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Diversity and ecological differentiation of mixed forest in northern Montenegro (Mt. Bjelasica) with reference to European classification

Diversität und ökologische Differenzierung von Bergmischwäldern im nördlichen Montenegro (Bjelsica-Gebirge) mit Bezug zur Europäischen Vegetationsklassifikation

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Abstract

The current state of forests as well as tree species composition in stands is the result of past development and somehow a record of all previous influences. As a base for better projections of future forest development and the development of sustainable management strategies we should recognize developmental processes in forests and understand their drivers. Mixed mountain forests in Montenegro, with an exceptionally large variation of environmental conditions, provide an excellent opportunity to study eastern-Mediterranean mixed mountain forests near their southern distribution limit. The goals of this study were 1) to floristically characterize mountain forests in an Eastern Mediterranean region and 2) to assess their physical site properties as determinants of forest types. Research was based on data collected from 158 sampling plots in the territory of the mountain Bjelasica, north-east Montenegro. The influence of topographic, climatic and edaphic site characteristics on the differentiation of vegetation and formation of forest types was assessed using numerical ordination and classification. Three types of mountain forests were separated based on their floristic composition, which can be easily characterized by the composition of their tree layer: 1) Mixed forests with spruce, silver fir and beech, 2) monodominant beech forests resulting from over-exploitation of type 1, and 3) heliophytic mixed forests with pioneer species (pine, aspen and birch) and European hop-hornbeam. The types are discussed regarding their physical site characteristics and put in a European context. Mountain forests of Montenegro are quite similar to forests in other regions of Europe and can be arranged into the existing "Classification of European beech forests" (Willner et al. 2017) and according to Willner & Grabherr (2007).

Keywords: mixed mountain forest, Montenegro, site classification, site conditions, stand structure, vegetation

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

In Europe mixed mountain forests are characterized by European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and Norway spruce (*Picea abies*). They are distributed across the temperate, continental and Mediterranean bioclimatic zones. Besides their similarity in dominant tree species these forest ecosystems also have similar field layers consisting of herbs, especially early flowering species. In the European map of natural vegetation (BOHN et al. 2000) this forest type is grouped under "mixed deciduous-coniferous communities (formation F)". Although there are many common characteristics, European mixed mountain forests differ in their species composition due to differences in regional species pools and bedrock geology (WILLNER et al. 2017). As tree species dominant in boreal and temperate mountain areas of Europe reach their southern limit in the Mediterranean bioclimatic zone, studies on these forests can serve as examples for climate change research.

The Mediterranean region is a hotspot of climate change (LUTERBACHER 2012). In this region, warming due to climate change is projected to exacerbate aridity through reduced vapor pressure and resulting soil moisture deficit (GIORGI & LIONELLO 2008, IPCC 2014). Recent drought events have caused a widespread decline in tree growth, decreasing productivity and inducing forest die-off of Mediterranean forests in dry (SARRIS et al. 2007, THABEET et al. 2009, VACCHIANO et al. 2012, DORMAN et al. 2013) as well as in mesic sites (JUMP et al. 2006, LINARES & CAMARERO 2012, CASTAGNERI et al. 2014). Conversely, other authors have reported growth improvements of tree species in Mediterranean sites (TEGEL et al. 2014). Responses in mixed stands are even more complicated, as each tree species shows an individual reaction to climatic changes (BOURIAUD & POPA 2009, CASTAGNERI et al. 2014). Thus, these forests constitute not only possible future states of central European mountain forests but also need careful monitoring and assessment regarding their response to climate change (REDŽIĆ 2007).

Forests are dynamic and complex ecosystems. For their description and for monitoring temporal changes, species composition and their horizontal and vertical structure need to be considered. The composition of forests is influenced by natural and anthropogenic factors (BONCINA et al. 2003) and it is often hard to separate their effects, as they can act mutually, directly and indirectly. In Montenegro, there was less intense forest management than in other regions and no extensive deforestation in the past 200 years (MOTTA et al. 2015). This makes this region very valuable for studies on mountain forest dynamics with silver fir compared for example with strongly managed mountain forests in Central Europe with several cycles of forest clearing throughout the past centuries (MCGRATH et al. 2015). Additionally to anthropogenic influences, species composition and structure of forests at a specific site are not static, but change after timber extraction or natural disturbances during succession. Early successional forest stages comprise higher light availability and therefore rather light demanding tree species as well as a rich field layer (WILLIS 1994). The current state of forests as well as tree species composition in stands is the result of past development and somehow a record of all previous influences (ŠERCELJ 1996, BONCINA et al. 2003). For close to nature forestry we should recognize developmental processes in forests and understand its drivers. This is the base for better projections of future forest development and the development of sustainable management strategies.

However, knowledge on eastern-Mediterranean mixed mountain forests is still lacking behind the knowledge on temperate and also western-Mediterranean types. Particularly, the number of relevant studies published in international scientific journals is very low. Mixed mountain forests in Montenegro provide an excellent opportunity to study eastern-Mediterranean mixed mountain forests near their southern distribution limit. Montenegro is characterized by an exceptionally large variation of environmental conditions, where climate can limit forest growth and succession but can also give rise to lush, mesic forest ecosystems (SCARASCIA-MUGNOZZA et al. 2000). According to the European Environmental Agency (EEA) Montenegro is divided into two zones, a Mediterranean and an alpine biogeographical region. Montenegro's land area is characterized by a high forest cover. According to DEES et al. (2013) forest (59.5%) and forestland (9.9%), high and coppice forests with equal shares, cover 69.4% of the total land area of 1,388,581 ha. The average volume per hectare forest area is estimated at 159.6 m³/ha. Most important species are European beech (*F. sylvatica*), oak species (*Quercus cerris*, *Q. petraea*), Norway spruce (*P. abies*), silver fir (*A. alba*), and pine species (*Pinus nigra*, *P. sylvestris*, *P. heldreichii*, *P. peuce*). In total 12 conifer species and 59 broadleaf species have been recorded in Montenegro (DEES et al. 2013). The share of coniferous and broadleaf species differs considerably with respect to area and wood volume.

The majority of forests are mountain forest which is located at elevations between 800 and 1800 m (78.7%) and on slopes between 6 and 35° (87.2%). Average volumes of more than 200 m³/ha occur at elevations of 1200 to 2000 m, while they are considerably lower at lower elevations (DEES et al. 2013).

Our study aims to increase the knowledge and data base on eastern-Mediterranean mixed mountain forests and discuss their characteristics in a European context. Therefore, we launched a vegetation survey and applied multivariate analysis. Aims of this study were (1) to floristically characterize eastern-Mediterranean mountain forests and (2) to assess their physical site properties as determinants of forest types.

2. Methods

2.1 Study area

The study area (9,205 ha) (Table 1) was the Bjelasica management unit (4756519 N, 395327 E, 585; 1850 m a.s.l) in northern Montenegro (Fig. 1). 53% of forest area is located on moderately steep slopes (11–20°) and 43% on steep slopes (21–30°). Most slopes are exposed to the north (N, NE, and NW). The region has a continental-montane climate. From 1961 to 1990 mean temperature at the hydrometeorological station „Bijelo Polje" (606 m a.s.l) ranged from 2.8 °C in winter to 15.1 °C in summer (mean 8.7 °C) and mean annual precipitation approximated 905 mm per year. The geological bedrock types are very diverse. At higher altitudes siliceous limestone bedrock prevails whereas at lower altitudes sandstone and shale prevails (FUSTIC & DJURETIC 2000). According to the management plan for the unit "Bjelasica" for 2003–2013 57% of the study area was covered by mountain forests

Table 1. Area and diversity summary statistics of 158 sampled plots in a mountain forest in the management unit „Bjelasica" of northern Montenegro.

Tabelle 1. Zusammenfassende Statistik zu Fläche und Diversität der 158 Vegetationsaufnahmen von Bergwäldern in der Bewirtschaftungseinheit "Bjelasica" im nordöstlichen Montenegro.

Parameter	Value
Study area (ha)	9205
Area sampled (ha)	1.61
α (average number of species per plot)	16
γ (total species richness)	160

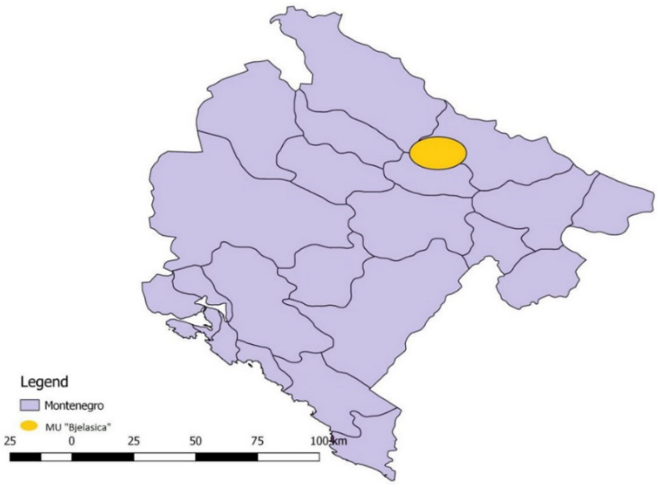

Fig. 1. Position of investigation area, Management Unit "Bjelasica", mountain Bjelasica, Montenegro (Source of the map: DIVA-GIS).

