

Article

Diversity of *Ostrya carpinifolia* Forests in Ravine Habitats of Serbia (S-E Europe)

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Abstract: We investigated vegetation in ravine habitats of Serbia, in order to classify hop hornbeam (*Ostrya carpinifolia* Scop.) forests in syntaxonomic terms, assess the effects of environmental factors on their floristic differentiation, and detect the biodiversity components of the analyzed communities. Both K-means clustering and Bayesian classification revealed five ecologically interpretable groups of forests that belong to the alliances *Ostryo carpinifoliae-Fagion sylvaticae*, *Ostryo carpinifoliae-Tilion platyphylli*, *Fraxino orni-Ostryion carpinifoliae*, *Pseudofumario albae-Ostryion carpinifoliae*, and *Achilleo ageratifoliae-Ostryion carpinifoliae*. Canonical correspondence analysis indicated that these alliances are clearly differentiated along a combined light–moisture gradient (from shade and mesic to sunny and xeric variants). The alpha diversity increases from xeric to mesic alliances. A lower alpha diversity in xeric forests may be explained by the stress conditions that prevent mesic species from colonizing the saxatile habitats. Extremely high—almost the greatest possible—values of both the species turnover and beta diversity were detected in all variants of the analyzed forests. Such high diversity may be the result of the strong environmental gradients in ravine habitats. The investigated forests represent an important pool of rare, paleo-endemic species that survived Quaternary glaciations in ravine refugia.

Keywords: alpha diversity; beta diversity; species turnover; K-means clustering; Bayesian clustering; phytosociology; endemic species; syntaxonomy; canonical correspondence analysis



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1. Introduction

Ostrya carpinifolia Scop., commonly known as hop hornbeam, dominates in xeric amph-Adriatic alliances *Carpinion orientalis* Horvat 1954 and *Fraxino orni-Ostryion* Tomažič 1940 of the class *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959 [1–4]. Čarni et al. [4] and Stupar et al. [5] analyzed the ecological, floristic, and chorological differences between these alliances. In addition to the zonal belt of sub-Mediterranean xeric forests, the hop hornbeam forms mesic communities that are extrazonally distributed in inland parts of the Apennines and the Balkan Peninsula [2–8].

Ostrya carpinifolia Scop. is a species that is adapted to a warm to moderate climate, but it avoids a strictly Mediterranean climate with a marked summer drought. This species has wide tolerance limits with respect to both light and moisture gradients [9]. Due to its high tolerance to adverse soil conditions, it is most commonly located in canyons [2,3,8]. The stress conditions found in skeletal soils, and on screes and bare rocks, prevent stronger competitors from replacing the hop hornbeam in ravine habitats.

Ravine refugia of the Balkan Peninsula were important for species survival during periodic glaciations and for the postglacial recolonization of northern Europe during interglacial stages of the Quaternary [10–14].

Despite numerous studies having been conducted on ravine vegetation in central parts of the Balkan Peninsula [3–8,15–23], available information on the biodiversity components of *Ostrya carpinifolia* forests is incomplete. Therefore, we performed investigations of ravine vegetation in Serbia, in order to (1) classify hop hornbeam forests, (2) assess the effects of environmental factors on their floristic differentiation, and (3) detect patterns of biodiversity components (alpha and beta diversity) in investigated communities.

2. Materials and Methods

2.1. Study Area and Sampling Procedures

Using the Braun-Blanquet [24] sampling procedure, we collected 144 relevés from canyons of the Gradac, Trešnjica, Derventa, Djetinja, Ljutina, Mileševka, and Lim rivers (Figure 1). The set of originally collected relevés is stored in the FLORA database, and it is available upon request. The geographic coordinates of the study area are presented in Table 1. The size of the sampling sites varied from 15 × 15 m in mesic forests to 20 × 20 m in xeric communities. The importance of a species at a site was assessed using the numeric scale of combined cover-abundance values [25]. The taxonomic nomenclature was harmonized with the nomenclature for vascular plants and bryophytes in the Plant List Database (<http://www.theplantlist.org>).

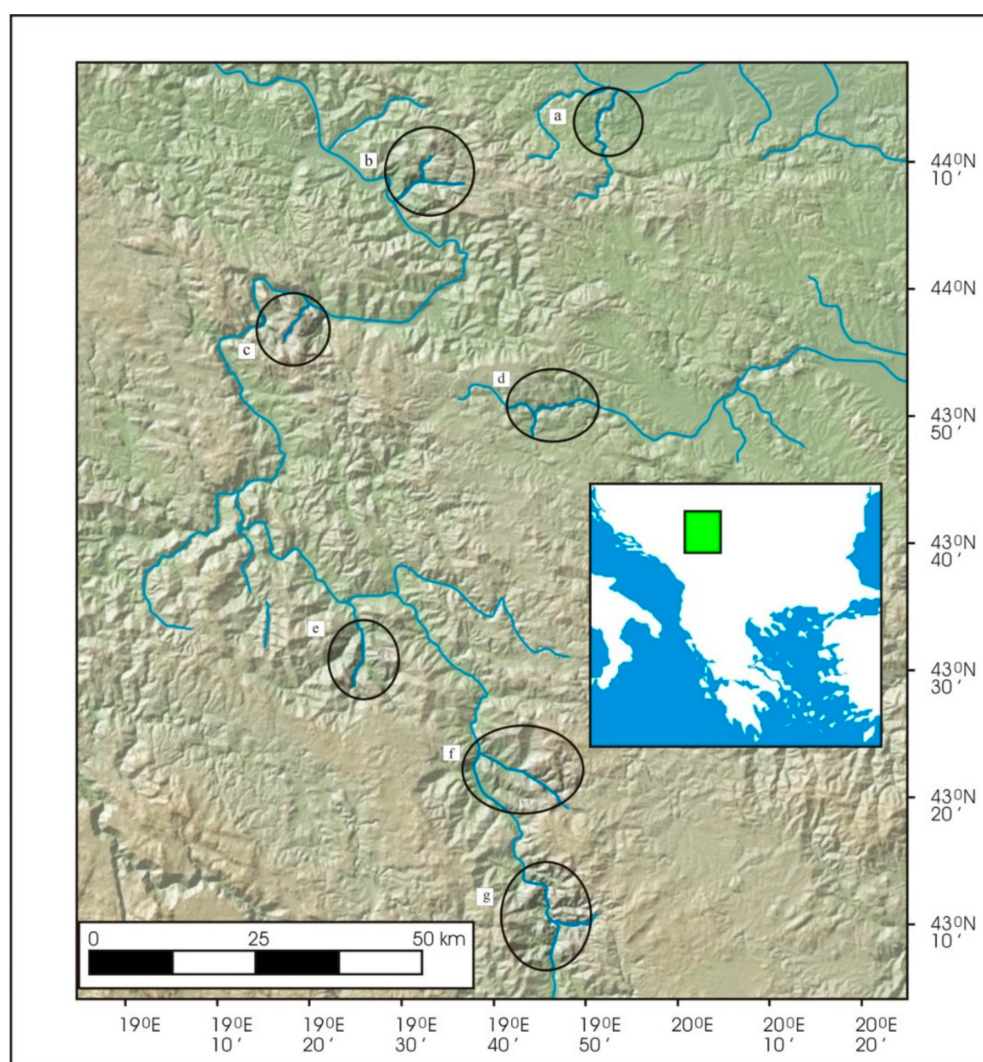


Figure 1. A map of the study area. The canyons of the Gradac (a), Trešnjica (b), Derventa (c), Djetinja (d), Ljutina (e), Mileševka (f) and Lim (g) rivers are circled.

