

Relationships between plant diversity, vegetation cover, and site conditions: implications for grassland conservation in the Greater Caucasus

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Abstract Overgrazing, land use abandonment and increasing recreational activities have altered the vegetation of high-montane and subalpine grassland of the Caucasus. The failure of previous restoration efforts with unsuitable and exotic plant species indicates the need for information on the present vegetation and in which way it might change. Within the Greater Caucasus, we have described and quantified the mountain grassland which develops under characteristic overgrazed and eroded site conditions. Further, we have proposed potential native plant species for revegetation to restore and conserve valuable mountain grassland habitats. We used non-metric dimensional scaling ordination and cluster comparison of functional plant groups to describe a gradient of grassland vegetation cover. For our study region, we identified four major vegetation types with increasing occurrence of ruderal pasture weeds and tall herb vegetation on abandoned hay meadows within the subalpine zone. Within high-montane grassland a decline of plant diversity can be observed on sites of reduced vegetation cover. Due to a low potential of the grassland ecosystem to balance further vegetation cover damage, the long-term loss of diverse habitats can be expected. We conclude with management recommendations to prevent erosion and habitat loss of precious mountain grasslands.

Keywords Land degradation · NMDS · Overgrazing · Functional plant groups · Mountain grassland restoration

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Introduction

The stability of mountain slopes is substantially influenced by site conditions such as vegetation cover, vegetation composition and species-richness (Martin et al. 2010; Pohl et al. 2009), which are in turn dependent on biotic environmental conditions and management practices (Tepnadze et al. 2014; Wellstein et al. 2007). Agricultural management practices under low stocking numbers and short grazing periods are of vital importance for a sustainable grassland management. Accordingly, a disregarded grazing regime harms the vegetation cover and induces grassland degradation processes. Furthermore, key plant species such as grasses can be replaced by unpalatable, invasive plants (Valentine 2001) and some of them e.g. *Veratrum lobelianum* and *Cirsium obvallatum* are referred to as ruderal pasture weeds (Callaway et al. 2000). In steep, mountainous terrain, trampling by ungulates creates a net of horizontal, diagonal and vertical tracks where small damage spots can occur when animals are crossing between the passages (Riedl 1983). During heavy rain the water runoff increases on downward facing pathways and vegetation damage spots, which further results in an erosion of the soil layer (Dommermuth 1995; Riedl 1983). Accordingly, similar effects were observed on sites where the vegetation cover had been trampled by tourists (Klug et al. 2002). Consequently, if there is no management action against the water runoff taken, then the soil erosion will be followed by larger mass wasting events which remove the entire soil layer and expose rubble and scree of the parent rock material (Stahr and Langenscheidt 2015). Compared to the surrounding grassland, such habitats of scree display drastically altered site conditions and are further characterized by pioneer communities which establish a first stage of succession (Jenny-Lips 1930; Körner 2003; Zöttl 1952). Due to climatic and topographic conditions, the natural soil formation on mountain slopes is an extremely protracted process. In mountainous regions, erosion is a natural process which is further accelerated by a reduced vegetation cover. Dense vegetation cover is a key prerequisite to balance the processes of rapid soil erosion and long lasting soil formation. Hence, the loss of vegetation cover and associated processes are based on complex interactions between land use, land use changes (intensification and abandonment) and regional mountain features, e.g. exposition, underlying parent rock material, soil type and topography. Investigating all interrelated causes of degradation are therefore essential to understand these relationships. However, to prevent larger degradation events the detection of early erosion stages which are made visible by changes in vegetation is essential. Therefore a thorough knowledge of the vegetation which establishes under characteristic site conditions is mandatory for any site conservation efforts. Consequently, a broad knowledge of early erosion stages and revegetation measures with indigenous, site specific seed mixtures has evolved for the European Alps (Florineth et al. 2002; Krautzer et al. 2013). Immediate revegetation of open vegetation with indigenous, site specific seed mixtures is an essential prerequisite for the success of ecological restoration (Krautzer et al. 2004; Krautzer and Wittmann 2006; Krautzer et al. 2011). However, despite ongoing erosion processes nothing is known about the suitability of native plant species for restoration measures in the Caucasus region.

Altogether, overgrazing influences grassland condition which results in a reduced grass cover, an increased abundance of unpalatable plant species and soil erosion. On a mountain landscape level it has to be considered that these complex effects appear spatially and temporally interdependent. Previous studies have mainly independently researched effects of either vegetation cover (Martin et al. 2010; Pohl et al. 2009) or pasture weeds (Callaway et al. 2000) in relation to the diversity of degraded grassland. The first goal of our study

was to describe and quantify the vegetation which develops under characteristic overgrazed and eroded site conditions. Therefore we have addressed the following research questions:

Which environmental variables are related to the species distribution on overgrazed and eroded sites?

How is species-richness related to the species distribution on overgrazed and eroded sites?

Our second goal was to give recommendations for a site-specific ecosystem restoration in the Caucasus. Therefore we aimed to describe and quantify functional plant groups in order to maintain ecosystem functions after restoration measures. Further, we aimed to suggest potential plant species for revegetation. Therefore we addressed the following questions:

Which species-richness and abundance of functional plant groups can be observed on sites of different vegetation cover?

Which native plant species occur along a gradient of vegetation cover at high frequencies and can therefore be considered for the restoration of grassland ecosystems in the Caucasus?

Methods

Study region

The Republic of Georgia is situated in the Caucasus region and borders on the Black Sea. Due to high topographic and climatic gradients, Georgia consists of various major ecosystems such as evergreen and deciduous forests, dry mountain shrub lands, steppes, semi-deserts, wetlands, and high mountain habitats (Critical Ecosystem Partnership Fund 2004). The whole Caucasus region comprises the high amount of 2791 endemic plant taxa (Solomon et al. 2014) and is therefore declared as one of the global biodiversity hotspots (Myers et al. 2000). Mountain grassland in the high-montane and subalpine zone of the Georgian Caucasus includes different types of meadows and pastures mixed with subalpine tall herb vegetation (Lichtenegger et al. 2006; Nakhutsrishvili 1999).

