.7	17.8	17.6	12.6	9.6	10.8
Carduus defloratus	h	.	.	2	.	16 *	7	.
Brachypodium sylvaticum	h	14	31	28	26	65 *	9	24
Buphthalmum salicifolium	h	.	.	2	.	14 *	.	.
Laserpitium latifolium	h	.	6	4	1	22 *	2	.
Saxifraga rotundifolia	h	2	13	8	13	6	70 *	18
Polystichum lonchitis	h	.	.	1	3	8	41 *	6
Adenostyles alliariae	h	.	1	.	3	.	36 *	8
Stellaria nemorum	h	2	1	6	12	12	50 *	19
Lonicera alpigena	h	.	1	20	7	16	52 *	8
Primula elatior	h	2	1	2	10	8	34 *	.
Cicerbita alpina	h	.	.	.	2	.	23 *	5
Polystichum aculeatum	h	3	21	29	38	24	80 *	40
Epilobium montanum	h	12	5	17	23	20	59 *	16
Paris quadrifolia	h	.	9	35	28	24	75 *	63
Picea abies	t	5	4	13	16	31	50 *	32
Picea abies	s	3	3	10	10	31	52 *	34
Streptopus amplexifolius	h	.	.	1	1	6	20 *	.
Rubus idaeus	s	20	1	14	14	22	52 *	16
Rumex alpestris	h	.	1	.	1	6	20 *	2
Lonicera nigra	s	.	.	2	1	8	20 *	2
Salix appendiculata	s	.	.	1	.	2	16 *	2
Valeriana montana	h	.	.	.	.	2	14 *	.
Crepis paludosa	h	.	1	.	2	4	18 *	2
Cystopteris montana	h	.	.	.	.	.	11 *	.
Cardamine pentaphyllos	h	.	.	22	9	8	41 *	19
Aconitum variegatum ssp. *paniculatum*	h	.	.	8	.	18	27 *	6
Veronica urticifolia	h	.	1	28	5	33	43 *	5
Ranunculus platanifolius	h	.	.	1	.	18	20 *	3
Species diagnostic for more than one subcluster								
Aconitum lycoctonum	h	5	18	10	6	69 *	68 *	10
Petasites albus	h	2	3	6	16	39	68 *	60 *
Athyrium filix-femina	h	2	9	20	33	31	80 *	90 *
Species diagnostic for broad-leaved ravine forests of SE Europe								
r *Symphytum tuberosum*	h	5	21	22	5	.	.	66 *
r *Lamium orvala*	h	.	13	25	2	.	.	56 *
r *Cardamine enneaphyllos*	h	7	28	27	5	2	9	63 *
r *Cyclamen purpurascens*	h	2	10	56 *	4	.	.	13
Polystichum setiferum	h	2	28	13	1	.	.	23
Other species with high frequency								
Fagus sylvatica	t	32	55	45	47	51	27	63
Fagus sylvatica	s	17	26	37	41	35	14	52
Lamiastrum galeobdolon	h	47	52	71	68	92	98	89
Geranium robertianum	h	85	56	61	75	73	73	45
Dryopteris filix-mas	h	51	38	67	69	53	89	87
Mercurialis perennis	h	39	52	62	71	80	41	48
Corylus avellana	s	59	60	84	51	35	16	44
Urtica dioica	h	63	33	16	61	33	48	71
Galium odoratum	h	39	44	29	66	61	41	42
Mycelis muralis	h	51	40	52	31	65	48	27
Senecio nemorensis	h	29	9	47	44	43	75	53
Actaea spicata	h	8	21	50	33	41	66	60
Salvia glutinosa	h	10	26	55	25	59	9	45
Campanula trachelium	h	37	33	43	16	59	18	8
Aegopodium podagraria	h	10	38	24	28	51	25	32
Asarum europaeum	h	25	44	42	30	8	5	29
Asplenium scolopendrium	h	3	27	39	36	6	27	42
Polygonatum multiflorum	h	19	48	46	27	4	5	29
Viola reichenbachiana	h	10	47	33	12	45	11	19
Pulmonaria officinalis	h	27	26	39	22	6	14	37
Aruncus dioicus	h	7	9	32	32	18	43	29
Arum maculatum	h	10	41	14	29	2	2	53
Fragaria vesca	h	22	20	38	9	37	18	5
Cystopteris fragilis	h	31	9	17	22	8	41	21
Asplenium trichomanes	h	24	21	48	21	10	11	13
Geum urbanum	h	34	34	14	18	18	11	11