Table 1. The geographic coordinates of the study area.

River	Geographic Coordinates	Number of Relevés
Gradac	44.188436 N, 19.868344 E–44.233333 N, 19.867778 E	23
Trešnjica	44.141667 N, 19.531667 E–44.150278 N, 19.540278 E	28
Derventa	43.954167 N, 19.356944 E–43.963056 N, 19.358333 E	21
Djetinja	43.848611 N, 19.808611 E–43.844444 N, 19.772778 E	18
Ljutina	43.475833 N, 19.405556 E–43.501389 N, 19.422500 E	20
Mileševka	43.364444 N, 19.728889 E–43.358889 N, 19.739722 E	15
Lim	43.190278 N, 19.766111 E–43.213056 N, 19.764167 E	19

2.2. Statistical Analyses

The classification of relevés may be performed using a wide spectrum of clustering methods. Hierarchical classification methods (different variants of agglomerative and divisive clustering) may produce a high number of misclassifications. To avoid the risk of misclassifications, we used both K-means clustering [26] and Bayesian classification [27]. These non-hierarchical methods enable the allocation of misclassified relevés and the formation of clusters that are as homogeneous as possible. Subjectivity in the initial estimation of the number of clusters is the main drawback of both methods. Marinković et al. [28] proposed a simple procedure to avoid this problem. It selects the number of clusters by maximizing the variance ratio:

$$VR = \frac{\sigma_B^2}{\sigma_W^2}, \quad (1)$$

where σ_B^2 denotes the between-group variance (i.e., variance of cluster centroids), and σ_W^2 is the within-group variance (the sum of variances within each of the k clusters). The fidelity of each species to different clusters was assessed using the phi coefficient [29].

The effects of environmental variables on the floristic differentiation of communities were assessed using canonical correspondence analysis [30]. Environmental variables included topographic parameters (altitude, slope, and aspect) and a set of variables (light, moisture, soil acidity, soil nutrients, temperature, and continentality) that were estimated indirectly, using the weighted average of Ellenberg's indicator values [31]. The stepwise forward selection procedure [27] was used to detect environmental variables with statistically significant effects on vegetation. During each step of the procedure, we expanded the multiple regression model by adding an environmental variable explaining most of the residual variance (i.e., the variance of vegetation data, not explained by previously selected environmental variables). The statistical significance of the hypothesis that vegetation is independent of selected environmental variables was assessed using the non-parametric Monte Carlo permutation test (3000 permutations, $p < 0.05$).

The alpha diversity was assessed using Shannon's entropy:

$$H = - \sum_{i=1}^s p_i \log p_i, \quad (2)$$

where p_i is the proportion of species i within a site, and s denotes the number of species within the site. Pielou [32] proved that the equitability component of alpha diversity can be calculated using the following equation:

$$E = \frac{H}{H_{max}} = - \sum_{i=1}^s p_i \log p_i / \log s, \quad (3)$$

where H_{max} is the greatest possible entropy.

The beta diversity represents the variability in species composition among communities [33,34]. Floristic difference between a pair of communities is attributable to both species turnover and species richness [35–41]. Two communities maximally differ if they have no species in common (Figure 2a). Such a situation corresponds to complete species

replacement from one to another community. However, a pair of communities may differ not because of species replacement, but due to a difference in species richness. In that case, the species-richer community may be considered a nest for the species-poorer community (Figure 2c). Therefore, the beta diversity component related to differences in species richness is frequently denoted as “nestedness”. Floristic differences between two communities are usually caused by both species turnover and nestedness (Figure 2b).

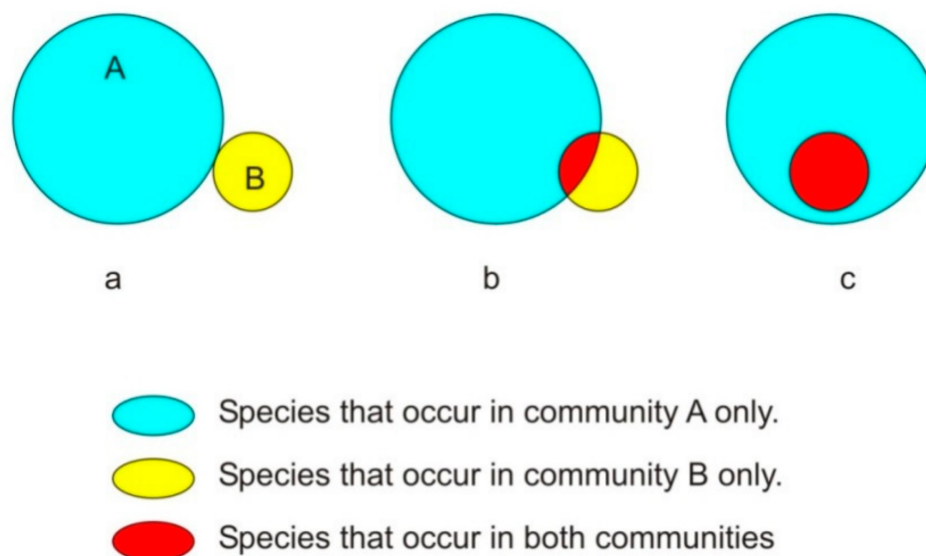


Figure 2. Venn diagrams of overlapping species in two communities. These diagrams may explain the concept of beta diversity components. The greatest beta diversity implies the complete replacement of a species from one to another community (a). Two communities may differ not because of species replacement, but due to differences in species richness (c). The beta diversity usually depends on both species turnover and nestedness (b).

Components of the beta diversity were determined using the procedures described by Baselga [35] and Podani et al. [37]. Statistical analyses were performed using the updated version of the FLORA software [42].