Abb. 1. Lage des Untersuchungsgebietes, Bewirtschaftungseinheit "Bjelasica", Bjelasica-Gebirge, Montenegro (Kartengrundlage: DIVA-GIS).

mainly composed of *F. sylvatica* (62.9%), *A. alba* (8.3%), *P. abies* (2.5%), *Acer pseudoplatanus* (3.4%), *Q. petraea* (2.7%), *Q. cerris* (2%), *Ostrya carpinifolia* (3.7%). Some relic stands (ca. 50 ha) of *Pinus heldreichii* (whitebark pine) forest occurred as well. The remainder of the area consisted of agricultural land or bare rock. The area has a long history of human settlement and forest utilization, including a high livestock grazing pressure.

2.2 Field survey

Data on vegetation composition and physical factors were collected at 158 sites from June to September in 2014 and 2015. The concept map which was used as a basis for sampling design included terrain structures, climatic zones and bedrock type. The selection of the patches is done in Microsoft Excel and the random sampling was done using a GIS. Sampling design focuses covering the feature space i.e., to ensure that all base saturation classes, all altitude levels and solar insolation classes as well as landform units are covered. The second aim is to reduce travel time since the area is not well accessible. To achieve both aims a sampling scheme based on non-overlapping 500 m x 500 m patches was developed. The general scheme is a stratified random sampling approach and works as followed: for each base saturation class, for each altitude level, for each solar insolation class, the patch was selected comprising all landform units with equal probability/area, and each landform unit was sampled randomly. As additional condition each stratum was to be sampled at least twice. This assured that relevant vegetation types were covered. In the first year were placed 38 and in the second 120 sampling plots.

The plot size was 100 m^2, represented homogeneous site conditions and had a shape either of 10 m × 10 m or 20 m × 5 m, depending on relief and forest structure. In the case of local disturbance, a strong site gradient or inaccessible areas within the plot area, the plot had to be shifted systematically (moved within 20 m if possible or replaced by other appropriate plot).

The structure of the vegetation was described by three layers: Field layer (height < 1 m), shrub layer (height 1–5 m) and tree layer (height > 5 m). For each layer, the occurring vascular plant species were listed and their cover abundance in the respective layer was estimated using the modified Braun-Blanquet-scale (ELLENBERG & MUELLER-DOMBOIS 1974, VAN DER MAAREL 1979). Finally, the total cover of each layer was estimated. Taxonomy followed PIGNATTI (1982), TUTIN et al. (1993) and DOMAC (1994).

At each site the following physical parameters were surveyed: location (latitude/longitude), landform (terrain form, slope, aspect, curvature, elevation, terrain position), land use and soil. Soil description was done on a pit of approximately 1 m width dug to 1 m depth (or reaching the parent material), on which soil depth and pH (extraction in KCl) were recorded (from the following depths: 0–30, 30–60 and > 60 cm).

Additionally to the data from our field survey, we used climate maps provided by the Institute of Hydrometeorology and Seismology of Montenegro. Distances to roads (public and forest) were calculated using maps from the Forestry Administration of Montenegro.

In statistical analysis we used the following variables: cover of plant species, plant species richness, Simpson index, total layer cover (tree, shrub and herb), elevation, slope, pH, soil depth, distance from road, northness (N, NE, NW).

2.3 Data analysis

2.3.1 Vegetation analysis

Data handling and vegetation analysis was done in R (R CORE TEAM 2014). In the vegetation analysis pseudo-species were used, i.e., tree species occurrences in the field, shrub, and tree layer were treated individually. Species occurring in less than three percent of relevés were excluded from the analysis because they were not considered relevant. Vegetation data were Hellinger-transformed (square root of species cover divided by total sum of cover in data-set) using the function decostand in the R-package vegan (LEGENDRE & GALLAGHER 2001). Plots were ordinated by non-metric multidimensional scaling (NMDS; OKSANEN et al. 2016), using the Bray–Curtis dissimilarity, with three axes, as determined by the decline of stress.

The Hellinger-transformed plot matrix was subjected to Isopam classification (non-hierarchical partitioning) (SCHMIDTLEIN et al. 2010) to obtain floristically defined vegetation types, which were projected in ordination space by plot symbols and group centroids. This algorithm is based on ordination and space partitioning. Ordination (isometric feature mapping; TENENBAUM et al. 2000) and partitioning (partitioning around medoids; KAUFMAN & ROUSSEEUW 1990) are applied in an iterative way with different parameterizations while searching for ordinations and partitions with high overall fidelity of species to groups of sites. The estimation of fidelity is based on the standardized G statistic (BOTTA-DUKÁT et al. 2005) and includes the number of species with a high standardized G value and the value itself. Isopam can be used in a hierarchical or non-hierarchical way and with or without optimization of cluster numbers. We went for the non-hierarchical mode and an automated optimization of cluster numbers. The isotab function calculated an ordered constancy table (Supplement S1) based on Isopam clustering results. In the table, the upper part lists typical species with a significant binding to single clusters (according to the *phi* coefficient of association; TICHÝ & CHYTRÝ 2006) combined with a maximum *p* value resulting from Fishers exact test; FISHER 1922). The lower part of the table is ordered by descending overall frequency.

Species diversity at the plot level was quantified as species richness and Simpson index (the probability that two individuals randomly selected from a sample will belong to the same species). Floristic heterogeneity within forest types was calculated as the median distance in ordination space (axes 1+2) of plots to the centroid of the respective forest type.

The statistical relationship of species composition with site characteristics was studied by fitting variables to NMDS axes 1 and 2 with 999 permutations (Supplement S1, Fig. 3; OKSANEN et al. 2016) and by testing differences between Isopam forest types displayed in boxplots by a Kruskal-Wallis test.

3. Results

In total we recorded 160 species in 158 vegetation plots (Table 1). The most common species was beech (*F. sylvatica*) (in 91% of the plots) (Supplement S1). Other common tree species were sycamore maple (*A. pseudoplatanus*) (56%), fir (*A. alba*) (52%) and spruce (*P. abies*) (26%). The most common herb species were *Rubus idaeus* (54%), *Pteridium aquilinum* (52%), *Galium sylvaticum* (48%), *Galeobdolon luteum* (41%) and *Fragaria vesca* (38%).

3.1 Ordination

Vegetation relevés were separated by the first two ordination axes. The first axis was defined by a gradient from rather low competitive species such as *P. nigra*, *O. carpinifolia*, *Potentilla erecta*, *P. alba*, *Populus tremula* and *Rosa canina* to competitive species in the tree layer, namely *F. sylvatica*. The floristic gradient of the second axis was determined by the presence of *A. alba*, *Anemone hepatica*, *Daphne blagaiana* with high scores, and *Hedera helix* and *Polytrichum formosum* with low scores. Species such as *Galium sylvaticum*, *Luzula luzuloides*, *Prenanthes purpurea*, *Galeobdolon luteum*, *Rubus fructicosus* agg. and *Pteridium aquilinum* had intermediate scores on both axes (Fig. 2).

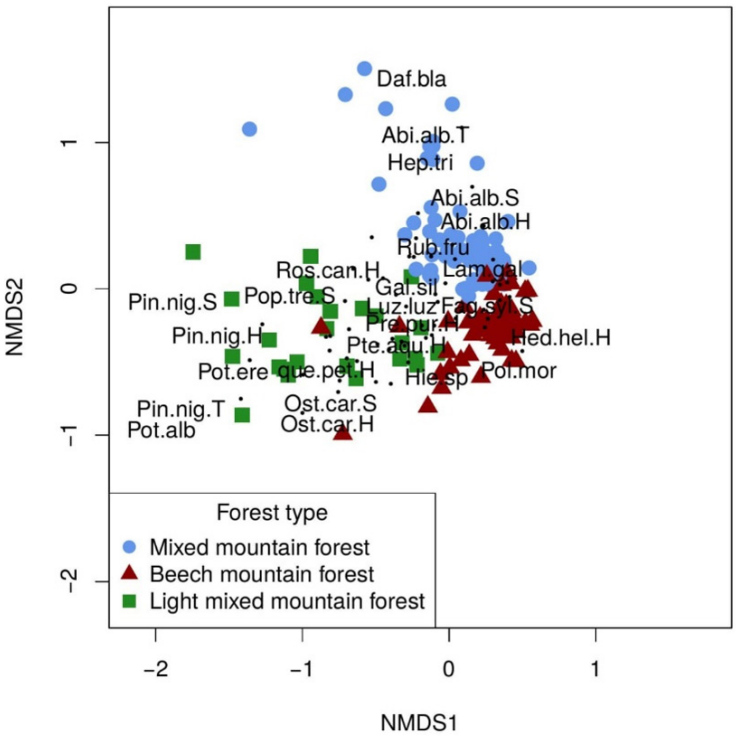

Fig. 2. NMDS ordination of 158 sample plots in a mountain forest in the management unit „Bjelasica“ of northern Montenegro; relevés grouped according to Isopam classes.

