The importance of plant community structure and soil seed banks for productivity and sustainable use of pastures and hay meadows on the slopes in Khevi, a high mountain region in the Central Greater Caucasus

A dissertation submitted to the School of Natural Sciences and Medicine of the Ilia State University

By **Giorgi Tedoradze**

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Scientific supervisor: Prof. Dr. Zaal Kikvidze

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As the author of the submitted dissertation "The importance of plant community structure and soil seed banks to productivity and sustainable use of pastures and hay meadows on the slopes in Khevi, a high mountain region in the Central Greater Caucasus", I declare that the work is my original work and does not contain material published, accepted or defended by other authors, which is not mentioned or cited in accordance with the relevant rules.

Giorgi Tedoradze

20.03.2022

Photos by Giorgi Tedoradze

აბსტრაქტი

ჩემი კვლევა არის ნაწილი მულტიდისციპლინური და ბინაციონალური პროექტისა AMIES II, რომელის მთავარი მიზანი გულისხმობდა მდგრადი მიწათსარგებლობის სცენარის შემუშავებას ცენტრალური კავკასიონისათვის (ყაზბეგი). პროექტის ამოცანათაგან ერთ-ერთი მოიცავდა სუბალპური მდელოს ციცაბო ფერდობების მცენარეულობის კვლევას. უფრო კონკრეტულად ჩემი სამუშაო დაკავშირებული იყო ციცაბო ფერდობების ბალახოვანი მცენარეულობის სტრუქტურის, ნიადაგის თესლის ბანკის და პროდუქტიულობის შესწავლასთან. თემატურად დისერტაცია შედგება ოთხი ნაწილისაგან. თითოეული თავის შემადგენლობაში შედის: ლიტერატურის მიმოხილვა, საკვლევი კითხვები, მეთოდები, შედეგები, დისკუსია და დასკვნები. დისერტაცია ეფუძვნება 2014-2017 წლებში ჩატარებულ საველე სამუშაოებს, რომელიც მოიცავდა ფიტოსოციოლოგიური ნაკვეთების შერჩევა-აღწერას, ნიადაგის ნიმუშების აღებას, როგორც ნიადაგის თესლის ბანკის ექსპერიმენტისთვის, ასევე ქიმიური ანალიზისთვის და ბიომასის აჭრებს. პირველ თავში მოცემულია ნიადაგის თესლის ბანკის ექსპერიმენტის შედეგები და განხილულია მისი გამოყენების პოტენციალი დაზიანებული ფერდობების აღდგენის პროცესში. ამასთან ნიადაგის თესლის ბანკის სიხშირე და მრავალფეროვნება დაკავშირებულია, როგორც ტოპოგრაფიასთან და მიწათსარგებლობასთან, ასევე არსებულ მცენარეულ საფართან. მეორე თავში მოყვანილია აღწერილი მდელოს მცენარეულობის ტაქსონომიური და გეოგრაფიული სტრუქტურა. მცენარეული მრავალფეროვნება მოცემულია სახეობრივ, გვარობრივ და ოჯახების დონეზე. განხილულია ენდემების რაოდენობა, წარმოდგენილია სასიცოცხლო ფორმები. მესამე თავში წარმოადგენილია აღწერილი ფიტოსოციოლოგიური ნაკვეთების საფუძველზე მცენარეულობის კლასიფიკაცია ბრაუნ-ბლანკეს მეთოდოლოგიით. მოცემულია თითოეული მცენარეული ტიპის ფლორისტული და ეკოლოგიური დახასიათება. ხოლო მეოთხე, ბოლო თავში განხილულია მდელოების პროდუქტიულობა, როგორც სხვადასხვა ტიპის მცენარეულობისთვის ასევე საკვლევი ტერიტორიის სხვადასხვა დასახლებული პუნქტისათვის, განსხვავებული მიწათსარგებლობის პირობებში. ოთხივე თავი ეყრდნობა საკვლევ ტერიტორიზე დანიმუშებულ ნაკვეთებზე შეგროვილ

ფიტოსოციოლოგიურ ინფორმაციას და შესაბამისად მდელოს მცენარეულობის სახეობების საერთო სიას.

ძირითადი საძიებო სიტყვები: მიწათსარგებლობა, სუბალპური მდელოები, ციცაბო ფერდობები, აღდგენის პოტენციალი, ტაქსონომიური და გეოგრაფიული სტრუქტურა, კლასიფიკაცია, ბიომასები.

Abstract

My study was based on multidisciplinary studies conducted within the frame of the binational project AMIES II, the overall aim of which was to develop a sustainable land use scenario for the Central Greater Caucasus (Kazbegi, Georgia). One of the tasks of the project was to study the vegetation of the steep slopes of the subalpine meadow. More specifically my work was related to the study of the structure of herbaceous vegetation on steep slopes, the soil seed bank and productivity. Thematically, the dissertation is structured in four parts. Each chapter has its own literature review, research questions, methods, results, discussion, and conclusions. The dissertation is based on fieldwork conducted in 2014-2017, which included selection and sampling of phytosociological plots, soil sampling for both soil seed bank experiments, as well as chemical analysis and biomass clipping. **The first chapter** presents the results of the soil seed bank experiment and discusses the potential of its use in the process of repairing damaged slopes. However, the frequency and diversity of soil seed bank is related to both topography and land use, as well as comparable to standing vegetation. **The second chapter** describes the taxonomic and geographical structure of the sampled meadow vegetation. Plant diversity is given at the species, genus and family level. The number of endemics is discussed and given the life forms of each species. **The third chapter** presents the classification of vegetation based on the described phytosociological plots according to the Braun-Blanquet methodology. The floristic and ecological characteristics of each plant community types are given. **The final fourth chapter** and discusses the productivity of meadows, for different types of plant community and for different settlements in the study area, under different land use conditions. All four chapters are based on data collected in phytosociological plots sampled in the study area and hence the overall list of meadow vegetation species.

Key Words: Land use, Subalpine Grasslands, Steep slopes, Revegetation potential, Taxonomic and geographical structure, Classification, Biomass.

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Abbreviations:

AC	*Astragalus captiosus* community type
ARDSG	Agriculture and Rural Development Strategy of Georgia
AGB	Aboveground biomass
ASN	Aboveground species number
BSN	Belowground species number
C	Carbon content in soil [%]
CC	Cover of cryptogams [%]
Ch	Chamaephyte
CH	Height of cryptogams [cm]
CL	Cover of litter [%]
CTI	Compound Topographic Index
DAM	Digital Altitude Model
DD	Data Deficient
DM	Dry mass
EEA	European Environment Agency
EN	Endangered
G	Geophyte
H	Hemicryptophyte
ISA	Indicator Species Analysis
L	Liana
LB	Legume biomass [%]
LC	*Lomelosia caucasica* community type
LCLU	Land cover and land use
LIM-MAX	Ecological Limits and Maximum Cattle
N	Nitrogen content in soil [%]
NBSAPG	National Biodiversity Strategy and Action Plan of Georgia
NE	Not Evaluated
NMDS	Non-metric multidimensional scaling
North	Northness
NT	Near Threatened
PA	*Plantago atrata* community type
PC	*Polygonum carneum* community type

pH	pH_{H2O}
Ph	Phanerophyte
PROT-MAX	Ecological Protection and Maximum Cattle
PROT-REG	Ecological Protection and Regional Orientation
RM	*Rhinanthus minor* community type
Roots	root weight [%]
SD	Seed density (m^{-2})
SR	Solar radiation
T	Therophyte
V semi-par	Vascular semi-parasite

Introduction to the thesis

The importance of plant diversity for our life is impossible to overestimate. Plant diversity plays a crucial role in supplying mankind with important natural resources, while diverse and intact plant communities that contain various life forms provide us with many vital ecosystem services (Körner 2003; EEA 2010). These services include, but are not limited to, the following: supplying fresh water, protection from erosion, providing food, fodder, medicinal plants, construction materials and supporting traditional subsistence economies in low-income societies. Further, plant diversity is important to maintain intact habitats that harbour diverse forms of animal life. Recreation and tourism depend greatly on the conservation of traditional landscapes where plant diversity is a fundamental component (Körner 2003; EEA 2010; NBSAPG 2014-2020 2014). The importance of plant diversity to primary and secondary habitats, which shelter many species of high conservation value is particularly noticeable in high mountains.

A diverse vegetation cover develops many forms of dense roots that penetrate into considerable depths and stabilize soils on the slopes. On the other hand, such vegetation can be maintained only on functioning/intact well-formed soils of a diverse structure. In general, there is a clear relationship between the soil type and plant species distribution in mountains (Körner 2003; Pohl et al. 2009; Martin et al. 2010).

Soil is a key component of high mountain ecosystems that can sustain a healthy and diverse vegetation cover. Soil contains the seed bank that can help restore plant communities and their ecosystem functions after natural and human-induced disturbances (e.g., flushing rains, avalanches, compaction, overexploitation). The higher the diversity of plants and their seed bank in the soil in mountain ecosystems, the higher their ability to withstand natural disasters such as falling rocks, landslides, mudslides and avalanches (Oades 1984; Tisdall 1994; Bird et al. 2007).

Over the millennia, natural alpine and subalpine forests were converted into semi-natural pastures and hay meadows in the central Caucasus; the traditional agriculture created here a rich cultural landscape with remarkably high plant diversity, which can help attract tourists interested in ecology and culture. In fact, the region currently is an important tourist destination that offers mountaineering, hiking, horseback riding, and skiing, and supports economic growth and diversification (Debarbieux et al. 2014; Gugushvili, Salukvadze, and Salukvadze 2017; Salukvadze, Gugushvili, and Salukvadze 2019).

Grasslands constitute an important part of vegetation in high mountains; traditionally, they are managed as pastures and some parts are hay meadows to provide fodder for winter time. These subalpine and alpine herbaceous plant communities appear to be very sensitive to climate change (Körner 2003), while the consequences of overexploitation such as intensive soil erosion has become a threat to plant diversity. Livestock husbandry in mountains is based on the resources that pastures and hay meadows provide. The impact of ongoing land use practices include overgrazing and disturbances owing to construction (roads, pipelines, other infrastructure) which can increase the risk of natural hazards, abrupt abandonment of pastures and hay meadows owing to depopulation of the remote high mountain villages (Nakhutsrishvili et al. 1999; Körner 2003; Nakhutsrishvili 2005; Gigauri et al. 2011; NBSAPG 2014-2020 2014). These changes bring about alterations in ecosystem functioning (Cernusca et al. 1996; Tasser et al. 2007; Theissen, Otte, and Waldhardt 2019) with consequences such as productivity loss (Tasser and Tappeiner 2002). All these factors reduce species diversity, the integrity of the vegetation, and prompt soil erosion.

It should be noted though that moderate grazing can in fact help maintain high plant diversity (Körner, Nakhutsrishvili, and Spehn 2006). Exclusion of grazing usually leads to a decline in species diversity, which becomes evident after only a few years. On the other hand, economic importance of mountain pastures to local economy is very high as this economy is essentially based on the production of meat and dairy, and this is also true for not only high mountain regions but also plains in other regions of Georgia. In fact, the existing grasslands provide food security, and satisfy to a large extent the increasing demands of growing urban populations (O'Mara 2012).

The state of affairs described above appears to be appreciated by the authorities as one can see a more or less realistic description of the existing situation in the legal frameworks issued by the Georgian government. First of all, there is the "National Biodiversity Strategy and Action Plan of Georgia 2014 – 2020" (2014), which assesses the state of the country's biodiversity and describes it as „challenging“, since data collection, analysis of species distribution, and the state of habitats and key ecosystems are poorly organized and unsystematic. The same document admits that the unregulated and chaotic use of pastures and hay meadows is aggravated by the absence of comprehensive legislation and regulations, while the existing law is ambiguous. At the same time, the lack of basic data and information on important variables, such as the area occupied by pastures and hay meadows, number of land plots per municipality, cattle density, vegetation type, their composition and conservation value and productivity, hinders the attempts to improve the existing legislation (NBSAPG 2014-2020 2014). One of the exceptions in this regard is Kazbegi district, where only in the last decade complex and multidisciplinary studies have been conducted (Magiera et al. 2013; 2016; 2017; Tephnadze et al. 2014; Magiera 2017; Hanauer et al. 2017; Hüller, Heiny, and Leonhäuser 2017; Shavgulidze, Bedoshvili, and Aurbacher 2017; Hansen et al. 2018; Theissen et al. 2019; Theissen, Otte, and Waldhardt 2019; Tedoradze et al. 2020; Togonidze 2020).

In spite of this background, it is remarkable that the development of animal husbandry, together with other sectors of agriculture, have been declared a priority of the state (ARDSG- 2015-2020 2015; ARDSG 2021 – 2027 2019). Livestock husbandry, if founded on knowledge-based practices and scientifically tested technologies, can be the core of sustainable agriculture. But, to achieve this, natural resources and land use must be managed correspondingly to maintain species composition and diversity, productivity and nutritional value of pastures and hay meadows. This aim cannot be reached without the prevention of slope soil erosion and restoring the degraded lands (Wiesmair 2016).

The aim of the present doctoral thesis is to fill the aforementioned gaps in our knowledge on the high mountain managed plant communities in Georgia. My study was based on multidisciplinary studies conducted within the frame of the binational project AMIES II (Scenario development for sustainable land use in the Greater Caucasus). The latter is a follow-up project of AMIES (the analysis of the interrelationship between environmental and societal processes in the Greater and Lesser Caucasus of Georgia). The overall aim of the AMIES II was to focus on the development of sustainable agricultural land-use scenarios for the rural development of the marginal Kazbegi region. The project was organized into four project units (Landscapes, Soils, Phytodiversity, and Socio-economic). In each unit, German and Georgian researchers collaborated. My research was related to the subalpine vegetation of steep slopes, more specifically my work was focused on plant community structure, soil seed banks, and productivity. Collaboration included fieldwork for vegetation sampling and collecting soil and plant material samples, laboratory analyses of samples and subsequent statistical analyses, the results of which are reported in this thesis.

Steep slopes are particularly prone to soil erosion (Jakšík et al. 2015; Wiesmair 2016), while the managed grassland communities in Khevi mostly occur on slopes of 20-30° inclination (Kavrishvili 1965). Therefore, one of the main aims of our study was to investigate the seed banks in the managed grasslands within our study region. Our task was assessing the impact of land use and topography on the composition and diversity of soil seed banks and testing whether the existing seed banks could be used in the restoration of vegetation on eroded and heavily disturbed areas (Chapter 1). Since the steepness of the terrain is directly linked to the threat of soil erosion, a dense, diverse, slope-protecting vegetation cover is greatly important to the conservation of high mountain grasslands. Understanding the dynamics of this vegetation requires the knowledge on species composition, taxonomic structure, as well as historical geography of Khevi's subalpine pastures and hay meadow communities (Chapter 2). The conservation of habitats on the steep slopes of Khevi also requires a constant monitoring of the current vegetation layer and its composition; for this having a workable vegetation classification is indispensable. Hence, one of my aims was to establish phytosociological groups and give their floristic and ecological characteristics. A workable vegetation classification can enable us to summarize this information in vegetation maps, an essential tool for nature conservation, landscape management, policy-making, and sustainable land-use (Chapter 3). In the frame of the AMIES project we also looked at the productivity of managed grasslands and their area (Magiera 2017), which are important variables in sustainable agriculture and helps determine the optimal cattle density under various scenarios for future land use development (chapter 4).

Thematically, the dissertation is structured in four parts. Each chapter has its own literature review, research questions, methods, results, discussion, and conclusions. The two chapters of the dissertation are based on two published articles, while the remaining two (second and third) chapters are based on unpublished data. As a study area, we choose the macro-slopes of Mt. Kazbegi located in Kazbegi Municipality, Georgia, the Caucasus.

With this thesis I will answer the following questions:

The persistent soil seed banks (Chapter 1):

i) to analyse whether the composition of soil seed bank in high mountains is linked to land use and terrain topography;

ii) to analyse whether persistent seed bank can restore plant communities in case of disturbance, and

iii) to address which species are most frequent and what is their share in the soil seed bank of the high mountain managed plant communities of the central Caucasus.

Floristic composition of the pastures and hay meadows on Khevi's slopes (Chapter 2):

i) what is the floristic composition of the managed plant communities on the slopes of Khevi, and

ii) which floristic centres contribute mostly to their species composition?

Phytosociological classification of Khevi's steep subalpine pasture and hay meadow communities (Chapter 3):

i) to classify subalpine pastures and hay meadow vegetation on the slopes of various steepness in Khevi, and

ii) to describe concrete phytosociological communities and examining what were the ecological and land use factors that determined their differences.

Productivity of pastures and hay meadows, and sustainable land use capacity in Khevi (Chapter 4):

i) what is the area of the managed herbaceous plant communities in the surroundings of Khevi villages, and what is the ratio of pastures to hay meadows, and

ii) what is the productivity of the managed herbaceous plant communities in the surroundings of Khevi villages, and how different is the yield among different pasture and hay meadow communities?

The species names are compared with four databases (i.e., “Euro+Med” 2006; “The Plant List” 2013; “GBIF.Org” 2020; “IPNI” 2021), the results are presented in the form of species lists see the appendices.

Some results and data of my study were published and used in two scientific articles:

1.Tedoradze, G., Nakhutsrishvili, G., Seip, M., Theissen, T., Waldhardt, R., Otte, A., & Magiera, A. (2020). Terrain impacts the composition of the persistent soil seed bank: A case study of steep high mountain grasslands in the Greater Caucasus, Georgia. Phytocoenologia,47–63. https://www.schweizerbart.de/papers/phyto/detail/50/92499/Terrain_impacts_the_composition_of_the_persistent_soil_seed_bank_A_case_study_of_steep_high_mountain_grasslands_in_the_Greater_Caucasus_Georgia

2.Theissen, T., Aurbacher, J., Bedoshvili, D., Felix-Henningsen, P., Hanauer, T., Hüller, S., Kalandadze, B., Leonhäuser, I.-U., Magiera, A., Otte, A., Shavgulidze, R., Tedoradze, G., Waldhardt, R. (2019). Environmental and socio-economic resources at the landscape level–Potentials for sustainable land use in the Georgian Greater Caucasus. Journal of Environmental Management, 232, 310–320. https://www.sciencedirect.com/science/article/pii/S0301479718312891

Chapter 1. The persistent soil seed banks of steep high mountain grasslands

1.1 Literature review

1.1.1 Overview

The study area is located in Khevi, the historical province of Georgia, on the northern slopes of the Central Caucasus. Khevi today constitutes Kazbegi Municipality and, together with four other neighbouring municipalities, is part of Mtskheta-Mtianeti Region. However, the 'municipality' as an official name has been introduced after the administrative reform conducted relatively recently, while the old name, 'district´, informally still remains in use. Therefore, 'Kazbegi Municipality', 'Kazbegi District' and 'Khevi' can be used interchangeably. Kazbegi Municipality includes 45 villages, 16 of which are completely abandoned. Geologically the study area is complex. The major bedrocks are represented by Paleozoic granitoids, Jurassic sediments, limestones, marls, conglomerates, clay shales, and sandstones (Maruashvili 1971; Abdaladze et al. 1998; Schürholz 2010; Urushadze, Tarasashvili, and Urushadze 2000).

The Caucasus in general, and Georgia in particular, are distinguished with outstandingly high biological diversity and are among the 36 biodiversity hotspots in the world (Myers et al. 2000; Habel et al. 2019). The flora of Georgia counts more than 4130 species of the vascular plants. Approximately 31% of the flora, or 1300 plant species, are endemic to Caucasus Ecoregion. Of them about 280 species are endemic to Georgia (Solomon, Schatz, and Shulkina 2013). If compared to the countries within the same climate zone, Georgia stands out for its floristic richness and endemism. The flora of Khevi is also very rich and includes 1347 vascular plant species. In Khevi, approximately 25%, or 337 species, are endemic to this region. Specifically, 322 species are endemic to the Caucasus Ecoregion and 15 species are endemic to Georgia (Sakhokia and Khutsishvili 1975; Gagnidze 2000, 2005).