3. Results

We recorded 353 species of vascular plants in the investigated forests. A high percentage of phanerophytes (trees and shrubs) was characteristic for the analyzed communities. The screes and cliffs are covered by sparsely distributed individuals of *Ostrya carpinifolia* Scop. and other xeric trees. On more favorable soils, the hop hornbeam occurs in combination with numerous xeric and mesic species. Compared to the phanerophytes, the herbaceous plants were more diverse. A high percentage of herbaceous species belonged to the group of endemic Tertiary relicts. A selection of the huge amount of paleo-endemic species occurring in the investigated forests is shown in Figure 3.



Figure 3. Important endemic species that occur in hop hornbeam forests: *Onosma stellulatum* Wald. et Kit (a), *Lathyrus binatus* Pančić (b), *Achillea ageratifolia* (Sibth. & Sm.) Boiss. (c), *Daphne malyana* Blečić (d), *Athamanta turbith* (L.) Brot. subsp. *haynaldii* (Borbas & Uechtr.) Tutin. (e), *Aquilegia grata* Zimmeter (f), *Campanula secundiflora* Vis. & Pančić (g), *Euphorbia glabriflora* Vis. (h), and *Hieracium waldsteinii* Tausch (i).

3.1. Classification of Communities

The results of K-means clustering and Bayesian classification showed that the analyzed forests can be grouped into five homogeneous clusters (Table 2).

Table 2. Dependence of classification results on a pre-selected number of clusters. The greatest ratio of between-group variance (B) to within-group variance (W) assures that the overlap of homogeneous clusters is minimized. In our data set, the greatest variance ratio (bold font) was obtained for five clusters.

Number of Groups	Classification Method					
	K-Means Clustering			Bayesian Classification		
	B	W	B/W	B	W	B/W
2	0.0359	1.4760	0.0243	0.0344	1.4721	0.0234
3	0.0534	2.1473	0.0249	0.0513	2.1435	0.0239
4	0.0714	2.7889	0.0256	0.0721	2.7865	0.0259
5	0.1026	3.2876	0.0312	0.0890	3.4257	0.0260
6	0.1097	3.8599	0.0284	0.0866	4.0811	0.0212
7	0.1094	4.5725	0.0239	0.0934	4.7242	0.0198
8	0.1115	5.2554	0.0212	0.1089	5.3205	0.0205
9	0.1123	5.9542	0.0189	0.1112	5.9612	0.0187
10	0.1221	6.5167	0.0187	0.1201	6.5223	0.0184

For each cluster, a set of diagnostic species was detected using the phi coefficient. A synoptic table of the analyzed forests is presented in Appendix A.

Cluster 1 comprises mesophilous, shady forests on deep soil. Diagnostic species of the cluster are mesic species (*Asperula taurina* L., *Epimedium alpinum* L., *Fraxinus excelsior* L., *Evonymus europaeus* L., *Alliaria petiolata* (M.Bieb.) Cavara & Grande, *Pulmonaria officinalis* L., *Melampyrum hoermannianum* K. Malý, *Angelica sylvestris* L., *Parietaria officinalis* L., *Athyrium filix-femina* (L.) Roth, *Cardamine bulbifera* (L.) Crantz, *Cyclamen purpurascens* Mill., *Acer pseudoplatanus* L., and *Brachypodium sylvaticum* (Huds.) P.Beauv.). The forests included in this cluster may be assigned to the mesic alliance *Ostryo carpiniifoliae-Fagion sylvaticae* Borhidi 1963 of the order *Fagetalia sylvaticae* Pawłowski 1928.

Cluster 2 consists of mesic forests on both deep and skeletal soils. Its diagnostic species included mesic species (*Salvia glutinosa* L., *Hedera helix* L., *Asarum europaeum* L., *Tilia platyphyllos* Scop., *Scrophularia nodosa* L., *Aremonia agrimonoides* (L.) DC., *Juglans regia* L., *Campanula rapunculoides* L., *Lilium martagon* L., *Campanula trachelium* L., *Sanicula europaea* L., *Arum maculatum* L., and *Sorbus torminalis* (L.) Crantz.) and more xeric species (*Helleborus odoratus* Waldst. & Kit. ex Willd., *Scutellaria altissima* L., *Digitalis grandiflora* Mill., *Calamintha grandiflora* (L.) Moench., *Arabis turrata* L., and *Galium schultesii* Vest). These forests belong to the alliance *Ostryo carpiniifoliae-Tilion platyphylli* Košir et al. 2008.

Cluster 3 includes the xeric hop hornbeam forests that belong to the alliance *Fraxino orni-Ostryion carpiniifoliae* Tomažič 1940. Its diagnostic species are *Potentilla micrantha* Ram. ex DC., *Carex caryophyllea* Latourr., *Glechoma hirsuta* Waldst. & Kit., *Clinopodium nepeta* (L.) Kuntze, and *Fraxinus ornus* L.

Cluster 4 comprises xerothermophilous forests on screes and shallow skeletal soils. Diagnostic species of the cluster are *Pseudofumaria alba* subsp. *acaulis* (Wulfen) Lidén, *Stachys recta* L., *Teucrium montanum* L., *Prunus spinosa* L., *Draba lasiocarpa* Rochel, *Allium flavum* L., *Evonymus verrucosus* Scop., *Melica ciliata* L., *Campanula lingulata* Waldst. & Kit., *Fritillaria montana* Hoppe ex W.D.J.Koch, *Minuartia bosniaca* (Beck) K.Malý, *Clinopodium thymifolium* (Scop.) Kuntze, *Stipa calamagrostis* (L.) Wahlenb., *Rhamnus saxatilis* Jacq., *Coronilla emerus* subsp. *emeroides* (Boiss. & Spuner) Holmboe, and *Galium purpureum* L. These communities, which are floristically and ecologically clearly separated from other variants of investigated hop hornbeam forests, may be included in a new alliance of *Pseudofumario albae-Ostryion carpiniifoliae* all. nova.

Cluster 5 is represented by the chasmophytic xeric communities in stony habitats. Its diagnostic species are *Achillea ageratifolia* (Sibth. & Sm.) Boiss, *Seseli rigidum* Waldst. & Kit., *Euphorbia glabriflora* Vis., *Frangula rupestris* Schur, *Amphoricarpos neumayeri* Vis., *Globularia cordifolia* L., *Hieracium waldsteinii* Tausch, *Geranium macrorrhizum* L., *Campanula secundiflora* Vis. & Pancic, *Genista radiata* (L.) Scop., *Saxifraga crustata* Vest., *Valeriana montana* L., *Cerastium decalvans* Schloss. & Vuk., *Jurinea mollis* (Torn.) Rchb., *Saxifraga tridactylites* L., and *Silene pusilla* Waldst. & Kit. We have included communities of the cluster in a new alliance of *Achilleo ageratifoliae-Ostryion carpiniifoliae* all. nova.

