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SUCCESSION, MANAGEMENT AND RESTORATION OF DRY GRASSLANDS

Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., Bulgaria

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Abstract

The area of semi-natural grasslands in Bulgaria has decreased tremendously in the past century due to agricultural intensification or abandonment. As these grasslands host valuable biodiversity, conservation measures are needed for their sustainable maintenance. We studied the effect of pastureland abandonment on plant communities at the Ponor Mt., a part of the Balkan Mts., Bulgaria. Data on floristic composition, vegetation structure and several abiotic parameters were collected in 137 randomly located 16-m^2 plots in 2008. Canonical correspondence analysis (CCA) was used to analyse how species composition is related to abiotic and land use factors. Analyses of covariance (ANCOVAs) were used to test for the effects of sheep grazing vs. abandonment on vegetation structure and composition. The main environmental factors explaining the compositional variation were related to the altitude, sheep grazing and soil depth. Pastureland abandonment led to an increase in vegetation height and of the richness of mesophytes and leafy plants, and red-list species. Grazed plots had higher total species richness, more xerophytes, rosette forming and spring-flowering species. To ensure the persistence of the species of both the open grasslands and mid-successional grassland communities, the management should be carried out in an extensive way and with a zonation regime.

Keywords: Festuco-Brometea, *pasture, Ponor Mt., sheep grazing, species composition, species richness*

Introduction

Traditional use of pastures is considered to be beneficial by providing high quality products for consumers and in the same time by supporting biodiversity including many rare and threatened species (Henle et al. 2008). In this respect, pastures represent an important habitat for both socio-economic and ecological reasons, and alterations in their management are known to have consequences on ecosystem services (Díaz et al. 2007). However, these habitats decline significantly throughout Europe, because of the loss of traditional grazing practices during the twentieth century and the subsequent natural succession or afforestation which reverted many semi-natural grasslands into scrub and woodland (Newton et al. 2009; Veen et al. 2009). Grazing impacts can vary substantially depending on factors such as stocking density, livestock type, grazing season, site characteristics and climate (Lake et al. 2001; Newton et al. 2009). Although many of these factors have been investigated so far, grazing has a wide range of different impacts on grasslands, leading to various ecological responses that still are not easy to predict and interpret (Bornkamm 2006). Some studies suggest that grazing increases plant species diversity by reducing competitive pressure and creating horizontal heterogeneity of sites, e.g. through gap formation (Dupré & Diekmann 2001). On the other hand, Bornkamm (2006) demonstrates species loss due to grazing, which is explained by the selective destruction of biomass, compression of soil and destruction of soil surface caused by the presence of grazing animals. Škornik et al. (2010) found in Slovenian dry pastures that species richness is highest under light grazing, but decreases significantly both through intensification and abandonment. Ruprecht et al. (2009) found that species richness of red-listed vascular plants did

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not differ significantly between grazed and 40-year abandoned steppic lowland pastures in Romania, while species composition changed strongly. Generally, pasture abandonment influences plant functional traits composition (Lavorel et al. 1998; Díaz et al. 2007; Kahmen & Poschold 2008) and foliage structure by favouring the development of more dense and patchy vegetation (Persson 1984; Křenová & Lepš 1996). According to certain studies, tall grasses and nitrophilous herbs increase due to pasture abandonment (Krahulec et al. 2001), while species with short life cycle decrease (Lennartsson & Svensson 1996). However, these effects have been identified as space- and time-scale dependent, and extrapolation of the results from one to another region is limited (František et al. 2001). Most of the existing knowledge of the topic was derived from Central and Western Europe (Newton et al. 2009), while Eastern European countries are still poorly studied. Within Eastern Europe, the Balkan Peninsula is of special interest as it hosts less transformed natural landscapes than most other regions in Europe as well as particularly high levels of biodiversity (Kryštufek & Reed 2004). In most Balkan countries, traditional pastoralism still exists, but in many areas it has decreased significantly (e.g. Veen & Metzger 2009; Nikolov 2010), resulting in land abandonment and subsequent changes in vegetation structure (Meshinev et al. 2000, 2009; Stevanović et al. 2008). Thus, for the sustainable management of the semi-natural grasslands and conservation of their biodiversity, scientifically based conservation recommendations are needed for the region. However, most studies dealing with grazing impacts on vegetation in the Balkan area were qualitative in nature, with only a few quantitative analyses to date (e.g. Stevanović et al. 2008; Başnou et al. 2009).

Semi-natural grasslands are presently still widespread in Bulgaria (Meshinev et al. 2005), but their cover has decreased tremendously. In the beginning of the twentieth century, the semi-natural grasslands covered 18,000 km^2 (16% of the country territory) (Ganchev et al. 1964), but this area was reduced significantly in the 1990s and currently these habitats cover about 8500 km^2 (EEA 2010). Meshinev et al. (2005) identified two main negative processes in semi-natural grasslands: the invasion of woodland species due to abandonment and the conversion of pastures to arable fields, both leading to a decrease in species richness of vascular plants. However, there is no quantitative study addressing the impact of grazing on vegetation composition and structure (at community and functional groups level), and on rare and endemic species.

In this study, we used a landscape-level approach to analyse the impact of pasture abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., a typical pastoral area of Bulgaria. The specific objectives of the study were (i) to compare community parameters and environmental variables between abandoned and extensively used pastures; (ii) to identify the main gradients in the vegetation compositional variation; (iii) to reveal the response of vascular plants to grazing or abandonment at the levels of species and functional groups.