Results

Clusters and their interpretation

Fig. 2 shows the result of the cluster analysis of the eight TWINSPAN groups of relevés (subclusters). The subcluster X comprises 17 relevés of xerothermophilous forests, 13 of which are from one author (Hierholzer 1957; *Acereto-Coryletum avellanae*, *Aceri-Fraxinetum*) from the northwestern Apennines with a high cover of *Corylus avellana*. Because of the small size, specific floristic composition and unclear interpretation of this subcluster, we decided to eliminate it from further analyses. Excluding subcluster X, the xerothermophilous forests and mesophilous forests divide at the next first level. At the second level, the two groups also divide geographically into a group of southeastern European and a group of central European forests, resulting in four main clusters. The list of the syntaxa in each subcluster and cluster is given in App. 1.

The classification of broad-leaved ravine forests is presented in a synoptic table (Table 1), in which statistically determined diagnostic species are indicated and ranked by decreasing fidelity.

Cluster 1 corresponds to subcluster 1.1 and is represented mainly by xerothermophilous forests from the middle European and Pannonian sector. The cluster is characterized by a group of thermophilous and nitrophilous species with Eurasian distribution, growing at lower altitudes in the *Quercus petraea* and *Carpinus betulus* belt. The central European *Tilia* associations *Aceri-Carpinetum*, *Aceri-Tilietum cordatae*, *Aceri-Tilietum platyphylli*, *Mercuriali-Tilietum*, *Roso pendulinae-Tilietum* and *Seslerio albicantis-Tilietum cordatae* are classified within this cluster.

Cluster 2 is characterized by thermophilous species of southeastern distribution, e.g. *Primula vulgaris*, *Ostrya carpinifolia*, *Fraxinus ornus*, *Cyclamen purpurascens*, *Helleborus odorus* and *Euonymus latifolius*. It comprises of two subclusters. Subcluster 2.1 is represented mainly by xerothermophilous forests from the Apennine, Illyrian and Pannonian sectors, and subcluster 2.2 by xerothermophilous forests from the Eastern Alpine, Illyrian, central Alpine and middle European sectors as it comprises the relict association *Asperulo taurinae-Tilietum* in the broader sense. Diagnostic species of subcluster 2.1 are thermophilous species with southeastern distribution (*Acer obtusatum*, *Lathyrus venetus*, *Galanthus nivalis*, *Tilia tomentosa*) and Eurymediterranean species (*Ruscus hypoglossum*, *Viola alba*, *Quercus cerris*). Diagnostic species of subcluster 2.2 indicate that the distribution of this subcluster is mainly related with the Alps (e.g. *Luzula nivea*, *Galium laevigatum*, *Anemone trifolia*).

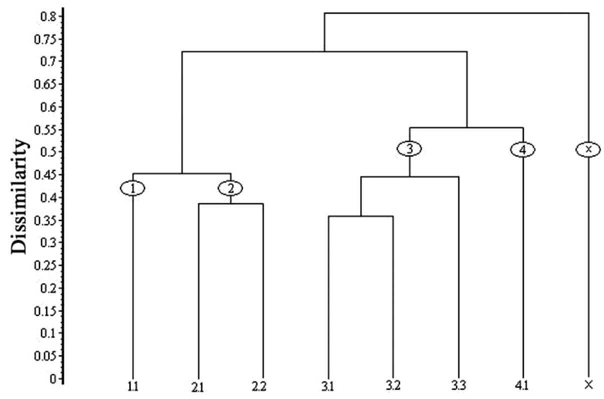

Fig. 2. Cluster analysis of the eight TWINSPAN groups of relevés (subclusters) of BLFs in southeastern and central Europe, resulting in four clusters.