These variants of the analyzed forests are distributed in clearly distinguishable habitat types (Figure 4). The mesic alliance *Ostryo carpiniifoliae-Fagion sylvaticae* occurs in shady habitats, on north-facing slopes or at the bottom of canyons, on deep soil (Figure 4a). Forests of the alliance *Ostryo carpiniifoliae-Tilion platyphylli* are also distributed in shady habitats but, unlike the previous alliance, on more skeletal soils (Figure 4b).

Xeric variants of the investigated forests usually occur in dry, sunny habitats. They differ with respect to soil conditions. Forests that belong to the alliance *Fraxino orni-Ostryion carpiniifoliae* occupy sunny habitats, either on gentle slopes, or at the foot of steep slopes, where the soil is relatively deep (Figure 4c). The new alliances proposed in this article (*Pseudofumario albae-Ostryion carpiniifoliae* and *Achilleo ageratifoliae-Ostryion carpiniifoliae*) occur in adverse scree and saxatile habitats (Figure 4d,e).



Figure 4. Habitats of the alliances *Ostryo carpinifoliae-Fagion sylvaticae* (a), *Ostryo carpinifoliae-Tilion platyphylli* (b), *Fraxino orni-Ostryion carpinifoliae* (c), *Pseudofumario albae-Ostryion carpinifoliae* (d), and *Achilleo ageratifoliae-Ostryion carpinifoliae* (e).

3.2. Patterns in the Vegetation–Environment Relationship

Forward selection analysis (Table 3) indicates that all of the environmental variables, except for the altitude, are significant for floristic differentiation of the analyzed forests.

A combined light–moisture gradient separates the analyzed forests from the shady and mesic variants (the alliances *Ostryo carpinifoliae-Fagion sylvaticae* and *Ostryo carpinifoliae-Tilion platyphylli*) to the sunny and xeric variants (the alliances *Fraxino orni-Ostryion carpinifoliae*, *Pseudofumario albae-Ostryion carpinifoliae*, and *Achilleo ageratifoliae-Ostryion carpinifoliae*). Light and soil pH gradients are correlated. Sunny and xeric variants of forests occur in screes and rocky cliffs. Due to the shallow soil on carbonate and serpentine rock, the soil pH in xeric variants of the forests (the alliances *Pseudofumario albae-Ostryion carpinifoliae* and *Achilleo ageratifoliae-Ostryion carpinifoliae*) is alkaline. In shady communities (the alliances *Ostryo carpinifoliae-Fagion sylvaticae* and *Ostryo carpinifoliae-Tilion platyphylli*), which are developed on relatively deep soil, the soil reaction is slightly acidic to neutral. The gradients of soil nutrients and soil pH are negatively correlated (Figure 5).

Both forward selection and canonical correspondence analysis indicate that the variants of the analyzed forests are clearly differentiated with respect to shade, moisture, and soil nutrient gradients. The environmental conditions of the investigated communities (Figure 6) additionally support these findings.

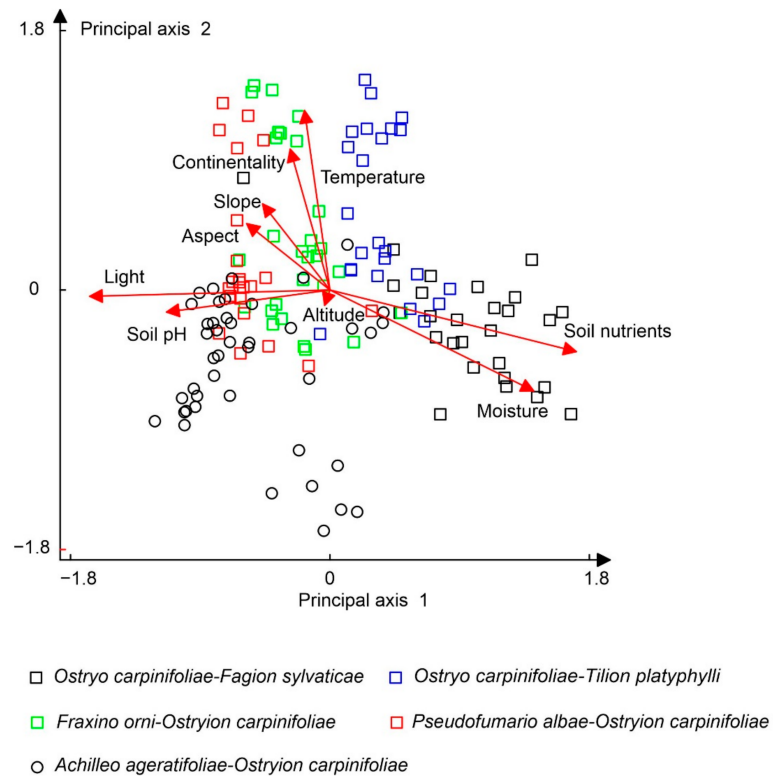


Figure 5. Canonical correspondence analysis of the investigated forests.

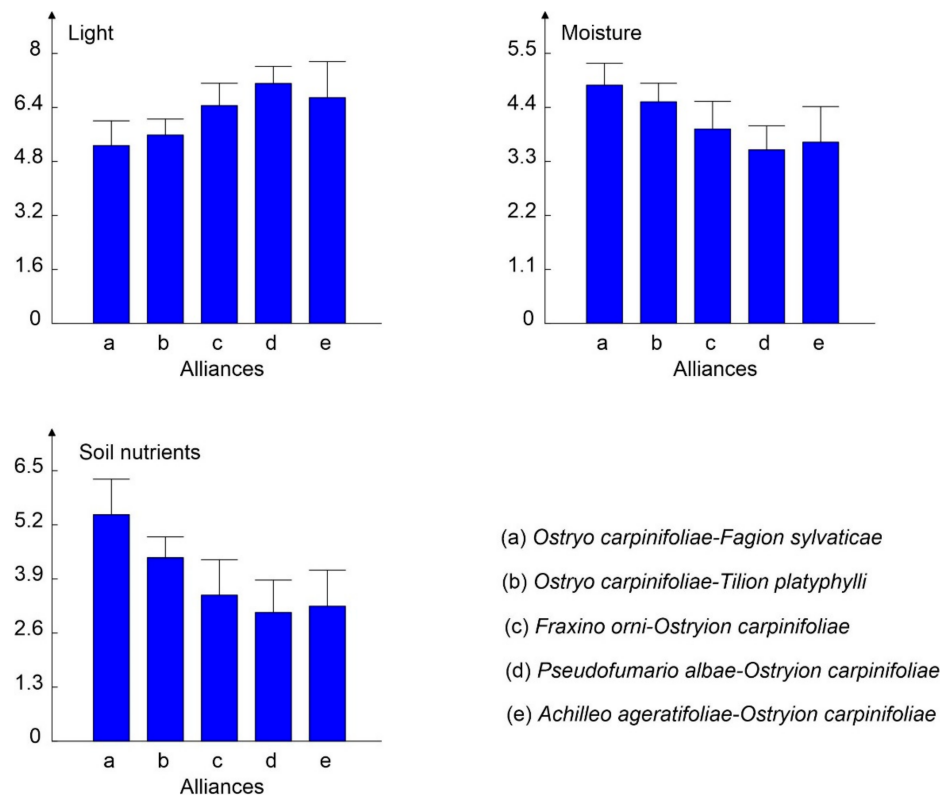


Figure 6. Environmental conditions in hop hornbeam forests. The blue bars are mean values and the lines are standard deviations of the light intensity, moisture, and soil nutrients in the investigated communities.