Study area

The study was carried out in the Ponor Mt., which is located in the western part of the Balkan Mts. The latter mountain range stretches 600 km along the Danube River from the Black Sea coast to northern Serbia. The Balkan Mts. show heterogeneous topography with peaks of more than 2000 m a.s.l. in the west but only 500–600 m in the east. The traditional land use is sheep farming in higher elevations and arable fields in the valleys with fertile soils.

The study area (43° 03′N–23° 10′E) covers about 300 km^2 located about 50 km northwest of the Bulgarian capital Sofia (Figure 1) and ranges from 389 to 1598 m a.s.l. The region is recognised as a part of the Natura 2000 network (Site of Community Interest BG0001040). Both limestone and dolomite with karst forms are characteristic for the landscape. The Ponor Mt. belongs to the temperate-continental climatic zone (Velev 2002) and is characterised by warm summers (mean July temperature 11°C) and cold winters (mean January temperature −8°C), resulting in a considerable annual temperature amplitude (Velev 2002). The mean annual precipitation is 1000 mm with a maximum from spring to summer and a minimum in winter (Velev 2002).

The vascular plant flora of the area comprises of 904 species from 408 genera and 84 families (K.V. & H.P. unpubl. results). The potential natural vegetation is dominated by *Quercus pubescens*, *Quercus daleshampii*, *Carpinus betulus* and *Fagus sylvatica* (Bohn et al. 2004). Presently, most of the territory is covered by xerophytic and mesophytic grasslands belonging to the alliances *Cirsio-Brachypodion* Hadač & Klika in Klika & Hadač 1944 and *Festucion valesiacae* Klika 1931 of the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944. Communities of the *Molinio-Arrhenatheretea* Tx. 1937 are distributed mainly near villages and are used as meadows. In the wetter parts of the mountain in the pot-holes, communities of the classes *Scheuchzerio-Caricetea fuscae* Tx. 1937 and *Calluno-Ulicetea* Br.-Bl. & Tx. ex Klika & Hadač 1944, dominated by *Nardus stricta*, occur locally (unpublished data). The major land management is related to traditional rural activities, such as grazing mainly with sheep and hay making,

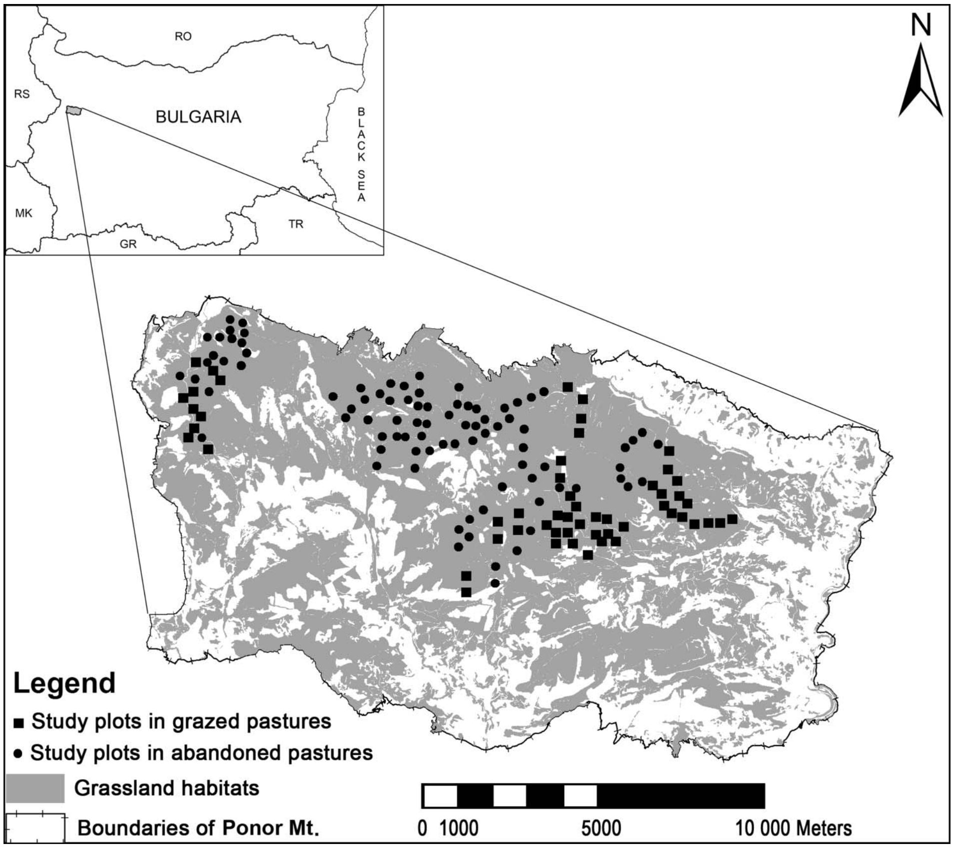

Figure 1. Location of the study plots in the Ponor Mt. and location of the study area in Bulgaria.

with a small fraction of arable fields. After the socio-economic changes in the 1990s, large areas of former pastures have been abandoned as a result of the tremendous decrease of livestock (Nikolov 2010).

Methods

Data collection

Interviews with local farmers and municipalities were carried out to find out which semi-natural grassland areas were abandoned (about 20 years ago) and which are still in use. These interviews resulted in a digital map of the area (Bulgarian Society for the Protection of Birds, unpublished data), which was used to allocate 140 study plots randomly in the accessible pastures of the Ponor Mt. (note that the southern parts are practically inaccessible by roads). Within each of the two mapping categories "abandoned" and "extensively grazed" 70 plots were selected randomly with the restriction that any two adjacent study plots should be at least 250 m apart. After verification in the field, three study plots were eliminated from the study as they were located in other habitats than grasslands, leaving 137 study plots for vegetation analyses. The categorisation in the field based on visible signs of livestock activity deviated from the *a priori* map-based classification, resulting finally in 52 grazed and 85 abandoned pastures.