The present state of the Georgian landscape results from a long tradition of human land use which shaped the mountain regions. Although archeological records of animal artifacts provide evidence of animal husbandry since ancient times (Lordkipanidse 1991), at first their number is likely to have been low due to the limited fodder resources during winter times (Itonishvili 1970). Over time, humans exploited the mountain forests and particularly replaced the subalpine birch forests by pastures, meadows, and arable fields (Nakhutsrishvili 1999). Nowadays, in the Aragvi and Tergi valley the once widespread deciduous, coniferous and mixed mountain forests of the high-montane and subalpine belt can only be found in small remaining patches within protected areas and remote places (Khetskhoveli et al. 1975; Parolly 2014). Due to the limited resources of mountain grassland for hay production as winter fodder, a transhumance system of pastoralism evolved with alternating grazing of northern grounds in the high-montane to alpine belt during summer times and winter grazing on the southern Georgian and Russian lowlands. Furthermore, the Russian annexation of Georgia in the early nineteenth century enabled the shepherders to use grazing grounds in the northern Caucasian territory (Plachter and Hampicke 2010). In

1861, the construction of the military road was finished (Kerashvili 2012; Schmerling and Dolidze 1991), which connected Tbilisi, the capital of Georgia, and Russia and enabled further local economic growth and development of the mountain region. The sheep husbandry profited from infrastructural developments and many arable fields were turned into pastures and meadows (Itonishvili 1970). Due to the collectivization during the Soviet period, the sheepherders took care of large state-owned flocks. Herding very large sheep herds through the mountain regions had consequences for the landscape, as was observed on the steep slopes along the migration routes of the upper Aragvi valley (Körner 1980). The upper Aragvi valley is asymmetrically shaped by an east side (south facing) that consists of andesite-basalt and a west side (north facing) which comprises clay-shale, shale marls and enclosures of limestone and sandstone (Gobejishvili et al. 2011; Khetskhovelidze et al. 1975). The slightly inclined, north facing side is covered by loose sediment which is prone to erosion and mudflows (Lichtenegger et al. 2006). For the upper Aragvi valley, a comparison of aerial images from the years 1958 and 2011 displayed a 10% increase in degraded and un-vegetated terrain (Klein 2011). This indicates ongoing erosion processes which are currently initiated by unregulated cattle grazing and logging of protected forests (Ministry of Environment Protection et al. 2009). The long lasting negative effects of the previous herding system collectivization followed by a de-collectivization, have been reported for several grassland ecosystems of former Soviet Union countries (Food and Agriculture Organization of the United Nations 2003). Additionally, recent development of an unrestricted increase in recreational activities (e.g. hiking) are further contributing to persisting erosion processes (Wiesmair et al. 2016).

In the Greater Caucasus, overgrazed grassland display vast areas of infestations by unpalatable plant species such as *Veratrum lobelianum* and *Cirsium obvallatum* (Callaway et al. 2000; Magiera et al. 2015). *Veratrum lobelianum* is closely related to *Veratrum album* which occurs in Central Europe and is, due to its acute toxicity and high abundance, a grazing weed of major concern (Schaffner et al. 2001). *Cirsium obvallatum* features sharp spines along its leaves and stems which protect the plant from being grazed (Callaway et al. 2000).

Study sites and field sampling

The village Mleta is divided into the two settlements Kvemo (Lower) Mleta [42°25′40″N, 44°29′52″E, 1455 m above sea level (m a.s.l.)] and Zvemo (Upper) Mleta (42°25′45″N, 44°29′23″E, 1535 m a.s.l.) which are situated on a talus fan in the upper Aragvi valley (Fig. 1). A large net of animal tracks and vegetation damage spots which were caused by cattle and sheep grazing, can be observed on the slopes next to Mleta (Fig. 2a). Minor construction works for hiking trails and forestation with maple (*Acer platanoides*) for wood production have been going on in the study region. Previous reforestation with coniferous trees (*Pinus* sp.) and leguminous bushes (*Amorpha fruticosa*) has failed to stop further land degradation and especially the planting of exotic plant species seems to be highly unsuitable for slope protection (Fig. 2b). Due to its accessibility from the military road and the occurrence of mass wasting events on a large scale, Mleta is a perfect study region for erosion processes from overgrazing. Furthermore, grassland on the north facing slope next to Mleta consists of a uniform geological layer of slate with homogeneous soil layers of Cambisol under grassland and Leptosol on eroded sites.

In July 2012 and 2013, we sampled 97 plots next to the village Mleta for vegetation and environmental parameters. We selected the plots according to their total vegetation cover in order to sample a gradient of grassland coverage (0–100%). Due to the high correlation

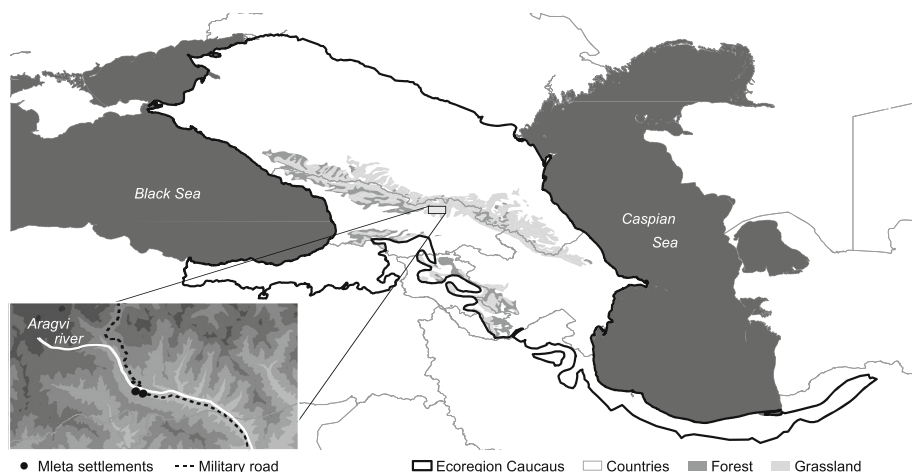


Fig. 1 Localization of Georgia and the study region within the Caucasus biodiversity hotspot with visualizations of montane pine forests combined with montane, submontane fir and mixed fir forests (Forest), and subalpine vegetation together with alpine grassland (Grassland). *Inlet* showing a contour map of the Upper Aragvi valley, with 500 m contour intervals starting from 1000–1500 m (light grey). *Sources* Caucasus Biodiversity Hotspot (Critical Ecosystems Partnership Fund), Map of the natural vegetation of Europe (BfN, Federal Agency for Nature Conservation Germany)

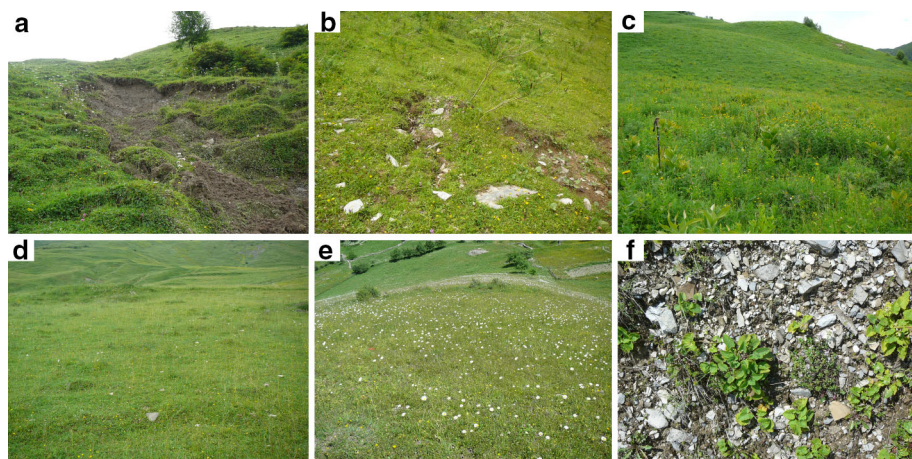


Fig. 2 Degradation- and grassland types of the upper Aragvi valley. **a** vegetation damage spot on high-montane pasture; **b** open soil on a site with *Amorpha fruticosa*; **c** *Seseli transcaucasica*-cluster with infestation of *Veratrum lobelianum*; **d** *Cynosurus cristatus*-cluster; **e** *Briza media*-cluster; **f** *Parnassia palustris*-cluster