Table 3. Results of the forward selection analysis.

Variable	Eigenvalue	F Statistic	Probability
Soil nutrients	0.4214	5.101	0.000 *
Light	0.2365	2.818	0.000 *
Temperature	0.2252	2.682	0.000 *
Continentality	0.1730	2.051	0.000 *
Soil acidity	0.1324	1.564	0.000 *
Moisture	0.1234	1.457	0.000 *
Aspect	0.1087	1.282	0.002 *
Slope	0.1025	1.208	0.006 *
Altitude	0.0799	0.939	0.326

* Signs indicate the environmental variables significant for floristic differentiation of the analyzed forests.

3.3. Alpha Diversity

The highest alpha diversity (expressed as Shannon's entropy) was recorded in mesic alliance *Ostryo carpinifoliae-Tilion platyphylli*, while the lowest entropy was detected in xeric alliance *Fraxino orni-Ostryion carpinifoliae* (Figure 7). A similar trend was observed for species richness. Contrary to the alpha diversity and species richness, the values of species equitability were almost identical (values near 1) in all variants of the analyzed forests.

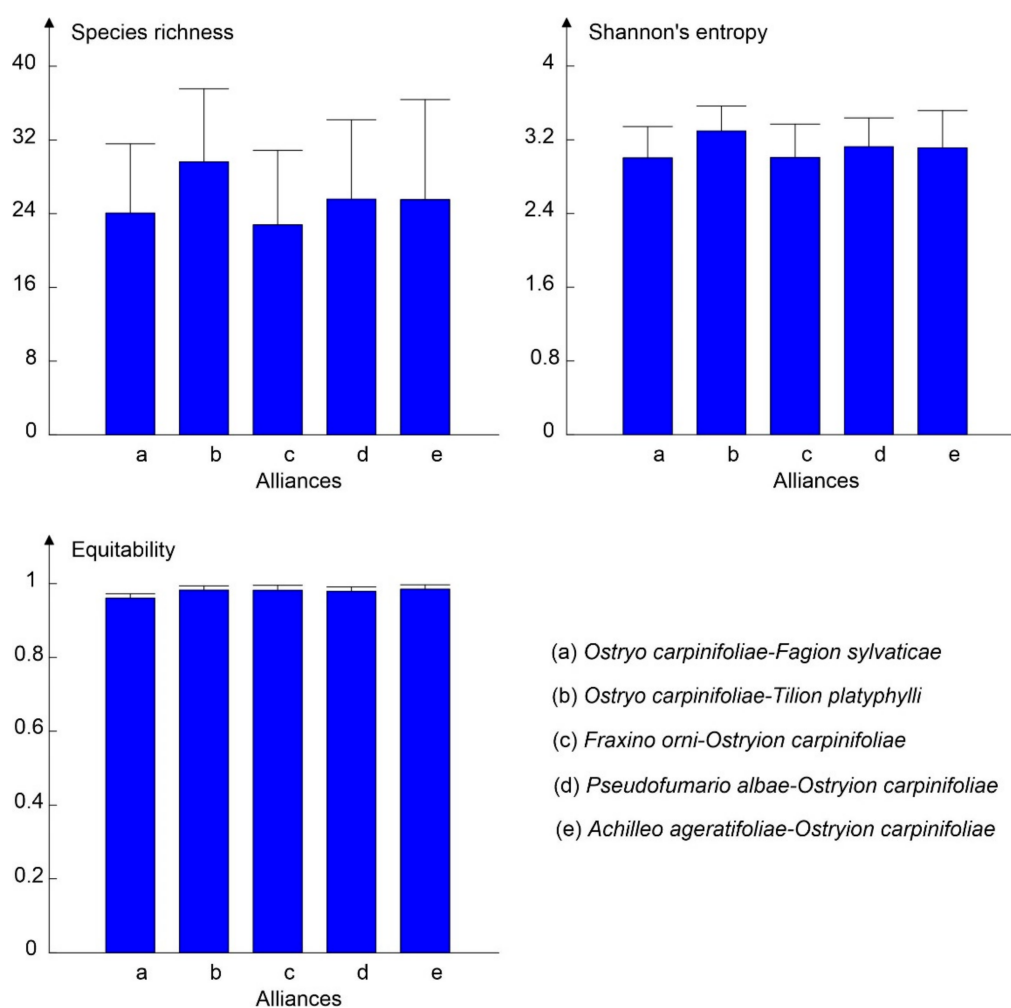


Figure 7. Alpha diversity components of the analyzed forests. The blue bars are mean values and the lines are standard deviations of the species richness, Shannon's entropy, and equitability in different variants of the analyzed forests.

3.4. Beta Diversity

Extremely high values for both species turnover and beta diversity were detected in all variants of the analyzed forests (Figure 8). The ternary graphs, presented in Figure 8, were obtained using Baselga's method [35]. We performed analyses of beta diversity using an alternative method, described by Podani et al. [37], but obtained essentially the same results, which are not presented in this article.