Vegetation relevés were sampled on 4 m × 4 m plots (size according to the suggestion of Chytrý & Otýpková 2003) from June to August 2008. The relevés analysed in this article are stored in and available from the Bulgarian vegetation database (Apostolova et al. in press; database EU-BG-001 according to GIVD, Dengler et al. 2011) with plot IDs 1974–2111.

Altitude and location were measured by Garmin eTrex Vista (GPS), the exposition was determined by a compass, and the slope was assessed visually in the following categories: (1) $<5^\circ$, (2) 5–10° and (3) $>10^\circ$. Soil depth was estimated by digging with a scoop in one corner of each study plot. Soils were classified as (1) shallow (<10 cm depth), (2) moderately deep (10–20 cm) or (3) deep (>20 cm). The cover of vascular plant species was estimated with the modified Braun-Blanquet scale of Westhoff & van der Maarel (1973). The vertical structure of the vegetation was described in three categories: (1) high-level vegetation layer (>60 cm), (2) mid-level vegetation layer (20–60 cm) and (3) low-level vegetation layer (<20 cm). The cumulative cover was calculated as a sum of the cover values of the three vegetation layers. Additionally, the cover of shrubs was estimated within a radius of 50 m around each study plot.

In order to investigate whether plant functional groups respond differently to pasture abandonment, we classified the vascular plant species into four groups following the approaches of McIntyre et al. (1999) and Lepš et al. (2006): (1) grasses, (2) sedges and rushes, (3) legumes and (4) other forbs. Because of their nature conservation importance, the rare and endemic species were additionally analysed as a separate group. We also considered in the analysis different groups of plants according to selected plant functional traits and further growth characteristics (Grime et al. 2007, supplemented by Kozhuharov 1992); each species was assigned to the predominant category only, namely life span (annual, biennial and perennial), life form (chamaephytes, therophytes, hemicryptophytes, phanerophytes and geophytes), canopy structure (basal, semi-basal and leafy), preference to soil moisture (mesophytes, meso-xerophytes and xerophytes), reproduction type (vegetative and non-vegetative), flowering period (winter, winter–spring, spring, spring–summer and spring–summer–autumn) and duration of the flowering period (0–90, 91–181 and >181 days).

The categorisation of threatened species corresponds to the Red List of Bulgarian vascular plants (Petrova & Vladimirov 2009), the Annexes 2, 3 and 4 of the Biological Diversity Act (Anon. 2007), and the Convention of International Trade in Endangered Species of Wild Flora and Fauna (CITES Secretariat 2010). The endemics (Balkan endemics) were recognised according to Petrova & Vladimirov (2010). Threatened and endemic species are collectively termed "species with conservation importance" in this article. Habitat types follow the Palearctic classification (Pal. Class.; Devillers & Devillers-Terschuren 1996).

Data analyses

Multivariate relationships between environmental variables and vegetation composition were determined by a canonical correspondence analysis (CCA), using CANOCO 4.5 (ter Braak & Šmilauer 2002) after having checked the gradient length and thus the suitability of a unimodal model by a detrended correspondence analysis (DCA). The length of the species data gradient was 3.163 and it was within the range for which both linear and unimodal ordination methods work well (Lepš & Šmilauer 2003). We preferred to use a CCA rather than a redundancy analysis (RDA) because the CCA better explained the variation in our data (the sum of all canonical eigenvalues was 0.604 for CCA and 0.134 for RDA). A Monte-Carlo permutation test was applied for the assessment of the statistical significance of canonical axes. Only one representative variable from a set of correlated variables ($|r_s| > 0.5$) was used in the ordination analyses. Species cover data were log-transformed before analysis and rare species were down-weighted (Lepš & Šmilauer 2003).

Before testing the effect of grazing vs. abandonment on various parameters, we checked distributions of all data visually (box-whisker plots etc.), following the suggestions of Quinn & Keough (2002). As we did not find strong deviations from normality or homoscedasticity, we applied parametric tests in the subsequent analyses. Furthermore, we checked by analyses of variance (ANOVAs) whether some of the measured abiotic parameters were sufficiently similar between grazed and abandoned plots. Those that showed significant differences (i.e. altitude and soil depth) were included as covariates in the subsequent analyses of covariance (ANCOVAs), with land use type as fixed effect. All the aforementioned analyses were computed using STATISTICA 7.0 (StatSoft 2004). Results are reported as means $\pm$ standard deviation (SD).

To test whether the distribution of species between the two land use types deviated from random, we used Fisher's exact test and quantified the degree of concentration with phi-values (Chytrý et al. 2002). The calculation of Fisher's exact test was done in JUICE (Tichý 2002), while the phi-values were calculated in MS Excel.

Results

Overall vegetation composition

Overall, 316 vascular plants species were identified in the studied semi-natural grasslands. The most frequent species was *Thymus longicaulis* (80%), while *Galium verum*, *Achillea millefolium*, *Asperula cynanchica*, *Filipendula vulgaris*, *Teucrium chamaedrys*, *Festuca rubra* and *Plantago lanceolata* were also present in more than 50 % of the plots (Table I). There were 16 species with conservation importance: six Balkan endemics, seven species protected by the law, four species included in the Red List of Bulgarian vascular plants and four species included in CITES (Table II).