of vegetation cover to slope inclination, we used a digital elevation model to predefine sampling areas. For our study area we sought for the full range of slope inclination and vegetation cover. Heterogeneous topographic conditions determined sampling at a minimum distance of 5 m to bordering habitat patches. All plots were located on the slope (3–43° inclination) whereas the flat valley ground and wetland were not sampled. Each plot

covered 25 m², within which we arranged three 1 m²-subplots. Species abundance was estimated for each 1 m²-subplot with the modified Braun-Blanquet cover-scale (Barkman et al. 1964). In order to include all occurring plant species on the plot without occurrences on the subplots, we assigned the lowest cover value (r) to species that were exclusively found on plot level. Vegetation, soil, rock and moss cover were visually estimated for each subplot. Maximum plant height was measured separately for grasses and herbs on subplot level. The subplot values were averaged to obtain a single plot value. Botanical nomenclature followed “The Plantlist” (The Plant List 2013).

Moreover, five samples of the top soil were randomly taken from each plot and pooled. Due to a very high stone content, we used a hand shovel to sample the upper soil layer (0–5 cm). The mixed samples were air-dried for 96 h. We sieved the soil samples to 2 mm to separate the coarse soil material from the fine soil. Coarse soil material was washed, all plant material removed, air-dried and weighed. We weighed the fine and coarse soil fractions in order to determine the percentage of stone content (>2 mm). The fine soil fraction was used for further chemical analyses. Soil samples were analyzed for their C and N values at the Institute of Soil Science and Soil Conservation at the University of Giessen, to retain information on total nitrogen (N_T) and total carbon (C_T). Calcium carbonate (CaCO₃) was determined using the Scheibler apparatus method and was used to calculate the ratio of organic carbon (C_{org}) to the total amount of carbon. C/N was calculated from the ratio of organic carbon to total nitrogen. Plant available phosphorus (P_{CAL}), potassium (K_{CAL}) and magnesium (Mg) were analyzed at the Agrofor Lab, Wettenberg, Germany. We determined pH-value in CaCl₂.

For each plot we measured the inclination with the SUUNTO PM-5 C 360 clinometer and the four coordinates of our plot corners with a GARMIN GPS62s. We marked the plot center with magnetic markers to re-locate the plots. The geographic direction was recorded to calculate the exposition values of northness (cosine of aspect) and eastness (sine of aspect) for each plot.

Analysis of functional plant groups

Following de Bello et al. (2010), we grouped plant species with similar responses to external factors and effects on ecosystem processes as functional plant groups. Therefore, the plant groups were first defined as herbs, graminoids (all grasses, including sedges) and woody plants (regenerating trees and shrubs). The herb group was further differentiated into *Fabaceae*, *Orchidaceae* and ruderal pasture weeds (*Cirsium obvallatum*, *Rumex obtusifolius*, and *Veratrum lobelianum*). *Fabaceae* play an important role in the input of nutrients due to their nitrogen-fixing capability. Plants of the *Orchidaceae* family belong to a group which has become endangered in many European grasslands due to the decline of suitable habitats (Calaciura and Spinelli 2008). Due to the high sensitivity of this plant family towards anthropogenic influences, conservation measures to protect these habitats would be as well necessary in Georgia (Akhalkatsi et al. 2003). Ruderal pasture weeds have the potential to replace grassland communities under intensive grazing when neglected by grazers (Vallentine 2001).

According to previous studies dealing with grassland conditions (Gao et al. 2006; Liu et al. 2007; Purevdorj et al. 1998), our dataset was classified into four vegetation cover intensities: 80–100% = dense, 60–79% = moderate, 30–59% = light, and 0–29% = sparsely. We used the classification scheme to further analyze the abundance and species-richness of functional plant groups within a gradient of vegetation cover. Therefore

we calculated the relative contribution of each functional plant group to the whole species number and abundance.

Analysis of vegetation and environmental data

We transformed the Braun-Blanquet cover values to percentage scale ($r = 0.3$, $+$ = 0.5, $1 = 2.5$, $2 = 4.0$, $2a = 8.75$, $2b = 18.75$, $3 = 37.5$, $4 = 62.5$, $5 = 87.5$), which was further log-transformed. To reduce noise in the data (in total 171 species), we omitted species with less than three occurrences prior to ordination analyses. Three outlier plots were detected with nearest single linkage/nearest neighbor classification and were removed from further analyses. Following analyses were run with a dataset of 94 plots (1505–2183 m a.s.l.) and 127 species. We used the “vegan” R-package (Oksanen et al. 2013) for Ward’s classification and Non-metric dimensional scaling (NMDS) ordination, both were performed with Bray–Curtis distance. The settings for the NMDS were: global Multidimensional scaling using monoMDS; two convergent solutions reached after twelve tries; scaling of centering, PC rotation and halfchange scaling. A detrended correspondence analysis (DCA) was performed to receive information on gradient length. To gain information about the indicator species of each vegetation cluster, we performed an indicator species analysis (Dufrêne and Legendre 1997) using the “indval” function of the “labdsv 1.7” R-package (Roberts 2013). Species-richness, Shannon and evenness diversity indices were derived with the “vegan” R-package. We used the Wilcoxon rank sum test with Bonferroni correction method for posthoc class comparison after Kruskal–Wallis cluster comparison. All analyses were performed using the R project statistical computing software (R Core Team 2014). Environmental percentage and degree values (slope, vegetation, soil, rock, moss and stone content) were arcsine transformed prior to analyses of cluster comparison and NMDS.