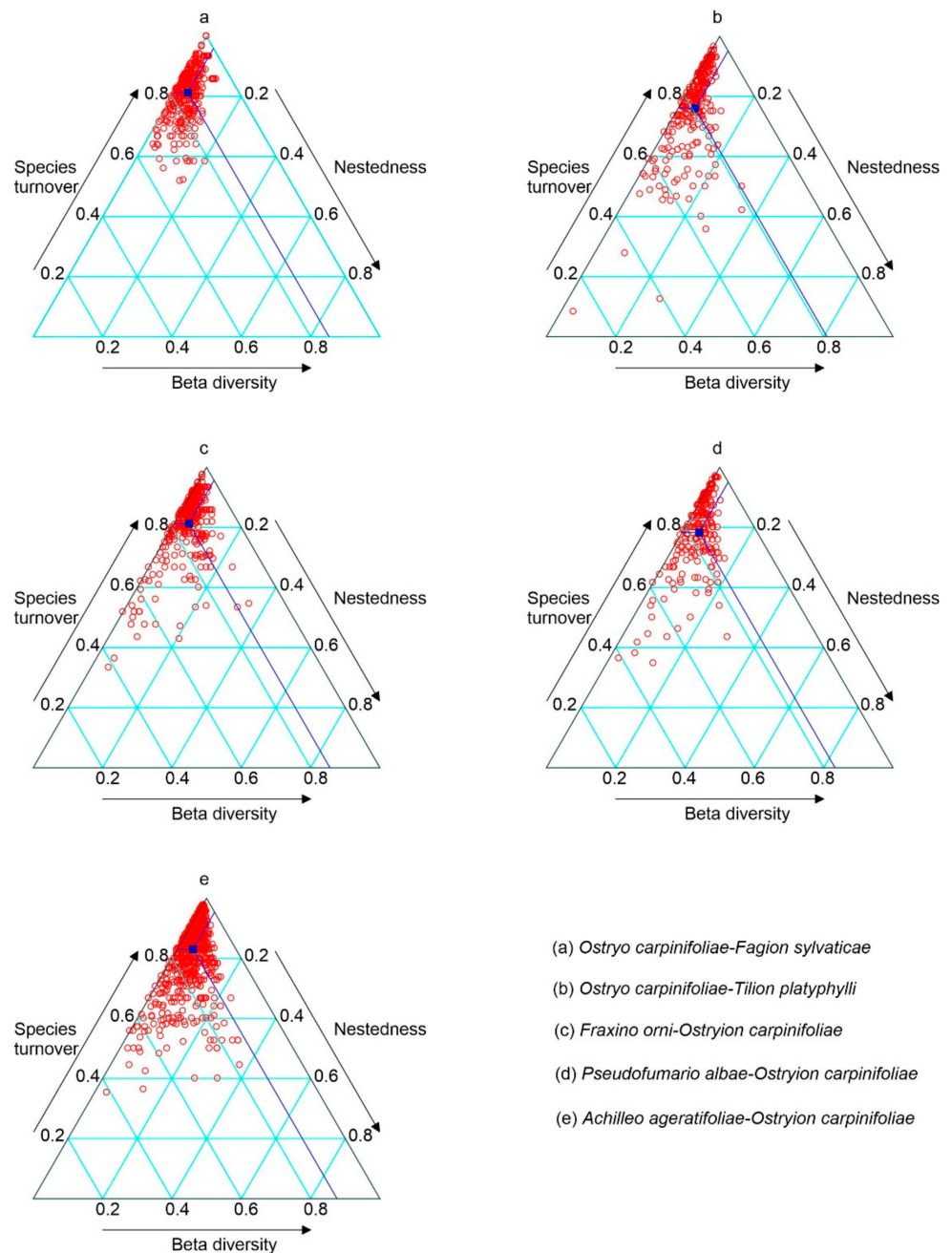


Figure 8. Beta diversity of the investigated forests. Each point (red circle) represents a pair of communities. Its position is determined by values of the beta diversity and its additive components (species turnover and nestedness). The blue rectangle corresponds to the centroid (average value) of the points.

4. Discussion

The classification of relevés may be performed using a wide spectrum of clustering methods [43–45]. Hill et al. [46] emphasized that the number of misclassifications is a key parameter in assessing the analytical power of clustering methods. Agglomerative classification procedures usually produce a huge number of misclassifications [43,46]. The most popular polythetic divisive methods perform well when the first principal axis accounts for most of the variation in a data set. However, if variances of principal axes are similar, these methods may produce serious misclassifications [47,48]. The inability to correct misclassifications is the main drawback of hierarchical classification methods. Non-hierarchical clustering methods, however, enable the allocation of misclassified relevés to their most similar cluster. Therefore, we performed classification of the analyzed communities using K-means clustering and Bayesian classification. These methods are the most powerful variants of non-hierarchical clustering methods [27]. The variance ratio indicates that K-means clustering produces more acceptable results than Bayesian classification. The main drawback of Bayesian classification is a rigid assumption that all variables must be normally distributed. Austin et al. [49] and Karadžić et al. [50] emphasized that the distribution of species along gradients usually deviates from the Gaussian distribution. Contrary to Bayesian classification, K-means clustering is not restricted by the normality assumption.

Using both methods, we revealed that the analyzed forests may be divided into five clusters. In addition to a clear floristic distinction (Table A1), these variants of hop hornbeam forests differ ecologically. The mesic alliances *Ostryo carpinifoliae-Fagion sylvaticae* and *Ostryo carpinifoliae-Tilion platyphylli* occur in shady habitats, on north-facing slopes or at the bottom of canyons. They differ with respect to soil conditions. While forests of *Ostryo carpinifoliae-Fagion sylvaticae* inhabit sites with deep soils, forests of *Ostryo carpinifoliae-Tilion platyphyll* occur on relatively shallow soils.

The syntaxonomy of the alliances can be represented by the following classification units:

Class: *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968;

Order: *Fagetalia sylvaticae* Pawłowski 1928;

Alliance: *Ostryo carpinifoliae-Fagion sylvaticae* Borhidi 1963;

Order: *Aceretalia pseudoplatani* Moor 1976;

Alliance: *Ostryo carpinifoliae-Tilion platyphylli* (Košir et al. 2008) Čarni in Willner et al., 2016.

Mucina et al. [1] included the basiphilous beech and mixed fir-beech forests of the Balkan Peninsula in the alliances *Aremonio-Fagion* (Horvat 1950) Borhidi in Török et al. 1989 (with the suballiances *Ostryo-Fagenion* and *Lonicero alpigenae-Fagenion*), *Geranio striati-Fagion* Gentile 1970, and *Fagion sylvaticae* Luquet 1926 (all basiphilous beech forests lacking numerous diagnostic species of *Aremonio-Fagion* and *Geranio-Fagion*). Such taxonomy may be questioned, because it excludes the Peri-Pannonian submontane lime-beech forests *Tilio tomentose-Fagion sylvaticae* (Marinšek, Čarni et Šilc 2013) Karadžić 2018. Moreover, it excludes the ravine forests of *Fagus sylvatica* and *Corylus colurna* that occur in eastern parts of Serbia and in Bulgaria. The geographically vicariant alliances *Ostryo carpinifoliae-Fagion sylvaticae* Borhidi 1963 and *Fago sylvaticae-Colurnion colurnae* Borhidi 1964 represent the most diverse variants of basiphilous beech forests in Serbia [51]. Therefore, we included the mesic forests of hop hornbeam and *Fagus sylvatica* in the alliance *Ostryo carpinifoliae-Fagion sylvaticae*, rather than in the alliance *Aremonio-Fagion*, which includes mesic forests from both canyon and non-ravine habitats.