Cluster 3 is characterized by a small group of mesophilous Eurasian species indicating colder and wetter sites. It comprises of three subclusters. Subcluster 3.1 is represented by mesophilous forests from the middle European, Eastern Alpine, western Alpine and central Alpine sectors; subclusters 3.2 and 3.3 are represented by mesophilous forests from the Eastern, western and central Alpine sectors. Subcluster 3.1 has no diagnostic species, as it represents, ecologically and phytogeographically, the core of central European BLRFs represented by the associations *Aceri-Fraxinetum*, *Arunco-Aceretum*, *Corydalido-Aceretum* and *Phylitido-Aceretum*. Subcluster 3.2 is characterized by species with Eurasian and Eurosiberian distribution indicating light and warm sites at higher altitudes; its relevés mainly belong to the central European associations *Sorbo-Aceretum* and *Asperulo taurinae-Aceretum*. Subcluster 3.3 is characterized by a species group indicating cold sites at higher altitudes, represented by the central European association *Ulmo-Aceretum*.

Cluster 4 corresponds to subcluster 4.1 and is represented almost exclusively by mesophilous forests from the Illyrian sector (*Aceri-Fraxinetum illyricum* s.lat.; *Chrysanthemo macrophylli-Aceretum*, *Dryopterido affinis-Aceretum*, *Hacquetio-Fraxinetum*, *Lamio orvalae-Aceretum*, *Omphalodo-Aceretum*). The cluster is characterised by the so-called Illyrian species, i.e. relic endemics of mesophilous forest sites with southeastern distribution, including *Stellaria montana*, *Lamium orvala*, *Cardamine trifolia*, *C. enneaphyllos*, *C. waldsteinii*, *Scopolia carniolica* and *Omphalodes verna*.

Phytosociological analyses

According to the phytosociological composition (Table 1), most species in all subclusters are classified as *Querco-Fagetea* and *Fagetalia sylvaticae* species, which is in accordance with the classification of these forests into the mentioned higher rank syntaxa. A relatively high proportion of *Quercetalia pubescentis* species is characteristic of xerothermophilous BLRFs of clusters 1 and 2. The proportion of *Fagetalia sylvaticae* is therefore greater in mesophilous BLRFs (clusters 3 and 4). A high proportion of *Carpinion orientalis* species characterizes both subclusters of cluster 2 (southeastern European *Tilia* forests). The proportion of *Aremonio-Fagion* species is considerably higher in cluster 4 (Illyrian *Acer* forests) than in other clusters of mesophilous forests. Within the xerothermophilous forests the proportion of *Aremonio-Fagion* species is the highest in both subclusters of cluster 2.

Indicator values and geo-elements

PCAs are presented of the seven subclusters with mean Pignatti indicator values (Fig. 3) and spectrum of geo-elements (Fig. 4) plotted as supplementary variables on the ordination diagram. Eigenvalues of the first two axes are 0.411 and 0.213. Xerothermophilous and mesophilous BLRFs are separated along the axis 1, while along axis 2 these forests are separated according to phytogeography.

Temperature and moisture (Fig. 3) show a high correlation with PCA axis 1, light and nutrient show moderately high correlation with axis 2. *Tilia* forests occur on warmer and drier sites, *Acer* forests on colder and wetter sites. Forests of SE Europe (Apennine-Balkan province) occur on nutrient richer soil and more shaded sites than C-European BLRFs. Nutrient richer soils are probably associated with thriving in the region of a warmer macroclimate. Together with the relatively wet sites, this suggests that decomposition of organic matter proceeds faster. *Acer* and *Tilia* forests, and forests generally, are better preserved in the Illyrian sector and less changed due to economic influences, and perhaps more shade.