Results

Vegetation types and site condition

The Ward classification resulted in four distinct clusters, which were plotted in an NMDS ordination (Fig. 3). The classification separated subalpine (*Seseli transcaucasica*-cluster, Fig. 2c) from high-montane grassland. Within the high-montane sites, the classification further differentiated between nutrient-rich pastures (*Cynosurus cristatus*-cluster, Fig. 2d), poor grassland (*Briza media*-cluster, Fig. 2e), and scree vegetation (*Parnassia palustris*-cluster, Fig. 2f). The NMDS included 127 plant species and revealed a stress level of 13.6. Environmental vectors were fitted against NMDS ordination and most important variables ($p < 0.001$) are shown in the ordination graph (Fig. 3). The corresponding vector values for the correlations of environmental vectors to the first and second NMDS axis are given in Table 1. The first axis displays a gradient of cover values (vegetation, soil and moss) and nutrient availability. The second axis represents a gradient of species diversity. Other variables such as canopy height, altitude, slope and rock cover display vectors in-between both axes. Northness, eastness and total carbon do not significantly correlate with the first two NMDS axes. Due to an intercorrelation of the environmental variables and for better visualization some of the variables were excluded from the ordination graph, as follows (Spearman correlation index, $p < 0.05$): Calcium carbonate ($R = 0.80$) with stone content;

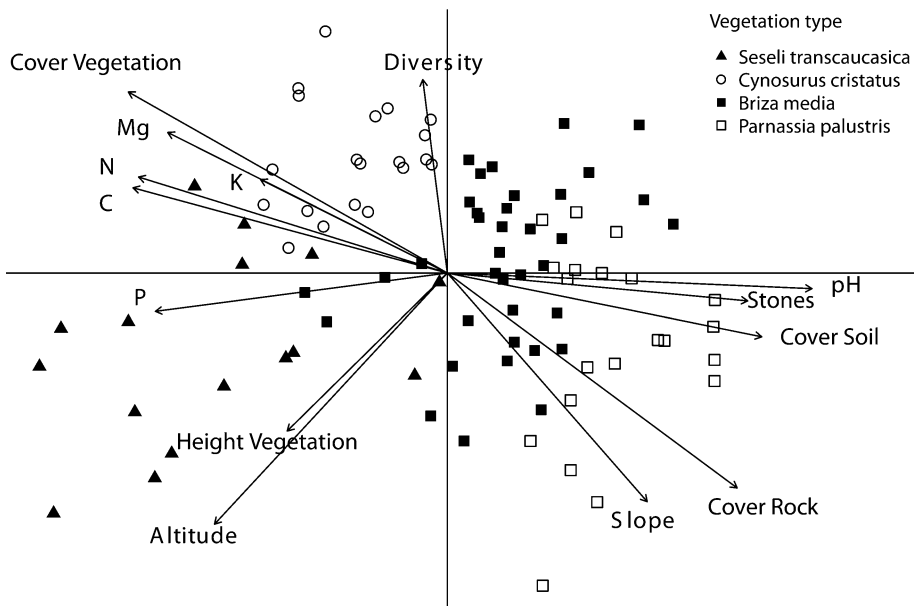


Fig. 3 NMDS ordination of 94 grassland plots and 127 species, displaying the first and second axis. The stress level revealed at 13.6, environmental variables are indicated by *arrows*. Abbreviations: *C* Organic carbon, *Diversity* Shannon diversity, *Mg* magnesium, *N* total nitrogen, *P* phosphorus, *stones* stone content, *K* potassium, *height vegetation* max. height herbs

Moss cover ($R = 0.52$) with rock cover; species-richness ($R = 0.91$) and evenness ($R = 0.64$) with Shannon diversity; Maximum height of graminoids ($R = 0.63$) with maximum height of herbs. The DCA showed a gradient length of 4.1, which indicates a complete species turnover.

The ordination shows that the nutrient-rich sites are restricted to the *Seseli transcaucasica*- and *Cynosurus cristatus*-cluster. These sites have higher contents of magnesium, potassium, phosphorus, total nitrogen, and organic carbon. The *Seseli transcaucasica*-cluster displays a higher maximum vegetation height. The *Briza media*- and *Parnassia palustris*-cluster display low nutrient values and can be characterized as nutrient-poor. These sites are characterized by a lower vegetation cover with conversely higher soil, rock, and moss cover values. Furthermore, these sites display higher stone contents with increased pH and CaCO_3 values. Additionally, these plots are characterized by a higher slope inclination. In total we revealed a median of 36 species per plot. Species-richness was highest for the *Cynosurus cristatus*- and *Briza media*-cluster, which differed significantly from the *Seseli transcaucasica*- and *Parnassia palustris*-cluster. The clusters differed significantly in 21 parameters (Table 2). A complete species list and environmental variables are shown in the Appendix (Electronic Supplementary Material).

The Indicator species analysis (ISA) identified 78 species as indicators of the four clusters. 29 species were assigned to the *Seseli transcaucasica*-cluster, 29 species to the *Cynosurus cristatus*-cluster, 9 species to the *Briza media*-cluster and 11 species to the *Parnassia palustris*-cluster. Species that occurred in the ISA with a relative frequency of $\geq 50\%$ were used to describe our clusters (Table 3), as follows: the *Seseli transcaucasica*-cluster is characterized by species of the subalpine tall herb vegetation such as *Astrantia maxima*, *Betonica macrantha*, *Cephalaria gigantea*, *Geranium ibericum*, *Hypericum*

Table 1 Direction cosines of the environmental vectors to the first and second axis of NMDS ordination and corresponding squared correlation coefficient (r^2)

	NMDS1	NMDS2	r^2
Altitude	-0.68	-0.73	0.66***
Slope	0.66	-0.75	0.52***
Cover vegetation	-0.87	0.49	0.76***
Cover soil	0.98	-0.20	0.58***
Cover rock	0.80	-0.60	0.73***
Cover moss	1.00	-0.02	0.21***
Height forbs	-0.71	-0.70	0.29***
Height graminoids	-0.91	-0.42	0.18***
Content stone	1.00	-0.09	0.51***
pH	1.00	-0.04	0.75***
CaCO ₃	0.97	-0.24	0.45***
P ₂ O ₅	-0.99	-0.13	0.49***
K ₂ O	-0.89	0.45	0.25***
Mg	-0.89	0.45	0.55***
N _(total)	-0.96	0.30	0.59***
C _(total)	-0.92	0.40	0.03
C _(org)	-0.97	0.26	0.60***
C/N	-0.65	0.76	0.11**
Northness	-0.73	-0.68	0.07
Eastness	0.60	0.80	0.04
Shannon diversity	-0.13	0.99	0.21***
Species richness	-0.14	0.99	0.17***
Evenness	-0.01	1.00	0.10**

* $p < 0.05$; ** $p < 0.01$; ***
 $p < 0.001$

bupleuroides, *Inula orientalis*, *Seseli transcaucasica*, and by “real” grassland species such as *Anthoxanthum odoratum*, *Bromus variegatus*, and *Dactylorhiza euxina*. Further, *Cirsium obvallatum*, *Rumex obtusifolius*, and *Veratrum lobelianum* are ruderal species indicative of overgrazed grassland. *Cynosurus cristatus*-cluster, the nutrient-rich high-montane pasture, is dominated by *Cynosurus cristatus* and further characterized by *Alchemilla caucasica*, *Carex caryophylla*, *Plantago lanceolata*, *Prunella vulgaris*, and *Trifolium repens*. The nutrient-poor *Briza media*-cluster is characterized by *Anthyllis variegata*, *Briza media*, *Leucanthemum vulgare*, *Linum catharticum*, *Polygala transcaucasica*, and *Thymus collinus*. Typical for the scree sites of the *Parnassia palustris*-cluster are the pioneer species *Campanula alliariifolia*, *Lactuca racemose*, *Parnassia palustris*, *Trisetum rigidum*, and *Tussilago farfara* which are characterized by a rapid establishment due to their abundant, anemochorous seed dispersal with further spread through water runoff.