In 1977, Kharadze estimated the number of species in Khevi to to be ca. 1300 with 28% rate of endemism including 60 species that were described uniquely from Khevi (Kharadze 1977). Other authors give similar estimates of endemism i.e., 25-28% of Khevi flora is endemic to the region (Grossheim 1936; Sakhokia and Khutsishvili 1975; Tephnadze et al. 2014). In any case, the endemism rate as an indicator of the conservation value of Khevi's plant communites reaches high levels. This is likely due to the geographical and ecological isolation of this region, together with the high diversity of environmental conditions of plant life that includes the wide range of microclimate types and abiotic stresses created by strongly variable topography (Dolukhanov 1978; Nakhutsrishvili 2000; Gagnidze et al. 2002; Körner 2003).

1.1.2 History of the studies on Khevi flora

The history of botanical exploration of Khevi begins with Johann Anton Güldenstädt, a renowned naturalist and explorer of the 18th century. He travelled through the northern Caucasus and Georgia, and Khevi was the first Georgian province that he entered. After Güldenstädt, Khevi was explored by many well-known naturalists and botanists, among them M. Adams, A. A. Mussin-Pushkin, C. C. Steven, J. J. F. W Parrot, K. H. E. Koch, F. J. Ruprecht, G. F. R. Radde, N. A. Desulavi, A. Rehman, N. Bush, N. A. Troitsky, and others. These explorations produced the first herbarium specimens of plant species from Khevi and contributed to the description of Khevi's flora (Sakhokia and Khutsishvili 1975). The regular botanical studies on the vegetation and flora of Khevi began in 1928 with the aim to produce a comprehensive description of plant species and vegetation types, as well as assessments of plant resources. Before this, the pastures and hay meadows in Khevi and elsewhere in the Soviet Union, were managed traditionally (Larin 1967), which was considered irregular and ineffective management by professional botanists (Larin 1967; Nakhutsrishvili 1990; 2003). Nonetheless, the knowledge produced by Georgian botanists was rarely applied in the management of pastures and hay meadows of Khevi, which until now, has largely remained based on traditions. The pioneer of studying the vegetation of Khevi, including its plant resources, pasture and hay meadow communities, is Ana Kharadze. Since 1937, Ecaterine Khutsishvili was involved in these investigations (Sakhokia and Khutsishvili 1975).

Between 1937–1951, botanists whose work was focused on the flora and vegetation of Khevi took active part in a nation-wide programme of land certification. Attention was paid to the productivity of the pastures and meadows. At the end, each Kolkhoz farm (a collective farm in the Soviet Union) received a 'land passport' of the agricultural lands allocated to them. The land passport detailed the floristic composition of hay meadows and pastures, soil types, terrain, and other ecological characteristics of plant communities. It was a very well-done job at the time. Studies on vegetation ecology (then it was called geobotany) in the Central Caucasus began in early 1960s, along with floristic and plant geographic research (Kharadze 1966a; 1977; Nakhutsrishvili and Gagnidze 1999). Experimental, plant ecological studies that included both mensurative and manipulative experiments were conducted from the 1970s and aimed at: determining temperature (Chkhikvadze 1970; Kikvidze 1988; Kikvidze and Abdaladze 1988) and water relations (Tulashvili 1970; Nakhutsrishvili 1988) in various plant communities; ecophysiological studies of CO_2 gas exchange between plant and environment (Abdaladze 1988b; 2011); light relations (Nakhutsrishvili et al. 1985); the effects of autotrophic and heterotrophic organisms on the productivity of meadows (Nakhutsrishvili 1965; 1977a; Khetsuriani 1966; Abdaladze and Kikvidze 1991); various adaptive mechanisms and strategies (Nakhutsrishvili 1965; Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980; Gamtsemlidze 1977; Larcher and Nakhutsrishvili 1982; Nakhutsrishvili and Gamtsemlidze 1984; Nakhutsrishvili et al. 1988; Nakhutsrishvili 1990; Nachuzrischwili et al. 1990); heat resistance (Abdaladze et al. 1988; Akhalkatsi et al. 2006); productivity of various pasture and hay meadow communities and drought resistance of plants (Lortkhiphanidze 1966; Chkhikvadze 1977; Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980; Nakhutsrishvili 1986); and human impacts on high mountain plant communities (Nakhutsrishvili 1965; Gamkrelidze 1986; Abdaladze 1988a), including impacts of grazing (Nakhutsrishvili and Cernusca 1982; Nakhutsrishvili 1990; Körner, Nakhutsrishvili, and Spehn 2006). Further, studies on the taxonomy and classification continued, and by 1975 a comprehensive checklist of Khevi flora was produced (Sakhokia and Khutsishvili 1975). The flora of Khevi was approached from the perspective of historical plant geography (Janelidze and Margalitadze 1977) and several publications have been devoted to different questions of vegetation classification (Bedoshvili 1988; Zazanashvili 1988, 1990; Pyšek and Šrůtek 1989; Bohn, Zazanashvili, and Nakhutsrishvili 2007).

The collapse of the Soviet Union in 1991, and the following severe economic crisis that protracted till the early 2000s, caused a notable decline in the intensity of botanical and ecological research in Georgia and, in particular, Khevi. Nonetheless, there were some noteworthy studies published over this difficult period. These works include studies on species interactions, specifically documenting facilitative interactions of plants in high mountain herbaceous communities (Kikvidze 1993; 1996; Kikvidze and Nakhutsrishvili 1998; Callaway, Kikvidze, and Kikodze 2000), and also the diurnal dynamic balance between facilitation and competition in hay meadows (Kikvidze et al. 2006). Additionally, important studies on the reproductive phenology of different species of seeds and seedlings were published (Akhalkatsi and Wagner 1996; Akhalkatsi et al. 2006). Vegetation ecologists have established permanent plots in 2001 at high altitudes and since then Khevi is included in large-scale monitoring networks (GLORIA-EUROPE and GLORIA-WORLDWIDE) to document the effects of climate change on the structure of high mountain plant communities (Nakhutsrishvili 2005; Gigauri et al. 2011; 2014). Comparative analysis of high mountain flora and vegetation in the Caucasus and other regions such as European Alps have also been conducted (Akhalkatsi and Wagner 1997; Nakhutsrishvili 2003; Erschbamer et al. 2010).

In 2010-2017, multidisciplinary research was conducted in Khevi, within the framework of two binational projects, AMIES I and AMIES II, which created opportunities for young scientists too. This helped increase the intensity of research because plant communities in Khevi were intensively sampled with phytosociological and experimental methods and resulted in a number of publications (Magiera et al. 2013; 2016; 2017; Tephnadze et al. 2014; Hanauer et al. 2017; Hüller, Heiny, and Leonhäuser 2017; Shavgulidze, Bedoshvili, and Aurbacher 2017; Theissen et al. 2019; Theissen, Otte, and Waldhardt 2019; Tedoradze et al. 2019; Tedoradze et al. 2020); new articles are expected to be published in the near future.

1.1.3 Soil seed banks and erosion

Georgia is a country with a distinctly mountainous terrain with a high risk of erosion, therefore protecting soils should be an important activity. Erosion prevention is especially important for areas where mountain ranges are mainly built of shale rocks and such are the ranges almost throughout eastern Georgia (S. Nakhutsrishvili 1960). The steepness of the terrain is directly linked to the threat of soil erosion (Wiesmair 2016). Therefore, dense, diverse, slope-protecting vegetation cover is of great importance for high mountain grasslands (Bazilevich, Davydova, and Yashina 1987; Körner 2003; Martin et al. 2010; Sharikadze et al. 2011). The denudation of slopes and loss of soils washed down (Fig. 1.1) by atmospheric precipitation are mainly caused by unsustainable management of forests and grasslands. This is especially true for the subalpine zone, where forests were largely converted into pastures and hay meadows. This strongly reduces water-retaining capacity of vegetation, while subalpine slopes receive abundant precipitation. Protective measures against erosion may include planting, use of anti-erosion blankets, digging diversions to help drainage, building terraces, however, these measures are efficacious only in conditions of sustainable management of standing plant communities (S. Nakhutsrishvili 1960).

Figure 1.1: Eroded slopes of Khevi (Photos by Giorgi Tedoradze).

Cattle herding has been practiced in the mountains of the Caucasus since ancient times, and so the high mountain grasslands of this region cannot be considered "virgin" (Troitsky 1924; Nakhutsrishvili 1990, 2003). Troitsky (1924) noted almost a century ago the deplorable condition of high mountain grasslands in the Caucasus, where the population complained about decline in pasture yields, degradation, and loss of pastures. Troitsky blamed the limited, or in some cases, complete lack of use of primitive methods of pasture improvement (Troitsky 1924). Our study area is no exception as it fits to the general picture. The grasslands were long been used by the locals as pastures and hay meadows, and it seems that the traditional management was sustainable owing to the moderate intensity of land use by subsistence agriculture. However, the sharp rise in livestock numbers during the Soviet period (Didebulidze and Plachter 2002) led to a wide spread of overgrazing and caused mass erosion that became very conspicuous on the slopes in Khevi. In heavily grazed areas, plant communities are mainly composed of species with high cellulose content, but of low nutritional value, such as the widespread grasslands dominated by matgrass (*Nardus stricta*) and fescue (*Festuca varia*) (Kharadze 1977). Fortunately, even though the nutritional value of fescue is not high, it can protect slopes from erosion. It should be noted that the area of distribution of these species is expanding, which on one hand is an ecologically positive phenomenon (protection of slopes from erosion), but on the other hand it is economically negative (low nutritional value) (S. Nakhutsrishvili 1962; Kimeridze 1965).

Nakhutsrishvili (1960) studied the effects of grazing on pasture communities using permanent plots and found that even a year of exclusion produced considerable positive changes in vegetation. Specifically, species diversity and biomass grew, while 50% of stripped soils were recovered by new growth (S. Nakhutsrishvili 1960). Grazing exclusion over 15-20 years led to 10-15-fold increase in the productivity of subalpine meadows (Nakhutsrishvili 1977b). Nakhutsrishvili documented the changes in Lagodekhi pastures after a 12-year break. The results showed that the restoration processes are more intense in the subalpine than in the alpine zone (S. Nakhutsrishvili 1962). Plants such as lady's mantle (*Alchemilla* spp.), sibbaldia (*Sibbaldia* spp.), matgrass (*Nardus stricta*), thistles (*Cirsium* spp.), dock (*Rumex* spp.) and other less valuable pasture species disappeared completely from the plots after the exclusion, and were replaced by grasses (*Poa* spp.), leguminous genera (*Trifolium* spp.) and other nutritious forbs. Unlike this, in alpine zone relatively less changes in vegetation were found, most probably owing to less intensive restoration processes (S. Nakhutsrishvili 1962).

Restoration also can depend on the characteristics of a given plant community and its soils, as well as its exploitation history and slope angle. Sites on steep soils where inclination exceeded 15°, restoration takes long time if it is possible at all (Gadzhiev 1979).

Subalpine plant communities (1,800-2,500 m a.s.l. in Khevi), particularly on steep slopes, are rich in species (Sakhokia 1983; Bazilevich, Davydova, and Yashina 1987; Nakhutsrishvili 2013). Certainly, the ongoing changes in climate and land use affects these communities (Bekker et al. 1997; Körner 2004; Magiera et al. 2013). Negative land use changes in traditionally used communities (moderate rotational grazing, regular moving) include not only overgrazing, but also abrupt and prolonged abandonment (MacDonald et al. 2000). The latter negatively affects plant community structure, productivity, and integrity of vegetation by disrupting the erosion-preventing capacity of the communities on the high mountain slopes (Tappeiner and Cernusca 1993). At the same time, extreme weather events that increase likelihood of disastrous events such as avalanches and landslides under ongoing climatic changes (Keggenhoff et al. 2014). In summary, restoration of these species-rich communities on the steep slopes of the Central Greater Caucasus has become a challenge.

Restoration ecology gives considerable importance to studies on seed banks (Bakker et al. 1996). In fact, the contribution of soil seed banks to vegetation restoration in degraded plant communities is among the most intensively discussed questions, however, this field is not free of controversies (Baskin and Baskin 1998; Vivian-Smith and Handel 1996).

Roberts (1981) defines the soil seed bank as a collection (reservoir) of viable seeds in the soil and on its surface. Seeds can stay dormant in the soil, some of them for years, and this depends on the species (Roberts 1981; Poschlod 1991). A soil seed bank may not contain seeds of all species that are present in a given community (Ungar and Woodell 1996; Baskin and Baskin 1998), while, in contrast, it is also possible to find seeds of species that are not members of a given community (Milberg and Hansson 1994; Baskin and Baskin 1998). Seed abundance and species composition can vary over time and space, depending on the rate of seed loss through germination, rotting and decomposition, physiological death, and animal transfer *versus* the rate of new seed arrival through seed rain from the fruiting plants of a given community and neighbouring vegetation (Poschlod 1991).

Various soil seed bank models were developed (Thompson and Grime 1979; Grime 1981; Bakker 1989; Thompson, Bakker, and Bekker 1997; Csontos and Tamás 2003). However, most of these models divide seeds found in soils into two categories: transient and persistent. Seeds that perish in the soil within one year constitute a transient seed bank, and seeds that survive in the soil longer than one year build a persistent seed bank (Thompson and Grime 1979; Grime 1981). However, there are also more detailed classifications of seed banks suggested, for example, some models distinguish the following three types of seed banks: transient with seed lifespan less than one year; short-term persistent with seed lifespan more than one year, but less than five years; and long-term persistent with seed lifespan of at least 5 years or more (Bakker 1989; Thompson, Bakker, and Bekker 1997). Other even more detailed classifications divide soil seed bank in four or more categories in which along with the seed lifespan include other criteria such as seed depth in soil, seed rain time, germination rate, and seed dormancy duration (Poschlod and Jackel 1993). There are extensive reviews of main approaches to soil seed banks classification available (Csontos and Tamás 2003; Walck 2005). Nowadays, most researchers prefer the models with fewer seed bank categories (Csontos and Tamás 2003; Walck et al. 2005). The presented thesis reports the results obtained from the analyses of persistent soil seed banks, since this is the category that can be used for restoring degraded plant communities (Bakker et al. 1996).

In general, soil seed bank is considered to be an important component of an ecosystem that supports long-term stability of plant communities and that can be effectively used for restoration (Bekker et al. 1997; Willems and Bik 1998; J. Bakker and Berendse 1999; Bossuyt and Honnay 2008; Kalamees et al. 2012), even though some authors question this opinion. The criticism is based on the fact that the dissimilarity of species compositions between aboveground plant community and the plant species that emerge from the seeds collected in the soil beneath the same plant community can be considerably different (Davies and Waite 1998; Miller and Cummins 2003; Handlová and Münzbergová 2006; Jacquemyn et al. 2011).

Germination and plant establishment are the factors that largely determine the success of restoration, yet the density of diaspores can play a decisive role too. The main resources for successful restoration of plant cover are provided by soil seed banks, seed rain, animal seed dispersal, the amount of seeds produced, root fragments, rhizomes, and tubers (Graham and Hutchings 1988; Kinucan and Smeins 1992; Bakker et al. 1996). Interrelated factors such as the successional stage of the site, local terrain, water content and oxygen level in the soil, soil temperature and chemical composition can play a role in success of germination and plant establishment (Karssen and Hilhorst 1992; Eriksson and Eriksson 1997; Christoffoleti and Caetano 1998; Thompson et al. 1998; 2001; Dölle and Schmidt 2009; Jacquemyn et al. 2011). Severe environmental conditions in high mountains such as cold generally reduces viability of seeds, while the lack of favourable sites can hinder germination and establishment of plants. In front of these challenges, persistent seed bank must be an important contributor to the regenerating of plant communities and the restoration of high mountain ecosystems (Holtmeier 2009).

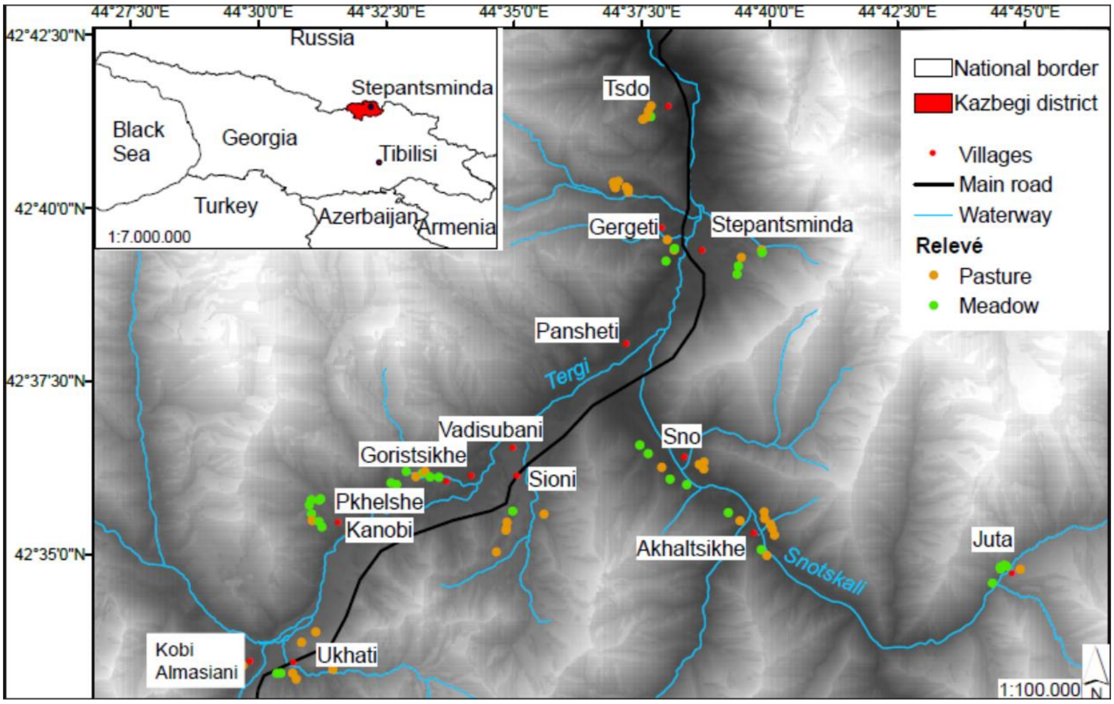
There is a consensus among restoration ecologists that aboveground vegetation, land use, and site environmental conditions can generally be linked to soil seed banks (Gutiérrez, Arancio, and Jaksic 2000; Waldhardt et al. 2011; Tephnadze et al. 2014; Klaus et al. 2018). However, there are only a few studies on the seed banks of high mountain plant communities, and even less conducted in the central Caucasus (Onipchenko 2004). Further, in the South Caucasus (Armenia, Azerbaijan and Georgia) no work on soil seed bank can be found (Shi, Zhang, and Wei 2020). This area belongs to a biodiversity hot-spot (Myers et al. 2000; Habel et al. 2019) where persistent traditional land use systems excluded any application of mineral fertilisers to the pastures and hay meadows (Onipchenko 2004; Tephnadze et al. 2014; Theissen et al. 2019). This circumstance permits conducting experimental tests on the relationship between topography, land use, and the soil seed bank composition under the traditional low intensity land use system (Thompson and Grime 1979; Walck et al. 2005). Therefore, my study was designed to collect quantitative data on soil seed banks found on steep slopes of the Greater Caucasus in high mountains of Khevi, Georgia. The aim of my study was to examine the effects of topography and land use on the seed bank composition and density, as well as analyse whether soil seed bank can be used in the restoration of degraded vegetation cover. To achieve this aim, I set three objectives for my research: (1) analyse whether the composition of soil seed bank in high mountains is linked to land use and terrain topography; (2) analyse whether persistent seed bank can restore plant communities in case of disturbance; and (3) address which species are most frequent and what is their share in the soil seed bank of the high mountain managed plant communities of the central Caucasus.