All 137 plots could be assigned to one of four habitat types: sub-continental steppic grasslands (Pal. Class. code 34.31, $n = 89$), Mountain hay meadows (Pal. Class. code 38.3, $n = 40$), Balkanic montane mat-grass swards (Pal. Class. code 35.73, $n = 7$), and Purple moorgrass meadows and related communities (Pal. Class. code 37.31, $n = 1$). The mean species richness in the 16-m^2 plots was 33.0,

Table I. Abridged synoptic table of the 137 studied grassland plots in the Ponor Mt. All vascular plant species are shown that are either significantly concentrated in one of the two land use types grazing ($n = 52$) or abandonment ($n = 85$) according to Fisher's exact test or that occurred in at least one-third of all plots.

Species	Acronym	Functional group	Constancy (%)			phi value × 100	
			All	Grazed	Abandoned	Grazed	Abandoned
Diagnostic species for grazing							
Medicago falcate	MedFal	L	30	60	12	51**	
Eryngium campestre	EryCam	F	31	60	13	49*	
Crupina vulgaris	CruVul	F	21	44	7	44*	
Cirsium vulgare	CirVul	F	28	52	14	41*	
Carex caryophyllea	CarCar	S	32	56	18	40*	
Sideritis Montana	SidMon	F	12	27	2	37*	
Centaurea stoebe	CenSto	F	18	37	7	37*	
Convolvulus arvensis	ConArv	F	20	38	8	37*	
Hieracium pilosella	HiePil	F	50	73	35	37*	
Leontodon crispus	LeoCri	F	38	60	25	35*	
Linum catharicum	LinCat	F	12	25	4	32*	
Carlina acanthifolia	CarAca	F	45	65	33	32*	
Prunella vulgaris	PruVul	F	11	23	4	30*	
Euphrasia sp.	EupSpp	F	27	44	16	30*	
Logfia arvensis	LogArv	F	5	13	–	30*	
Festuca dalmatica	FesDal	G	34	52	24	29*	
Trifolium repens	TriRep	L	7	15	1	28*	
Cichorium intybus	CicInt	F	4	12	–	27*	
Daucus carota	DauCar	F	4	12	–	27*	
Potentilla cinerea	PotCin	F	47	63	36	26*	
Salvia nemorosa	SalNem	F	6	13	1	25*	
Phleum montanum	PhlMon	G	6	13	1	25*	
Vicia sativa	VicSat	L	6	13	1	25*	
Minuartia viscose	MinVis	F	23	37	15	24*	
Carduus nutans	CarNut	F	7	15	2	24*	
Cynodon dactylon	CynDac	G	3	8	–	22*	
Trifolium dalmaticum	TriDal	L	3	8	–	22*	
Trifolium aureum	TriAur	L	7	13	2	22*	
Asperula purpurea	AspPur	F	26	38	19	22*	
Poa pratensis	PoaPra	G	23	35	16	21*	
Asperula cynanchica	AspCyn	F	58	71	51	20*	
Koeleria macrantha	KoeMac	G	47	60	39	20*	
Poa badensis	PoaBad	G	4	10	1	20*	
Diagnostic species for abandonment							
Agrostis capillaris	AgrCap	G	32	10	46		38*
Chamaespartium sagittale	ChaSag	L	46	25	59		33*
Hypericum perforatum	HypPer	F	47	27	59		31*
Artemisia chamaemelifolia	ArtCha	F	18	4	27		29*
Inula salicina	InuSal	F	18	4	27		29*
Veratrum nigrum	VerNig	F	11	–	18		27*
Seseli peucedanoides	SesPeu	F	20	6	28		27*
Festuca rubra	FesRub	G	51	35	61		26*
Genista tinctoria	GenTin	L	15	4	21		24*
Potentilla pedata	PotPed	F	14	4	20		23*
Viola dacica	VioDac	F	14	4	20		23*
Phleum pratense	PhlPra	G	11	2	16		23*
Briza media	BriMed	G	43	29	52		22*
Luzula campestris	LuzCam	S	21	10	28		22*
Silene roemeri	SilRoe	F	7	–	12		22*
Carex montana	CarMon	S	7	–	12		22*
Primula veris	PriVer	F	26	13	33		22*
Polygala major	PolMaj	F	13	4	19		22*
Chamaecytisus calcareus	ChaCal	L	27	15	34		20*
Potentilla alba	PotAlb	F	18	8	24		20*
Geranium sanguineum	GerSan	F	9	2	14		20*
Most frequent non-diagnostic species							
Thymus longicaulis	ThyLon	F	80	81	79	2	
Galium verum	GalVer	F	68	58	74		17

(continued)

Table I. (*Continued*).

Species	Acronym	Functional group	Constancy (%)			phi value × 100	
			All	Grazed	Abandoned	Grazed	Abandoned
Achillea millefolium	AchMil	F	63	69	59	10	
Filipendula vulgaris	FilVul	F	55	50	59		9
Teucrium chamaedrys	TeuCha	F	53	63	46	17	
Plantago lanceolata	PlaLan	F	50	62	44	17	
Anthoxanthum odoratum	AntOdo	G	50	38	56		17
Brachypodium pinnatum	BraPin	G	44	48	41	7	
Sanguisorba minor	SanMin	F	43	52	38	14	
Scabiosa columbaria	ScaCol	F	42	54	34	19	
Lotus corniculatus	LotCor	L	40	50	34	16	
Plantago media	PlaMed	F	40	48	35	13	
Veronica austriaca	VerAus	F	39	27	47		20
Trifolium alpestre	TriAlp	L	39	29	45		16
Cerastium banaticum	CerBan	F	39	31	44		13
Hypericum linarioides	HypLin	F	37	25	45		20
Bromus riparius	BroRip	G	37	40	35	5	
Galium heldreichii	GalHel	F	34	27	39		12

Each species is assigned to one of four functional groups (L = legumes, F = other forbs, G = grasses, S = sedges and rushes) and followed by its acronym (used in Figure 2). The concentration of species is indicated by their positive phi-values and by the significance level according to Fisher's exact test (*$P < 0.05$, **$P < 0.01$).