Species that occurred within the densely vegetated plots (*Seseli transcaucasica*- and *Cynosurus cristatus*-cluster) at a relative frequency of $\geq 50\%$ were *Anthoxanthum odoratum*, *Campanula glomerata* ssp. *caucasica*, *Centaurea salicifolia*, and *Luzula stenophylla*. Species that we found within the high-montane plots (*Cynosurus cristatus*-, *Briza media*-, and *Parnassia palustris*-cluster) at a relative frequency of $\geq 50\%$ were *Cruciata laevipes*, *Euphrasia* sp., *Leucanthemum vulgare*, *Linum catharticum*, *Phleum pretense*, *Prunella vulgaris*, *Trifolium pretense*, and *Thymus collinus*. Species that displayed a relative frequency of $\geq 50\%$ within the nutrient-poor plots (*Briza media*- and *Parnassia palustris*-cluster) were *Anthyllis variegata*, *Briza media*, *Campanula alliariifolia*, *Parnassia*

Table 2 Median values and quartiles of environmental variables from vegetation type clusters

Vegetation cluster	<i>Seseli transcaucasica</i> (n = 16)	<i>Cynosurus cristatus</i> (n = 20)	<i>Briza media</i> (n = 37)	<i>Parnassia palustris</i> (n = 21)
Altitude (m a.s.l.)*	1989.5 ± 111.5 ^a	1747.0 ± 266.5 ^{b,c}	1689.0 ± 258.0 ^b	1640.0 ± 252.0 ^c
Slope (°)*	22.5 ± 15.3 ^a	17.5 ± 7.5 ^a	37.0 ± 10.0 ^b	37.0 ± 5.0 ^b
Cover vegetation (%)*	100 ± 5 ^a	93.5 ± 6.5 ^b	60 ± 40 ^c	28 ± 31 ^d
Cover soil (%)*	0 ± 5 ^a	5 ± 3 ^a	15 ± 10 ^b	18 ± 7 ^b
Cover rock (%)*	0 ± 0 ^a	1 ± 5 ^a	15 ± 23 ^b	40 ± 17 ^c
Cover moss (%)*	0 ± 0 ^a	1 ± 2 ^b	5 ± 4 ^{b,c}	5 ± 9 ^c
Height forbs (cm)*	69.2 ± 18.3 ^a	28.3 ± 18.8 ^b	35.0 ± 15.0 ^b	31.7 ± 21.7 ^b
Height graminoids (cm)*	76.7 ± 8.3 ^a	39.2 ± 23.2 ^b	41.7 ± 20.0 ^b	45.0 ± 33.3 ^c
Content stone (%)*	4.1 ± 2.0 ^a	11.4 ± 8.8 ^b	19.3 ± 17.1 ^b	31.3 ± 13.8 ^c
pH (CaCl ₂)*	4.49 ± 0.77 ^a	5.47 ± 2.17 ^a	7.11 ± 0.31 ^b	7.35 ± 0.39 ^c
CaCO ₃ (%)*	0.00 ± 0.00 ^a	0.14 ± 3.58 ^b	13.40 ± 23.73 ^c	32.46 ± 25.82 ^d
P ₂ O ₅ (mg/100 g)*	3.04 ± 2.15 ^a	1.60 ± 1.91 ^a	0.42 ± 0.60 ^b	0.20 ± 0.38 ^b
K ₂ O (mg/100 g)*	11.13 ± 3.40 ^a	7.88 ± 4.89 ^{a,b}	7.73 ± 5.36 ^b	5.56 ± 2.49 ^c
Mg (mg/100 g)*	9.06 ± 3.46 ^a	9.23 ± 5.87 ^a	3.99 ± 1.80 ^b	2.94 ± 0.99 ^b
N _(total) (%)*	0.74 ± 0.17 ^a	0.52 ± 0.16 ^b	0.34 ± 0.21 ^c	0.19 ± 0.09 ^d
C _(total) (%)*	7.08 ± 1.38 ^{a,c}	4.98 ± 1.91 ^b	5.21 ± 2.66 ^{b,c}	5.44 ± 2.42 ^{b,c}
C _(org) (%)*	6.83 ± 1.63 ^a	4.83 ± 1.64 ^b	3.12 ± 2.36 ^c	1.53 ± 0.68 ^d
C/N (%)*	9.41 ± 0.56 ^a	9.05 ± 1.07 ^a	8.91 ± 1.69 ^a	7.68 ± 1.31 ^b
Northness	0.53 ± 0.47 ^a	0.53 ± 0.14 ^a	0.53 ± 0.14 ^a	0.67 ± 0.47 ^a
Eastness	0.85 ± 0.85 ^a	0.85 ± 0.11 ^a	0.85 ± 0.11 ^a	0.75 ± 0.85 ^a
Shannon*	3.00 ± 0.21 ^a	3.15 ± 0.16 ^b	3.18 ± 0.31 ^b	2.95 ± 0.36 ^a
Richness*	34 ± 4 ^a	38 ± 7 ^b	39 ± 13 ^b	32 ± 9 ^a
Evenness*	0.84 ± 0.04 ^a	0.87 ± 0.02 ^{a,b}	0.87 ± 0.02 ^b	0.84 ± 0.04 ^{a,b}

Superscript letters (a, b, c, d) indicate significant variable differences for the Wilcoxon rank sum test of a posthoc cluster comparison using Bonferroni correction method ($p < 0.05$)

Asterisk indicates significant differences between clusters from Kruskal–Wallis comparison ($p < 0.05$)

palustris, *Polygala transcaucasica*, and *Salvia verticillata*. Common grassland species which occurred within all plots at a relative frequency of $\geq 50\%$ were *Agrostis vinealis*, *Festuca pratensis*, *Leontodon hispidus*, *Lotus corniculatus*, *Pimpinella rhodanta*, *Plantago lanceolata*, *Ranunculus caucasicus*, and *Veronica gentianoides*.