Abb. 2. NMDS-Ordination der 158 Vegetationsaufnahmen von Bergwäldern in der Bewirtschaftungseinheit “Bjelasica“ im nördöstlichen Montenegro; die Aufnahmen sind entsprechend der Isopam-Klassen gruppiert.

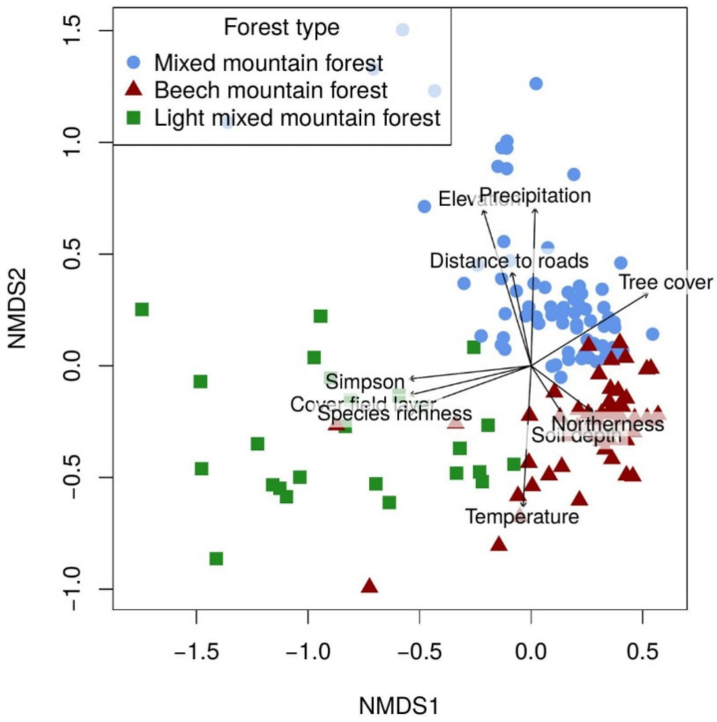

Fig. 3. NMDS ordination of 158 sample plots in a mountain forest in the management unit „Bjelasica“ of northern Montenegro; relevés grouped according to Isopam classes: Site and vegetation variables.

Abb. 3. NMDS-Ordination der 158 Vegetationsaufnahmen von Bergwäldern in der Bewirtschaftungseinheit “Bjelasica“ im nördöstlichen Montenegro; die Aufnahmen sind entsprechend der Isopam-Klassen gruppiert: Standorts- und Vegetationsvariablen.

The environmental fit on the ordination showed that vegetation variables related to cover and diversity varied across the first axis, i.e., the first axis represented a diversity gradient. Physical site variables related to climate and soil had higher axis loading on the second axis, i.e., the second axis represented an environment gradient.

The most significant (Fig. 3, Table 2) vegetation variables were cover of trees and herbs ($p < 0.001$), species richness ($p < 0.001$) and Simpson diversity ($p < 0.001$). The environmental fit additionally revealed correlations with physical site variables. Elevation, temperature, precipitation and soil depth intercorrelated. The most significant site variables (Fig. 3, Table 2) were elevation ($p < 0.001$), temperature and precipitation ($p < 0.001$). Soil depth and northerness were significant site variables, but less ($p < 0.004$) significant than elevation. Other site variables such as slope and pH of soil were not significant.

3.2 Classification of mountain forests

Clustering the sample plots using the Isopam algorithm provided three plot groups (Table 2, 3 and Supplement S1), that were clearly separated in NMDS-space (Fig. 2 and 3).

The first group was located at higher altitudes (mean altitude 1218.7 m a.s.l.), where precipitation was higher and temperature was lower (Fig. 4). Also, this Isopam group was located farthest from roads and had the highest tree cover (mean 0.77). Compared to the other

Table 2. Results of the environmental fit of site parameters on ordination axes 1 and 2 with 999 permutations. Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Tabelle 2. Ergebnisse der Ladung von Umweltvariablen auf die Ordinationsachsen 1 und 2 mit 999 Permutationen. Signifikanzcodes: 0 '***' 0,001 '**' 0,01 '*' 0,05 '.' 0,1 ' ' 1.

	NMDS1	NMDS2	r^2	Pr(>r)
Site parameter				
Elevation	-0.29448	0.95566	0.3305	0.001***
Slope	-0.04079	-0.99917	0.0297	0.099
pH	-0.30635	0.95192	0.0131	0,35
Soil depth	0.54217	-0.84027	0.0633	0.004**
Temperature	-0.05699	-0.99837	0.2495	0.001***
Precipitation	0.02445	0.99970	0.3079	0.001***
Northerness	0.79836	-0.60217	0.0758	0.004**
Distance road	-0.20125	0.97954	0.1138	0.001***
Vegetation parameter				
cover_trees	0.84958	0.52746	0.2354	0.001***
cover_shrub	-0.27280	-0.96207	0.0010	0.92
cover_herbs	-0.97209	-0.23460	0.1946	0.001***
species_richness	-0.94002	-0.34111	0.1567	0.001***

two groups, this group was moderately rich in plant species (species richness 15.58, Simpson index 0.68). Three tree species were characteristic for this group (Supplement S1): European beech, silver fir and Norway spruce. Other tree species in this group were birch (*Betula pendula*) and maple (*A. pseudoplatanus*). The shrub layer was characterized by regenerating beech, fir and spruce, as well as the species composition of the field layer. Important species in the field layer were *A. pseudoplatanus*, *Galeobdolon luteum*, *Oxalis acetosella*, *Pteridium aquilinum* and *Fragaria vesca*. This group was considered to be a mixed mountain forest.

The second Isopam group occurred at lowest altitudes (mean altitude 960 m a.s.l.), with higher temperature and lower precipitation (Fig. 4). The soil depth was the largest (mean 89 cm) and this group was the most homogeneous (0.23 medium distance to group center in NMDS). Compared to the other two groups (Supplement S1), this group was poorest in plant species (richness 14.68, Simpson index 0.61). Beech dominated in the tree, shrub and herb layer (Supplement S1). Accompanying tree species were *B. pendula* and *A. pseudoplatanus* but at lower frequency than in the other two groups, as well as *Abies alba* in the shrub layer. The field layer was richer, additionally to beech other important vascular plant species were *Pteridium aquilinum*, *Rubus idaeus*, *A. pseudoplatanus*, *A. alba* and *Galium sylvaticum*. This group was characterized as beech mountain forest. Floristically, the third Isopam group clearly differed from the two others by a higher species richness (Fig. 4) and the occurrence of rather light demanding tree species such as black pine (*P. nigra)* and other pioneer tree species (*Populus tremula*, *B. pendula*). Because of low tree layer cover (mean 0.51), shrub and herb layers were rich in plant species (species richness 21.07, Simpson index 0.83). The most important plant species in the shrub layer were beech, sycamore maple, black pine, European hop-hornbeam (*Ostrya carpinifolia*), aspen (*P. tremula*). Next to *F. sylvatica*, *P. tremula*, *P. nigra* in the herb layer other important tree species were *A. pseudoplatanus*, *Fraxinus excelsior*, *Q. cerris*, *Q. petraea* and *P. abies*. Other plant species in the field

Table 3. Mean variable values of site parameters for three forests types of 158 sampled plots in a mountain forest in the management unit „Bjelasica“ of northern Montenegro.

Tabelle 3. Mittlere Kennwerte von Standortsvariablen für die drei Waldtypen, basierend auf den 158 Vegetationsaufnahmen von Bergwäldern in der Bewirtschaftungseinheit “Bjelasica“ im nordöstlichen Montenegro.

Site parameter	Mixed montane forest	Beech montane forest	Light mixed montane forest
Elevation (m a.s.l)	1220	960	1200
Soil depth (cm)	66	89	59
Tree layer (%)	77	71	51
Field layer (%)	35	38	61
Species richness	15.58	14.68	21.07
Simpson index	0.68	0.61	0.83
Within group diversity	0.36	0.23	0.77

layer were *Fragaria vesca*, *Pteridium aquilinum*, *Viola odorata*, *Rosa canina* and *Euphorbia amygdaloides*. This group and the second group had several species in common: *F. sylvatica*, *Luzula luzuloides* and *Galium sylvaticum* (Supplement S1). This group was the most heterogeneous one (Supplement S1) (0.77 medium distance to group center in NMDS), this confirmed its diverse floristic composition. This group was characterized as light mixed mountain forest.