Table II. Vascular plant species of conservation importance (according to Anon. 2007, Petrova & Vladimirov 2009, CITES Secretariat 2010) found in the studied plots in the upland pastures of the Ponor Mt.

Species	Constancy (%)		Balkan endemic	Red List Bulgaria	Biological Diversity Act	CITES
	Grazed	Abandoned				
Alchemilla erythropoda	15	16		VU		
Artemisia chamaemelifolia	4	27*		CR	Annex 3	
Asyneuma anthericoides		1	+			
Bupleurum affine	4				Annex 4	
Chamaecytisus calcareus	15	34*	+			
Dactylorhiza cordigera		1			Annex 4	+
Hypericum linarioides	25	45		NT		
Orchis coriophora	4	.			Annex 4	+
Orchis morio		1			Annex 4	+
Orchis tridentata		5			Annex 4	+
Pastinaca hirsuta	2	11	+			
Pedicularis grisebachii	2	1	+			
Scabiosa triniifolia	8	2	+			
Sesleria latifolia	15	22	+			
Stipa pennata		7			Annex 4	
Thesium linophyllon	2	5		DD		

Species with significantly increased constancy in one of the two land use categories are marked with * (see Table I). VU – vulnerable, CR, critically endangered; DD, data deficient; NT, near threatened.

with a minimum of 14 and a maximum of 60 vascular species per plot.

Ordination of the vegetation plots

The first (eigenvalue 0.249) and the second canonical axis of the CCA (eigenvalue 0.123) accounted for 61.7% of the variance in the species composition with respect to the measured environmental variables. Both axes were statistically significant (Monte-Carlo test: $F = 2.13$, $P < 0.01$). The first axis was correlated with soil depth and abandonment, while the second accounted for the slope (see Figure 2).

Differences between grazed and abandoned grasslands

The two habitat types Mountain hay meadows (Pal. Class. code 38.3; 86% of the assigned plots) and Balkanic montane mat-grass swards (Pal. Class. code

35.73; 73%) were largely found in abandoned pastures, while 56% of the stands of the sub-continental steppic grasslands (Pal. Class. code 34.31) were still grazed. Abandoned pastures were located at higher altitude (1308 ± 59 m a.s.l. for abandoned *vs.* 1205 ± 49 m a.s.l. in used pastures; $P < 0.001$) and on deeper soils (Figure 3; $P = 0.019$) than grazed pastures.

Grazed and abandoned pastures differed for 9 of the tested 17 structural and diversity parameters after accounting for the covariates altitude and soil depth (Table III). However, most of the significant differences were so small that they are hardly of any ecological relevance, namely species richness and cover of grasses. Most importantly, total vascular plant species richness was 6% higher in grazed pastures, while that of species with conservation importance was twice as high in abandoned than in grazed pastures. The vegetation height and correspondingly the cover of the uppermost vegetation layer was higher in abandoned plots, while the two lower vegetation layers were more pronounced in grazed plots. On the contrary, cover and richness of the four distinguished functional groups did not show a significant grazing effect, except for negligibly small effects for grasses that were even opposing for the two parameters.

Regarding specific functional traits (Table IV), the strongest effect of grazing vs. abandonment was found regarding the soil-moisture preference of plants. While the mesophytes (e.g. *Agrostis capillaris*, *Phleum pratense*, *F. rubra*, *Briza media*, *Chamaespartium sagittale*, *Luzula campestris*, *Primula veris*, *Seseli peucedanoides* and *Inula salicina*) were the largest

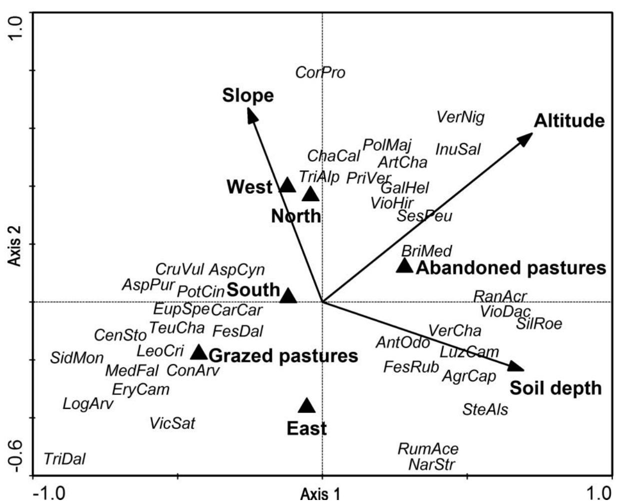

Figure 2. Two-dimensional CCA ordination diagram of vascular plant species composition in the upland pastures of the Ponor Mt. Only species with fit range over 10% ($n = 40$ species) are shown. Black triangles indicate categorical predictors, arrows indicate continuous predictors, and species are indicated by acronyms (for species acronyms, see Table I).