1.2 Materials and Methods

1.2.1 Study area

The study was conducted on pastures and hay meadow communities found on the slopes of various steepness in the subalpine zone of Khevi, where the altitudinal range of this zone is 1,800 to 2,500 m a.s.l. Administratively this area belongs to Kazbegi Municipality, Mtskheta-Mtianeti Region, Georgia. All study sites were located on the northern macro-slope of the Central Greater Caucasus (Fig. 1.2).

Figure 1.2: Map of the study region, Tedoradze et al. 2020.



Khevi's climate is relatively continental with mean annual temperature of 4.6 °C at 1,850 m (1970-2000). Temperature varies strongly seasonally. Specifically, the annual mean minimum and maximum temperatures range from of –12.9 °C in January 19 °C in July. Annual precipitation is ca. 910 mm (1970-2000), and also seasonally very variable. Most of the precipitation occurs during the late spring and early to mid summer and is followed by a relatively dry spell that lasts from August to March. (The climate data were obtained from the WorldClim database, Fick and Hijmans 2017).

The major bedrocks are built by volcanic andesite and dacite with a considerable occurrence of sandstones. The major soil types are leptosols, skeletic regosols, skeletic cambisols, and umbrisols (Maruashvili 1971; Urushadze, Tarasashvili, and Urushadze 2000; Hanauer et al. 2017). Humic components mostly spread on the steep, north-exposed slope soils. By the former Soviet classification this soil type is a 'mountain forest meadow and mountain meadow soil' (Urushadze, Tarasashvili, and Urushadze 2000).

There are various herbaceous communities on the slopes of Khevi mountains (Nakhutsrishvili 2003), but *Bromus variegatus, Agrostis capillaris, Lomelosia caucasica,* and *Trifolium alpestre* dominate the steep subalpine slopes (1,800-2,500 m a.s.l.) (Sakhokia 1983). In contrast, the most common species on the moist north-east or north-exposed slopes are *Anemone narcissiflora* subsp. *fasciculata*, *Lomelosia caucasica, Betonica macrantha* (Nakhutsrishvili and Abdaladze 2017a). Forests are mostly made up of *Betula litwinowii* and *Sorbus caucasigena* and occur mainly on steep north-exposed slopes (Akhalkatsi et al. 2006). The southern slopes are often dry and eroded, hence herbaceous communities are more xerophilous, which is caused by the land use along with other factors (Sakhokia 1983; Tephnadze et al. 2014; Nakhutsrishvili and Abdaladze 2017a).

1.2.2 Vegetation sampling

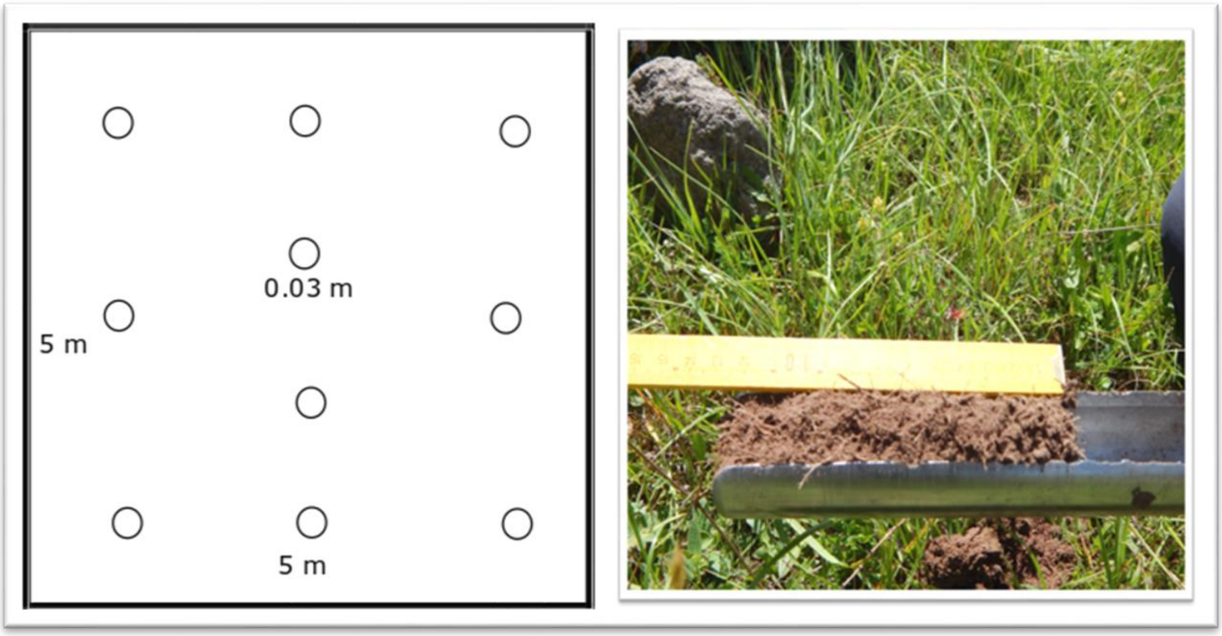
Vegetation was sampled on subalpine herbaceous communities found on the slopes of variable steepness (10°-45°) between the altitudes of 1,750 and 2,350 m a.s.l. Sampling was conducted in July-August of 2014 and 2015 (species were recorded for each plot in subsequent years 2016-2017 too). 5m X 5m plots were set for sampling, which follows the traditional protocol used in phytosociological studies (Braun-Blanquet 1964). The recorded species abundances were estimated by the modified scale of Braun-Blanquet (r, +, 1, 2m, 2a, 2b, 3, 4, 5) (van der Maarel 2007).). Plant species were identified using keys and synopses given in the following publications: Ketskhoveli, Kharadze, and Kutateladze (1964; 1969) and Ketskhoveli, Kharadze, and Gagnidze (1971-2011 vols. I–XVI). Species that not identified in field were collected and compared to the samples in the National Herbarium of Georgia of the Institute of Botany (TBI), Ilia State University, Georgia. Because multiple herbarium specimens were often collected from the same plant in different plots, we found 82 herbarium specimens taken from these 43 plants (herbarium specimens is available at the TBI). The botanical nomenclature primarily follows Gagnidze (2005) updated from other databases such as The Plant List 1.1, "Euro+Med" 2006 and "GBIF.Org" 2020 as well as the renewed nomenclatural list of the Flora of Georgia (Davlianidze et al. 2018) (Annex 1).

In total we sampled 81 plots in pastures and hay meadows belonging to nine settlements (Akhaltsikhe, Juta, Stepantsminda, Kanobi, Kobi, Pkhelshe, Sioni, Sno, and Tsdo). The mean distance between the villages and sampling sites was 900 m, and the plots were at least 15 m apart. There were eight to 10 plots per village. Vegetation cuttings were collected from the plots for measuring standing mass. To obtain an acceptably balanced data set, a stratified random sampling design was employed in which the slope aspect (north *versus* south), slope angle (mild - 10-25° *versus* steep 25-45°), and land use (pasture *versus* hay meadow) were used as strata. Digital Elevation Model (DEM) was used to obtain the basic data on environmental conditions for each plot. These data, except the altitude, included the Compound Topographic Index (CTI), eastness and northness, roughness of the terrain, slope inclination, and solar radiation. The following two land use category was also added as a variable: hay meadow (33 plots) *versus* pasture (48 plots).

1.2.3 Soil sampling

To measure the soil seed bank and nutrients, 10 subsamples (Fig. 1.3) of the upper soil layer at a depth of 0-5 cm were taken at random from each plot using a soil corer (Ø 3 cm). Soil samples were collected in 2014. A deeper, 10 to 15 cm soil sampling often was impossible owing to soil shallowness and the frequent presence of stones (Csontos 2007).

Figure 1.3: Soil sampling in the study area.



The ten randomly taken subsamples were mixed in the field into a combined sample, totalling in volume at 350 cm³, and brought in the laboratory. From this, 95-100 cm³ sample was used for chemical analysis and the rest was used for seed bank experiment. The samples intended for chemical analyses were dried, sieved with 5 mm mesh to separate stones and roots, and then the sieved soil, stones and roots were weighed separately. Next, the 5 mm sieved soil was sieved (2 mm mesh) and dried again for soil nutrient analyses. Soil pH was determined in H_2O solution with pH Meter p325, WTW. For determining total carbon (C_t) and total nitrogen (N_t) the Duma method with an EA1110 elemental analyzer of CE Instruments was used. Plant available phosphorus (P_{cal}), potassium (K_{cal}), and magnesium (Mg_{cal}) were assayed with calcium-acetate-lactate extraction method (Amelung et al. 2018). The chemical analyses were conducted in the Laboratory of Soil Science and Conservation of the University of Giessen.

1.2.4 Preparation of the soil seed bank samples

The soil samples intended for seed bank analyses were stored in a refrigerator at 3 °C until February 2016. The prolonged storage period was necessary to obtain the persistent seed bank. This procedure imitates wintering of the seeds, therefore my persistent seed bank consisted of species whose seeds survived two winters in the soil (one winter in the field, and a second 'winter' in the refrigerator in 2016). A similar method was used to study persistent seed bank in the Andes (Arroyo et al. 1999) and British Islands (Warr, Kent, and Thompson 1994).

Figure 1.4: Soil seed bank experiment in Linden-Leihgestern, close to Giessen (Hesse, Germany), (Photos by Giorgi Tedoradze)

The seed bank was examined with the seedling emergence method, in which the number of emerged seedlings is a measure of the germinable seed bank (Thompson, Bakker, and Bekker 1997). In spring 2016, soil samples were sieved (2 mm mesh-size), placed in styrofoam trays containing sterilised soil on the bottom, and spread evenly over the top of the sterilised soil as a layer of 2 cm thickness. For control, we used sterilised soil samples. The trays were covered with a fine net to prevent airborne seeds from contaminating the germination experiment, and placed outdoors at the experimental site in Linden-Leihgestern, close to Giessen (Hesse, Germany, N50°32'10.536" / E8°41'35.782, 178 m a.s.l.), for four months (Fig. 1.4). The annual mean temperature at this site is 9 °C, and annual precipitation is 600-700 mm per year (Umweltatlas Hessen, 2013; 30-year average).

The cold stratification outdoor continued till mid-December 2016, then the trays were moved indoors, in a heated greenhouse in which air temperature was maintained between 18-24 °C at day and between 12-18 °C at night. The trays received artificial light of more than 10,000 lx through 6:00 a.m. and 10:00 p.m. and were watered every third day to maintain sufficient soil moisture. The experimental trays were monitored regularly to identify and record the emerging seedlings. The seedlings that could not be safely identified were transplanted into small pots and continued their growth there till their flowering phase (Fig. 1.5). In this way we avoided ambiguities in plant species identification, although data collection from the germination experiment has been prolonged up to 12 months.

Seed density was calculated per m^2 for 0-5 cm deep soil layer. The volume of the soil sample was calculated by dividing the mass of the soil sample by 1.3 $g*cm^{-3}$ (mean soil density), while the mass of the stones was divided by 2.7 $g*cm^{-3}$ (mean stone density); their sum was taken as the total volume of the sampled soils. Since the volume of $1m^2$ plot at depth 0.05m=50 000$cm^{-3,}$ I calculeted the factor, by dividing 50,000 cm^{-3} by each sample volume and the resulting number (factor) was multiplied by the seedling number to obtain the germinable seed density.

Figure 1.5: Greenhouse. Seedlings transplantation into small pots, Giessen (Hesse, Germany), (Photos by Giorgi Tedoradze)

1.2.5 Statistical analyses

Three community matrices were constructed. The first one included the list of all species and their abundance in plots. The second matrix contained only species that emerged after the germination experiment and their abundances. The third matrix included plots and their environmental conditions. To reduce the number of environmental variables and reveal the patterns of species and their germinable seed bank distributions, the first two matrices were analysed together with the third matrix using an ordination method of non-metric multidimensional scaling (nMDS, Kruskal 1964). The plants species abundance data both for standing plant communities and seed bank were log-transformed. The nMDS was performed using Euclidean distances with 200 iterations and random starting settings (Clarke and Ainsworth 1993).

A two-step approach was used to analyse the patterns in species distribution across the plots. The first was a cluster analysis based on Ward's method (Ward 1963). At the next step, plant community types were identified through the procedure described by Dierschke (1994), which consist in modifying slightly the obtained clusters on the basis of phytosociological criteria (see appendices 3). Land use category determined for the study region in the field by Theissen (2011), together with these modified clusters or plant community types, were used as grouping variables in the nMDS ordination. The identified plant communities were also used in the indicator Species Analysis (ISA), commonly employed to identify indicator species in already known plant community types (Legendre and Legendre 2012).

The Mantel test was used to compare species compositions between the standing plant communities and their germinable soil seed bank (Mantel 1967). Statistical significance of the differences in environmental variables among plant community types was tested by Kruskal-Wallis rank sum test, followed by the Nemenyi's pairwise *post hoc* comparisons test that is based on the chi-squared approximation for independent samples.

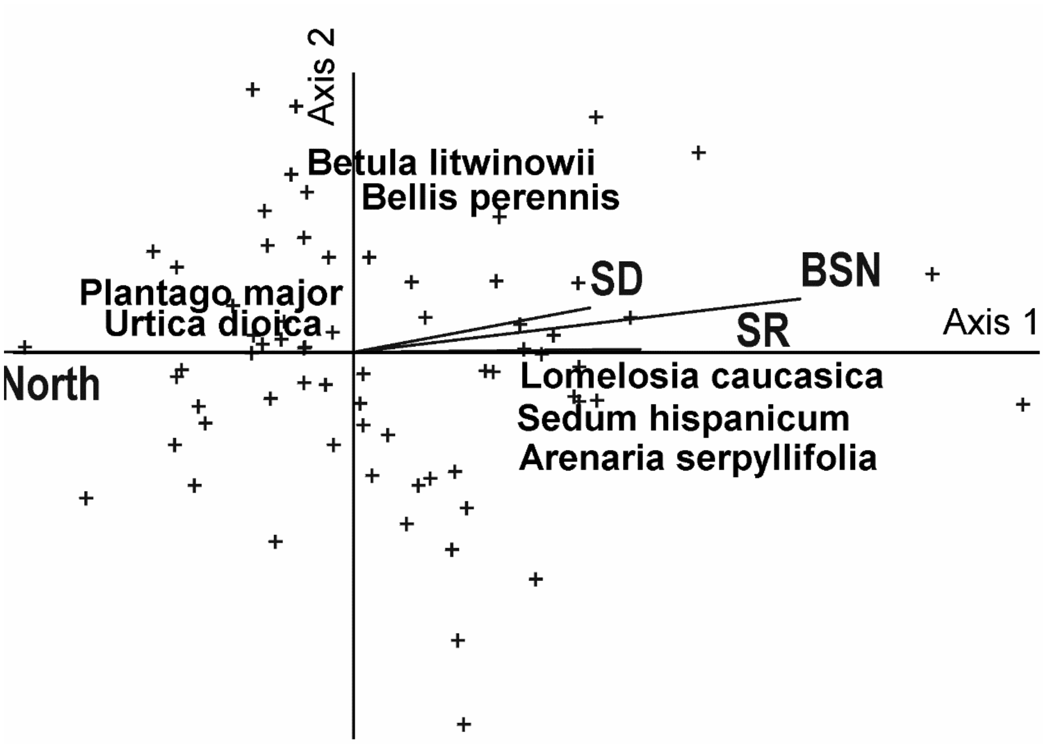
Ordination was performed using software PC-Ord Version 7 (McCune and Mefford 1999). For other statistical tests (Mantel, Kruskal-Wallis and Nemenyi) the package PMCMR in R programme Version 3.3.2 was used.

1.3 Results

1.3.1 Distribution of species germinable from the soil seed bank along ecological gradients

Germination experiment produced 70 vascular plant species (Appendix 1). These species germinated from soil samples of 74 plots, while soil samples from five plots did not produce any seedling, therefore these plots were discarded from the analyses. One sample produced only one species (*Trifolium spadiceum*), but in very large numbers and was discarded too. Finally, one more plot had to be discarded through the statistical analyses as a clear outlier. In total, out of the original 81 plots, 74 were included in downstream analyses.

Figure 1.6: Non-metric multidimensional scaling (NMDS) of the reweighted soil seed bank at the species level, with a stress level of 17.15. Indicator species are labelled. Arrows represent environmental gradients with correlations to the ordination of r ≥ 0.2 and r ≥ -0.4. BSN = belowground species number, North = northness, SD = seed density (m^{-2}), SR = solar radiation. Tedoradze et al. 2020.



The soil seed bank as represented by the community of germinated species was dominated by *Lomelosia caucasica* (mean seed density 438.8 ± 91 m^{-2}), *Potentilla crantzii* (mean seed density 394.5 ± 123 m^{-2}), *Agrostis vinealis* (mean seed density 290.4 ± 82 m^{-2}), *Plantago atrata* (mean seed density 204.4 ± 56 m^{-2}), *Arenaria serpyllifolia* (mean seed density 187.7 ± 48 m^{-2}), *Sedum hispanicum* (mean seed density 172.3 ± 52 m^{-2}), *Trifolium pratense* (mean seed density 118.2 ± 38 m^{-2}), *Urtica dioica* (mean seed density 90 ± 28 m^{-2}), and *Carex* sp. (mean seed density 133.4 ± 52 m^{-2}, see Appendix 2).

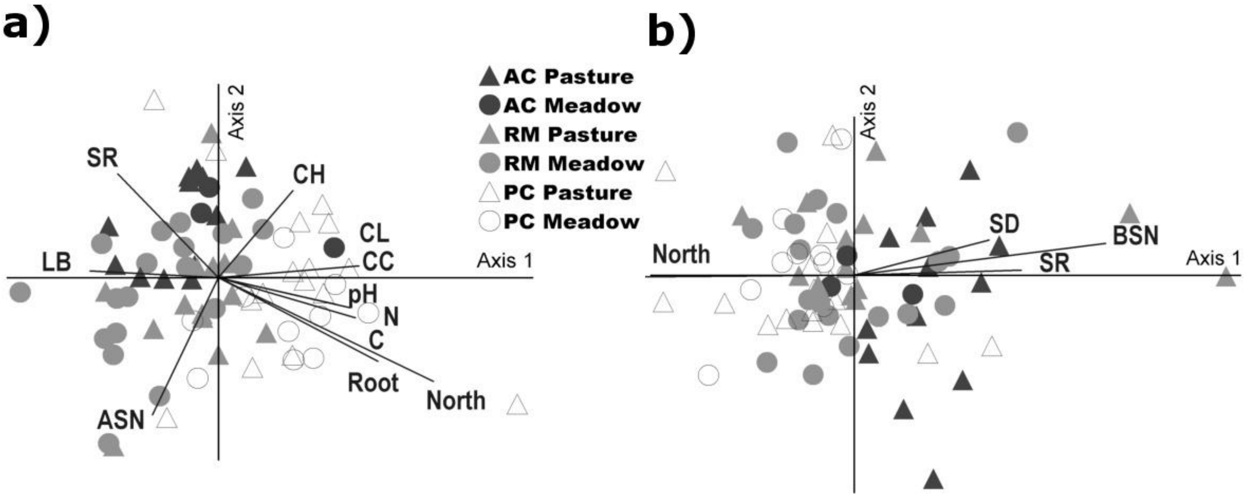
Cluster analysis with phytosociological modification grouped plant communities (both the standing plant community and their germinable seed composition) in three main types: *Polygonum carneum* community type (PC) on 26 plots, *Rhinanthus minor* community type (RM) on 33 plots and *Astragalus captiosus* community type (AC) on 15 plots (Table 1.1).

Then, plant community type was included as a group variable in the nMDS ordination. The ISA was also based on the distinction of these three plant community types (Tab. 1.1, Fig. 1.6).