4. Discussion

Based on our vegetation survey in Bjelasica, Montenegro, we separated three types of mountain forests by their floristic composition. They can be easily characterized by the composition of the tree layer. 1) Mixed mountain forest with the three tree species spruce, silver fir and beech, 2) beech mountain forest with absolutely dominating beech in the tree layer, and 3) light mixed mountain forest with pioneer species (pine, aspen and birch) and European hop-hornbeam. In the following we compare these types by their physical site characteristics and discuss them in the European context.

4.1 Physical site characteristics

Our results showed that climate separated the three types and caused the elevation gradient. This was expected because with increasing altitude climate changes systematically (MILOSAVLJEVIĆ 1985). Micro-climatic factors modify the macroclimate which affects the distribution of plant communities (TOMIĆ 2004). Spruce could be found in areas with rather continental climate, at lower temperature and higher precipitation than beech and Silver fir. Silver fir occurred at higher precipitation and higher relative humidity, but it is not tolerant to as low temperatures as spruce (TOMIĆ 2004). The analysis of the influence of exposition revealed that the northern exposure of Bjelasica favored beech, because there it was protected from summer heat and winter frost.

Soil depth also differed significantly among forest types and followed the expected pattern of lower soil depth at higher elevation (multi-collinearity among elevation, soil depth and climate). Likely, forest types are not separated due to different soil types but the influence of lower soil depth at higher elevation due to erosion and slower soil formation caused this pattern. However, slope was not significant in our study.

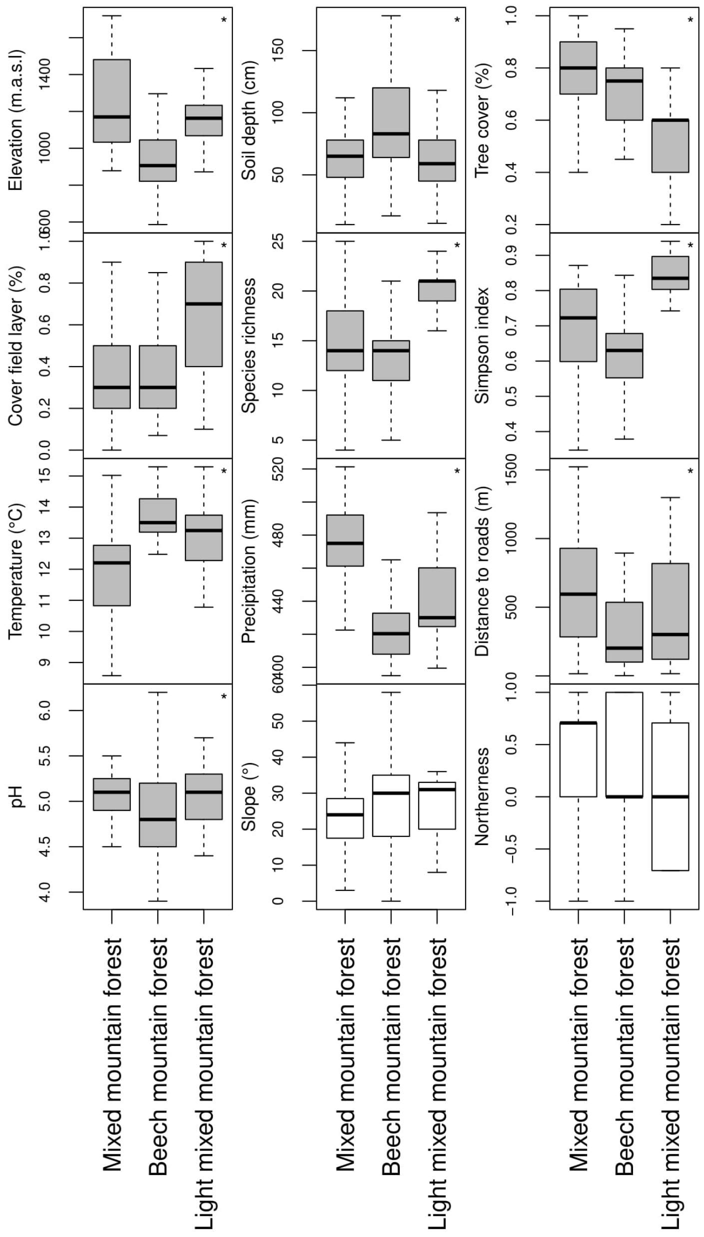

Fig. 4. Differences among Isopam forest types in site and vegetation variables and results of Kruskal-Wallis test; significant variables: elevation, soil depth, tree cover, cover field layer, species richness, Simpson index, temperature, precipitation, distance to roads, pH; Not significant variables: slope, northerness.

Abb. 4. Unterschiede zwischen Isopam-Waldtypen in Standorts- und Vegetationsvariablen und Ergebnisse des Kruskal-Wallis Tests; signikante Variablen sind Höhenlage, Bodentiefe, Baumschicht- und Krautschichtdeckung, Simpson-Index, Temperatur, Niederschlag, Entfernung zu Straßen, pH. Nicht signfikante Variablen sind Hangneigung, Schattseitigkeitsindex.

Surprisingly, soil pH did not differ significantly among groups. However, this could be caused by the coarse resolution of the used scale (Hellinger pH meter with 6 classes only). A study with stronger focus on the effect of soil pH on forests with higher measurement accuracy and a study design across a soil gradient could come to different results.

Besides physical site factors, we added a proxy for management to the data set. Distance to roads was used as proxy for accessibility and management intensity. It differed significantly among the three forest types, and was lowest for beech mountain forests. This indicates that economically valuable tree species such as silver fir and spruce may have been removed from these forest stands in the recent past. In contrast, for mixed mountain forests in Bjelasica distance to roads was larger than for the other two forest types. The distance from roads prevented the uncontrolled cutting of fir and spruce. Furthermore, distance to roads was correlated to cover of tree layer, which was higher at larger distance to roads.

Vegetation parameters had higher axis loadings than physical site parameters in the ordination and correlated with the first axis. Species richness is negatively correlated with the number of trees in upperstorey as the tree cover represent the proxy for light availability and thus optimal conditions for the species in the understorey.

4.2 Regional and European classification

4.2.1 Mixed mountain forests

Mixed forests with silver fir, Norway spruce, and European beech ("*Piceo-Abietetum*" Čolić 1965) are widespread throughout the Balkan Peninsula, from Mt. Plješevica in Croatia to the Rhodope Mountains in Bulgaria. On the territory of Montenegro, they approach their southern limit (Curovic et al. 2011). Mixed mountain forests are considered to range from 800 to 1700 m a.s.l. with silver fir-beech forests occupying the lower areas (800 to 1650 m a.s.l.) and stands with additionally spruce occur at higher areas (1000 to 1550 m a.s.l.) (Diklić et al. 1997, Tomić 2004). Dinaric beech-fir forests in Croatia range from 600 to 1100 m a.s.l. In Bulgaria, fir-beech forests are mostly at altitudes of 1000 to 1400 m a.s.l. (Tzonev et al. 2006). In our study, forest stands with spruce occurred at elevation 900 to 1700 m a.s.l., which was outside its recently described range of distribution.

The distribution of these forest types in Bjelasica was influenced by the specific conditions. A large number of canyons and watercourses, as well as exposition of the terrain modify the climatic and soil conditions (Gazdić et al. 2016).

The so-called "*Piceo-Abietetum"* Čolić 1965 has an equal share of all three tree species under natural conditions, which can be shifted due to management (Tomić 2004). It appears that this also happened in Bjelasica, where stands had lower share of conifers closer to roads due to good accessibility and stronger harvesting of conifers. This means that the absence of fir from plots cannot necessarily related to abiotic conditions. The boundaries ("thresholds") of the potential natural distribution of silver fir are of particular interest, which also has implications for further management, i.e., tree species selection and subsequent stand treatment in montane production forests of the region.