The proportions of Pontic, Eurymediterranean and Eurosiberian species are highly correlated with axis 1 and the proportions of SE-European and Mediterranean-montane species are correlated with Axis 2 (Fig. 4). This means that Pontic and Eurymediterranean species are characteristic of subclusters of *Tilia* forests on the left side of the diagram, Eurosiberian species of subclusters of *Acer* forests on the right side, SE-European and Mediterranean-montane species of Apennine-Balkan subclusters in the upper part, and Eurasian species of C-European subclusters in the lower part of the diagram.

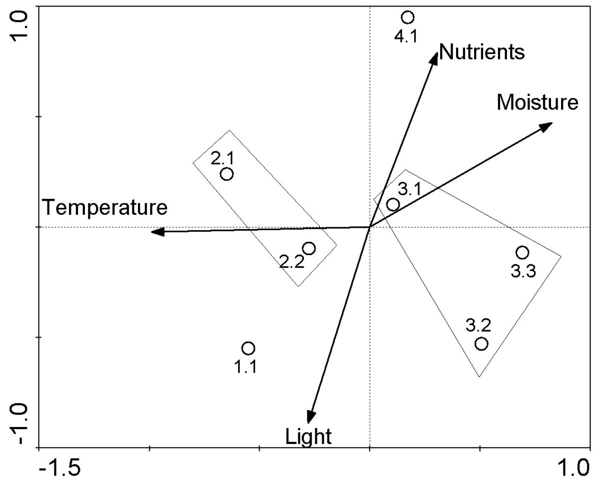

Fig. 3. Principal components analysis (PCA) of subclusters and Pignatti indicator values plotted as supplementary data on the diagram. The subclusters are numbered as in Table 1. Clusters are framed. Only indicator values with the highest correlations with the first two PCA axes are shown. The highest correlations with the first axis have the indicator values for temperature (–0.988) and moisture (0.824), with the second axis the values for light (–0.889) and nutrients (0.789).

Discussion

Many authors have found that broad-leaved ravine forest communities in SE Europe differ from C-European communities. However, there are different views on the synsystematic classification of BLRFs:

1. Classification within the alliance of *Fagus* forests *Aremonio-Fagion* (Horvat 1938, 1962; Glavač 1958; Accetto 1991; Vukelič & Rauš 1998);
2. Classification within the separate suballiance *Polysticho setiferi-Acerenion*, still within *Fagus* forests of the alliance *Aremonio-Fagion* (Košir 1972; Marinček 1990; Borhidi & Kevey 1996; Dakskobler 1999; Košir & Marinček 1999; Košir 2002);
3. Classification into the broadly conceived central European alliance *Tilio-Acerion* (Zupančič & Žagar 1999; Taffetani 2000; Biondi et al. 2002; Catorci et al. 2003; Angiolini et al. 2005);
4. Classification into an independent SE- European alliance *Fraxino-Acerion* Fukarek 1969 (Fukarek 1969; Jovanović et al. 1986; Stefanović 1986; Sarić 1997; Kojić et al. 1998; Košir 2005 a, b) or heterogeneous alliance *Euonymo latifolii-Fagion* (Ubaldi 2003), vicariating with *Tilio-Acerion* in the Apennines.

The idea of classifying the SE-European BLRFs into the alliance *Aremonio-Fagion* was proposed after a study of *Acer* dominated forests occurring intrazonally within an area of Illyrian *Fagus* forests (Horvat 1938; Marinček