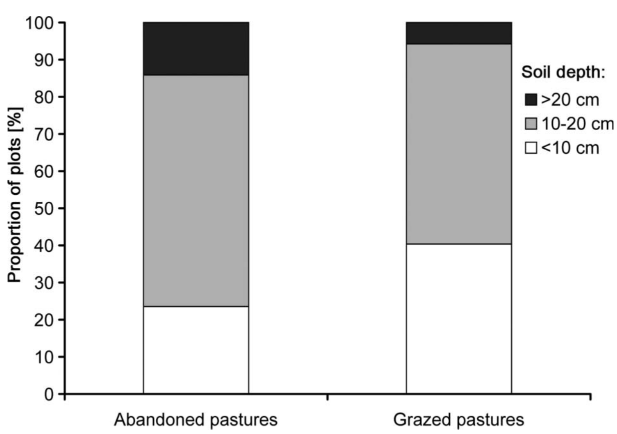

Figure 3. Proportion of study plots in different soil depth categories for grazed pastures and abandoned plots.

Table III. Comparisons of vegetation structure and species richness (per 16 m^2) between extensively grazed ($n = 52$) and abandoned ($n = 85$) pastures in the Ponor Mt. using ANCOVA (covariates: altitude and soil depth).

Variable	Grazed	Abandoned	*P*
Total vascular plant species richness	**34.3 ± 8.1**	32.3 ± 8.7	**0.002**
Vegetation height (cm)	61.1 ± 20.4	**74.4 ± 27.1**	**<0.001**
Number of vegetation layers	2.7 ± 0.7	2.9 ± 0.6	0.241
Cover of high-level vegetation layer (%)	6.3 ± 14.3	**12.4 ± 21.0**	**<0.001**
Cover of mid-level vegetation layer (%)	63.8 ± 14.9	63.9 ± 20.7	0.375
Cover of low-level vegetation layer (%)	**25.4 ± 11.5**	22.0 ± 13.5	**0.048**
Cover of shrubs (%)	**4.2 ± 5.7**	2.6 ± 4.6	**0.032**
Cover of grasses (%)	60.4 ± 13.9	**63.5 ± 14.1**	**<0.001**
Species richness of grasses	**6.1 ± 1.7**	5.8 ± 1.6	**0.001**
Cover of legumes (%)	5.6 ± 3.2	5.7 ± 4.3	0.202
Species richness of legumes	3.8 ± 1.6	3.7 ± 1.9	0.067
Cover of sedges and rushes (%)	2.8 ± 4.6	2.3 ± 4.7	0.441
Species richness of sedges and rushes	0.9 ± 0.7	1.0 ± 0.7	0.563
Cover of other forbs (%)	26.1 ± 8.5	26.4 ± 10.3	0.114
Species richness of other forbs	22.1 ± 6.2	21.9 ± 6.7	0.060
Cover of species with conservation importance (%)	5.8 ± 14.1	7.6 ± 15.8	0.473
Number of species of conservation importance	1.0 ± 1.2	**1.7 ± 1.3**	**0.002**

The values are reported as true means ± SD. This means that we did not correct them for difference in the influential covariates, which can lead to the situation that minor differences in the true means associated with considerable variances are still highly significant. For significant differences, the *P*-values and the respective higher values are set in bold.

Table IV. Comparisons of the species richness of functional groups (16-m^2 plots) between extensively grazed ($n = 52$) and abandoned ($n = 85$) pastures in the Ponor Mt. using ANCOVAs (covariates: altitude and soil depth).

Grouping criteria	Functional group of plants	Grazed	Abandoned	*P*
Life span	Annuals	0.9 ± 0.6	0.7 ± 2.8	0.620
	Biennials	**0.4 ± 0.3**	0.1 ± 0.2	< **0.001**
	Perennials	30.0 ± 15.7	33.5 ± 18.4	0.138
Life forms	Chamaephytes	0.02 ± 0.07	0.2 ± 0.8	0.189
	Therophytes	1.3 ± 0.8	0.8 ± 2.8	0.393
	Hemicryptophytes	29.9 ± 15.7	33.3 ± 18.3	0.138
	Geophytes	0.2 ± 0.4	0.2 ± 0.4	0.097
	Phanerophytes	**0.05 ± 0.20**	0.01 ± 0.05	**0.041**
Canopy structure	Plants with basal canopy	**5.2 ± 6.9**	2.5 ± 4.8	< **0.001**
	Plants with semi-basal canopy	21.4 ± 13.2	20.8 ± 15.3	0.435
	Plants with leafy canopy	4.7 ± 4.7	**11.0 ± 10.5**	< **0.001**
Preference to soil moisture	Mesophytes	8.9 ± 12.4	**20.9 ± 19.2**	< **0.001**
	Meso-xerophytes	**22.3 ± 16.2**	13.4 ± 13.6	< **0.001**
	Xerophytes	**6.6 ± 7.3**	2.0 ± 3.1	< **0.001**
Reproduction type	Vegetative	26.1 ± 15.9	26.6 ± 17.9	0.209
	Non-vegetative	5.1 ± 4.7	7.7 ± 10.4	0.064
Flowering period	Winter	0.1 ± 0.1	**0.2 ± 0.2**	< **0.001**
	Winter–spring	**0.3 ± 0.3**	0.1 ± 0.2	< **0.001**
	Spring	**3.2 ± 6.3**	1.5 ± 3.6	< **0.001**
	Spring–summer	27.1 ± 14.1	32.3 ± 18.4	0.211
	Spring–summer–autumn	**0.7 ± 1.0**	0.1 ± 0.2	< **0.001**
Duration of flowering period	0–90 days	3.9 ± 6.3	5.8 ± 10.5	0.545
	91–181 days	26.9 ± 13.9	28.4 ± 16.4	0.179
	> 181 days	1.1 ± 0.95	**2.3 ± 0.22**	**0.007**

The values are reported as true means ± SD (for interpretation, see Table III). For significant differences, the *P*-values and the respective higher richness values are set in bold.

group in abandoned grasslands and their richness was more than two times higher than in grazed pastures, the number of meso-xerophytes and xerophytes (e.g. *Festuca dalmatica*, *Poa badensis*, *Medicago falcata*, *Centaurea stoebe*, *Eryngium campestre*, *Sideritis monana*, *Leontodon crispus* and *Potentilla cinerea*) was higher under grazing, with the first group being the dominant one. Plants with basal canopy were favoured under grazing while plants with leafy canopy were favoured under abandonment. The number of spring flowering plants was higher in actual pastures. Neither life-form composition nor reproduction type was significantly influenced by land use type, and life span categories showed a significant but minor effect only in the case of biennials.