In the former Yugoslavia, the bioclimatically defined belt of beech-fir (*Abieti-Fagetum* (Ht. 1938) Treg. 1957 s. lat.) forests is very pronounced and occupies large areas. Beech-fir forests are characterized by a dense tree layer dominated by beech and fir (Jovanović 1980). This forest formation was described under various geographic and climatic conditions, therefore includes a large number of names of associations throughout the former Yugoslavia. Beech-fir forests in Slovenia were described under the name *Abieti-Fagetum* "*dinaricum*" Treg. 1957 emend. Pun. 1977; *Abieti-Fagetum* "*praealpino-dinaricum*" Pun. 1979 (mscr.), *Abieti-Fagetum* "*praealpinum*" Robič. 1965 (prov.), *Abieti-Fagetum* "*praepannonicum*" Fab. 1963, *Luzulo-Abieti-Fagetum* "*praealpinum*" Mar. 1977 (prov.); in Croatia as *Fagetum* "*croaticum*" *abietetosum* Ht. 1938; in Bosnia & Hercegovina as *Abieti-Fagetum* "*illyricum*" Fuk. et Stef. 1958, *Fago-Abietetum* "*serpentinicum*" H. Ritter-Strudnička 1970, *Fago-Abietetum* Stef. 1963; in Serbia as *Abieti-Fagetum* "*serpentinicum*" B. Jov. (1957) 1979, *Abieti-Fagetum* "*serbicum silicicolum*" B. Jov. 1955, *Abieti-Fagetum* "*serbicum calcicolum*" B. Jov. 1955; in Macedonia as *Fagetum* "*montanum*" *abietetosum* Em 1965, *Fago-Abietetum* "*borisii-regis meridionale*" Em 1973; and in Montenegro as *Fagetum sylvaticae* "*montenegrinum abietetosum*" Bleč. 1958 (JOVANOVIĆ et al. 1986).

The association described as *Abieti-Fagetum* (Fuk. et Stef.) FUKAREK 1969 forms an altitudinal belt from 900 to 1400 (1500 m), and occurs also at lower altitudes in some regions depending on orographic and edaphic conditions (STEFANOVIĆ 1977).

Beech-fir forests in former Yugoslavia in general can be found under high precipitation (over 1200 mm), and on variable soils with pH ranging from 4,5 to 7,5 (ĆIRIĆ et al. 1971). The floristic composition of of these forests is very similar to beech-fir (-spruce) forests on Mt. Bjelasica. From Slovenia, through Croatia, Bosnia and Montenegro, many subassociations of this community have been described.

The two forest types *Polypodio-Fagetum moesiacae* and *Piceo-Abietetum*, in the former Yugoslavia, formed the intermediate mountain belt. This zone is characterized by precipitation sums between 1100 and 2800 mm per year and a mean annual temperatures between 5 and 8 °C, and between 10 and 14 °C in the vegetation period (JOVANOVIĆ et al. 1986). Beech has a much wider ecological and geographical range and builds many ecotypes which are adapted not only to different climatic conditions from the oak's to the spruce's belt, but also very different habitats within each zone of the mountain (MIŠIĆ & POPOVIĆ 1960). Silver fir, however, has a much narrower elevation range, and its distribution is limited to the subalpine zone (HORVAT 1954, JOVANOVIĆ 1980, MIŠIĆ et al. 1982). This beech and silver fir zone merges into the hot and dry oak zone (500–1000 m a.s.l.) and cold and harsh subalpine zone (spruce zone) (1550–1750 m a.s.l.) (MIŠIĆ et al. 1982). The community with tree dominant three species (*Piceo-Abietetum*) is usually located above the belt of beech-fir, in Bosnia it is widespread as well as in the northern Montenegro and southwestern Serbia (JOVANOVIĆ et al. 1986). As the Dinaric the Montenegrin beech-fir forests are much richer in species than the Pannonian ones (VUKELIĆ 2012), where species as *Picea abies*, *Sorbus aucuparia*, *Rhamnus fallax* and *Lonicera alpigena* are less frequent. The differential species in the beech-fir forests of the Sava-Drava and Montenegro are *Festuca drymeia*, *Carex pilosa* and *Luzula luzuloides* (VUKELIĆ 2012).

In the northwest Balkan beech-fir forests are also widespread. They belong to the alliance *Aremonia-Fagion* and suballiance *Lamio orvalae-Fagenion*, with an avarage altitude of 1086 m. Its diagnostic species are *A. alba*, *Rubus fruticosus*, *Oxalis acetosella*, *Rhamnus alpina* (MARINŠEK et al. 2013). The floristical composition of these forests is also very similar to mountain beech-fir forests on Mt. Bjelasica.

However, according WILLNER et al. (2017), Mixed Mountain forests in Mt. Bjelasica can be classified into unit Meso-basiphytic beech forests, subunit *Eu-Fagenion* I (Montane beech and fir-beech forests on moderately acidic brown soils). Also, these forests can be assigned to the *Galio odorati-Fagetum* Sougnez & Thill 1959 on the higher altitudes. *F. sylvatica* is very competitive species, often forming almost mono-dominant stands in Europe (WILLNER et al. 2017). In some mountain ranges such as Mt. Bjelasica, *A. alba* and *P. abies* are frequently codominant. These forests occupy moderately fresh to fresh soils with moderate or good base supply. Such soils can be found on silicate rocks (Gneiss, Schist, Amphibolite, etc.), Brown soils, Luvisols, Pseudogleys. Shrub layer of these forests is usually poor species (WILLNER and GRABHERR 2007).

4.2.2 Beech mountain forests

Montane beech forests (*Fagetum* "*montanum*" Ht. 1938 s. lat.) are widespread throughout Balkan and are usually assigned to the alliances *Fagion* "*illyricum*" Horv. 1950 and *Fagion* "*moesiacae*" Bleč. et Lakš. 1970. In former Yugoslavia, this group includes a large number of associations: *Fagetum* "*submontanum praedinaricum*" Mar. et Zup. 1978, *Fagetum* "*submontanum praealpinum*" Mar. 1978, *Lamio orvalae-Fagetum* "*praealpinum*" Mar. 1981, *Lamio orvalae-Fagetum "praedinaricum"* Mar., Pun. et Zup. (1982) 1984, *Fagetum* "*altimontanum praedinaricum*" (Košir 1962) Mar. 1980, *Fagetum* "*altimontanum dinaricum*" Mar. 1983, *Fagetum* "*altimontanum praealpinum*" Mar. 1978 (Slovenia); *Fagetum* "*croaticum boreale*" Ht. 1938, *Fagetum* "*croaticum australe montanum*" Ht. 1938 (Croatia); *Lathyro verni-Fagetum* (Ht. 1938) Fab. 1963, *Melico-Fagetum* Fab., Fuk. et Stef. 1963, *Fagetum* "*montanum illyricum*" Fuk. et Stef. 1958 (Bosnia and Herzegovina); *Fagetum* "*moesiacae montanum s. l.*" (Kosovo); *Fagetum* "*submontanum*" (Rud. 1940) B. Jov. 1967, *Fagetum* "*submontanum mixtum*" Mišić 1972, *Tilio-Fagetum* "*submontanum*" (Jank. et Mišić 1960) Mišić 1972, *Juglando- Fagetum* "*submontanum*" (Mišić 1966) B. Jov. 1979, *Ilici-Fagetum* "*submontanum*" B.Jov. 1979, *Dentario glandulosae-Fagetum* "*submontanum*" B. Jov. 1975, *Hyperico androsaemi- Fagetum* "*submontanum*" E. Vuk. 1966, *Fagetum* "*montanum serbicum*" B. Jov. 1953 (non Rud. 1940), *Fagetum* "*altimontanum moesiacum*" B. Jov. (1950, 1957, 1959) 1985 (Serbia), *Festuco heterophyllae-Fagetum* Em. 1965, *Calamintho grandiflorae-Fagetum* Em. 1965, *Aristolochio-Fagetum* Em 1965 (Macedonia) (JOVANOVIĆ et al. 1986).

Humidity in the montane areas of Montenegro is lower than in the Illyrian province (Croatia and Bosnia), where annual rainfall is significantly higher. Because of this, the Moesian beech prevails here, which is better adapted to drier conditions. According to JOVANOVIĆ et al. (1986), montane beech forests in Montenegro belong to the association *Fagetum* "*moesiacae montanum*" Bleč. et Lkšč. 1970.

The association *Fagetum* "*montanum*" (Fuk. et Stef.) FUKAREK 1969 is widely distributed and forms a continuous elevation belt along the Dinaric mountains. These forests occur from 800 (900) to 1100 (1200) m, depending on the size of the mountain massif. There are examples of close to virgin forests in Croatia, Bosnia and Montenegro (HORVAT 1958, e. g., in the strict reserves of Biogradsko Lake and Mt. Bjelasica). In modern times they were degraded by irregular forest management, and removed from their natural state (STEFANOVIĆ 1977) also in Mt. Bjelasica. Compared to the beech forests of Central Europe these forests are characterized by a greater richness of species. They are differentiated into several subassociations. Beech forests on the Bjelasica are very similar to the subassociation *cardaminetosum* Fab. 1966.