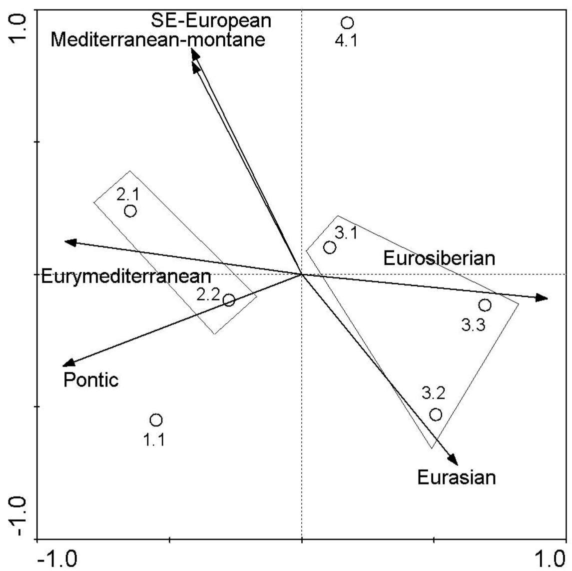

Fig. 4. PCA of subclusters and proportion of geo-elements in subclusters plotted as supplementary data on the diagram. The subclusters are numbered as in Table 1. Clusters are framed. Only geo-elements with the highest correlations with the first two PCA axes are shown. The highest correlations with the first axis have the values for Eurymediterranean (–0.897), Pontic (–0.903) and Eurosiberian (0.928) geoelement, with the second axis the values for SE European (0.853), Mediterranean-montane (0.804) and Eurasian (–0.719) geoelement.

1990). However, not all the BLRFs are spatially related to *Fagus* communities. In fact, *Tilia* dominated forests are more often linked to the zonal forests belonging to the alliances *Erythronio-Carpinion* or *Carpinion orientalis*. This suggests that classifying the southeastern European BLRFs into the alliance *Aremonio-Fagion* is not the most suitable solution.

Classification into an independent alliance, as proposed by Fukarek (1969), is not a suitable solution as we could not confirm it by the numerical analyses. Numerical analyses (Fig. 2) show that xerothermophilous or mesophilous BLRFs of different phytogeographic regions are more similar than xerothermophilous and mesophilous BLRFs of a single region. Despite this, there are a few species linking together mesophilous and xerothermophilous BLRFs of southeastern Europe (e.g. *Polystichum setiferum*, see Table 1).

Cluster analysis has suggested that BLRFs in southeast Europe differ from central European ones and that they form separate groups (Fig. 2). However, the central European alliance *Tilio-Acerion* is characterized by the dominance of some tree species such as *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos*, *Ulmus glabra*, which dominate ravine forests not only in central Europe but also in a large part of SE Europe. Therefore, we propose the assignment of BLRFs of southeastern Europe into the alliance *Tilio-Acerion*, and a further subdivision into two new suballiances of southeastern European distribution, one of which includes xerothermophilous and the other mesophilous BLRFs. These suballiances, named *Lamio orvalae-Acerenion* and *Ostryo-Tilienion* (see description below), are parallel to the already established central European suballiances *Lunario-Acerenion* and *Tilienion* (Table 1).

There are more plant species in BLRFs of SE Europe than in those of C Europe due to the general richness of woody species of SE Europe due to the effect of glacial refugia and the possible relic character of some stands (Trepp 1947). SE-European suballiances are, therefore, defined by groups of geographical differential species which are also ecologically coherent. We think that the classification based on ecological, as well as geographical, differential groups is more generally applicable than the classification which considers only ecological differences. After all, the differences in geographical position that result in different macroclimatic conditions are always reflected together with ecological ones.

Syntaxonomical classification

The suggested syntaxonomical classification of broad-leaved ravine forests in central and southeastern Europe is as follows:

Class: *Querco-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937
Ordo: *Fagetalia sylvaticae* Pawłowski et al. 1928
Alliance: *Tilio-Acerion* Klika 1955
Suballiance: *Tilienion platyphylli* (Moor 1975) Th. Müller 1992 (cluster 1 in Table 1)
Suballiance: *Lunario-Acerenion pseudoplatani* (Moor 1973) Th. Müller 1992; (cluster 3 in Table 1)
Suballiance: *Lamio orvalae-Acerenion pseudoplatani* suball. nova hoc loco (cluster 4 in Table 1)
Suballiance: *Ostryo carpinifoliae-Tilienion platyphylli* suball. nova hoc loco (cluster 2 in Table 1)

The nomenclatural type (holotypus) of the *Lamio orvalae-Acerenion pseudoplatani* is the association *Omphalodo vernae-Aceretum* P. Košir et Marinček 1999 *holotypus hoc loco*. Illyrian mesophilous BLRFs are classified into this suballiance.