Effect of land use on species constancies

For 54 out of 316 species, the land use type had a significant effect on their distribution in the area, with 33 species showing increased constancy in grazed plots, but only 21 being more frequent in abandoned plots (Table I). The proportion of species with decreasing and increasing trend due to abandonment was similar for the four distinguished functional groups: grasses, sedges and rushes, legumes as well as other forbs. Most indicative for grazed plots were *M. falcata*, *E. campestre* and *Crupina vulgaris*, whilst *Logfia arvensis*, *Cichorium intybus* and *Daucus carota* were even restricted to these. For abandoned plots, *A. capillaris*, *C. sagittale* and *Hypericum perforatum* had the highest diagnostic value, whilst *Veratrum nigrum*, *Silene roemeri* and *Carex montana* were restricted to these.

Discussion

Methodological aspects

In this study, we used a landscape-level approach, i.e. a space-for-time substitution to analyse the medium-term effects of abandonment. While an experimental approach could have better controlled potential confounding factors (Quinn & Keough 2002), this obviously was not applicable *post hoc*. Regarding the comparison of diversity and structural parameters, we believe that we included the relevant covariates in our ANCOVAs so that the results are reliable. On the contrary, we could not partial out the effects of covariates, when determining the differential species of the two land use types. However, knowing the ecology of the determined differential species (Table I), it is very unlikely that the pronounced shifts in constancy are due to the significant but small differences between the land use types regarding altitude or soil depth. By contrast, most of the differences could be well explained as direct or indirect grazing effects (see below). Post-study interviews with local farmers confirmed that 20 years ago the now abandoned pastures looked similar to the currently grazed pastures in their structure and species richness.

Land abandonment and landscape features

It is known that the spatial pattern of grazing regimes strongly depends on the distribution of food resources, water and minerals in terrestrial ecosystems (Adler et al. 2001). Therefore, it is to be expected that more distant and hardly accessible pastures in the study area have been abandoned first. Grassland communities of the Balkan mountains have been intensively exploited in the past, but nowadays mainly grasslands in the valleys and lower slopes and those close to the villages at lower altitude are used for grazing, whereas pastures remote from settlements and located on the upper slopes and crests at higher altitude were abandoned (Nikolov 2010). In our results, this statement is supported by the statistically significant difference in the altitude between grazed and abandoned pastures.

While succession theory assumes that in regions where forests are the potential natural vegetation, grassland communities gradually transform to shrubland and forest following land abandonment, and this has been corroborated by studies in other grassland systems of the Balkan Mts. (Stevanović et al. 2008, Velev & Apostolova 2008), we found even higher densities of woody plants in the grazed pastures. Also Kahmen & Poschlod (2008) found a relative increase of phanerophytes at low grazing pressure (on Ponor Mt., the sheep density was 0.03 animal units ha^{-1}; Nikolov 2010). The higher shrub cover within active pastures of the Ponor Mt. could also be accounted for by a possible decrease of the reforestation rate with altitude as it was found in the Alps (Gellrich et al. 2008). Furthermore, the local environmental conditions in valleys and lower slopes (i.e. higher rates of clay, organic matter, nitrogen and water retention) might be more favourable to shrub encroachment than on upper slopes and crests (see also Peco et al. 2006). Finally, disturbance by grazing animals might facilitate the establishment of phanerophytes, while litter accumulated after abandonment might have a negative effect.

Land use and plant communities

In the present study, a significant, but small positive effect of grazing was found for total vascular plant species richness, while the majority of studied functional groups of plants were not affected significantly. This is in agreement with results of Dupré & Diekmann (2001) and Škornik et al. (2010), who found an increase of species richness under low and intermediate grazing intensity and its decrease under intensive grazing, but differs from Ruprecht et al. (2009) who report no significant richness changes due to abandonment. Despite the small differences in species richness (see Table II) our results confirm that grazing effects on plant communities are mostly species-specific and that species abundances may change much more than species richness (Dumont et al. 2009). Accordingly, we found much stronger patterns for specific traits, in particular regarding the moisture preference of the species (see Table III) or at the species level (see Table I), with 51 species showing significant responses to the land use type.

Most of these effects were related to the direct impact of grazing animals such as trampling and foraging, resulting in biomass removal and disruption of plant growth processes. These impacts also lead to a more xeric environment favouring xerophytic species. In our study, plant height and cover of tall plants were positively correlated with land abandonment, as found in other studies (e.g. Krahulec et al. 2001). At the same time, taller plants were probably favoured by deeper soils which were more frequent in abandoned grasslands. Additionally, this plant group creates more shade on the soil surface and a greater amount of litter, both factors reducing evaporation from the soil and supporting a moister microclimate.