In Mt. Bjelasica anthropo-zoogenic impacts are particularly high, as forests are located near villages and surrounded by meadows and pastures. Long-term irregular management has led to degradation, so that a significant part of these forests is converted to coppice forests, with stunted trees of poor quality small height. This way of managing of these forests has also led to soil degradation. However, in some places, more distant and more hidden, which are harder to access, vigorously growing beech stands are well-preserved.

These forests are floristically richer than the forests of Central Europe, some of the characteristic species are: *F. sylvatica*, *A. pseudoplatanus*, *A. platanoides*, *Ulmus glabra*, *Daphne mezereum*, *Euonymus latifolius*, *Cardamine bulbifera*, *Galium odoratum*, *Paris quadrifolia* and *Mercurialis perennis*. All of these species are also characteristic for beech forests in the Mt. Bjelasica at higher altitude (over 900 m), and described site conditions correspond to those on the Mt. Bjelasica. However, in our research area many degraded forms of these forests occur.

The beech forests on Mt. Bjelasica below 800 m are very similar to the association *Helleboro odori-Fagetum* "*moesiacae*" Soo & Borhidi 1960, based on floristic composition and site conditions. The tree layer is highly structured with dominance of the beech and admixed *Carpinus betulus*, *A. pseudoplatanus*, *A. platanoides*, *Prunus avium* and *Q. petraea*. The shrub layer with *Sambucus nigra*, *Corylus avellana* and *Rubus hirtus* is poorly developed. Characteristic and common species of the herb layer are *Galium odoratum*, *Cardamine bulbifera*, *Geranium robertianum*, *Lamium galeobdolon*, *Asarum europeum* and *Pulmonaria officinalis* s. l.

In Balkan, beech forests occurs in a very wide belt from 100–300 m to 1400–1600 m a.s.l (Tomić 2004). In Croatia, belt of beech forests width is over 1000 m (Horvat 1954). *Fagetum* "*montanum*" in the Mt. Kopaonik (Serbia) occurs at an altitude from 1100 to 1600 m a.s.l., in northern exposure with slope 5–30^{o} (Mišić & Popović 1960); the floral composition of these forests is very similar to the beech mountain forests from Mt. Bjelasica. In Kosovo and Metohia mountain beech forests are widespread at altitudes above 1000 m, and predominantly on silicate surface (Krasnići 1972), floristic composition is pretty similar with the presence of some differential species such as *Cyclamen neapolitanum* and *Lathyrus inermis*. In the beech stands (from 800 to 1200 m a.s.l.) a many conifer stumps were observed, which suggests to regard this forest type as a degradation stage of deciduous-conifer forests (Diklić et al. 1997). Many authors assume that montane beech forests below 1100 m a.s.l. were stands of beech-fir forests in the past, but under the influence of management fir was removed (Tomić 2004). This is supported by the observed proximity of the stands to roads used as a proxy for management intensity and accessibility. Mixed mountain forests were far away from roads than beech mountain forests. However, it needs to be considered that road density decreases with altitude. Thus, further research is needed to untangle these confounded variables.

In Bjelasica montane beech forests (with *F. sylvatica* being the main tree species) occur below ca. 960 m a.s.l. Beech was actually dominant in all layers and diversity was rather low due to strong canopy shading. Mesophilic species, mainly of the Central European distribution type, such as *A. pseudoplatanus*, *A. platanoides*, *Q. petraea*, *Prunus avium*, *Pyrus pyraster* and *Fraxinus excelsior* occurred in the tree layer.

According Willner et al. (2017), this group can be classified into unit Meso-basiphytic beech forests, subunit *Eu-Fagenion* I (Montane beech and fir-beech forests on moderately acidic brown soils). Floristically and ecologically, these forests can be assigned to the *Galio odorati-Fagetum* Sougnez & Thill 1959.

4.2.3 Light mixed mountain forests

This forest group was the most heterogeneous. Main tree species were *P. nigra*, *O. carpinifolia* and accompanying species were pioneers such as *Betula pendula* and *Populus tremula*. Also, this group was the richest in species. In Bjelasica mountain this forest is young forest, but the high cover of beech and fir in shrub layer indicates that this type of forest is in the natural process of succession.

Pine species are an important component of Mediterranean forests. Characteristics of species such as high light demands, strong drought tolerances, and relatively fast growth-rates (HANLEY & FENNER 1997, RICHARDSON & RUNDEL 1998), allow them to succeed in the difficult conditions of the Mediterranean. Because of the ability of the seeds for "rapid migration and explosive population increase" (HIGGINS & RICHARDSON 1998) usually reinforce their invasive nature, especially in ecosystems that are susceptible to fire.

Pioneer tree species form early succession stages on abandoned lands and after natural or anthropogenic disturbances such as wind throw and (mainly anthropogenic) fires. In the last few decades the human population declined in the countryside of Montenegro, therefore the cultivated land decreased and has recently been overgrown by forest. Additionally, human-caused fires are not uncommon in the north of Montenegro, because in spring local people use fire to prepare the meadows for the next grazing period. Moreover, local people burn the forest field layer because after the fire they expect a better crop of mushrooms for collection and sale. These are some of the disturbances affecting this type of forest. However, light mixed mountain forests also occur on sunny, usually steep wind-exposed localities on the Dinaric karst in Montenegro, where *A. alba* is absent as a forest tree. The competitiveness of beech is also reduced on the usually rather shallow rankers and rendzinas to such an extent that sub-Mediterranean species like *O. carpinifolia* and *Fraxinus ornus* become admixed in the tree layer.

According to WILLNER and GRABHERR (2007) light mixed mountain forests with *O. carpinifolia* and *F. ornus* can be assigned to the association *Erico-Ostryetum* Horvat 1959 s. l. Situated on steep slopes, undeveloped land shallow and immature soils these forests form islands surrounded by more monodominant and closed beech forests.

The community with *P. nigra* occurred in a mosaic of coarse rock walls, and warm steep slopes with immature soils from limestone and dolomite. Other stands were interpretable as replacement communities of beech and beech- silver fir forests, mainly on recently burned sites or after clear cut, on steep slopes with recent landslides, colluvial drift, etc. *P. nigra* is the dominant tree species in the tree layer, and xerothermic species characterize these species rich forests. Frequent regeneration of silver fir and beech in these forests shows that during succession they might develop into mixed mountain forests during the next decades.

In the region of beech-fir forest in Croatia, *Helleboro-Pinetum* Horv. 1958 occupies large areas (HORVAT 1958) with similar habitat conditions and rather similar plant species as in Montenegro. The *Pinetum nigrae* "*submediterraneum*" Anić. 1957, as the coldest variant in an altitude from 450 to 1800 m a.s.l. was described in Mt. Velebit (Croatia). In Macedonia the *Fago-Pinetum nigrae* Em. 1981 is a widespread secondary forest type (JOVANOVIĆ et al. 1987, TOMIĆ 2004) very similar to the successional pine community in Mt. Bjelasica. *Pinus nigra* prevails in the community, while *P. sylvestris* occurs only at higher elevations, and the proportion of beech increases in more mature stands. Also the composition of terrestrial vegetation is similar, with prevailing acidophilic species such as *Vaccinium myrtillus*, *Pteridium aquilinum* and *Galium rotundifolium*. Even more extreme communities are found in the canyon of the river Piva (*Pinetum nigrae* "*montenegrinum*" Bleč. 1958) on Mt. Goč (Serbia, *Potentillo-Pinetum nigrae gončensis* Jov. 1959 with a greater number of subassociations). The subassociation *abietetosum* occurs above 1000 m, as in Mt. Bjelasica this mature successional stage approaches beech-fir forests (TOMIĆ 2004). However, these beech forests with pine in Mt. Bjelasica can be classified as *Fago-Pinetum nigrae* Em. 1981.

4.3 Implications for sustainable use and conservation

The current average annual increment of standing wood in Bjelasica is 5,8 m^3/ha in high forests and 3,7 m^3/ha in coppice forests (DEES et al. 2013). The current average annual increment in mixed beech-fir-spruce forests of Montenegro is 8,3 m^3/ha. Also, the current average annual increment of fir (10,3 m^3/ha) and spruce (8,7 m^3/ha) is larger than beech`s (5,1 m^3/ha). In Montenegro, beech forest area is about 20% of all forests, only 10% of all forests are beech-fir and beech-fir-spruce forests together (DEES et al. 2013).

Timber harvest of silver fir and especially spruce is highest in mixed beech-fir, beech-spruce, and spruce-beech-fir forests (PRETZSCH et al. 2010, 2013). However, this was studied for central European forests and needs to be shown for forests of Montenegro. Nevertheless, reducing the area of mixed deciduous-coniferous forests poses a threat to Montenegrin forestry, not only because beech stands are already more frequent than the more productive silver fir and spruce stands, but also because mixed forests are more stable regarding natural regeneration after harvest, disturbances and also facing climate change. Thus, common illegal cutting and anthropogenic fire threaten the resilience of forest stands. In the period from 2006 to 2010, 40226 ha of forests or 4.7% of the total area under the forests were destroyed by anthropogenic fire (DEES et al. 2013). Any disturbance of beech-fir forest structure changes the floristic composition and usually decreases timber yield.