Xeric variants of the investigated forests usually occur in dry, sunny habitats. They differ with respect to soil conditions. Forests that belong to the alliance *Fraxino orni-Ostryion carpinifoliae* are distributed on skeletal, but relatively deep, soil. The new alliances proposed in this article (*Pseudofumario albae-Ostryion carpinifoliae* and *Achilleo ageratifoliae-Ostryion carpinifoliae*) occur in adverse scree and saxatile habitats. It is the stress gradient (from relatively deep but skeletal soils to screes and bare rocks) that clearly separates these three

variants of xeric hop hornbeam forests. The classification of xeric hop hornbeam forests involves the following syntaxa:

Class: *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959;

Order: Quercetalia pubescenti-petraeae Klika 1933;

Alliances: *Fraxino orni-Ostryion* Tomažič 1940,

Pseudofumario albae-Ostryion carpinifoliae all. nova, and

Achilleo ageratifoliae-Ostryion carpinifoliae all. nova.

Species-rich hop hornbeam forests are widely distributed in central parts of the Balkan Peninsula [3–8,16–23]. Due to their extremely heterogenous structure, the syntaxonomy of these forests is still unresolved. Our article clearly indicates that hop hornbeam forests in Serbia may be divided into five ecologically and floristically distinguishable alliances. Similar communities are extended outside the study area. Therefore, a detailed chorological and ecological analysis of associations within each of these alliances requires further vegetation studies. The forward selection analysis indicates that all environmental variables, except for the altitude, are significant for floristic differentiation of the analyzed forests. Most of the analyzed communities are distributed within a narrow altitudinal range (from 300 to 550 m). Therefore, the effects of altitude on the differentiation of communities is insignificant. The specific topography of canyons forms strong thermal and moisture gradients [8]. As canonical correspondence analysis indicates, the investigated ravine forests are clearly differentiated along the moisture and temperature gradients. A strong light gradient is a consequence of the different density of dominating trees in the analyzed forests. The screes and cliffs are covered by sparsely distributed individuals of hop hornbeam and other xeric trees. The shade increases from the extremely xeric alliances *Pseudofumario albae-Ostryion carpinifoliae* and *Achilleo ageratifoliae-Ostryion carpinifoliae* to forests of the alliance *Ostryo carpinifoliae-Fagion sylvaticae*, which are dominated by dense populations of *Fagus sylvatica* and other broad-leaved trees.

Analyses of the species diversity involved investigations of both alpha (within-community) and beta (between-community) diversity. The alpha diversity depends on both species richness and species equitability (evenness of species abundance) [52,53]. The high alpha diversity of the investigated forests is attributable to the diverse environmental conditions that enable the coexistence of numerous species with different ecological requirements [8,50]. A heterogeneous, patchy environment prevents the dominance of one species and promotes a polydominant community structure [6].

The beta diversity can be partitioned into two additive components: Species turnover and nestedness (the difference in species richness) [35,37,42]. Extremely high—almost the greatest possible—values of both species turnover and beta diversity were found in all variants of the analyzed forests. Such high diversity can be explained by the heterogeneous microclimatic conditions along strong thermal and moisture gradients [8].

The high diversity of phanerophytes, the presence of numerous Tertiary relicts, and a high proportion of paleo-endemic species are the main characteristics of ravine vegetation in the Balkan Peninsula [6–8]. The high diversity of phanerophytes suggests that broad-leaved ravine forests are remnants of Tertiary subtropical vegetation [8].

The Balkan Peninsula is one of the most important biodiversity hotspots in Europe [54–56]. According to Velčev et al. [57], Balkan endemic taxa can be divided into two main categories: Paleo-endemics and neo-endemics. Paleo-endemics include relict species from the Tertiary period, which dominated Europe at the beginning of the so-called Quaternary period. The high percentage of paleo-endemic species in canyons can be explained by the ‘chasmophytic divergence’ hypothesis [7,8,58]. The hypothesis is based on three main assumptions: (1) A strong selective pressure in adverse rocky habitats; (2) reduced gene flow between populations; and (3) genetic drift.

The expansion of chasmophytes into adjacent non-ravine habitats is prevented by more efficient competitors. Due to dispersion barriers, the chasmophytic populations are isolated and their gene flow is reduced. Even within the same saxatile habitat, the gene flow may be considerably inhibited due to obstructions in the formation of progeny. The

failure of seed to establish new individuals occurs frequently, because most of the holes and crevices that are suitable for ecesis are already occupied. Such a situation reduces gene flow significantly. A combination of reduced gene flow, a strong selective pressure, and genetic drift may contribute to the fast speciation of endemic taxa. Examples of the amazing diversification of chasmophytes are genera *Edraianthus* A. DC. and *Amphoricarpos* Vis. [59,60].

The effective size of chasmophyte populations is usually very low. In such a situation, the genetic drift stochastically eliminates alleles. The fixation of (often non-adaptive) alleles and increased proportion of homozygous individuals reduce the ecological plasticity of chasmophytes. Therefore, most of the species that are adapted to saxatile habitats belong to the group of critically endangered taxa.

Due to the high diversity, the protection of broad-leaved ravine forests should be the top priority in biodiversity conservation projects [61].

5. Conclusions

We used both K-means clustering and Bayesian classification to obtain maximally homogeneous clusters of relevés. The optimal number of clusters was determined by maximizing the ratio of between-group to within-group variances [28]. The results of both the K-means clustering and Bayesian classification indicate that the analyzed forests may be divided into five variants (alliances *Ostryo carpinifoliae-Fagion sylvaticae*, *Ostryo carpinifoliae-Tilion platyphylli*, *Fraxino orni-Ostryion carpinifoliae*, *Pseudofumario albae-Ostryion carpinifoliae*, and *Achilleo ageratifoliae-Ostryion carpinifoliae*). Despite a great overlap of species distributions, these alliances are clearly distinguishable floristically and ecologically.

A combined light–moisture gradient clearly separates the analyzed forests. Due to shallow soil on carbonate and serpentine rock, the soil pH in xeric variants of the forests (the alliances *Pseudofumario albae-Ostryion carpinifoliae* and *Achilleo ageratifoliae-Ostryion carpinifoliae*) is alkaline. In shady communities that are developed on relatively deep soil, the soil reaction is slightly acidic to neutral.