The first three axes of the nMDS ordination explained 81% of the variation in my data set of seed bank species, with a stress level of 17.15 (Fig. 1.6). Axiswise, the first, second and third axes explained the 49%, 17%, and 15% of variation respectively.

The first nMDS axis coincided with the transition from *Polygonum carneum* community type (PC) (seed bank indicator species *Urtica dioica* and *Plantago major*) to AC grassland (seed bank indicator species *Lomelosia caucasica*, *Arenaria serpyllifolia*, *Sedum hispanicum*), which correlated with increasing north exposure of the PC community and an increasing richness of germinable species (belowground species number or BSN, r = 0.54), also with seed density (r = 0.4), and solar radiation (r = 0.44) (see also Fig. 1.7b).

Figure 1.7: Non-metric multidimensional scaling (NMDS) of a) the aboveground vegetation composition with a stress level of 18.7, explaining 72% of the initial distances, with axes one, two, and three explaining 31%, 23%, and 18%, respectively, and b) the reweighted soil seed bank with a stress level of 17.15, explaining 81% of the initial distances, with axes one, two, and three explaining 49%, 17%, and 15%, respectively. In both diagrams, arrows represent environmental gradients with correlations to the ordination of r ≥ 0.3 and r ≥ -0.3 and for b) r≥ 0.2 and r ≥ -0.4. The length of the arrow was fitted to the relationship between ordination and environmental gradient. ASN = aboveground species number, BSN = belowground species number (m^{-2}), C = carbon content in soil [%], CH = height of cryptogams [cm]; CL = cover of litter [%], CC = cover of cryptogams [%], LB = legume biomass [%], NDVI = the normalized difference vegetation index, N = nitrogen content in soil [%], Roots = root weight [%], pH = pH_{H2O}, SD = seed density (m^{-2}), North = northness, SR = solar radiation. Tedoradze et al. 2020.



The second nMDS axis correlated with the intermediate *Rhinanthus minor* community type (RM) characterised by the seed bank indicator species *Bellis perennis*, *Bromus variegatus* and *Betula litwinowii* (r= 0.3, 0.2, 0.4 respectively).

PC communities on the slopes of north aspect were characterised by a high soil nutrient content (N_{org} = 0.8%, C_{org} = 8.8%, phosphorus content = 19.1 mg*kg^{-1}), deeper soils (14.3 cm), and higher acidity (pH = 5.8) (Appendix 3). Conversely, the AC communities that largely occurred on the slopes of south aspect were exposed to increased solar radiation and grew on poor soils with considerably low levels of available nutrients (N_{org} = 0.4%, C_{org} = 3.5%, phosphorus content = 6.1 mg*kg^{-1}); these soils were notably shallower (7.9 cm), but less acid (pH = 6.49). Similar findings for soil pH have been reported for the alpine zone of Kazbegi district (Jolokhava et al. 2020)

Table 1.1: Indicator species analysis of the aboveground vegetation and the soil seed bank for the three grassland types: *Polygonum carneum* (PC), *Rhinanthus minor* (RM), and *Astragalus captiosus* (AC), with a significance level of $p < 0.05$ and an indicator value (IV) > 12. Tedoradze et al. 2020.

Indicator species	IV	Rel. frequency (%)			*p*
		PC n=26	RM n=33	AC n=15	
PC grassland					
Aboveground vegetation					
Polygonum carneum	54.5	62	3	7	0.0002
Betonica macrantha	46.7	54	12	0	0.0004
Cyanus cheiranthifolius	45.8	65	24	7	0.0006
Pimpinella rhodantha	42.6	62	18	7	0.0002
Ranunculus oreophilus	41.2	81	45	27	0.0042
Carex humilis	39.7	54	0	20	0.0008
Vicia alpestris	39	62	30	13	0.0028
Cirsium obvallatum	37.1	65	21	40	0.0066
Geranium ibericum	29	38	15	0	0.0088
Calamagrostis arundinacea	27.5	31	6	0	0.0046

Cruciata glabra	25.7	42	21	13	0.041
Gymnadenia conopsea	18.3	27	6	7	0.0492
Gentiana septemfida	17.2	23	6	7	0.0412
Daphne glomerata	15.4	15	0	0	0.0328
Soil seed bank					
Urtica dioica	20	31	12	7	0.0394
Plantago major	11.5	12	0	0	0.0498
RM grassland					
Aboveground vegetation					
Trifolium alpestre	45.3	35	79	27	0.0006
Rhinanthus minor	41.5	77	82	20	0.008
Phleum phleoides	41.2	54	91	67	0.0072
Anthyllis variegata	39.9	38	76	47	0.0094
Polygala anatolica	36.1	12	48	13	0.0028
Galium verum	29.6	19	58	33	0.0384
Seseli transcaucasicum	27.4	8	36	7	0.0098
Gentianella caucasea	23.2	12	30	0	0.022
Echium rubrum	17.5	4	21	0	0.0486
Soil seed bank					
Bellis perennis	18.5	8	24	0	0.0368
Bromus variegatus	15.3	4	18	0	0.044
Betula litwinowii	15.2	0	15	0	0.0364
AC grassland					
Aboveground vegetation					
Astragalus captiosus	95.1	4	9	100	0.0002
Dianthus cretaceus	63.3	8	12	73	0.0002
Sedum acre	46.7	0	0	47	0.0002
Sempervivum pumilum	43.6	0	6	47	0.0002
Thymus collinus	42.1	46	39	80	0.0026
Poa alpina	41.8	8	0	47	0.0002
Campanula collina	39.8	69	61	93	0.0194

Festuca ovina	38.9	35	48	80	0.0082
Euphrasia caucasica	36.2	0	6	40	0.0004
Silene ruprechtii	33.7	42	33	73	0.0174
Achillea millefolium	28.5	12	18	47	0.0092
Erigeron caucasicus	23.9	0	3	27	0.0032
Artemisia vulgaris	23.3	0	6	27	0.004
Echium vulgare	20	0	0	20	0.0064
Alyssum murale	20	0	0	20	0.007
Asperula molluginoides	20	0	0	20	0.0074
Onosma caucasica	13.3	0	0	13	0.0354
Scutellaria oreophila	13.3	0	0	13	0.037
Lolium rigidum	13.3	0	0	13	0.042
Securigera varia	12.3	0	3	13	0.0238
Sempervivum caucasicum	12	0	3	13	0.0244
Soil seed bank					
Sedum hispanicum	47.8	4	12	60	0.0002
Arenaria serpyllifolia	40	8	21	60	0.0002
Lomelosia caucasica	39.5	15	45	73	0.0018
Medicago lupulina	28.3	4	3	33	0.001
Gnaphalium supinum	20	0	0	20	0.0058
Verbascum sp.	16.7	4	0	20	0.0236
Myosotis alpestris	13.3	0	0	13	0.0386
Juncus tenuis	13.3	0	0	13	0.0388

1.3.2 Restoration potential of the persistent soil seed bank

The analysed 74 relevés contained 269 vascular plant species found in pasture and hay meadow communities, while the germination experiment produced much less, only 70 species. These two sets of plant species shared 47 species, i.e., only 18% of species from standing plant communities were represented in their germinable seed bank. The other 23 species from the soil seed bank were not found in pastures and hay meadows. In sum, the relevés were dominated by *Bromus variegatus* (in 96% of relevés), *Medicago glomerata* (77%), *Phleum phleoides* (73%), *Agrostis vinealis* (72%), *Campanula collina* (70%), *Lotus corniculatus* (70%), *Rhinanthus minor* (68%) and *Trifolium ambiguum* (66%). Conversely, the germinable seed bank was dominated by *Lomelosia caucasica* (from 43% of plots), *Potentilla crantzii* (30%), *Agrostis vinealis* (29%), *Arenaria serpyllifolia* (26%), *Plantago atrata* (24%) and *Sedum hispanicum* (20%) demonstrating that the compositions of the most frequent species in two datasets were very dissimilar. The ISA showed that there was not a single shared indicator species between standing plant communities and their seed bank representatives. The ISA also showed that the AC plant community type possessed more indicator species than RM and PC (Tab. 1.1).

The plant community types also differed widely in species richness: the relevés from AC contained less species (ASN = 30.9) than those from RM (ASN = 34.9) and PC (ASN = 34.2). Nonetheless, plant community types did not differ notably in the richness of germinable seed bank species: the values of the BSN equalled to five, five and four for AC, RM and PC, respectively.

The mean seed density was found to be the highest in the AC plant community type (4,386 m^{-2}) followed by PC (3,584 m^{-2}) and RM (3,916 m^{-2}). The AC plant community also showed the highest shared species rate (25%) followed by the RM (24%) and the PC (21%) plant community types.

The differences in species composition between the standing plant communities and their germinable soil seed bank can be easily discerned on ordination plots (Fig. 1.7). The Mantel test also found only a weak correlation ($r = 0.21$ by the standardised Mantel test) between the two data sets. At the same time, the first axis of the nMDS ordination correlated with the northness ($r = 0.54$), root mass ($r = 0.46$) and litter cover ($r = 0.44$) and thus clearly differentiated the plant community types along the north-to-south gradient with increasing root and litter mass. Specifically, AC tended to the south aspect whilst RM and PC tended to the north aspect. The second axis of the nMDS ordination correlated negatively with species richness of standing plant communities ($r = -0.44$) and soil C/N ratio ($r = -0.37$), but positively with solar radiation ($r = 0.38$); the AC plant community type separated again from

RM and PC along the gradients of the solar radiation and soil organic content, which coincided with decreasing species richness.

1.4 Discussion

1.4.1 Topography and soil seed banks

Slope aspect and solar radiation, which are the variables that are determined by topography, can be linked with species composition (Peco, Ortega, and Levassor 1998). My results show that species richness and seed density in the soils varied greatly between the slopes of north versus south aspects. This is a clear gradient from the cool and moist (north aspect) to warm and dry (south aspect) plant life conditions. Warmer slopes generally enjoy more abundant seed rain resulting in a higher density of seeds in soils (Bertiller 1992). Theoretically, topography can have effects on seed density by other mechanisms too, such as seeds brought by surface run-off. However, my results do not show any statistically significant relation of seed density with the altitude, curvature, or topographical wetness (Caballero et al. 2003; Havrdová, Douda, and Doudová 2015).

The difference in plant community structure between two slope aspects could also be accentuated by grazing impacts (Bekker et al. 1997), since the AC plant community type contains abundant species characteristic to poor pastures (*Lomelosia caucasica*, *Arenaria serpyllifolia*). The relatively rich and dense soil seed bank of the AC communities could help adapt to the overgrazing disturbance, yet this might not always repair the damaged plant cover as indicated by the relatively high occurrence of shallow and bare soils, especially on steeper slopes (Appendix 3). Therefore, my results suggest that the steep slopes of the south aspect run an increased risk of soil erosion.

The PC plant community type, contrary to AC, are found mostly on the slopes of the north aspect. Remarkably, the soils beneath PC contain abundant seeds of ruderal species (for example *Plantago major* and *Urtica dioica*), which can persist in the soils over a long time (Christoffoleti and Caetano 1998; Bossuyt and Hermy 2003). The soils under the PC communities are relatively more acid, deep, and rich in available nutrients. These characteristics and the proximity of cattle paths can explain the abundance of ruderal species in the soil seed bank (Appendix 3). At the same time, the relative scarcity or the absence of seeds of standing species in these soils might indicate a reduced ability of post-disturbance regeneration of this type of plant communities.

The RM plant community type occupies the middle (intermediate) part of the north-to-south gradient of environmental conditions where soil seed banks show a high abundance of *Bellis perennis* and *Betula litwinowii.* The seeds of these two species are dispersed by wind and run-off water, and often germinate and emerge within the vegetation gaps (Schmid and Harper 1985; Gibson 1996). As Bossuyt and Hermy (2003) showed, *Betula* can form a persistent seed bank, a rare phenomenon among the tree taxa whose soil seed banks were examined. These authors also report that seed density in the soils increased with increasing disturbance. These results were confirmed by the studies conducted in the mountains of Belgium (Jacquemyn et al. 2011). High seed density of *Betula* was also found in alpine eutrophic fens of the North Caucasus (Onipchenko 2004). These fens might function as a seed trap or as a sink of the seeds of *Betula* brought by winds and run-off water.

1.4.2 Potential of the soil seed bank to re-vegetate the disturbed sites

The similarity of species composition between standing communities and their soil seed bank can be 50-60% (Bakker and Berendse 1999), however, along a disturbance gradient the mean density of seeds in the soil can vary (Ma, Zhou, and Du 2010). Therefore, my results show that on the relatively steep slopes of Khevi the mean density of seeds in soils was not high (4,249 seeds*m^{-2}), and the percent proportion of the species that standing communities shared with soil seed banks was as low as 18%. The mean seed density of seeds can be 18,108 seeds*m^{-2} as reported by a study on a managed grassland in the Czech Republic, where 27% of standing plant species were found also in its germinable seed bank (Handlová and Münzbergová 2006). In the grasslands of the Central European mountainous region, the mean seed density was found to be 10,367 seeds*m^{-2}, while 56% of the species were shared between the soil seed bank and the standing plant communities (Wellstein, Otte, and Waldhardt 2007). Communities with high levels of disturbance show the values of seed density and shared species percentage that are comparable with the values found in my study: in green rooftops the soil seed density was 4,814 seeds*m^{-2}, with 34% of species shared (Vanstockem et al. 2018), and in semiarid grasslands the seed density was found to be 3,749 seeds*m^{-2}, with 32-51% species shared (Kinucan and Smeins 1992). Therefore, the values of seed density and shared species percentage rather indicate moderate to high levels of disturbance in the pastures and hay meadows of Khevi, characteristic of high mountain environments (Christoffoleti and Caetano 1998; Bossuyt and Hermy 2003). Most probably, many of the species of standing communities that did not emerge in the germination experiment mostly contributed to transient seed bank (Lopez-Marino et al. 2000). The dissimilarities between standing and germinated species could also owe to the fact that, depending on the type and strength of disturbance, standing plant community and its seed bank can be affected in different ways (Hölzel and Otte 2004). However, there were 23 species not found in standing plant communities; in other words the soil seed bank of a plant community can contribute to the persistence of species from other communities too and this effect can be important for conservation at larger, regional scale. Out of 70 species that emerged in germination experiment eight appeared to be endemic to the Caucasus ecoregion, while another five species (they are identified only to the genus level) had an unknown red list status (Gagnidze 2005; Solomon, Schatz, and Shulkina 2013). This emphasises the general importance of seed banks for restoration at a large spatial scale. As for the studied plant communities, their restoration to the original state after a considerable disturbance seems not to be easy since the similarity in community structure between the standing vegetation and germinable seed bank beneath it is low. Besides, 10 percent of soil samples did not produce any seedlings at all indicating the scarcity of persistent seeds in the soils under some of my study plots. Restoration efforts can be further hindered by high mortality of seedlings, typical of alpine environments (Schlag and Erschbamer 2000; Erschbamer, Kneringer, and Schlag 2001). We conclude that the prevention of disturbances appears to be the most effective measure against soil erosion and degradation of subalpine pastures and hay meadows (Miller and Cummins 2003). Nonetheless, the species found in the persistent soil seed bank still might have a certain ability to establish an erosion-preventive vegetation cover, yet this potential requires further investigation.

Conclusions

We found evidence that soil seed banks in the high mountain pastures and hay meadows of Khevi have a limited potential for restoring damaged and disturbed vegetation to its original state. This evidence is based on the considerable mismatch between the standing plant communities and their persistent soil seed bank, particularly on the slopes of the north aspect. If a given plant species is lost after a strong disturbance, this species might not reappear from the soil seed bank. Prevention of disturbances and damage by careful management, therefore, is highly recommended. At present, such management can be based on the moderate grazing and regular mowing practice characteristic of the traditional, low-intensity subsistence agriculture. However, studies shall continue to test innovative restoration strategies. Given that the persistent soil seed bank from my study showed a considerable admixture of species that were not members of standing plant communities, testing the direct diaspore transfer methods might be promising in the high mountains of the central Caucasus.

Chapter 2. Floristic composition of the pastures and hay meadows on Khevi's steep slopes

2.1 Literature review

The species as the major unit of classification is the basic concept of plant systematics and taxonomy, and play a central role in the related disciplines such as plant community ecology, plant geography, plant phylogenetics, description and analysis of vegetation, conservation, and restoration. Therefore, it is crucial to have a well-developed nomenclature in an authoritative and internationally recognised list of species (Korovina 1986; Rao 2004).

Flora represents a comprehensive list of all species recorded in any geographically defined area (country, region, island, river valley) (Tolmachev 1974). Floristic analyses are comprised of quantitative descriptions of the relations among major taxa (families, genera, species), and also examinations of the geographic origin of species included. Floristic analyses, therefore, also have to consider climatic characters and the history of terrestrial systems, as well as current human impacts such as land use and climate change (Wulff 1943; Tolmachev 1974; Mirkin, Naumova, and Solomeshch 2001).

The knowledge of plant species current distributions can be understood as the geographical structure of a given flora, being one of the main aims of floristic studies. Such knowledge can be gained using an approach that in the Soviet Union termed as 'the arealogical method' with 'areal' as the main unit that in fact means the area of distribution of a given species. The geographic structure is based on the concept of geographical element, which R. Gagnidze and M. Ivanishvili consider to be a part of a floristic element and is established by the arealogical method (Gagnidze and Ivanishvili 1975a).

The geographical element refers to the set of the representative taxa of a given phytochorion, the major area of which is covered by these species where they supposedly find optimal life conditions (Wulff 1943; Portenier 1993). Chorotype, area type, and chorological category are often used as synonyms for a geographical element (Passalacqua 2015).

Therefore, a geographical element denotes the group of species that have similar distribution. Identifying a geographical element helps generalise and systematise the existing knowledge on the geographical distribution of a species, and also facilitates the storage and synthesis of the required data (Portenier 1993; Pedrotti 2013). The analysis of area types can provide additional knowledge on the ecology and evolutionary history of species, and aid also the identification of phytochorions and plant geographical regions at higher scales (Portenier 2000; Mirkin, Naumova, and Solomeshch 2001). The species that typically occupy the Arcto-alpine environments *versus* the species typical for Central Asia clearly differ ecologically. Yet, there can be also plants of different ecological types within each of the large geographical areas more narrowly adapted to local environmental conditions. These can vary, for example, in soil types, water and temperature relations. Therefore, even an exact knowledge of geographical distribution provides only an approximate knowledge of the ecology of a given species, and might not be sufficiently accurate. This is because species within the same area may be ecologically different, and conversely, species with different areas may be ecologically similar (Mirkin and Naumova 2012). Nonetheless, identifying the geographical element enables exact mapping of species distribution, which is crucial for conservation purposes because an accurate knowledge of the distribution of species of high conservation value is indispensable for planning, establishing, and monitoring of protected areas. At the same time, distribution maps are essential to creating and updating "red lists" both at national and regional levels (Pedrotti 2013).

Distribution areas can vary in size being either continuous or disjunct (Mirkin and Naumova 2012; Pedrotti 2013). Furthermore, various systems were suggested to organise the knowledge of plant species distributions into a comprehensible and operable system. In the Caucasus, the first attempt to construct such a system was undertaken by Grossheim (1936). This system is based on the principle of geographical zonation, which proved to be difficult to use due to the lack of standartization (Portenier 1993), and many authors attempted to modify this system. The consequence is that different authors consider the same species to represent different geographical elements. The matter becomes even more complicated when different authors use different floristic systems and employ different species concepts. In sum, the comparison of the results of floristic analysis from different regions of the Caucasus and neighbouring regions often becomes impossible (Portenier 1993). It should be noted, though, that Caucasian botanists often use common approaches when defining plant geographical zones at large scale. Important differences emerge at the level of botanical provinces and below, where there are discrepancies in identifying districts, and the descriptions of districts often lack important details (Portenier 1993).