From a natural conservation viewpoint mixed mountain forests of Montenegro constitute habitat for a diverse and special wildlife including protected mammals such as brown bear (*Ursus arctos*) and roe deer (*Capreolus capreolus*) as well as birds such as *Aquila chrysaetos*, *Buteo buteo*, *Tetrao urogallis*, *Strix aluca* etc.

Thus, restoration of mixed beech-fir, beech-fir-spruce forests should be imperative in the future, from the forestry as well as the nature conservation viewpoint.

5. Conclusion

Mountain forests of Montenegro are quite similar to forests in comparable regions of Europe and can be arranged into existing "Classification of European beech forests" (WILLNER et al. 2017) and according to WILLNER & GRABHERR (2007). These forests are subject to dynamics due to the combination of current land abandonment and forest regrowth on the one hand and fire disturbance for improvement of pastures and mushroom yields. Special attention needs to be paid to potential over-exploitation of well accessible forests stands, which are potential mixed mountain forests with beech, fir and spruce, but have been degraded to mere beech stands. The interplay of these dynamics and its impact on forestry and timber production as well as protected habitats and wildlife requires further study.

Erweiterte deutsche Zusammenfassung

Einleitung – Der derzeitige Zustand von Wäldern wie auch ihre Baumartenzusammensetzung sind das Ergebnis ihrer ehemaligen Entwicklung und letztlich ein Beleg für alle ehemaligen Einflüsse (ŠERCELJ 1996, BONCINA et al. 2003). Für bessere Vorhersagen ihrer zukünftigen Ausprägung und zur Entwicklung nachhaltiger Forstwirtschaftsstrategien ist die Kenntnis der Entwicklungsprozesse in Wäldern und ihrer treibenden Kräfte wichtig. Bergmischwälder in Montenegro bieten eine exzellente Möglichkeit, ostmediterrane Bergmischwälder an ihrer südlichen Verbreitungsgrenze zu untersuchen. Montenegro ist durch eine außergewöhnlich große Variabilität von Standortsbedingungen gekennzeichnet, wo das Klima Waldwachstum und Sukzession limitiert, aber auch zu üppigem Waldwachstum

führen kann (Scarascia-Mugnozza et al. 2000). Ziele dieser Studie waren 1) die Bergwälder einer östlichen Mediterranregion floristisch zu charakterisieren und 2) ihre abiotischen Standortsbedingungen als bestimmende Faktoren zu beurteilen.

Material und Methoden – Die Untersuchung basiert auf Daten von 158 Vegetationsaufnahmen im Gebiet des Bjelsica-Gebirges im nordöstlichen Montenegro. Die Größe der Probeflächen betrug 100 m^2 mit homogenen Standortsbedingungen. An jedem Standort wurden die folgenden Parameter erhoben: Lage (Längengrad/Breitengrad), Geländeform (Exposition und Hangneigung, Höhe, Krümmung, Lage im Gelände), Landnutzung und Boden. In den statistischen Analysen nutzten wir die folgenden Variablen: Deckung der Pflanzenarten, Artenzahl, Simpson-Index, Gesamtdeckung der Schichten, Meereshöhe, pH, Bodentiefe, Entfernung zur Straße, Schattseitigkeitsindex. Der Einfluss topographischer, klimatischer und edaphischer Standortsfaktoren auf die Differenzierung der Vegetation und Ausbildung von Waldtypen wurde anhand numerischer Ordination und Klassifikation beurteilt.

Ergebnisse – Unter den Vegetationsvariablen zeigten Deckungsgrad der Bäume und Kräuter ($p < 0{,}001$), Pflanzenartenzahl ($p < 0{,}001$) und Simpson Diversität ($p < 0{,}001$) die deutlichsten Beziehungen zu den Hauptachsen der floristischen Variabilität. Die signifikantesten Standortsvariablen waren Höhenlage ($p < 0{,}001$), Temperatur und Niederschlag ($p < 0{,}001$). Drei Bergwaldtypen wurden anhand ihrer Artenzusammensetzung definiert, die leicht anhand ihrer Baumartenzusammensetzung unterschieden werden können: 1) Mischwälder mit Fichte, Tanne und Buche, 2) monodominante Buchenwälder, die aus der Übernutzung von Typ 1 resultieren, und 3) lichte Mischwälder mit Pionierarten (Kiefer, Zitterpappel und Birke) sowie Hopfenbuche. Die erste Isopam-Gruppe kam in größeren Höhenlagen vor, wo der Niederschlag höher und die Temperatur niedriger war. Diese Gruppe war außerdem am weitesten von Straßen entfernt und hatte die höchste Deckung der Baumschicht. Nach Willner et al. (2017) können diese Wälder dem *Galio odorati-Fagetum* Sougnez & Thill 1959 höherer Lagen zugeordnet werden. Die zweite Isopam-Gruppe kam in den geringeren Höhenlagen vor, mit höheren Temperaturen und geringerem Niederschlag. Die Bodentiefe in dieser Gruppe war die größte und homogenste. Nach Willner et al. (2017) können diese Wälder ebenfalls dem *Galio odorati-Fagetum* zugeordnet werden. Die dritte Isopam-Gruppe unterschied sich klar von den beiden anderen durch eine höhere Artenzahl und das Vorkommen von relativ lichtbedürftigen Baumarten. Nach Willner & Grabherr (2007) lassen sich die lichten Bergwälder mit *Ostrya carpinifolia* und *Fraxinus ornus* dem *Erico-Ostryetum* Horvat 1959 s. l. zuordnen; andere Bestände stellen Pineten dar.

Diskussion – Die Waldtypen werden entsprechend ihrer abiotischen Standortsbedingungen diskutiert und in einen europäischen Kontext gesetzt. Die Bergwälder Montenegros sind den Wäldern in anderen Regionen Europas recht ähnlich und können in die existierende Klassifikation der europäischen Buchenwälder von Willner et al. (2017) eingeordnet sowie nach Willner & Grabherr (2007) klassifiziert werden. Besonderes Augenmerk wurdeauf die mutmaßliche Übernutzung gut zugänglicher Waldbestände gelegt, die potenzielle Bergmischwälder mit Buche, Tanne und Fichte darstellen, aber zu reinen Buchenbeständen degradiert sind. Das Zusammenspiel zwischen natürlicher und nutzungsbedingter Dynamik und ihr Einfluss auf Forstwirtschaft und Holzproduktion wie auch geschützte Habitate und die Tier- und Pflanzenwelt bedürfen weiterer Untersuchungen.

Author contribution

MG, AR and KD conceived the idea, designed the experiment and performed the data analysis. MG, MK and DP conducted the field sampling, MG wrote the manuscript. MK, DP and MS revised the manuscript and participated in the discussion of the results.

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Supplements

Supplement S1. Constancy table as provided by Isopam classification.

Beilage S1. Stetigkeitstabelle als Ergebnis der Isopam-Klassifikation.

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Supplement S1. Constancy table as provided by Isopam classification; species occurrences per forest type (%); significance levels according to Isopam output: < 0.0001 ***, < 0.001 **, <0.01 *; gray shading: the diagnostic species.

Beilage S1. Stetigkeitstabelle als Ergebnis der Isopam-Klassifikation; Vorkommen der Arten nach Waldtyp (%), Signifikanzniveaus entsprechend der Isopam-Ausgabe: < 0,0001 ***, < 0,001 **, <0,01 *; graue Schattierung: diagnostische Arten.