The change in species composition was related to the change in structure from open to semi-open grasslands under active grazing to closed in abandoned sites. The observed pattern in vegetation composition in active pastures could also be explained by the selective grazing of sheep. They graze vegetation close to the soil surface and create spots of bare ground (Ausden 2007). Under such conditions, gap colonisers with rhizomes or stolons (*Convolvulus arvensis*, *Hieracium pilosella*, *Trifolium repens* and *Cynondon dactylon*) as well as annuals (*L. arvensis* and *Vicia sativa*) have an advantage over other species because of their ruderal strategy (Grime et al. 2007). Therefore, these species are widely distributed in grazed pastures (František et al. 2001; Pavlů et al. 2006; Firincioğlu et al. 2009). The higher abundance of rosette plants in grazed pastures found in our study corresponds to the results from many other studies (e.g. Lavorel et al. 1998, McIntyre et al. 1999). Finally, we found a strong increase of some spiny species (*E. campestre*, *Cirsium vulgare*, *Carlina acanthifolia* and *Carduus nutans*) in pastures which benefit from selective grazing and are known as pasture weeds (Dierschke & Briemle 2002). Compared to the study by Škornik et al. (2010) in Slovenia, we found for many of the joint species similar preferences along the grazing gradient.

Medicago sativa agg., *T. repens* and *Poa pratensis* were for example much more frequent under (heavy) grazing than without while *C. montana* was lacking in heavily grazed pastures. However, some species also showed a regionally different behaviour, such as *F. rubra*, which was restricted to heavily grazed places in Slovenia, but preferred abandoned pastures in Bulgaria.

Looking more closely into the list of species benefitting from abandonment, one can realise that many of the increasing species (e.g. *H. perforatum*, *Geranium sanguineum, I. salicina* and *Genista tinctoria)* are diagnostic for the class *Trifolio-Geranietea sanguinei* T. Müller 1962 (Mucina 1997; Dengler et al. 2006). *Trifolio-Geranietea* communities are known to be particularly species rich and to contain many threatened species (Korneck et al. 1998). It is not untypical that a *Trifolio-Geranietea* stage follows *Festuco-Brometea* communities after abandonment and such stands can be highly valuable. We also found more species with conservation importance in abandoned pastures (Table II). This could be explained by the persistence of such species most remote from settlements but also by their low forage quality (e.g. *Chamaecytisus calcareous, Hypericum linarioides* and *Sesleria latifolia*) which could have stimulated the abandonment of such pastures.

Some groups of plants were not affected significantly by the analysed medium-term abandonment. Among these are endemics that have wide distribution in the country (*Scabiosa triniifolia* and *Tragopogon balcanicum*). Similarly, many species with very broad distribution in the country and characteristic for the grasslands (*G. verum, A. millefolium, P. lanceolata, A. cynanchica, T. chamaedrys, F. vulgaris* and *T. longicaulis*) were equally represented in grazed and abandoned plots. These are generalist species with long-term persistence in pasturelands. For some of them (e.g. *A. millefolium* and *P. lanceolata*), there is evidence for presence in grasslands since the Neolithic age (Poschlod & WallisDeVies 2002).

Conclusions for conservation

Although species composition differed much between continuously grazed and abandoned sites, the community structure and overall functional composition of the studied grasslands were essentially the same. Even approximately 20 years after abandonment, the cover of woody species was low and not higher than in the grazed pastures. While overall species richness was slightly higher in grazed pastures, the density of conservation-relevant (i.e. threatened or endemic) species was higher in abandoned pastures. From a plant conservation perspective, we can thus conclude that 20 years of succession on a subset of grassland areas probably did not negatively affect the overall plant diversity of the Ponor Mt., but rather might have increased it by providing suitable habitats for mid-successional species (e.g. of the class *Trifolio-Geranietea sanguinei*). This will help for maintaining a sufficient number of managed grassland patches for those species adapted to these conditions.

The support of traditional land use could be a relevant tool to ensure the continuation of these favourable conditions as it is generally known to be beneficial to conservation values (as opposed to modern intensive farming practices) (Henle et al. 2008; Veen et al. 2009). With the aim to maintain species rich upland semi-natural grasslands in the region, extensive grazing should be promoted with sheep density $> 0.15\ ha^{-1}$ animal units as advised by the National Standard 4.1 for maintaining the land in good agricultural and ecological condition (Anon. 2010). However, zones with a concentration of red listed species as well as low-productive xeric grasslands on shallow soils should be grazed at much lower intensity. On the other hand, the high abundance of species such as *A. capillaris*, *P. pratense*, *F. rubra* and *B. media* with fodder values of 6–9 according to Dierschke & Briemle (2002) in presently abandoned localities would provide a forage resource of sufficient quality for sheep, making the grazing also economically sustainable. In the light of the result that pastureland abandonment was observed mostly in less accessible sites, establishment of sheep pens in the remote areas of the mountain may be beneficial for a more spatially uniform grassland management within the mountain. Such a measure could be supported by the European Agricultural Fund for Rural Development as non-productive investments – Articles 36 & 41 from the Council Regulation (EC) No 1698/2005 (European Union 2005).

Control of shrub encroachment is a necessary part of good practice in pasture management (Stevanović et al. 2008), but it should be done with care: (1) shrubs are an important structural feature of the landscape, beneficial for other components of biodiversity, such as insects (Söderström et al. 2001) and birds (Nikolov 2010); (2) some of these shrubby habitats are under protection of the Habitats Directive themselves (i.e. *Juniperus communis* formations on heaths or calcareous grasslands).

To prevent both encroachment of woody species in remote pastures under low-intensity grazing and overgrazing in the areas close to the settlements, yearly rotational grazing ensuring regular movement of the herds throughout the whole area should also be supported (Başnou et al. 2009). Such a practice was traditionally applied in the 1920s with a rotation period of 3–4 years (Jordanov 1924).

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Nomenclature

Vascular plants: Kozhuharov (1992).

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