It is clear from the above that there is no common approach and understanding among plant geographers in the classification of geographical elements in the Caucasus. The flora, as well as the geography, of this region are uniquely complex and rich, and defining its geographical elements based on the concept of phytochorion and plant geographical area types might produce acceptably comparable results. This is exactly the approach initially formulated by Josias Braun-Blanquet (1919; 1923), Alexander Eig (1931), Revaz Gagindze (1974), Marine Ivanishvili (1973) and others (Braun-Blanquet 1919; 1923; Eig 1931; Ivanishvili 1973; Gagnidze and Ivanishvili 1975a; Yurtsev and Kamelin 1991; Portenier 2000), which in the Soviet references is often called ‘a regional principle’ or ‘floristic approach’ (Gagnidze and Ivanishvili 1975a). Following these authors, the regional principle might be more ‘flexible’ and effective in the Caucasus with its complex terrain.

The question of which plant geographical area a species belongs to should be resolved on the basis of current distribution area of this species (Portenier 1993; White 1993), taking also into account its core distribution (Wulff 1943). A geographical element can be considered a species that falls within the boundaries of a certain chorion. Some species are found in two or more provinces and are referred to as linking species. These linking species can be identified by their occurrence linked to one or more provinces (Portenier 1993; White 1993; Dowsett-Lemaire, and Müller 2021).

Depending on the researcher's goals and the aims of floristic analysis, the description of area types can be very detailed or general, and determined by the spatial scale at which the geographical element is defined. For example, the geographical element of the Apennines belongs to the Euro-Siberian region at the regional scale, to the boreal level at the sub-regional scale, and to the Holarctic kingdom at the global level (Gagnidze and Ivanishvili 1975a; Passalacqua 2015). At any rate, however, defining the geographical element based on plant geographical areas will require use of one of the existing schemes of the division of a given territory into floristic regions, and these schemes are more than one. One of them is the well-known and widely accepted system of Armen Takhtajan (Takhtajan 1978). A similar system was produced by Salvador Rivas-Martinez (2004), who despite some differences, also considers the Caucasus, and Georgia in particular, as part of the Euro-Siberian (corresponding to circumboreal in the scheme of Takhtajan) and the Irano-Turanian regions (Rivas-Martinez and Rivas-Saenz 2004)

Revaz Gagnidze placed the main part of the Caucasus into the sub-Mediterranean region (Gagnidze and Ivanishvili 1975b), which coincides with the Macaronesia-Mediterranean region by Hermann Meusel and Eckehart Jäger (Meusel, Jager, and Weinert 1965). In his later works, Gagnidze lifted the Ancient Mediterranean region to a higher rank of kingdom, and this is one of the main features distinguishing his system from other classifications (Gagnidze 1996, 2004; Gagnidze and Davitadze 2000).

The flora of the Caucasus can be linked to the Mediterranean as well as the Irano-Turanian and Boreal floras. Clearly, the relative contribution from these floras will vary through the complex gradients of Georgia's environment. Since the aim of the present study was to establish general connections of the flora of Khevi's subalpine pastures and hay meadows with other regional floras, we addressed the following questions: i) what is the floristic composition of the managed plant communities on the slopes of Khevi? and ii) which floristic centres contribute mostly to their species composition?

2.2 Materials and Methods

A floristic analysis approach was used to determine the types of species areas based on identified geographical elements. This method largely relies on the hierarchy of botanical-geographical units of the country (Portenier 2000).

The list of plants obtained from the sampling of pastures and hay meadows on the slopes of various steepness in the subalpine zone of Khevi was used in floristic analyses. There were 81 plots sampled following the usual phytosociological protocol in 2014-2017 (see the previous chapter). All species within the plots were recorded and their sum was considered to represent the floristic composition of high mountain pastures and hay meadows of Khevi.

Species nomenclature is in accordance with the checklist of vascular plant species of Georgia (Gagnidze 2005). The list was updated from international plant databases (“IPNI” 2021; “GBIF.Org” 2020; “Euro+Med” 2006; “PESI” 2021; “The Plant List” 2013), the second edition of the list of vascular plant species of Georgia (Davlianidze et al. 2018), and the checklist of the Khevi’s flora (Sakhokia and Khutsishvili 1975). see Annex 1. I collected data on the geographical range of each species using the following floras: Flora of Georgia, Flora of Turkey, Flora of USSR, Flora of Armenia, Flora of Europe, Caucasian flora conspectus (Komarov 1934-1960; Takhtajan 1954-2009, 2003-2012; Tutin et al. 1964-1993; Davis 1965-2001; Ketskhoveli, Kharadze, and Gagnidze 1971-2011). Additionally, we crosschecked databases (“GBIF.org” 2020; “Euro+Med” 2006; “World Flora Online” 2021). If the area of distribution of a given species, or at least its center of distribution, was confined to the boundaries of a chorion, it was considered to be a geographical element of this chorion. Although quite often a species’ distribution was not confined to any one chorion, but instead was found spread across two or more chorions. In such cases the species was considered to be a linking species. A similar type of linking species whose distribution area did not extend beyond a higher-ranked phytochorion was included in this higher phytochorion (Passalacqua 2015). Since in the Caucasus the high-rank botanical-geographical units are established using generally the same principles, these areas are relatively consistent from author to author (Portenier 1993). The same cannot be said about the phytochoria of lower ranks (provinces, districts), where inconsistencies are conspicuous owing to the lack of shared principles for delineating these areas (Yurtsev and Kamelin 1991). Therefore, in this study, only the chorions of provinces and above are used.

2.3 Results

2.3.1 Taxonomic structure

Khevi’s flora is comprised of 1347 vascular plant species (Sakhokia and Khutsishvili 1975; Gagnidze 2005). Out of these species, 269 were found in 81 sampling plots, which constitutes 20 % of Khevi's flora. The recorded species belonged to 143 genera and 42 families (Table 2.1).

Table 2.1: General taxonomic structure of the recorded species in subalpine pasture and hay meadow communities in Khevi.

Higher Taxa	Families		Genera		Species	
	Number	%	Number	%	Number	%
Angiospermae	42	100	143	100	269	100
Among these:						
Dicotyledonae	34	81	118	82.5	222	82.5
Monocotyledonae	8	19	25	17.5	47	17.5

The largest 10 families included 92 genera (64.5 %). All in all, the composition of these families and their size (the number of genera in them) is very similar to the general taxonomic structure of Khevi's flora (Sakhokia and Khutsishvili 1975) (Table 2.2).

Table 2.2: Number of genera in the largest 10 families in the vascular flora of subalpine pasture and hay meadow communities in Khevi.

N	Family	Number of Genera	%
1	*Asteraceae*	21	14.7
2	*Poaceae*	15	10.5
3	*Fabaceae*	11	7.7
4	*Apiaceae*	10	7
5	*Lamiaceae*	9	6.3
6	*Brassicaceae*	6	4.2
7	*Caryophyllaceae*	5	3.5
8	*Orobanchaceae*	5	3.5
9	*Ranunculaceae*	5	3.5
10	*Rosaceae*	5	3.5

Total	92	64.4

Measuring family size by the number of species produced the same 10 families with one exception: *Campanulaceae* replaced *Ranunculaceae*. These families included 173 (64.3 %) species (Table 2.3). The top three families remained the same through all analyses, but the order of families was variable.

Table 2.3: Number of species in the largest 10 families in the vascular flora of subalpine pasture and hay meadow communities in Khevi.

N	Family	Number of Species	%
1	*Asteraceae*	39	14.7
2	*Poaceae*	*31*	11.7
3	*Fabaceae*	*23*	8.7
4	*Caryophyllaceae*	*14*	5.3
5	*Rosaceae*	*14*	5.3
6	*Apiaceae*	*12*	4.5
7	*Orobanchaceae*	*12*	4.5
8	*Lamiaceae*	*12*	4.2
9	*Campanulaceae*	*9*	3
10	*Brassicaceae*	*7*	2.6
Total		173	64.5

The largest genus as measured by the number of species is *Trifolium*. Twenty-eight genera are represented by three or more species, 40 genera by two species each, while more then half of genera contain a single species (Table 2.4).

Table 2.4: Number of species in the genera of the vascular flora in subalpine pasture and hay meadow communities in Khevi.

N	Genera	Number of Species	N	Genera	Number of Species
1	*Trifolium*	10	17	*Gentiana*	3
2	*Campanula*	8	18	*Geranium*	3

3	*Alchemilla*	7	19	*Hypericum*	3
4	*Silene*	6	20	*Luzula*	3
5	*Festuca*	6	21	*Veronica*	3
6	*Cirsium*	5	22	*Koeleria*	3
7	*Pedicularis*	5	23	*Poa*	3
8	*Carex*	4	24	*Thalictrum*	3
9	*Euphorbia*	4	25	*Potentilla*	3
10	*Plantago*	4	26	*Galium*	3
11	*Phleum*	4	27	*Salvia*	3
12	*Erigeron*	3	28	*Polygonum*	3
13	*Tanacetum*	3		**In The rest**	
14	*Taraxacum*	3			
15	*Dianthus*	3		40 genera	2-2
16	*Sedum*	3		75 genera	1-1

Out of 269 species in the list, 64 were endemic (23.8%), among them 56 –NE, five – LC, two - NT, one - DD categories (Solomon, Schatz, and Shulkina 2013).

The most frequent among the life forms were hemicryptophytes with 188 species (69.9%), chamephytes with 25 species (9.3%), therophytes with 21 species (7.8%), geophytes with 19 species (7.1%), hemiparasites of vascular plants with eight species (2.9) and phanerophytes with six species (2.2%), and lianas with two species (0.7%).

2.3.2 Geographical structure

We recorded 269 species of vascular plants, and these were grouped into 18 geographical range types or chorotypes (Table 2.5).

The proximity of the study area to the Western and Eastern Caucasus, the connections with Central Dagestan, and the colonisation of the Caucasus by the Boreal and South-West Asian flora might explain the high percentage of linking species in the flora of Khevi's (Sakhokia and Khutsishvili 1975; Kharadze 1966a; 1977; Grossheim 1936). In our data set, the Caucaso-Southwest Asian species were most prominent among the linking species with 26 species (9.6% of the flora of Khevis subalpine pastures and hay meadows). This was followed by 16 species (5.9%) from the European-Mediterranean region, 14 species (5.2%) from the Caucaso-Anatolian, six species (2.2%) from European-South-west Asian, and four species (1.5%) from the Hyrcanian-Euxinian region. The remaining chorotypes of this group did not exceed 1% each.

Table 2.5: Chorotypes and their proportions in the vascular flora of subalpine pasture and hay meadow communities in Khevi.

Geographical range types (chorotypes)	Number of Species	%	Number of Species	%
Widespread Species				
Palearctic	59	21.9	86	31.9
Holarctic	25	9.3		
Cosmopolitan	2	0.7		
Linking Species				
Caucaso-SW Asian	26	9.7	82	30.5
Euro-Mediterranean	16	5.9		
Caucaso-Anatolian	14	5.2		
Euro-Mediterranean-SW Asian	11	4.1		
Euro-SW Asian	6	2.2		
Hyrcano-Euxinian	4	1.5		
Mediterranean-SW Asian-Eurasian steppe	2	0.7		
Euro-Ancient Mediterranean	1	0.4		
Caucaso-East Mediterranean	1	0.4		
SW Asian-Caucasian-Eurasian steppe	1	0.4		
Ancient Mediterranean Species				
Mediterranean-SW Asian	8	2.9	9	3.3
Mediterranean-SW Asian-Turanian	1	0.4		
Boreal Species				
Caucasian	73	27.1	92	34.2
Caucaso-Euxinian	10	3.7		
Euro-Siberian	9	3.3		

2.4 Discussion

2.4.1 Taxonomic structure

The vascular flora of Khevi's pasture and hay meadow communities was represented by only angiosperms, where the number of dicotyledonous species exceeded that of monocotyledonous fourfold. My results clearly show the disproportional distribution of species and genera among families, which is characteristic of the vegetation developed under harsh environmental conditions (Tables 2.2 and 2.3). Species diversity within the genera was visibly low (Table 2.4) as 75 genera (52.4%) had a single species and 40 genera (27.9%) contained only two species; in other words, 80.4% of genera were represented by one or two species. Therefore, the high species richness in the floristic composition was strongly influenced by the relatively high number of small-sized genera.

The species composition of the top 10 largest families gives a good idea of the contribution of different floristic centres to the flora of Khevi's pasture and hay meadow communities.

The largest family in the flora of Khevi's subalpine pastures and hay meadows was *Asteraceae* and *Poaceae* - the families of a very wide distribution over various regions. Conversely, other large families showed more distinct distribution and could indicate connection to a specific floristic region. For instance, *Fabaceae*, *Caryophyllaceae*, *Brassicaceae* and *Apiaceae*, which were among the top largest families in Khevi, are associated with Mediterranean floras (Tolmachev 1986). In contrast, *Ranunculaceae* and *Rosaceae*, also among the largest families in Khevi, are characteristic of, and indicate a link to, the Boreal floras (Tolmachev 1986). These are two large floristic regions with which Khevi's flora can be connected.

Being in the top ten families *Campanulaceae* and *Orobanchaceae* (the latter also includes genera *Pedicularis*, *Rhinanthus*, and *Rhynchocorys*), indicates the specificity of the high mountain flora and its influence on Khevi's pastures and hay meadows.

The composition of the 10 largest families from Khevi's subalpine pastures and hay meadows generally mimicked the taxonomic structure of the flora of all of Khevi. The only difference was *Campanulaceae*, which replaced *Cyperaceae*, as the tenth largest family in the entire flora (Sakhokia and Khutsishvili 1975). The reduced prominence of *Cyperaceae* in my data can be explained by the fact that the study area was located on relatively steep slopes where the moist meadows with abundant *Cyperaceae* were rarely represented.

The contribution of boreal and Mediterranean flora is even more evident in the analysis of the number of species in the genus. In this case, the representatives of the boreal flora are *Alchemilla, Carex,* and *Plantago*. Further, the Mediterranean connections are indicated by *Trifolium, Silene,* and *Euphorbia*. In addition, the flora of the high mountain Caucasus is characterized by presence of diverse species of *Campanula* and *Pedicularis*.

Out of the 64 endemic species, 51 were confined to the Caucasus Ecoregion (Solomon, Schatz, and Shulkina 2013). The distribution of the remaining endemics went beyond the borders of the Ecoregion: ten of them were Caucaso-SW Asian (e.g. *Sedum spurium*, *Euphorbia iberica*, *Pedicularis wilhelmsiana*) and Caucaso-Anatolian (e.g. *Cirsium caucasicum, Draba hispida, Vicia alpestris*) with five species in eachtype, two were Caucasian (with irradiation) (*Cirsium obvallatum* and *Pulsatilla violacea*), and one was Euro-Mediterranean-SW Asian (*Draba siliquosa*).

2.4.2 Geographical structure

The species showed the following three prominent patterns of geographical distribution (chorotypes): boreal (34.2%), linking (30.5%) and 'widespread' (31.9%). The proportion of the Ancient Mediterranean chorotype was minor (3.3%). At the finer spatial scale, the Caucasian, Palearctic, Holarctic and Caucaso-Southwest Asian chorotypes had a total share of 68% of the species, whilst European-Ancient Mediterranean, Caucaso-Eastern Mediterranean, Southwest Asian-Caucasian-Eurasian-steppe, and Mediterranean Southwest Asian-Turanian chorotypes appeared to be very minor, with their total share not exceeding 1.5%.

The prominence of Palearctic species, represented by 59 (21.9%) species, was large. At the finer spatial scale, this included 50 Palearctic species, six Western Palearctic species, and three Palearctic (conditional) species. Holarctic species accounted for 9.3% (25 species). The number of cosmopolitan species was negligible with two only species (0.7%).

The 97.7% of the widely distributed species appeared to be Palearctic and Holarctic. The high proportion of such species in the flora of Khevi's subalpine plant communities was in fact as expected. Indeed, the species were recorded on mainly mesic meadows, while, the Central Great Caucasus is a part of the Holarctic kingdom (Takhtajan 1978; 1986).

According to Ana Kharadze (Kharadze 1966b), Khevi's flora belongs to the sub-province of high mountain Caucasus, which is part of the province of the Great Caucasus.

The high mountain flora of the Caucasus mainly consists of Arcto-alpine elements, which colonised Khevi as early as in Pleistocene (Nakhutsrishvili 2003). Nakhutsrishvili (2003) also notes the opinion of Fedorov (1952) and Kharadze (1960) that the flora of the high mountain Caucasus is mostly autochthonous and evolved in the Tertiary and Quaternary. Finally, Grossheim (1936) in his analysis of endemics remarked that the central Caucasus was colonised by both Boreal and Western Asian elements (Fedorov 1952; Kharadze 1960; Nakhutsrishvili 2003).

In the Ancient Mediterranean group, Mediterranean-Southwest Asian is represented by eight (2.9%) species, and Mediterranean-Southwest Asian-Turanian by a single species. The Mediterranean chorotype has a much higher percentage in the scrub vegetation of the Khevi, which is as expected since the vegetation in the study area is mesophilic and developed in a climate notably different from the Mediterranean (Ivanishvili 1973). However, if we look at the linking group, it becomes clear that all the species in this group are related to the Mediterranean region. Consequently, the relation to the Mediterranean flora is not as weak as it may seem at first glance, but the contribution of the Boreal flora is the largest and most easily observed.

Among the Boreal species, the most frequent was the Caucasian chorotype with 73 (27.1%) species, followed by 10 (3.8%) Caucaso-Euxinian species, and 9 (3.3%) Euro-Siberian species. The high proportion of the Caucasian chorotype is an indication of the autochthonous origins of a flora (Kharadze 1966). There were 51 endemics among the Caucasian chorotypes, 42 of them of status NE, five of LC, two of NT, and two of DD. The high proportion of the Caucasian chorotype is natural and conforms to the results of analysis of the scrub-like vegetation on the northern slopes of the great Caucasus range (Ivanishvili 1973).

For the sake of comparison, floristic analysis of the pistachio woodlands in the south-east of Georgia on the Iori plateau and the Eldar plain showed a large contribution from the Mediterranean flora, and a reduced Boreal element. This contrasting difference is not unexpected, since Khevi lays to the north of the Great Caucasus main range and thus much closer to Boreal ecosystems (Lachashvili, Eradze, and Khetsuriani 2020).

In summary, it can be stated that the Caucasian, Caucaso-Southwest Asian and Palearctic floras play the most important role in shaping the vegetation of Khevi's subalpine pastures and hay meadows. Holarctic and European-Mediterranean species also contribute considerably. Finally, the chorotypes such as Caucaso-Anatolian, European-Mediterranean-Southwest Asian, European-Southwest Asian and Hyrcanian-Euxinian are notable and diversify Khevi's floristic spectrum.

Conclusions

The taxonomic structure of Khevi's subalpine pasture and hay meadow communities shows the influence of both the Boreal and Mediterranean flora. At the same time, the share of widespread families is high.

The chorotype analysis confirmed the strong influence of the Boreal flora, which was expressed in the high percentage of Caucasian chorotypes. The latter points to the autochthonous origin of the flora. The influence of the Mediterranean flora is mainly expressed by the linking chorotypes. At the same time, the percentage of species with a wide distribution is large.