The greatest alpha diversity (expressed as Shannon's entropy) was recorded in mesic alliance *Ostryo carpinifoliae-Tilion platyphylli*, while the lowest entropy was detected in the xeric alliance *Fraxino orni-Ostryion carpinifoliae*. The extremely high species turnover and beta diversity in the analyzed forests can be explained by the heterogeneous microclimatic conditions along strong thermal and moisture gradients.

The investigated forests represent an important pool of rare, paleo-endemic species that survived the Quaternary glaciations in ravine refugia.

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Appendix A

Table A1. Synoptic table of the analyzed forests. Each row of the table specifies the fidelity (expressed as the phi coefficient, multiplied by 100) of a species to the alliances *Ostryo carpiniifoliae-Fagion sylvaticae* (A), *Ostryo carpiniifoliae-Tilion platyphylli* (B), *Fraxino orni-Ostryion carpiniifoliae* (C), *Pseudofumario albae-Ostryion carpiniifoliae* (D), and *Achilleo ageratifoliae-Ostryion carpiniifoliae* (E). Diagnostic species are shaded.

Species	Alliances				
	A	B	C	D	E
<i>Asperula taurina</i> L.	38
<i>Epimedium alpinum</i> L.	47
<i>Fraxinus excelsior</i> L.	39
<i>Evonymus europaeus</i> L.	39
<i>Alliaria petiolata</i> (M.Bieb.) Cavara & Grande	39
<i>Heracleum sphondylium</i> L.	39
<i>Primula veris</i> L.	30
<i>Pulmonaria officinalis</i> L.	39
<i>Melampyrum hoermannianum</i> K. Malý	44
<i>Angelica sylvestris</i> L.	35
<i>Galeopsis speciosa</i> Mill.	35
<i>Parietaria officinalis</i> L.	37	3	.	.	.
<i>Convallaria majalis</i> L.	35
<i>Athyrium filix-femina</i> (L.) Roth	43
<i>Cardamine bulbifera</i> (L.) Crantz	29	1	.	.	.
<i>Equisetum telmateia</i> Ehrh.	30
<i>Cyclamen purpurascens</i> Mill.	53
<i>Acer pseudoplatanus</i> L.	30
<i>Brachypodium sylvaticum</i> (Huds.) P.Beauv.	50	11	.	.	.
<i>Salvia glutinosa</i> L.	38	22	.	.	.
<i>Hedera helix</i> L.	45	37	.	.	.
<i>Asarum europaeum</i> L.	28	18	.	.	.
<i>Tilia platyphyllos</i> Scop.	10	22	7	.	.
<i>Helleborus odorus</i> Waldst. & Kit. ex Willd.	11	55	.	.	.
<i>Scutellaria altissima</i> L.	15	39	.	.	.
<i>Scrophularia nodosa</i> L.	4	47	.	.	.
<i>Aremonia agrimonoides</i> (L.) DC.	10	26	4	.	.
<i>Juglans regia</i> L.	.	41	.	.	.
<i>Cornus mas</i> L.	.	29	9	2	.
<i>Campanula rapunculoides</i> L.	.	27	6	4	.
<i>Digitalis grandiflora</i> Mill.	.	36	2	.	.
<i>Calamintha grandiflora</i> (L.) Moench.	.	26	16	.	.
<i>Arabis turrata</i> L.	.	27	1	.	1
<i>Lilium martagon</i> L.	.	37	.	.	.
<i>Rubus hirtus</i> Wald. et Kit.	.	42	.	.	.
<i>Campanula trachelium</i> L.	.	33	14	.	.
<i>Sanicula europaea</i> L.	.	37	.	.	.
<i>Arum maculatum</i> L.	.	32	.	.	.
<i>Sorbus torminalis</i> (L.) Crantz.	.	37	.	.	.
<i>Galium schultesii</i> Vest	.	40	.	.	.
<i>Cornus sanguinea</i> L.	.	35	10	.	.
<i>Potentilla micrantha</i> Ram. ex DC.	.	7	29	.	.
<i>Carex caryophyllea</i> Latourr.	.	5	26	.	.
<i>Glechoma hirsuta</i> Waldst. et Kit.	.	3	25	5	.
<i>Lathyrus sylvestris</i> L.	.	.	29	2	.
<i>Clinopodium nepeta</i> (L.) Kuntze	.	.	34	.	.
<i>Geranium sanguineum</i> L.	.	7	21	.	.
<i>Fraxinus ornus</i> L.	.	15	30	17	.
<i>Pseudofumaria alba</i> (Mill.) Lidén	.	.	5	30	10
<i>Stachys recta</i> L.	.	.	19	26	.

Table A1. Cont.

Species	Alliances				
	A	B	C	D	E
<i>Teucrium montanum</i> L.	.	.	11	29	.
<i>Prunus spinosa</i> L.	.	.	12	24	.
<i>Draba lasiocarpa</i> Rochel	.	.	2	28	.
<i>Allium flavum</i> L.	.	.	6	22	.
<i>Evonymus verrucosus</i> Scop.	.	.	3	25	18
<i>Melica ciliata</i> L.	.	.	.	32	12
<i>Campanula lingulata</i> Waldst. & Kit.	.	8	.	33	.
<i>Fritillaria montana</i> Hoppe ex W.D.J.Koch	.	.	.	27	.
<i>Minuartia bosniaca</i> (Beck) K.Malý	.	.	.	27	.
<i>Micromeria thymifolia</i> (Scop.) Fritsch	.	.	.	32	9
<i>Stipa calamagrostis</i> (L.) P.Beauv.	.	.	.	29	.
<i>Rhamnus saxatilis</i> Jacq.	.	.	.	34	.
<i>Galium purpureum</i> L.	.	.	.	24	24
<i>Globularia cordifolia</i> L.	.	.	.	13	21
<i>Hieracium waldsteinii</i> Tausch	50
<i>Geranium macrorrhizum</i> L.	48
<i>Campanula secundiflora</i> Vis. & Pancic	39
<i>Genista radiata</i> (L.) Scop.	37
<i>Saxifraga crustata</i> Vest.	34
<i>Valeriana montana</i> L.	34
<i>Cerastium decalvans</i> Schloss. & Vuk.	30
<i>Jurinea mollis</i> (Torn.) Rchb.	31
<i>Saxifraga tridactylites</i> L.	.	.	.	2	32
<i>Silene pusilla</i> Waldst. et Kit.	31
<i>Achillea ageratifolia</i> (Sibth. & Sm.) Boiss	38
<i>Seseli rigidum</i> Waldst. & Kit.	35
<i>Edraianthus graminifolius</i> (L.) A.DC.	.	.	.	4	37
<i>Euphorbia glabriflora</i> Vis.	.	.	.	7	34
<i>Frangula rupestris</i> Schur	34
<i>Amphoricarpos neumayeri</i> Vis.	.	.	.	2	21

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