Functional plant groups

The relative abundance and species-richness of functional plant groups were calculated for each of the vegetation cover classes (Fig. 4). Due to a contribution of high-montane and subalpine vegetation to the plant composition within the densely vegetated class, we

Table 3 Indicator species analysis of vegetation types ordered by relative frequency

Species name	Cluster	I (n=16)	II (n=20)	III (n=37)	IV (n=21)	IndVAL
<i>Agrostis vinealis</i>		88	100	70	62	44 **
<i>Seseli transcaucasica</i>		81	10	5	0	77 ***
<i>Betonica macrantha</i>		75	0	3	0	75 ***
<i>Astrantia maxima</i>		75	5	3	0	75 ***
<i>Anthoxanthum odoratum</i>		75	60	16	0	43 ***
<i>Dactylorhiza euxina</i>		75	25	22	19	42 ***
<i>Cirsium obvallatum</i>		69	20	22	10	64 ***
<i>Trifolium caucasicum</i>		69	40	46	10	48 **
<i>Centaurea salicifolia</i>		69	50	24	29	41 **
<i>Carex umbrosa</i> ssp. <i>huetiana</i>		69	35	19	5	29 **
<i>Cephalaria gigantea</i>		63	5	19	10	54 ***
<i>Rumex obtusifolius</i>		63	5	0	0	51 ***
<i>Hypericum bupleuroides</i>		63	10	14	5	46 ***
<i>Bromus variegatus</i>		63	45	35	29	40 ***
<i>Veratrum lobelianum</i>		56	0	0	0	56 ***
<i>Inula orientalis</i>		50	0	5	0	50 ***
<i>Geranium ibericum</i>		50	15	3	0	49 ***
<i>Cynosurus cristatus</i>		38	100	46	14	76 ***
<i>Trifolium repens</i>		81	100	57	24	52 ***
<i>Festuca pratensis</i>		56	100	70	71	49 ***
<i>Leontodon hispidus</i>		81	100	95	100	38 ***
<i>Carex caryophyllaea</i>		6	95	54	19	55 ***
<i>Plantago lanceolata</i>		56	95	97	81	55 ***
<i>Alchemilla caucasica</i>		50	95	89	43	46 ***
<i>Prunella vulgaris</i>		31	95	84	71	41 **
<i>Pimpinella rhodantha</i>		100	95	89	86	39 *
<i>Gentiana septemfida</i>		50	95	54	33	36 *
<i>Cerastium fontanum</i> ssp. <i>vulgare</i>		38	90	27	14	57 ***
<i>Phleum pratense</i>		31	85	59	52	49 ***
<i>Trifolium pratense</i>		25	85	62	57	44 **
<i>Euphrasia</i> sp.		0	85	62	90	37 ***
<i>Poa alpina</i>		25	75	70	48	36 **
<i>Achillea millefolium</i>		6	70	43	29	48 ***
<i>Festuca ovina</i>		25	70	46	14	36 **
<i>Phleum alpinum</i>		50	55	14	0	25 *
<i>Nardus stricta</i>		13	50	3	0	49 ***
<i>Medicago lupulina</i>		0	50	70	48	32 *
<i>Luzula stenophylla</i>		69	50	19	0	32 **
<i>Thymus collinus</i>		19	70	97	86	52 ***
<i>Leucanthemum vulgare</i>		6	90	95	86	40 ***
<i>Linum catharticum</i>		19	70	92	100	40 **
<i>Polygala transcaucasica</i>		6	45	84	86	40 ***
<i>Briza media</i>		25	45	81	76	39 **
<i>Anthyllis variegata</i>		0	15	59	52	45 ***
<i>Trisetum rigidum</i>		56	45	84	100	37 **
<i>Parnassia palustris</i>		6	10	49	86	48 ***
<i>Campanula alliariifolia</i>		0	0	68	81	47 ***
<i>Lactuca racemosa</i>		13	0	41	76	40 **
<i>Alchemilla</i> cf. <i>laeta</i>		38	0	16	71	28 *
<i>Tussilago farfara</i>		0	0	19	57	53 ***

Table 3 continued

No group assigned, non-significant indicator values					
<i>Ranunculus caucasicus</i>	100	100	97	90	31
<i>Lotus corniculatus</i>	75	90	97	100	29
<i>Veronica gentianoides</i>	56	95	76	43	32
<i>Rhinanthus minor</i>	88	35	54	29	28
<i>Campanula glomerata</i> ssp. <i>caucasica</i>	50	60	32	5	22
<i>Cruciata laevipes</i>	44	50	76	62	26
<i>Salvia verticillata</i>	13	30	57	62	22
<i>Origanum vulgare</i>	25	40	43	57	18

Species with a relative frequency of $\geq 50\%$ (grey shading) and highly significant indicator values (***) are shown as indicator species (bold). Boxes indicate cluster assignment of indicator species, cluster I: *Seseli transcaucasica*, cluster II: *Cynosurus cristatus*, cluster III: *Briza media*, cluster IV: *Parnassia palustris*

* $p < 0.05$; ** $p < 0.01$; $p < 0.001$ ***

separately visualized the *Seseli transcaucasica*-cluster. The herbs' contribution to the overall abundance increases with decreasing vegetation cover from 47% on dense sites of the high-montane zone up to 62% on sparsely vegetated plots. Further, the proportion of graminoid abundance decreases from 35% on dense sites to 22% on lightly vegetated sites, whereas the relative abundance of the *Fabaceae* group remains stable at 15–16% throughout the same vegetation cover ranges. Sparsely vegetated sites display a different trend for *Fabaceae* (10% abundance) and graminoids (26% abundance). Woody species (*Betula litwinowii*, *Daphne glomerata*, *Fagus orientalis*, *Prunus cerasifera*, *Pyrus caucasica*, *Salix caprea*, *Salix kazbekensis*, *Sorbus aucuparia*), orchids and ruderal pasture weeds contribute each to less than 1% abundance for the high-montane zone. However, for the subalpine *Seseli transcaucasica*-cluster, ruderal pasture weeds display about 10% relative abundance. Further, abundance of the *Seseli transcaucasica*-cluster is comprised by the overall lowest abundance value for the *Fabaceae* group (9%) in addition to herb and graminoid abundance which is similar to the densely vegetated high-montane sites.

Generally, herbs contribute most to overall species-richness which indicates the abandonment of former grassland management (haymaking). The herb species-richness ranges from 57% for the densely vegetated sites of the high-montane zone up to 61% at the sparsely vegetated sites and densely vegetated *Seseli transcaucasica*-cluster. Graminoids contribute to the second largest proportion of species-richness of 19–21% for open vegetation cover and 25% for the densely vegetated sites. *Fabaceae* contribute 8% of species-richness at the sparsely and lightly vegetated sites and display the lowest value of 5% on the densely vegetated *Seseli transcaucasica*-cluster sites. *Orchidaceae* show the lowest contribution to the species-richness on sparsely vegetated sites (3%), whereas the other vegetation cover classes display a relative species-richness of 5 and 4% for the *Seseli transcaucasica*-cluster. The highest shares of woody species to species-richness show the lightly (8%) and sparsely vegetated sites (6%). Woody species (*Sorbus aucuparia*) contribute only 1% to the relative species-richness on the densely vegetated *Seseli transcaucasica*-cluster sites. However, the *Seseli transcaucasica*-cluster displays the highest proportion of ruderal pasture weeds (4%). Whereas the plant group of ruderal pasture weeds is absent on the sparsely vegetated sites.