Chapter 3. Phytosociological classification of Khevi's steep subalpine pasture and hay meadow communities

3.1 Literature review

An ideal classification of vegetation is difficult to achieve, since plant communities are dynamic systems with various biomorphs characterised by seasonal fluctuations, variable phenology, successional change, also man-made or transient communities (Rabotnov 1978). To address these complexities, an array of approaches have been proposed (Braun-Blanquet 1964; UNESCO 1973; Whittaker 1980; Hill 1989; Dierschke 1994; De Cáceres et al. 2015; Faber-Langendoen et al. 2017; MacKenzie and Meidinger 2018), each of which has its own advantages and disadvantages (De Cáceres and Wiser 2012). This chapter discusses and compares two approaches, one is the classification based on dominant species (Whittaker 1980) and another is the phytosociological method of Braun-Blanquet (Braun-Blanquet 1964). The Braun-Blanquet approach is currently the most accepted and used, whilst the dominant-based method was widely used in the former USSR (Mirkin and Gareeva 1978) including in Georgia (Nakhutsrishvili 2013; Etzold, Münzner, and Manthey 2015). One of the first attempts to classify the vegetation of Georgia can be attributed to Grossheim (Grossheim, Sosnowsky, and Troitsky 1928), who built a classification scheme that provides a general overview of the Georgian vegetation. In addition to the dominant species, a classification of vegetation requires environmental data such altitude, exposure, slope, and soil composition (Kavrishvili 1965; Etzold, Münzner, and Manthey 2015; Nakhutsrishvili and Abdaladze 2017b). The named variables were used by Kavrishvili (1965) for the classification of natural pastures (Kavrishvili 1965).

Since the 1950s, however, the dominance-based method was criticised by some prominent Soviet vegetation ecologists, namely Ramensky (1952), Rabotnov (1974) and Mirkin (Mirkin and Gareeva 1978). These authors indicated the advantages of the phytosociological classification and its theoretical foundation, which could also be readily used in practice (Ramensky 1952; Mirkin and Gareeva 1978; Rabotnov 1984). Certainly, a striking advantage of the dominance-based classification is its simplicity, which allows for the determining of plant community categories even in the process of fieldwork. The use of this method may be justified for forest ecosystems, as well as for other plant communities where the dominance of one or a few species is strongly pronounced (Mirkin, Naumova, and Solomeshch 2001). Nevertheless, this method stumbles over a number of obstacles in other types of vegetation, especially when it comes to classifying meadows or man-made systems. Here the dominant species change both yearly and seasonally, and some species dominate only over certain years due to their life cycle. Furhter, the dominance of some species is associated with environmental disturbances. In such cases, an establishment of plant associations based only on dominant species cannot be recommended (Rabotnov 1978; Mirkin, Naumova, and Solomeshch 2001). Conversely, the Braun-Blanquet approach and its modern versions were successfully used in Europe and also other continents (Rabotnov 1978; Dengler, Chytrý, and Ewald 2008). Rabotnov and other authors emphasise that this approach provides the most effective method of vegetation classification compared to other methods (Rabotnov 1978; Dengler, Chytrý, and Ewald 2008). The Braun-Blanquet method usually produces detailed and accurate results (Kent 2011). Even though the use of this method is somewhat complicated in the northern latitudes and other countries with species-poor vegetation, but there are successful cases of classification from such places too (Rabotnov 1978; Dengler, Chytrý, and Ewald 2008). The frequent criticism of this method was that some authors deem it to be subjective, and also that the constructing and arrangement of phytosociological tables, despite being based on general principles, is a tedious and complicated process for students and young scientists (Kent 2011). Indeed working with large tables and community matrices might be complicated, but the classification process can now be automated by means of computers and the use of multivariate methods of analyses. These methods can be considered to be more objective due to their repeatability (Kent 2011).

Even though the standard protocol for sampling herbaceous communities introduced by Braun-Blanquet (1964) was routinely used in the Caucasus, this work was rarely concluded with a vegetation classification system. A few publications come from the North Caucasus alpine meadows (Korotkov and Belonovskaya 2000; Onipchenko 2004). Similarly, there are several studies from Khevi that used the original Braun-Blanquet method (Bedoshvili 1985; Lichtenegger et al. 2006) or its modern versions that included multivariate ordination (Pyšek and Šrůtek 1989; Magiera et al. 2013; Tephnadze et al. 2014) to produce a classification of Khevi's alpine meadows. The scarcity of works on vegetation classification in Georgia can be easily seen from the results of bibliometric analysis of trends in the publishing on the classification of Palearctic herbaceous communities, which included all the journals embedded in the Web of Science database (Janišová, Dengler, and Willner 2016). The vegetation composition was assessed using the standard Braun-Blanquet scale and thus acquired necessary data for phytosociological classification (Chapter 1). This was an opportunity to fill in the existing gaps in knowledge, and thus we conducted a phytosociological analysis of Khevi's managed subalpine herbaceous vegetation. My aim was to establish phytosociological associations and give their floristic and ecological characteristics. To achieve this goal we performed two-step investigation. The first step was to classify subalpine pastures and hay meadow vegetation on the slopes of various steepness in Khevi, under more or less similar land use conditions, using the Braun-Blanquet methodology. The objective of step two, in case of successful step one, was the description of concrete phytosociological associations established under the named conditions and examining what were the ecological and land use factors that determined their differences.

3.2 Materials and methods

The phytosociological analysis used the field data collected in the study area in 2014-2017 (Chapter 1, the Materials and Methods section). The number of plots was 81. The classification process could be represented as six consecutive steps. 1) Construct a community matrix organised into columns (relevé numbers) and rows (species). 2) Calculate the constancy of each species (the percentage of relevés in which a given species is present) and reorder species (table rows) to form a constancy table. 3) Find good diagnostic species - the groups of species that characterise various associations - these are primarily species of intermediate constancy; species with high constancy are characteristic of the entire set of relevés and species with very low constancy are not likely to be characteristic of relevé groups. 4) Draw up partial tables to order the relevés and species by their floristic similarity. 5) Sort again (secondary sorting) to produce the final arrangement of relevés within the preliminary community types, and group all the species into associations with the most constant on the top and accidental species listed at the bottom. 6) Each of these groups should be treated as an association or plant community and given formal names in accordance with the Braun-Blanquet system and to show the relationship to existing units (called syntaxa) (Braun-Blanquet 1964; Dierschke 1994; Dengler, Chytrý, and Ewald 2008; Kent 2011).

Dengler et al (2008) give a succinct description of the differential, character and diagnostic species used in the process of phytosociological classification:

> "*Within the Braun-Blanquet approach, the concept of character and differential species is important for the recognition of previously defined syntaxa. Differential species are those that positively differentiate, by their occurrence, the target syntaxon from other syntaxa. Character species are a special case of differential species: they positively differentiate the target syntaxon from all other syntaxa. The differential and character species combined are called diagnostic species*" (Dengler, Chytrý, and Ewald 2008).

That is, the character species of a particular syntaxon can also be differentiated between other plant groups and *vice versa* (Westhoff and Van Der Maarel 1978; Dengler, Chytrý, and Ewald 2008). Differential species show a distinct pattern of their distribution across the relevés and are usually included in several syntaxa, while character species are found in only one (or mainly one) syntaxon (Westhoff and Van Der Maarel 1978; Mirkin, Naumova, and Solomeshch 2001).

The diagnostic species are established on the concept of constancy and fidelity. Traditionally, to be constant in the target group, the species must occur at least two times more frequently in this than in any other group (Dengler, Chytrý, and Ewald 2008). The value of constancy is calculated as the percentage of plots where the species is found and then is categorised as degrees of constancy often expressed in Roman numerals (I: 1-20%; II: 21-40%;… V: 81-100%; Dengler, Chytrý, and Ewald 2008). Differential species can usually be found at degrees II, III and IV, or within 20 to 80% of relevés (Westhoff and Van Der Maarel 1978). As for the fidelity value, it is a quantity that shows how often a species is found in an established group. A species is considered to be faithful to a group if its frequency of distribution coincides with a given group and is diminished or absent elsewhere (Dengler, Chytrý, and Ewald 2008). The name of the group is represented by the species, which possesses the maximum level of fidelity value and constancy degree. In my case, working with the table revealed a tendency in plants to group along a diagonal that coincided with the direction from the dry to wet community groups; such a pattern usually emerges in phytosociological tables when there is a clear ecological gradient that can affect plant species distribution (Dengler, Chytrý, and Ewald 2008).

3.3 Results

The phytosociological analysis of Khevi's subalpine managed herbaceous vegetation initially established two well-distinguished groups: of *Astragalus captiosus* and *Rhinanthus minor.* However, the latter group appeared to be rather large and included most of the relevés, at the same time this group possessed a structure that allowed for its further division. At the next stage, we performed this division into two subgroups and, as a final result, obtained three community types: *Astragalus captiosus, Rhinantus minor* proper and *Polygonum carneum*. In Chapter 1. we used these three communities in the analysis of indicator species and the soil seed bank comparisons. This chapter describes the further phytosociological analysis of the above three plant communities. First, when looking at these phytosociological groups in relative detail (see Annex 2 and Figure 3.1), it became noticeable that, with the exception of *Astragalus captiosus* community, each of the other two communities contained two subgroups. Since these subgroups were well-defined and possessed more than three character species, I proceeded in my classification and, all in all established five community types (their details are given below). Their floristic and ecological characterisation enabled a comparative approach to these five community types. In their descriptions below, the species of the groups are arranged in a descending order of constancy values.

Group I included 16 plots. Diagnostic species of this group usually grow on dry and stony slopes and were represented by the following species (see the table below).

Diagnostic species of **Group I**. Frequency refers to the number of plots out of 81 sampled ones where a given species was recorded.

Species	Total frequency	Frequency in Group I	Fidelity	Constancy
Astragalus captiosus	19	16	84.2	25.7
Dianthus cretaceus	18	12	66.7	24.3
Sempervivum pumilum	10	7	70	13.5
Sedum acre	7	7	100	9.5

The floristic composition of this community was not rich, with maximum 24 species recorded in some plots. The plots of this group are found within the range of 1791 – 212^2 a.s.l., usually on the slopes that are highly illuminated by the sun (south, southeast, east). The mean vegetation coverage is 75%, with slope inclination ranging from $15\text{-}45^0$ (mean = 23.4^0). The mean height of vegetation was in the range of 15-20 cm. The coverage of legumes was relatively high as compared to other communities and varied in the range of 30-70% (mean = 50%). Graminoids made up 9-78% (mean = 34.4%) of aboveground biomass, while forbs and legumes accounted for 5-58 (mean = 31.3%) and 3-50% (mean = 23.8%), respectively. The biomass ratio of graminoids : forbs : legumes is 1.4:1.4:1. The soil here is loamy and thin (mean = 8.8 cm). The content of roots in the soil varied from 1–3% (mean = 1.9), while the mean content of stones in the soil was 22.4%; the pH_{H20} varied between 5.84–6.83 (mean = 6.4). Nitrogen content in soil varied from 0.2 to 0.9% (mean = 0.4%) and carbon C_{org} from 1.23 to 8.21% (mean = 3.7%). As for the content of potassium (K_{cal}), phosphorus (P_{cal}) and magnesium (Mg_{cal}) in the soil varied from 9 -81 (mean = 39.6), 1.3-16 (mean = 6.3) and 159.2-492.3 (mean = 283) mg/kg, respectively. All plots in this group are used as pastures, most of them have traces of heavy grazing (paths, compaction, open ground).

Group II included 21 plots (eight plots are covered by the first group) - see Annex 2.

Diagnostic species of **Group II**. Frequency refers to the number of plots out of 81 sampled ones where a given species was recorded. See the table below for the diagnostic species.

Species	Total frequency	Frequency in Group II	Fidelity	Constancy
Plantago atrata	36	20	55.6	48.6
Potentill acrantzii	29	17	58.6	39.2
Scabiosa bipinnata	19	11	57.9	25.7
*Bupleurum falcatum**	17	8	47.1	22.9
Campanula rapunculoides	12	5	41.7	16.2
Phleum pratense	8	4	50	10.8
Leontodon caucasicus	6	3	50	8.1

*subsp. *Polyphyllum*

The floristic composition of this plant community was rich, included 26 to 46 species per plot (mean richness 36 species). This group represents a transitional plant community from Group I (AC community) to other groups. Out of 21 plots, 14 were pastures, seven were hay meadows. Seven plots faced the south-east, three plots faced the north-east, and three more faced to north or north-east. This group is typical for the subalpine belt, the plots included in this group are presented in the range of 1791-2262 m a.s.l., usually on the slopes that are well-irradiated by the sun (south, east). Vegetation coverage averaged 85%, with slope inclination ranging from 15 to 35^0 (mean 21.6^0). However, the coverage of legumes varied from 10-70% (mean = 44%), and the mean height of vegetation was in the range of 15-75 cm. Graminoids made up 6-78% (mean = 39%) of aboveground biomass, while forbs and legumes made up 5-88 (mean = 31.4%) and 2-50 (mean = 21%), respectively. The biomass ratio of graminoids : forbs : legumes was 1.9:1.3:1. The soil was shallow (mean depth = 9.7 cm). The content of roots in the soil varied from 1 to 4 % (mean = 2.4%), while the mean content of stones in the soil was 22.3%. Soil pH_{H2O} varied between 5.57-6.58 (mean = 6.2). Nitrogen content in soil varied from 0.25-0.87% (mean = 0.49%) and organic carbon C_{org} from 2.19-9.93% (mean = 5.28%). Finally, the content of potassium (K_{cal}), phosphorus (P_{cal}) and magnesium (Mg_{cal}) in the soil varied from 26-186 (mean = 76.1), 3-22 (mean = 11.1) and 220-585 (mean = 369.3) mg/kg, respectively. Some of the plots in this group were used as regularly mown hay meadows and some as pasture, although there were traces of medium or light grazing on the hay meadows too.

Group III included 14 plots - see the table below for the diagnostic species.

Diagnostic species of **Group III**. Frequency refers to the number of plots out of 81 sampled where a given species was recorded.

Species	Total frequency	Frequency in Group III	Fidelity	Constancy
Lomelosia caucasica	29	11	37.9	39.2
Polygala anatolica	23	12	52.2	31.1
Salvia verticillata	17	11	64.7	22.9

The floristic diversity of this plant community was, on average, 25 to 40 species per plot, and the mean number of species reached 34. This group is typical for the subalpine belt, the plots included in this group are presented in the range of 1750-2170 m a.s.l., it seemed that thus group did not have any preference for slope exposure, although the north and the north-west expositions were presented by only one plot. The mean coverage of vegetation was 84.3%, and slope inclination ranged from 15 to 50^0 (mean = 31.8^0). Legume coverage varied within 30-75% (mean = 61.1%). The mean height of the vegetation varied within 30-65 cm. Graminids made up 19-58% (mean = 45%) of surface biomass, while forbs and legumes accounted for 8-40.9% (mean = 23%) and 6.4-72.8% (mean = 23.7%), respectively. The biomass ratio of graminoids : forbs : legumes is 2:1.9:1. The soil here was relatively deep (mean = 12.9 cm). The content of roots in the soil varied from 0.88 to 5.35% (mean = 2.8%), while the content of stones in the soil ranged from 10 to 28% (mean = 18.8%). Soil pH_{H20} varied between 5.8-7.5 (mean = 6.4). Nitrogen content in soil was 0.27-1.06% (mean = 0.55%) and carbon C_{org} was 3.57-12.59% (mean = 5.6%). The content of potassium (K_{cal}), phosphorus (P_{cal}) and magnesium (Mg_{cal}) in the soil varied between 16.4-120 (mean 67.4), 1.27-79.08 (mean 16.3) and 112-838.9 (mean 386.4) mg/kg, respectively. All plots of this group were used as regularly mown hay meadows, and there were no observable signs of grazing.

Group IV included 31 plots -- see table below for the diagnostic species.

Diagnostic species of **Group IV**. Frequency refers to the number of plots out of 81 sampled where a given species was recorded.

Species	Total frequency	Frequency in Group IV	Fidelity	Constancy
Cirsium obvallatum	31	20	64.5	41.9
Pimpinella rhodantha	26	19	73.1	35.1
Cyanus cheiranthifolius	27	19	70.4	36.5
Polygonum carneum	23	21	91.3	31.1
Betonica macrantha	21	19	90.5	28.4
Carex humilis	18	15	83.3	24.3
Anthoxanthum odoratum	18	11	61.1	24.3

The floristic diversity of this plant community was, on average, 23 to 41 species recorded per plot, and the mean number of species reaching 34.9. This group is typical of the subalpine belt, and it is closely related to and partly overlaps with, the fifth group (below). The plots included in this group are presented in the range of 1795-2317 m a.s.l., this group can be found in different exposures. Vegetation coverage was high (mean = 88.4%), slope inclination was 10 to 400 (mean = 29.60). Legume coverage varied from 15-70% (mean = 45.3%). The mean height of vegetation was in the range of 20-80 cm. Graminoid species made up 2-95% (mean = 38.9%) of biomass, while forbs and legumes made up 1–86 (mean = 44%) and 1–36 (mean = 10.3%), respectively. The biomass ratio graminoids : forbs: legumes is 3.8:4.3:1. The soil here is relatively deep (mean = 14.7 cm). The content of roots in the soil varied from 2-11% (mean = 4.2%), while the mean content of stones in the soil was 16.5%. Soil pH H_2O varied between 4.47-6.6 (mean = 5.76). Nitrogen content in soil was 0.45-1.53% (mean = 0.84%) and carbon C_{org} was 4.71-18.3% (mean = 9.3%). Finally, the content of potassium (K_{cal}), phosphorus (P_{cal}) and magnesium (Mg_{cal}) in the soil varied within 34-517 (mean = 98.2), 5-50 (mean = 20.8) and 58-832 (mean = 376.5) mg / kg, respectively. More than half of the plots in this group were used as pastures. There are signs of grazing on some of the plots and there are regularly mown hay meadows in this group.

Group V included seven plots (all seven plots are covered by the fourth group) - see Annex 2.

Diagnostic species of **Group V**. Frequency refers to the number of plots out of 81 sampled ones where a given species was recorded. See the table below for the diagnostic species.

Species	Total frequency	Frequency in Group V	Fidelity	Constancy
Silene linearifolia	8	5	62.5	10.9
Helictotrichon adzharicum	9	5	55.6	12.2
Deschampsia cespitosa	5	5	100	6.8
Veratrum lobelianum	4	4	100	5.4
*Anemone narcissiflora**	4	4	100	5.4
Fritillaria collina	4	4	100	5.4
Potentilla reptans	4	3	75	5.4
Chaerophyllum roseum	3	3	100	4.1
Carex panicea	3	3	100	4.1
Calamagrostis arundinacea	11	5	45.5	14.9

**subsp. fasciculata*

The floristic composition of this plant community is consistently rich, with 36-40 per plot. This group is typical of Khevi's subalpine belt, and the plots included in this group were located within the range of 1822–2317 m a.s.l. on relatively moist slopes of N and NW aspect. Vegetation coverage was high and averaged 85%, with slope inclination ranging from 10 to 40^0 (mean = 19.7^0). The mean coverage of legumes was 15-60% (mean = 41.8%). The mean height of the vegetation varied within 25-60 cm. Graminoids made up 18.9-53% (mean = 38%) of surface biomass, while forbs and legumes accounted for 22.2-68.7 (mean = 44.8%) and 1.2-24 (mean = 8.6%), respectively. The biomass ratio graminoids: forbs: legumes is 4.4: 5.2: 1. The soil here is relatively deep (mean = 19.2 cm). The content of roots in the soil varied from two to 11% (mean = 5.5%), while the average content of stones in the soil was 11.8%. Soil pH_{H2O} varied between 4.55–6.47 (mean = 5.5). The content of soil nitrogen and carbon C_{org} were 0.45–1.53% (mean = 0.95%) and 4.71-18.27% (mean = 11%), respectively.

Figure 3.1: Defined groups of plant communities in a subalpine pasture and hay meadow in Khevi (Photos by Giorgi Tedoradze)

Finally, the content of potassium (K_{cal}), phosphorus (P_{cal}) and magnesium (Mg_{cal}) in the soil varied within 44-517.4 (mean = 170.6), 5-50 (mean = 26.5) and 201.19-494.2 (mean = 339.4) mg/kg, respectively. The plots of this group were used as pastures, with signs of medium or weak grazing.

In total, these groups included 74 plots out of sampled 81 ones since seven plots could not be resolved between the second and third groups and did not form a specific group. Accordingly, we excluded them.