The holotypus of the *Ostryo carpinifoliae-Tilienion platyphylli* is the association *Saxifrago petraeae-Tilietum platyphylli* Dakskobler 1999 holotypus hoc loco. Xerothermophilous BLRFs with the distribution centre in SE Europe (Apennine-Balkan province) are classified into this suballiance.

Mesophilous forests of the suballiance *Lamio orvalae-Acerenion* are geographically bound to the Illyrian subprovince (Fig. 1), as they are defined with mesophilous Illyrian species which are gradually disappearing towards the South and the east of the region as a result of the unfavourable climate (higher temperatures, unfavourable precipitation regime). Stands of *Acer* forests appear intrazonally within the range of zonal Illyrian beech forest communities of alliance *Aremonio-Fagion*.

The suballiance *Ostryo-Tilienion* includes xerothermophilous BLRFs from a great part of the Apennine-Balkan province (Fig. 1), especially from the regions with sub-mediterranean climate. They are defined by a diagnostic species combination which is partly shared with the alliance *Carpinion orientalis*. Only few associations of the *Ostryo-Tilienion* can be found also outside the limits of the Apennine-Balkan province as scattered islands of thermophilous relic BLRFs (e.g. association *Asperulo taurinae-Tilietum* in the Central Alpine and Eastern Alpine sectors and more sporadically in the Middle European sector, or associations *Scutellario altissimae-Aceretum* and *Tilio tomentosae-Fraxinetum orni* at the edge of the Pannonian sector).

In the southern Apennines and Balkans, the presence and cover of tree species characteristic of the *Tilio-Acerion* drastically decrease, while other tree species such as *Acer obtusatum*, *A. lobelii*, *Aesculus hippocastanum*, *Alnus cordata*, *Tilia platyphyllos* ssp. *pseudorubra* and *T. tomentosa* become dominant (Bonin 1978; Bergmeier 1990; Mazzoleni & Ricciardi 1995; Brullo et al. 2001; Corbetta et al. 2004; Amanatidou 2005). The syntaxonomic affinity of these tree species is not yet clear. As the alliance *Tilio-Acerion* is defined by dominance of *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos* and *Ulmus glabra*, we support the opinion that communities from the extreme south of Europe should be classified into a separate alliance vicariating with *Tilio-Acerion* (Brullo et al. 2001) or a separate suballiance within the alliance *Carpinion orientalis* (Blasi et al. 2006).

Vegetation in SE Europe (the Apennine-Balkan province) is chorologically uniform. This is because the refugia where the Apennine-Balkan vegetation, as well as European *Tilia* species (*Tilia cordata*, *T. platyphyllos*, *T. rubra, T. tomentosa*), survived the Quaternary glaciation were in the Apennine and the Balkan peninsula and on the southern and southeastern edges of the Alps (Lang 1994, 2003; Šercelj 1996; Magri 1998).

The distribution centre of mesophilous BLRFs is in the Central European and Alpine provinces. We can find most southern mesophilous stands only in the Illyrian sector of the Apennine-Balkan province. In contrast the distribution centre of xerothermophilous BLRFs is in southeastern Europe, namely in the Apennine-Balkan province.

Conclusions

It was found that broad-leaved ravine forests in the Apennine-Balkan province differ from the Central European BLRFs and can be differentiated as two suballiances within the alliance *Tilio-Acerion*, characterized geographically, ecologically and chorologically, sharing the same history. There are still some open questions about classification of BLRFs from the southern Apennine and Balkan peninsula that need further investigations. In the future, classification of BLRFs in southeastern Europe, especially within suballiance *Ostryo-Tilienion*, should be done also at the level of associations. This article establishes the similarity between the vegetation on both sides of the Adriatic Sea and thus confirms certain contemporary phytogeographical findings.

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