Column	**1**	**2**	**3**
Forest type	**Mixed montane forest**	**Beech montane forest**	**Light mixed montane forest**
relevés per cluster	**61**	**72**	**25**
Tree layer			
Abies alba	61 ***	5 ***	12 *
Picea abies	21 **	7	0 *
Fagus sylvatica	94	97 *	64 ***
Pinus nigra	0 **	0 **	40 ***
Populus tremula	6	7	32 ***
Ostrya carpinifoilia	3 *	8	32 ***
Quercus petraea	1 **	7	32 ***
Betula pendula	35 **	15 *	20
Acer pseudoplatanus	17	7	16
Pyrus pyraster	1.3	0	0.6
Fraxinus excelsior	0	0.6	0.6
Shrub layer			
Abies alba	90 ***	21 ***	12 ***
Fagus sylvatica	92	97	76 *
Pteridium aquilinum	6 **	25 *	24
Pinus nigra	3	0 **	36 ***
Ostrya carpinifoilia	1 ***	11	36 ***
Corylus avellana	4 *	8	32 ***
Quercus petraea	0 *	0	24 ***
Acer pseudoplatanus	17	8 *	40 **
Populus tremula	10	3 *	32 **
Juniperus communis	6	0 **	24 **
Picea abies	22	15	8
Betula pendula	10	15	12
Fraxinus excelsior	7	5	16
Prunus avium	3	2	12
Rhamnus fallax	1.9	0	0
Crategus oxyacantha	0	0.6	1.3
Rossa canina	1.3	0	0
Salix caprea	0.6	0.6	0
Sambucus nigra	0.6	0.6	0
Herb layer			
Galeobdolon luteum	51 **	34	20 *
Rubus fruticosus	35 *	16	20
Oxsalis acetosella	39 ***	16	4 **
Abies alba	78 ***	41 *	8 ***
Fagus sylvatica	92	89	72 *
Acer pseudoplatanus	62	43 **	76 *
Viola odorata	46 *	10 ***	63 ***
Luzula forsteri	38	23 *	44
Anemone apennina	19	5 **	28
Rubus idaeus	42 *	62	64
Quercus petraea	4 ***	30 **	28
Ostrya carpinifolia	0 ***	18 *	20
Lamium galeobdon	2 *	24 **	18
Fragaria vesca	19 ***	41	88 ***
Populus tremula	25	11 ***	76 ***
Rosa canina	14	7 **	64 ***
Euphorbia amygdaloides	14 **	25	60 ***
Pinus nigra	3 *	0 ***	52 ***
Luzula luzuloides	12	3 **	44 ***
Hypericum perforatum	0 **	2	28 ***
Quercus cerris	11	16	32 *
Veronica urticifolia	3 **	13	28 **
Fraxinus excelsior	10 *	20	32 *
Pteridium aquilinum	38 **	56	80 **
Juniperus communis	6	7	24 *
Corylus avellana	4	7	20 *
Potentilla erecta	0	0	16 ***
Galium sylvaticum	56	38	48
Festuca drymeia	18 *	38 *	28
Picea abies	25	28	28
Aremonia agrimonioides	28	21	32
Viola reichenbachiana	24	25	24
Galium robertianum	11	21	28
Dentaria bulbifera	14	16	8
Vaccinium myrtillus	11	13	12
Epimedium montanum	15	13	0 *
Betula pendula	7	13	16
Dryopteris filix-mas	8	15	4
Prenanthes purpurea	11	7	12
Anemone nemorosa	4	18 **	0
Epilobium angustifolium	11	7	8
Luzula sylvatica	4	11 *	0
Galium odoratum	6	7	8
Sorbus aucuparia	7	3	8
Sambucus nigra	4	7	4
Asarum europaeum	6	3	8
Daphne blagayana	11 **	0 *	0
Mercurialis perennis	3	7	8
Saxifraga rotundifolia	7	0 *	8
Hedera helix	1	10 *	0

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Fortsetzung auf der Rückseite

Column	1	2	3
Forest type	Mixed montane forest	Beech montane forest	Light mixed montane forest
relevés per cluster	61	72	25
Anemone hepatica	8 *	2	0
Athyrium filix-femina	1	8 *	0
Hieracium sp.	0	1	8 *
Crataegus oxyacantha	1	1	4
Helleborus odorus	3	1	1
Polystichum aculeatum	0	4	1
Hepatica triloba	0	3	1
Allium ursinum	0	0.6	2.4
Epilobium angustifolium	1.3	1.3	0
Potentilla alba	2.5	0	0
Atropa belladonna	0.6	1.3	0.6
Polytrichum formosum	0.6	0.6	1.3
Polygala vulgaris	1.9	0.6	0
Hypericum perforatum	1.9	0	0.6
Sanicula europaea	0	1.9	0.6
Calamintha nepeta	1.9	0	0.6
Lonicera alpigena	0	1.9	0.6
Dryopteris dilatata	0	1.9	0
Polystichum lonchitis	0.6	1.3	0
Clematis vitalba	0.6	0	1.3
Pyrus pyraster	1.3	0.6	0
Pulmonaria officinalis	0	0.6	1.3
Trifolium repens	1.9	0	0
Galium lucidum	1.9	0	0
Sedum acre	1.9	0	0
Euonymus latifolia	0	1.9	0
Prunus avium	0	0	1.9
Poa nemoralis	0	0	1.9
Agrimonia eupatoria	0.6	0.6	0.6
Hieracium tomentosum	1.3	0.6	0
Verbascum divisma	0	1.3	0.6
Ruscus hypoglossum	0	0.6	1.3
Colchium autumnale	0.6	0.6	0
Viola odorata	0.6	0.6	0
Polygonatum multiflorum	0.6	0.6	0
Epipactis helleborine	0.6	0.6	0
Heracleum sphondylium	0.6	0.6	0
Circaea lutetiana	0.6	0.6	0
Sorbus aucuparia	0.6	0.6	0
Achillea millefolium	0.6	0	0.6
Urtica dioica	0.6	0	0.6
Polystichum setiferum	0	0.6	0.6
Lunaria rediviva	0	0.6	0.6
Carex pendula	0	0.6	0.6
Daphne mezereum	0	0.6	0.6
Polypodium vulgare	0	0.6	0.6
Hieracium bauhinii	1.3	0	0
Convallaria majalis	1.3	0	0
Campanula pyramidalis	1.3	0	0
Juniperus nana	1.3	0	0
Briza minima	1.3	0	0
Stachys officinalis	1.3	0	0
Carduus nutans	1.3	0	0
Globularia cordifolia	1.3	0	0
Trifolium medium	1.3	0	0
Leontodon crispus	1.3	0	0
Thymus alpestris	1.3	0	0
Carex sylvatica	1.3	0	0
Homogyne alpina	1.3	0	0
Asperula scutellaris	1.3	0	0
Geum urbanum	1.3	0	0
Paris quadrifolia	0	1.3	0
Neottia nidus-avis	0	1.3	0
Coronilla coronata	0	1.3	0
Euphorbia angulata	0	1.3	0
Geranium sylvaticum	0	1.3	0
Lilium martagon	0	1.3	0
Tussilago farfara	0	0	1.3
Pinus sylvestris	0	0	1.3
Sorbus aria	0	0	1.3
Lonicera nigra	0	0	1.3
Glechoma hirsuta	0	0	1.3
Asplenium viride	0	0	1.3

Rare species in only one column (column/frequency):

Tree layer: Pinus sylvestris 1/0.6, Hedera helix 1/0.6, Salix caprea 2/0.6, Corylus avellana 3/0.6, Acer campestre 3/0.6, Quercus cerris 3/0.6.

Shrub layer: Sorbus torminalis 1/0.6, Euonymus latifolia 1/0.6, Sorbus aucuparia 1/0.6, Ulmus glabra 1/0.6, Prenanthes purpurea 1/0.6, Pyrus pyraster 1/0.6, Lonicera nigra 1/0.6, Tilia cordata 2/0.6, Alnus incana 2/0.6, Hedera helix 2/0.6, Malus sylvestris 3/0.6, Quercus ceris 3/0.6.

Herb layer: Polypodium vulgare 1/0.6, Cirsium sp. 1/0.6, Pinus heldreichii 1/0.6, Avenella flexuosa 1/0.6, Sesleria autumnalis 1/0.6, Brachypodium sylvaticum 1/0.6, Campanula bertolae 1/0.6, Thymus serpyllum 1/0.6, Trifolium pratense 1/0.6, Gentiana asclepiadea 1/0.6, Salix caprea 1/0.6, Acer platanoides 1/0.6, Astragalus glycyphyllos 1/0.6, Cynodon dactylon 1/0.6, Plantago major 1/0.6, Asarum europaeum 1/0.6, Phyllittis scolopendrium 1/0.6, Sedum ochroleucum 1/0.6, Thalictrum aquilegiifolium 1/0.6, Linaria vulgaris 1/0.6, Euonymus latifolia 1/0.6, Fritillaria montana 1/0.6, Pyrola secunda 1/0.6, Asperula longiflora 1/0.6, Ligusticum cornubiense 1/0.6, Hypericum maculatum 2/0.6, Ajuga reptans 2/0.6, Senecium sp. 2/0.6, Ceterach officinarum 2/0.6, Lotus corniculatus 2/0.6, Dryopteris dilatata 2/0.6, Asperula purpurea 2/0.6, Veratrum album 2/0.6, Helianthemum alpestre 2/0.6, Plantago lanceolata 2/0.6, Silene vulgaris 2/0.6, Veronica officinalis 3/0.6, Salvia glutinosa 3/0.6, Saxifraga cruciata 3/0.6, Rhamnus fallax 3/0.6, Acer campestre 3/0.6, Dianthus sp. 3/0.6, Muscari racemosum 3/0.6, Bromus sp. 3/0.6.