3.4 Discussion

***Astragalus captiosus* (AC) group.** Character species with high fidelity and constancy in this group are *Astragalus captiosus* and *Dianthus cretaceous*. As for the other two species (*Sempervivum pumilum, Sedum acre*) with high fidelity, their constancy was below 20%. Therefore, it was not advisable to consider them as character species (Dengler, Chytrý, and Ewald 2008). However, these species can be considered to be differential species, as they more or less differentiate the dry group AC from the PA and LC groups of intermediate moisture (Westhoff and Van Der Maarel 1978).

The AC stands out sharply from the established plant community types. The meadows of *Astragalus captiosus* are mentioned by Sakhokia (1983) as a representative of dry steppe meadows, specifically the forb and legume species (Sakhokia 1983). For rocky slopes with a thin soil cover, for relatively small areas, this plant group is referred to as *Astragaleta captiosus* (Sakhokia 1983; Nakhutsrishvili 2013; Nakhutsrishvili and Abdaladze 2017a). This group of meadows is also mentioned by Magiera (2017), where *Astragalus captiosus, Potentilla crantzii* and *Silene linearifolia* (Tephnadze et al. 2014; Magiera et al. 2017) are the character species. The last two species, are in my character species too, though not specifically in the AC group. However, *Potentilla crantzii* occurs in plant communities which directly extend from AC group and even overlap with it in a number of plots. As for *Silene linearifolia*, in my case it is a character of relatively humid meadows, which might be an effect of peculiar topography, especially on steep slopes.

AC plant communities are mainly found on sunny slopes of the south and south-east aspect, where the soil is thin and gravelly. Vegetation coverage is the lowest here, compared to other groups. However, the coverage of legumes at these sites is high, with the height of vegetation in the range of 15-20 cm. Soil organic nitrogen content is the lowest as compared to other groups and conforms to the high coverage of legumes (Dvorakovsky 1983). Organic carbon is one of the most important component in the soil because it helps to retain water in the soil and increases its fertility (Lal 2008). Like organic nitrogen, the content of organic carbon in AC soils is the lowest, although within the range characteristic for high mountain soils (Troeh and Thompson 2005). Likewise, available potassium and phosphorus are very low (Espinoza, Slaton, and Mozaffari 2012). The availability of magnesium depends on many factors such as the chemical composition of rocks in the soil. Like other elements, the magnesium content in the soil is low (Cowan, n.d.). Soil pH, topographical characteristics, together with the chemical composition of the soil and land use practice could lead to the low productivity of 3 t/ha (the methods of biomass measurements are described in Chapter IV, the Materials and Methods section).

***Plantago atrata* (PA) group.** Character species with high fidelity and constancy are *Plantago atrata*, *Potentilla crantzii*, *Scabiosa bipinnata*, and *Bupleurum falcatum* subsp. *polyphyllum*. The constancy of the remaining three species (*Campanula rapunculoides, Phleum pratense, Leontodon caucasicus*) did not reach 20% and we did not include them as character species according to common practice (Dengler, Chytrý, and Ewald 2008).

PA is closely related with AC. First of all, a part of the plots overlap, and there are shared species. For example *Potentilla crantzii* was already mentioned as a character species of the AC group (Magiera et al. 2017). The same can be said for *Plantago atrata* and *Scabiosa bipinnata*, which are found in both meadows and scree slopes. Typical species of dry meadows are *Leontodon caucasicus*, *Phleum pratense,* and *Bupleurum falcatum subsp. polyphyllum*, the latter is also associated with the forest boundary (Sakhokia 1983). As for *Campanula rapunculoides*, it is found in various habitats and, thus, its fidelity is low. This species can be found in forests, in meadows, arable lands or along riverbanks. *Phleum pratense* is one of the character species of hay meadows, which are dominated by *Hordeum violaceum* (Tephnadze et al. 2014; Magiera et al. 2017; Nakhutsrishvili and Abdaladze 2017a).

PA meadows are usually found on sunny (south, east) slopes. The vegetation cover is high compared to the first group (85%), but the soil is shallow, though not as thin as in AC. However, the coverage of legumes in PA is less compared to AC, while the vegetation height is variable but taller than in AC (15-75 cm). The percentage of legumes is relatively reduced also in biomass. Soil organic nitrogen, carbon available nutrients, potassium, phosphorus and magnesium are higher than the first group. Soil pH is still close to neutral, yet slightly more acidic in the case of the AC group. These characteristics, together with the chemical composition of the soil, could lead to a slightly higher productivity of 3.8 t/ha. Land use is a mixed grazing and mowing.

***Lomelosia caucasica* (LC) group.** Character species in this group with high fidelity and constancy are *Lomelosia caucasica* (*Scabiosa caucasica*), *Polygala anatolica*, *Salvia verticillata*.

According to Tephnadze (2014) *Salvia verticillata* is a character species of hay meadows, while *Lomelosia caucasica* (*Scabiosa caucasica* in her publication) is that of pastures (Tephnadze et al. 2014). In my case, these species form a group represented by hay meadows, although this does not exclude grazing at different times of the year. Sakhokia (1983) also notes that *Lomelosia caucasica* is less tolerant to grazing and is found in wet or moderately dry meadows, forest edges, and shrublands (Sakhokia 1983). In the Teberda reserve, Onipchenko (2002) established a group of vegetation *Bromopsietosum varigatae*, with participation of *Lomelosia caucasica*. Similar to my findings, *Bromus variegatus* (*Bromopsis variegata* in the original publication) dominated the community (Onipchenko 2002).

For the LA meadows no exposure seems to be a priority, although they occur on the north and north-west slopes less often. Vegetation coverage is high compared to the first group and slightly lower compared to the PA group (84.3%), while the height of vegetation is within 30–65 cm. Interestingly, the coverage of legumes exceeds that in the previous two groups (61.1%). Accordingly, the percentage of legumes in biomass appeared to be relatively high too (23.7%). The soil here is deepper (12.9 cm) with quite high organic nitrogen and carbon, as well as high amounts of other available nutrients, excluding K. Soil pH (mean 6.4) is slightly acidic, similar to the AC group. These characteristics, together with the chemical composition of the soil, could lead to a relatively high productivity of 4.5. All plots of this group are used as hay meadows, no signs of grazing were observed.

***Polygonum carneum* (PC) group**. Many species of this group can be character species due to their high fidelity and constancy. *Polygonum carneum* shows a remarkably high fidelity of 91.3 and constancy of 31.1%. This led to the conditional name for the group, as in the case of other groups (Dengler, Chytrý, and Ewald 2008). The other six character species are *Cirsium obvallatum, Pimpinella rhodantha*, *Cyanus cheiranthifolius*, *Betonica macrantha*, *Carex humilis*, and *Anthoxanthum odoratum*.

PC contains species that are somewhat identical to the graminoids-mixtoherbosa vegetation of Sakhokia (1983). This plant community spreads mainly on steep slopes. Sakhokia (1983) includes in it *Bromus variegatus, Agrostis vinealis* (then *Agrostis planifolia*) (*Agrostis vinealis subsp. Planifolia*) *Anthoxanthum odoratum, Koeleria eriostachya* (*Koeleria caucasica* in the original publication) (Sakhokia 1983). From these species, graminoids (*Bromus variegatus, Agrostis vinealis, Koeleria eriostachya*) are represented in my PC group as companion species, while *Anthoxanthum odoratum, Polygonum carneum* and *Betonica macrantha* are among the character species. A similar plant community type with *Polygonum carneum* and *Betonica macrantha* from subalpine and alpine pastures have been established by Lichtenegger et al. (2006). For the subalpine belt of the Teberda reserve, Onipchenko (2002) describes the association *Betonici macranthae-Calamagrostietum arundinaceae*, which is characterized by the following species: *Betonica macrantha, Bupleurum falcatum,* and *Rhinanthus minor* (Onipchenko 2002). In my case, these species are shared by PA and similar groups.

PC Meadows of this group are found across various exposures. Vegetation coverage is high and exceeds all considered groups (88.4%). Legume coverage is high (45.3%). The height of vegetation is in the range of 20-80 cm. The percentage of legumes in biomass is notably less (10.3%). The soil here is relatively deeper (12.9 cm) with also quite high organic nitrogen and carbon as well as available nutrients exceeding similar characteristics of the AC and PA groups, with the exception of Kcal. Soil pH_{H20} (mean 5.76) is relatively acidic. These characteristics, together with the chemical composition of the soil, could lead to a high productivity of 4.5 t/ha. All plots of this group are used as regular hay meadows and exclude grazing.

***Calamagrostis arundinacea* (CA) group.** Most of the species in this group have a high degree of fidelity, although the constancy is problematic, its value appeared to be much lower than the recommended threshold for character species, in many cases this value was even below 10. *Calamagrostis arundinacea* has a relatively high values of fidelity (45.5) and constancy (14.9), and thus was chosen as given name to this group. It should also be noted that the species characteristic of the group are listed only conditionally, as they are not recommended as character species due to their low constancy value (Dengler, Chytrý, and Ewald 2008). However, the species associated with this group can be considered differential species, as they more or less differentiate the humid group of the CA from the PA and LC groups of intermediate humidity (Westhoff and Van Der Maarel 1978). In my case, the CA group extends from the PC community type. Certainly, this does not mean that there not many communities in the study region where *Calamagrostis arundinacea* is dominant, many studies document their existence, yet more commonly in the plains (Sakhokia 1983; Tephnadze et al. 2014; Magiera et al. 2017; Nakhutsrishvili and Abdaladze 2017a). Other species of this group distinguished by relatively high fidelity and constancy are *Silene linearifolia*, *Helictotrichon adzharicum*, and *Deschampsia cespitosa*. For the subalpine belt of the Teberda reserve, Onipchenko (2002) cites an association referred to as *Calamagrostion arundinaceae*, where the character species are *Calamagrostis arundinacea, Anemone narcissiflora,* and *Anthoxanthum odoraum* (Onipchenko 2002). The wide distribution of *Calamagrostion arundinaceae* syntaxon in the central Caucasus has been also noted Ermakov (2012).

Calamagrostis arundinacea is mainly found in moist forest clearings. The forest in the study area is mostly formed by *Betula litwinowii*, which is found on the northern slopes. The *Calamagrostis arundinacea* group is also found in the same exposition, which confirms the connection of this species with *Betula* forest and the preference for less sunny but moist exposures. *Calamagrostis arundinacea* is often accompanied by *Agrostis planifolia* (*Agrostis vinealis subsp. planifolia*), *Anemone fasciculata, Betonica macrantha, Inula orientalis, Lomelosia caucasica, Helictotrichon adzharicum, Geranium ibericum* (Sakhokia 1983; Tephnadze et al. 2014; Nakhutsrishvili and Abdaladze 2017a). These species are shared among the groups established by us. A different species composition for *Calamagrostion arundinaceae* is given by Ermakov (2012), where the character species are *Bupleurum longifolium, Calamagrostis arundinacea, Delphinium elatum, Avenella flexuosa,* and *Digitalis grandiflora* (Ermakov 2012).

The CA group, as already mentioned, is found on relatively moist slopes exposed to west and north-west. Vegetation coverage is high (85%), the legumes contributing a considerable share (42%). The height of the vegetation varies within 25-60 cm, which is average among the vegetation types. Yet the portion of legumes in the biomass is sharply reduced to 8.6%. The soil is relatively deep (19.2 cm) and acidic (mean soil pH_{H20} = 5.5). The resulting character species include acidophilic plants (*Deschampsia cespitosa, Calamagrostis arundinacea*) (Dvorakovsky 1983; Gamzatova 2018). Organic carbon content is (11%) close to the typical organic soils (12% -18%) (Troeh and Thompson 2005). Organic nitrogen, available potassium, phosphorus and magnesium also exceed the respective values in AC and PA groups, but available potassium is less. This is the most productive community type yielding 4.7 t/ha. It is an exclusively hay meadow group without any signs of grazing.

The comparison of established community types allows for arranging them along a gradient from dry to moist conditions. AC is the driest community type, while CA is the most moist. Productivity increases from 3 t/ha to 4.7 t/ha on this gradient. While AC communities are mainly located on the south or south-east exposure, CA grasslands are found on the north or north-west slopes. Chemical composition of the soil also tracks the same gradient; organic nitrogen increases from 0.4 to 0.95%, organic carbon from 3.7 to 11%, available potassium from 39.6 to 170.6 mg / kg, phosphorus from 6.3 to 26.5 mg / kg. However, the impacts of land use on the studied plant communities is obvious. AC communities used as mostly pastures are much less productive than CA used exclusively as hay meadows. However, it should be noted that productivity, soil chemical composition, land use, and topography are interdependent and directly or indirectly always affect each other (Sakhokia 1983; Fraterrigo et al. 2005).

Remarkably, the plant groups discussed above overlap with the communities *Rhinanthus minor* (RM), a notable exception being AC. Therefore, RM can be used as a kind of 'umbrella' under which the four groups (PA, LC, PC, CA) can be collected. This overlap must be a consequence of the homogeneity of the vegetation shaped by the common land use traditions in Khevi. The methodology of plot selection in the study area with less subjective approach might also lead to a narrower range of plant communities that exist in Khevi. The groups established in my study show partial, but not complete, similarity with plant community types established in other studies. This is probably a result of using non-dominant plants as character and differential species. Certainly, the established groups cannot be understood as separately standing vegetation types, but instead as part of a much bigger picture of dynamic vegetation.

Conclusions

- The homogeneity of subalpine herbaceous managed plant communities caused by a more or less common land use traditions pose a challenge for the full resolution of syntaxa based on the Braun-Blanquet methodology.
- Nonetheless, even under similar management, the established community groups arrange along a gradient from dry to wet meadows. The established plant groups differ from each other floristically, topographically, by soil characteristics, and land use. However, all of this variation builds a gradation where environmental conditions change from relatively dry to relatively moist, and where the species composition of plant communities at the ends of gradient are sharply dissimilar.

Chapter 4. Productivity of pastures and hay meadows, and sustainable land use capacity in Khevi

4.1 Literature review

Livestock husbandry in the Caucasus, including Georgia, has a long history because it was a basis of low intensity subsistence agriculture over three millennia (Kikvidze 2020). However, in the Soviet period of planned economy, there was a sharp increase in the number of cattle which led to intensified land use (i.e., grazing and hay-making). An abrupt reduction in the heads of domestic cattle that led to the abandonment of pastures and meadows followed soon after the collapse of the Soviet system. For example, the heads of sheep in the Mtskheta-Mtianeti region decreased from 470,000 (1990) to 65,000 (1996) (Didebulidze and Plachter 2002), which in turn had an impact on vegetation (Togonidze and Akhalkatsi 2015). Both the sharp increase and the sudden decline in agriculture intensity had detrimental effects on the structure and composition of managed plant communities in Khevi. Indeed, biodiversity and ecosystem functions can be damaged not only by unsustainable intensive land use, but also by abandonment of traditionally managed lands (Tasser, Mader, and Tappeiner 2003; Uchida and Ushimaru 2014).

Grazing is generally considered a natural process that can be both beneficial and harmful, depending on its intensity and duration. Moderate grazing reduces dominant species and subsequently creates niches for other species. However, overgrazing, especially in early spring, can reduce productivity and soil absorption capacity and increase the risk of leaching and erosion. This eventually can lead to a complete destruction of vegetation. Further, multiple studies have also shown that a sudden abandonment of pastures increases the risk of erosion (Kavrishvili 1965; Tasser, Mader, and Tappeiner 2003; Körner, Nakhutsrishvili, and Spehn 2006; Fischer et al. 2008).

Healthy pastures and hay meadows not only prevent soil erosion and disruption of ecosystem functions, but also provide invaluable food resources to livestock husbandry. Further, this helps to supply dairy products and meat which contribute to food security amidst the demands of a growing world population (O'Mara 2012). Sustainable development of livestock husbandry is impossible without a knowledge of the area of existing pastures and hay meadows, their species composition, nutritional value, and productivity. Pastures and hay meadows can provide 9/10 of food for livestock, which is cheap, nutritious, and rich in vitamins and proteins (Grossheim, Sosnowsky, and Troitsky 1928; Kavrishvili 1965; Larin 1967).

Different authors provide contrasting estimates of the area of pastures and hay meadows in Georgia. For example, Troitsky in 1924 found that there were 180 thousand ha of summer pastures and 265 thousand ha of winter pastures (Troitsky 1924). The 1955 data, in contrast, found pastures and hay meadows occupied 1/4 of Georgia's area (i.e., 1638.4 thousand ha). Of these, 1479.3 thousand ha were pastures (1168.7 thousand ha of summer and 310.6 thousand ha of winter pastures). The area of hay meadows appeared to be much less at 159.1 thousand ha (Kavrishvili 1965; Ketskhoveli 1966). The current assessment given by the Agriculture and Rural Development Strategy of Georgia, is that natural pastures and hay meadows occupy 38% of agricultural land and amount to 300,004 ha (ARDSG 2021 - 2027 2019).

For Khevi, the estimates are that 48136 ha (44.5% of the total area of Khevi) is occupied by agricultural lands. The largest part is pastures with 41,856 ha (39%), while the hay meadows occupy only 1851 ha (1.6%) (Sakhokia 1983). The proportions of the pastures in the upper montane, subalpine and alpine belts were 12.4, 34.5, and 53.1%, respectively. However, due to density of stones and erosion, only 50–60% of pastures were suitable for grazing (Sakhokia 1983).

Studies on the productivity of the Caucasus mountain grasslands are crucial for their sustainable use. The productivity of pastures and hay meadows depends on many factors, including vegetation types and land use intensity. The subalpine plant communities of the Central Caucasus show relatively high productivity that strongly depends on precipitation and temperature over the vegetation period (Nakhutsrishvili 1977; Bazilevich, Davydova, and Yashina 1987).

A number of studies have been conducted to study the productivity of grasslands in the subalpine belt of the Kazbegi district. Nakhutsrishvili et al. (1980) reported the results of a long-term study of grassland productivity in four meadow communities, where their productivity was estimated for different periods of growing season. The communities were classified by the dominance method and the top dominant species were used for plant community names. Their results, presented below, refer only to the aboveground biomass (AGB) measured in mid-summer when the productivity is at its maximum: *Agrostis tenuis-Bromus variegatus-Trifolium ambiguum-Festuca ovina* 6.06 t/ha; *Festuca varia-Carex meinshauseniana-Mixtoherbosa* 7.93 t/ha; *Bromus variegatus- Agrostis planifolia- Carum caucasicum* 6 t/ha (while when it was 4.7 t/ha); *Festuca ovina- Pulsatilla violacea- Carex buschiorum* 3.57 t/ha (Chkhikvadze 1977; Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980). Grazing could strongly affect the productivity of hay meadows; for example, a limited grazing in *Agrostis tenuis-Bromus variegatus-Trifolium ambiguum-Festuca ovina* community reduced the hay biomass yields twice (Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980).

The use intensity and nutritional value of pastures and hay meadows can be strongly reduced by the spread of unpalatable and poisonous plants. Many of our high mountain grasslands are considerably infested with unpalatable and low-nutrition weeds such as *Aconitum, Anemone, Anthriscus, Aquilegia, Astrantia, Chaerophyllum, Cirsium, Colchicum, Delphinium, Digitalis, Euphorbia, Fritillaria, Galega, Gentiana, Lilium, Nardus, Pedicularis, Pulsatilla, Ranunculus, Rumex, Scrophularia, Swertia, Trollius, Rhinanthus,* and *Veratrum.* On the one hand, this indicates overgrazing, and on the other hand, it shows that almost no weed control is in practice (Troitsky 1924; Nakhutsrishvili 2003). In 1965 Kavrishvili reported that erosion, abundant rocks and stones, fragmented vegetation, and other signs of pasture degradation are common in 35.5% of summer pastures and 21.5% of winter pastures. Weeds occupied 35.6 thousand ha of summer pastures, while poisonous plants such as *Veratrum* took 18.7 thousand ha; likewise, plants of low nutritional value such as *Sibbaldia* and *Alchemilla* spread widely on 321.5 thousand hectares, while *Nardus* occupied 100 thousand ha. 18 thousand ha of winter pastures was infested with unpalatable weeds (Kavrishvili 1965). A study conducted in the Eastern Caucasus found that the percentage of weeds such as *Veratrum, Cirsium and Rumex* in the biomass of the subalpine plant communities often reached 48.1%, 27.9%, 81.1%, respectively (Vagabov 1974).