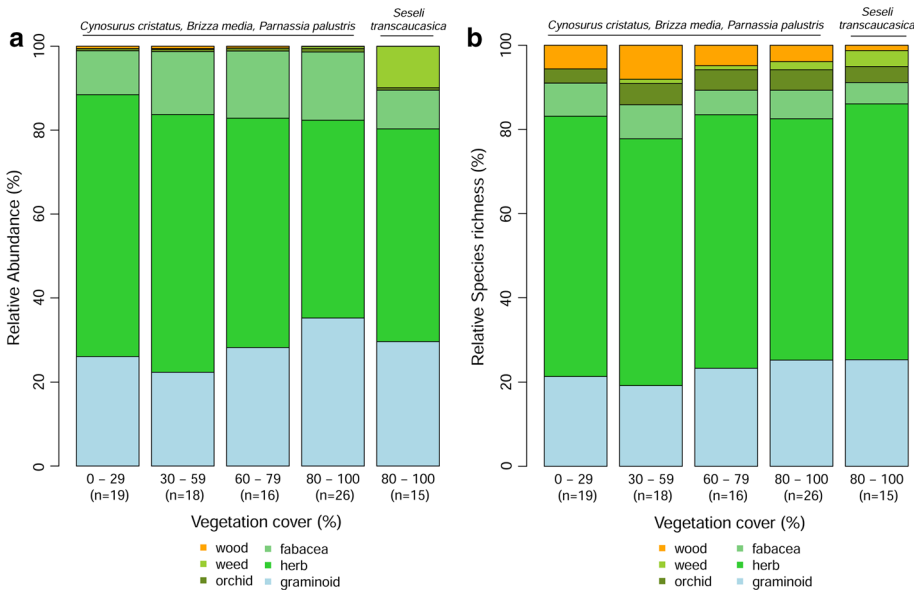


Fig. 4 Relative abundance (a) and species-richness (b) within varying vegetation cover

Discussion

Our study has examined the vegetation which develops under characteristic site conditions of overgrazed and eroded sites in order to establish conservation measures for mountain grassland within the Caucasus biodiversity hotspot.

Site condition and vegetation types

Our ordination results indicate the changeover of species composition and site conditions of the subalpine and high-montane zone which is in accordance with the well-known altitudinal gradient of mountain vegetation (Ozenda 1988). In our data set, the altitudinal gradient can be further seen in an overlap of shared species within the nutrient-rich sites of the subalpine and high-montane zone. Nevertheless, the distinct position for most of the *Seseli transcaucasica*-cluster sites is further confirmed by the ISA that shows most of the subalpine species at highest frequency. Besides altitudinal influences, changes in land use have further affected the subalpine sites in our research area (Tephnadze et al. 2014). The laborious haymaking on remote slopes of the subalpine zone was replaced by hay production at more favorable locations near the villages which were former used as arable fields. Indicators for hay production in the subalpine belt are *Agrostis vinealis*, *Bromus variegatus*, and to a smaller extent *Hordeum brevisubulatum* which are typical hay meadow species of the Kazbegi region (Tephnadze et al. 2014; Magiera et al. 2013). Ruderal species such as *Cirsium obvallatum* and *Veratrum lobelianum* are zoochorously dispersed by grazing animals and are therefore characteristic for grazed habitats. Callaway et al. (2000) discovered so-called safe sites in the surrounding of these species where certain species (e.g. *Trifolium ambiguum* and grasses) benefit from the protection of herbivory.

These safe sites on overgrazed grassland are characterized by high plant diversity whereas the subalpine grassland of our study region is dominated by highly competitive tall herbs such as *Seseli transcaucasica*, *Betonica macrantha*, *Astrantia maxima*, or *Cephalaria gigantea* which infest the abandoned hay meadows. However, we found a single specimen of *Traunsteinera sphaerica*, a considerably rare orchid species (Akhalkatsi et al. 2003), within the *Seseli transcaucasica*-cluster. Further, the subalpine meadows of the Kazbegi region have been described to substantially contribute to the phytodiversity on a landscape level (Tephnadze et al. 2014). Therefore future development of the productive subalpine grassland will be of interest as the low occurrence of meadow species indicates the loss of a valuable subalpine hay meadow habitat.

Our class comparison of environmental variables illustrates the changing site conditions along the slope of the high montane zone. Although we found a changing high-montane vegetation composition along the slope, these changes most likely contributed to a gradient of land use intensity. Tasser et al. (2003) identified effects related to a change in land use as an additional factor contributing to topographical factors causing the loss of vegetation cover and erosion events. We assume a higher grazing pressure within the slopes nearby the villages as it is known from former Soviet Union countries (Food and Agriculture Organization of the United Nations 2003). Furthermore, the altitudinal differences of vegetation types correspond to the distance from settlements and therefore the site conditions of the lower slope display lower vegetation cover. The location of erosion events on the lower part of the mountain slope was also found on steep overgrazed slopes of the Alps (Domermuth 1995). In the high-montane zone, we observed the *Cynosurus cristatus* grassland vegetation which develops under less inclined, dense site conditions of the upper slope. This vegetation type displays a high vegetation cover density and high species-richness. As we further approach downslope, the *Briza media*-cluster indicates a transition towards the *Parnassia palustris*-cluster. As the slope ascents we found less vegetation cover on *Briza media* grassland and the lowest coverages on the lower slope at *Parnassia palustris*-cluster vegetation. Although the site conditions of slope inclination, stone content and phosphorus content are in accordance with the sparsely vegetated sites, a higher vegetation cover and a lower rock cover distinguish the unique features of the *Briza media*-cluster from the *Parnassia palustris*-cluster. Due to its low nutrient values and high species-richness, the *Briza media*-cluster of our study area has to be recognized as a habitat as valuable as poor grassland of other mountain regions. This is further confirmed by the occurrence of one native *Gladiolus* population, a genus which has become particularly endangered in the European Alps. The *Parnassia palustris*-cluster sites carry the first stage of vegetation succession on habitats of scree. Other than the species-rich habitats of rock and scree of the Kazbegi region which are considered as valuable habitats for Georgia (Nakhutsrishvili et al. 2006), our described scree habitats are neither of any danger nor of conservation value. Considering the long-lasting period of soil formation in mountainous regions, the long-term loss of diverse grassland and the development towards habitats of no conservation value has to be expected once the vegetation cover is removed.

Seseli transcaucasica- and *Cynosurus cristatus*-cluster display acidic soil conditions whereas the high stone content on *Briza media*- and *Parnassia palustris*-cluster creates basic substrates. The content of calcium carbonate content indicates a mixture of calcareous and alkaline parent rock material, as it has been described for the study area (Gobejishvili et al. 2011; Khetskhoveli et al. 1975). Soil phosphorus content is generally very low, whereas potassium and magnesium values seem to be sufficient compared to grassland nutrient demands of managed European grassland (VDLUFA 1997, 1999). The strong decline of nutrients from vegetated to open sites that we observed was also reported

from sites of the Alps (Florineth et al. 2002; Zöttl 1952). Nutrient values of our sparsely vegetated study sites are comparable to site conditions which were recorded on a comparable study site in Italy (Florineth et al. 2002). However, phosphorus content within poor grassland (*Briza media*-cluster) and scree sites (*Parnassia palustris*-cluster) was several times lower compared to the Alps and similar low values were observed on study sites within the nearby Kazbegi region (Tephnadze et al. 2014). Additional factors such as the upper soil horizon thickness and fractions of coarse soil material where not incorporated into our soil analyses and might further influence the nutrient availability for plants.

Functional plant groups

Differences between the functional plant groups can be explained by the varying structural conditions of different vegetation cover classes. Graminoids play an important role to benefit the density of vegetation structure on densely vegetated sites where they are responsible for the higher abundance and species-richness. Accordingly, a sparsely vegetated structure enables the establishment of higher herb abundance. The *Fabaceae* is a light-demanding plant group which therefore seems to be most affected by the structure and site conditions of sparsely vegetated sites and densely vegetated *Seseli transcaucasica*-cluster sites. *Fabaceae* play an important role in the revegetation of sparsely vegetated sites due to their nitrogen-fixing capabilities (De Deyn et al. 2011). Due to their low competitiveness their relative abundance needs to be increased when considering restoration efforts. The decrease in the number of species of *Orchidaceae* on vegetation cover <30% indicates the decline of a species group of high conservation value once the soil layer has been completely eroded. These outcomes support the demand for the protection of valuable and diverse grassland habitats in Georgia.

The occurrence of ruderal pasture weeds is largely restricted to the *Seseli transcaucasica*-cluster. We conclude for our study region that the high abundance of ruderal pasture weeds indicates a high competitiveness to tall herb vegetation. The open vegetation structure of sparsely vegetated sites seems to enable more shrub and tree species to regenerate. Further, we assume that a high grazing pressure prevents further reforestation as the abundance of woody species is generally very low. The occurrence of woody species (*Sorbus aucuparia*) in the subalpine zone is a remnant from the original forest which indicates the potential for reforestation in the subalpine belt. However, the distance to mature trees influences the process of seedling recruitment and was not tested within our study.

Potential plant species for ecosystem restoration

Due to the tolerance to varying site conditions of plant species which we could find within all vegetation types of the high-montane zone, we assume these species to be suitable for grassland restoration in the Greater Caucasus. Although some single species may possess the capability to quickly restore vegetation cover, the necessity to restore species-rich grassland for erosion control has been reported (Martin et al. 2010; Pohl et al. 2009). From the plant species' characteristics to grow on nutrient-poor sites, we suggest grasses which form the matrix of grassland such as *Agrostis vinealis*, *Briza media*, *Festuca pratensis*, and *Poa alpina*. Additionally *Festuca ovina* might be suitable for revegetation, as the closely related *Festuca valesiaca* has been found to secure erosion edges in subalpine grassland of the Georgian Caucasus (Caprez et al. 2011). Moreover we suggest the following herb species which also grow under poor soil conditions: *Anthyllis variegata*, *Campanula*

alliariifolia, *Leontodon hispidus*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Medicago lupulina*, *Pimpinella rhodantha*, *Polygala transcaucasica*, *Ranunculus caucasicus*, *Salvia verticillata* and *Trifolium pratense*. However, due to small biomass we assume that *Parnassia palustris*, and *Veronica gentianoides* can be neglected for revegetation. In comparison to other species suggestions for restoration of mountain grassland (Krautzer et al. 2004), we further assume that *Achillea millefolium*, *Koeleria luerssenii*, *Phleum alpinum*, and *Trifolium repens* might be appropriate species. Further, *Trifolium ambiguum*, a native *Fabaceae* species of the Georgian mountain region, is globally used for grazing in permanent pastures and forms dense structures once established (Cuomo et al. 2003). Although *Festuca varia* plays an important role for slope protection in the Alps we do not recommend this species for the Caucasus region as it has the potential to replace grassland communities under intensive grazing (Nakhutsrishvili 1999). We further identified *Trisetum rigidum* as being able to take the ecological position of pioneer on high-montane scree habitats as it is known for *Trisetum distichophyllum* in the subalpine region of the European Alps. The seed production and suitability of the proposed species for restoration measures in the Caucasus region should be further tested in field studies.

Conclusion for grassland management and conservation

We found four major vegetation types which have developed under the site conditions of overgrazing and erosion in the Upper Aragvi valley. Our results indicate the loss of species-rich high-montane pastures once the vegetation cover is damaged. This is further confirmed by Tasser et al. (2003) who described larger erosion events on steep slopes after damage being done to the vegetation cover. Furthermore, Klug et al. (2002) reported little revegetation potential after the vegetation cover has been trampled. Due to the observed low individual numbers on sparsely vegetated sites, we assume also a low potential for the natural succession through seed production on these sites. Therefore, indigenous, site-specific seed material has to be produced to ensure restoration success. We strongly recommend applying our suggested native plant species and neglecting exotic species [e.g. *Chrysopogon zizanoides*] for revegetation. Therefore, for the *Cynosurus cristatus* pastures on steep slopes nearby the settlements we suggest focusing on early grassland revegetation once the vegetation cover gets damaged. Immediate seeding and grazing enclosures on vegetation damage spots are essential for grassland restoration success and slope protection (Krautzer and Wittmann 2006). Due to the high costs of large scale restoration methods we suggest putting emphasis on restoring recent small scale damages of pastures and recreational areas for the region of interest and other transition countries of the Caucasus region to stop land degradation and further habitat loss. The poor grassland vegetation of our study area showed the highest diversity and proved to also be habitat of specialist plants of high conservation value. Therefore the loss of these valuable stands needs to be halted. Further, these sites of *Briza media*-cluster displayed a median vegetation cover of 60% which should be the minimum goal for restoration management since Moismann (1984) proposed 70% vegetation cover to secure mountain slopes.

Due to site conditions, the highly productive *Seseli transcaucasica* grassland seems to be most suitable for grazing or haymaking. However, the high infestation with ruderal pasture weeds reduces the value as animal fodder. Therefore, strategies to reduce ruderal pasture weed abundance and to maintain the subalpine vegetation for animal use would be highly advisable. Further, on the more favorable, less inclined slopes of the subalpine zone cutting and haymaking should be again intensified towards the re-establishment of diverse *Hordeum* and *Bromopsis* community meadows in order to conserve habitat diversity.

Overall, we suggest establishing an appropriate management plan on collective land of Caucasian grassland as it has been proposed for other countries which experienced collectivization (Food and Agriculture Organization of the United Nations 2003).

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