An additional challenge at national scale is the disproportion between the winter and summer pastures. A full use of summer herding lands, the productivity of which is three times higher than that of winter pastures and hay meadows together, is usually limited because of the above (in Soviet times this was compensated by using winter pastures beyond the borders of Georgia). Food requirements of livestock can be met either with larger winter pastures or by feeding livestock with expensive products of agriculture (Kavrishvili 1965; Theissen et al. 2019). Perhaps the share of hay meadows shall be increased at the expense of summer pastures to be able to provide sufficient hay in winter.

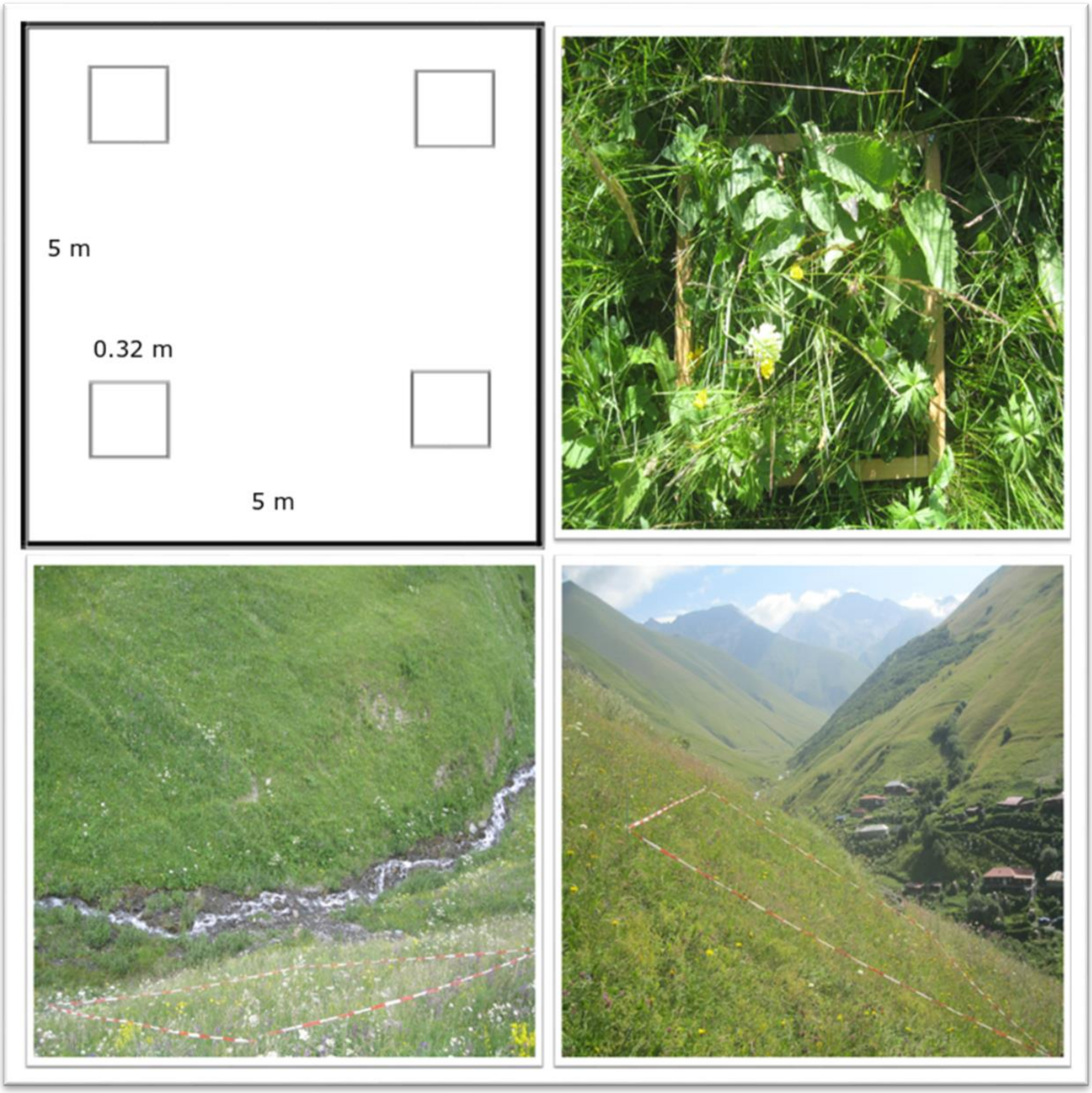
Even though the problem of sustainable and productive livestock husbandry is declared to be a national priority for the government of Georgia (ARDSG - 2015-2020 2015; ARDSG 2021 - 2027 2019), there is an acute lack of the research on grassland productivity in the central Caucasus (Lichtenegger et al. 2006; Magiera et al. 2017). Most of such research was conducted during the Soviet period (Chkhikvadze 1977; Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980). Studies on grassland productivity since the 1990s are rare in Khevi (Lichtenegger et al. 2006; Magiera et al. 2017) whilst already 30 years have passed after the collapse of Soviet Union and these three decades are rather long time period over which visible changes took place in the land use. These changes could affect both the species diversity and productivity of plant communities in both managed or abandoned pastures. These changes, as well as the appreciation of pastures and hay meadow resources as a cheap and abundant food base for livestock husbandry, motivated our study on the productivity of plant communities. The specific objectives were answering the following questions: i) what is the area of the managed herbaceous plant communities in the surroundings of Khevi villages, and what is the ratio of pastures to hay meadows? ii) what is the productivity of the managed herbaceous plant communities in the surroundings of Khevi villages, and how different is the yield among different pasture and hay meadow communities?

4.2 Materials and methods

4.2.1 Biomass sampling

Plant biomass can combine various components and subcomponent. For example, the aboveground biomass (AGB) is the mass of all living plant parts above the ground that includes stems, branches, bark, seeds and foliage (Poniatovskaia 1978; Nakhutsrishvili, Chkhikvadze, and Khetsuriani 1980). Our study measured the AGB. In the past, the most often used method was direct cutting, which not only damages the sampled vegetation, but also is a tedious procedure requiring time and resources. Nowadays, non-invasive remote methods are increasingly used and, in our case, the AGB estimates were obtained through a limited direct cutting combined with remote sensing (Magiera et al. 2017; Mikeladze 2020).

Figure 4.1: Vegetation and biomass sampling in the study area (Photos by Giorgi Tedoradze)



The cuts were carried out in the summer of 2015 and 2016 (late July, when the biomass reaches its peak). The AGB was harvested with scissors. A frame of 0.1 m^2 was placed four times at random within a sampling plot (25 m^2), and all the AGB was cut inside the frame. Therefore, we cut an area of 0.4 m^2 per plot. To obtain biomass per 1 m^2, we multiplied the weight of the cut biomass by a factor of 2.5 (0.4 * 2.5 = 1 m^2).

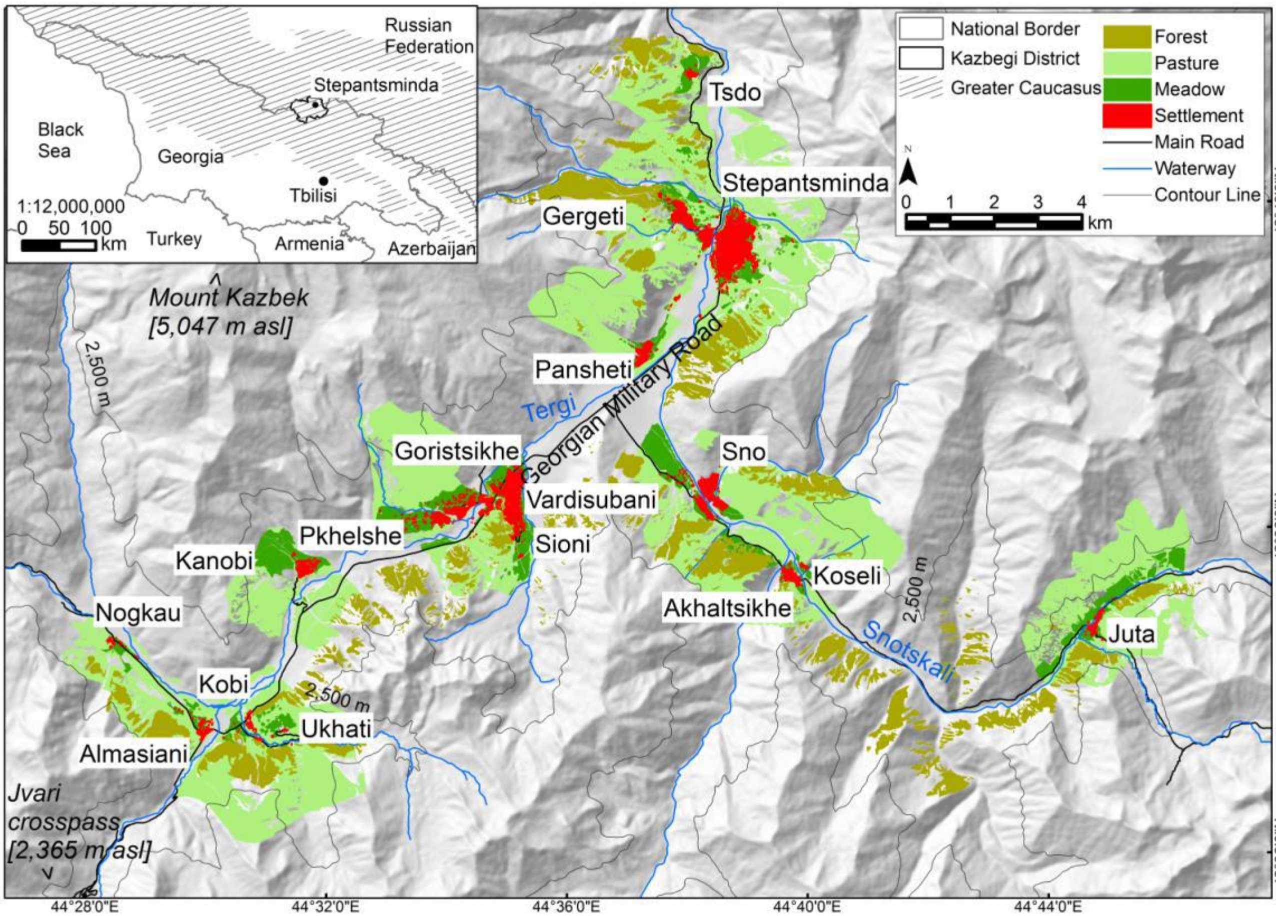
The resulting harvested vegetation was collected, sorted (into four groups consisting of either graminoids, legumes, forbs, and the rest), dried at 60 °C in an oven for 48 hours and the dry mass weighed. The obtained data were used for the extrapolation of the biomass per hectare. Drying and weighing procedures were performed at the Justus Libig University in Giessen (Germany).

4.2.2 Modelling

Plant community productivity map was generated by the same general modelling technique as described in Magiera et al. (2017). It incorporates the records of vegetation sampling in the field, biomass clippings, multispectral imagery, vegetation indexes, and topographic information (Magiera et al. 2017). We combined two years of clipped biomass data to base the modelling on a larger data set and thus improve the statistical power of analyses (Magiera et al. 2017; Theissen et al. 2019). The mapping of biomass that depends on the variable productivity in plant communities was conducted in two steps. First, all the vegetation sampling plots was subjected to the ISOMAP ordination (52% of initial distances were transferred to the ordination axis, (Tenenbaum, De Silva, and Langford 2000) to reduce the high-dimensional floristic data to three major gradients. The latter were then linked to satellite imagery using three random forest models (Breiman 2001), vegetation indices, and topographic variables (R^2 = 42%, R^2 = 27%, and R^2 = 5.62% explained variance). The resulting ISOMAP modelled/species composition maps were again used to predict biomass by a random forest algorithm. The resulting model explained 43% of variance.

The estimated biomass yield was expressed as tons per ha. The mapping and calculation of area for different land uses was performed with ArcGIS 10.2 (ESRI, Redlands, CA, USA) (Theissen et al. 2019). The area of the plant communities was limited by the areas where the biomass cuts took place, thus both the slope inclination and the altitude remained within a certain range representing mainly the subalpine belt.

Figure 4.2: Selected settlements and their surrounding lands, Theissen et al. 2019.



4.3 Results

Data were collected around 17 settlements. However, if the settlements were located close to each other, we merged them so that all in all we analysed data from nine research areas: 1) Stepantsminda and Gergeti; 2) Pansheti; 3) Koseli, Sno, Akhaltsikhe; 4) Tsdo; 5) Sioni, Vardisubani; 6) Pkhelshe, Goristsikhe; 7) Kanobi; 8) Kobi, Almasiani, Nogkau, Ukhati; 9) Juta. The productivity map model was prepared for pastures, meadows and forests around the named villages, and excludes areas with low (<0.2) NDVI. Further, the study areas were limited also to the sites where field descriptions and biomass clippings were conducted.

The area and productivity of the studied plant communities were calculated for the three (PROT-REG, PROT-MAX and LIM-MAX) scenarios, however, since in the PROT-REG and

PROT-MAX scenarios the land use system and biomass results were equal (the only difference was the number of cattle which was not analysed in the current dissertation; for more details see Theissen et al. 2019.), here we will discuss only two models (PROT-REG and LIM-MAX). The PROT-REG model was more conservative, included restrictions to protect agricultural land use, regional biodiversity, soil integrity, and slope stability. The land use system in this scenario encompassed all herbaceous plant communities on the slope of up to 30° inclination. Most of them were pastures. Steeper slopes (> 30°) were excluded to prevent the adding of damage to the vegetation cover already caused by the trampling effect of grazing cattle. In this scenario, the total grassland area for the study area was 3312 ha, of which 599 ha was hay meadows and 2713 ha was pastures.

Figure 4.3: Haymaking in the study area (Photos by Giorgi Tedoradze).

The total AGB estimate was 9276 tons (1967 tons of hay meadows and 7309 tons of pastures). The mean productivity of hay meadows was 3.44 t/ha, and the average productivity of pastures ass 2.7 t/ha.

A considerable number of hay meadows were found in Sno, Akhaltsikhe, and Koseli, as well as in Stepantsminda and Gergeti. On the study area, the hay meadows in the surroundings of Stepantsminda-Gergeti area occupied 106 ha. The mean productivity of hay meadows was 3.17 t/ha, total expected yield of 336 t of hay. Hay meadows around Sno, Akhaltsikhe and Koseli occupied 127 ha, productivity was 3.28 t/ha, or 416 t expected hay harvest in total.

Figure 4.4: Grazing in the study area (Photos by Giorgi Tedoradze).

Hay meadow area was the least around Phansheti and Tsdo (20 and 24 ha, respectively), although here the productivity per hectare was high 3.75 and 4.25 t/ha with corresponding estimates of the total yield of 75 and 102 t/ha, respectively.

Pastures dominated the areas below the Jvari Pass in the most southern part of the Tergi valley around Kobi and Ukhati, as well as lower in the Tergi valley around Stepanthsminda and Gergeti. In the area of Kobi-Ukhati pastures occupied 643 ha, mean productivity was 2.68 t/ha and the total expected hay harvest 1721 t. Pastures in the area around Stepantsminda and Gergeti occupied 614 ha, the mean productivity was 2.71 t/ha and the total expected harvest is 1661 t of hay. The Pastures occupied the least area (mean = 122) around Tsdo (118 ha), Kanobi (123 ha), and Sioni-Vardisubani (127 ha), and mean productivity was 3.26, 2.43 and 2.48 t/ha in Tsdo, Kanobi and Sioni-Vardisubani, respectively.

In the second (LIM-MAX) scenario, the ecological limits were loosened. In this scenario, the environmental barriers were weakened and consequently become tolerable. Land use in this scenario included all locations up to a 40° inclined slopes. The same hay meadows were included in this scenario, yet pastures increased by 44% as compared to the first scenario and amounted to 4844 ha (increment 2131 ha). Total pasture productivity was 14056 t (increment 6747 t), which is 48% more than in the previous scenario. The productivity of pastures was 2.9 t / h. In the second scenario, most of pasture areas were around Kobi-Ukhati (958 ha) and Stepantsminda-Gergeti (960 ha), and also the villages of Sno gorge (Koseli, Sno, Akhaltsikhe) with 965 hectare pastures. The productivity was 3.03, 2.87 and 2.94 t/ha found around Kobi-Ukati, Stepanthsminda-Gergeti and Koseli-Sno-Akhaltsikhe, respectively.

Area (ha) and DM biomass (t * a−1) for different land cover and land use (LCLU) types in 2015 and for scenarios PROT-REG, PROT-MAX and LIM-MAX, for the 17 study settlements. The area calculation was based on the LCLU pattern and the defined scenario maps. The biomass yield calculation for meadow and pasture were derived from the biomass model.

4.4 Discussion

Grassland productivity is closely related to temperature, seasonal distribution of precipitation, soil types, and topography (S. Nakhutsrishvili 1960; Martin et al. 2010; Hanauer et al. 2017; Tedoradze et al. 2020). In general, the growing season shortens with increasing altitude (Nagy and Grabherr 2009). Also, meadow productivity is often directly related to the distribution of fertile soils, mostly *Cambic umbrisols* on volcanic plateaux. These fertile soils are restricted to loamy colluvium at the volcanic plateaus in the study area, for example, around the villages of Ukhati, Kanobi, Tsdo, as well as Pkhelshe and Goristsikhe (Hanauer et al. 2017). In the past, the fields around the settlements in Khevi were used as agricultural lands, now covered by pastures and hay meadow. These lands are fertilised naturally, with the faeces of grazing cattle and horses, and represent the highest hay production sites in the study area (Lichtenegger et al. 2006; Tephnadze et al. 2014; Magiera et al. 2017).

Scenario development is often used to analyse the interaction between humans and the environment, which helps understand how the situations might develop under different conditions (Van Notten et al. 2003). In our particular case, the scenarios should help find the desirable direction of land use change (Theissen et al. 2019). In addition, one of the prerequisites for sustainable land use is the detailed knowledge of the specific area and productivity of each site for determining its sustainable capacity for grazing, that is, the appropriate number of livestock per each pasture (Hancock 2006).

In the first scenario, the total area of pastures is 4.5 times larger than that of hay meadows, the corresponding total yield of aboveground biomass is 3.7 times higher. This disproportion is a major challenge for feeding the cattle in winter (Kavrishvili 1965; Theissen et al. 2019). Although a considerable area of hay meadows is found in Sno, Akhaltsikhe and Koseli, as well as in Stepantsminda and Gergeti, the disproportion becomes clear if we compare this area to that of pastures even around the same villages. The pastures of Stepantsminda and Gergeti exceed the hay meadows 5.8 times in area, while in Sno, Akhaltsikhe and Koseli the difference is three times. In this respect, the area ratio of hay meadows to pastures seems to be more balanced in Sioni-Vardisubani and Kanobi, where the ratios are 89/127 and 77/123, respectively, and the existing difference is almost entirely balanced by the high yields of the hay meadows as compared to pastures. The total yield ratios of hay meadows to pastures were 280/315 and 271/299 in Sioni-Vardisubani and Kanobi, respectively. The situation is dramatically different in Pansheti and Kobi-Ukhati where the area of pastures is nine and 11.5 times larger than that of hay meadows, respectively. Clearly, this can lead to a sharp difference between total yields from hay meadows and pastures in these areas (Appendix 4). The mean productivity of pastures and hay meadows including all sampled plots in Khevi were 2.7 t/ha and 3.44 t/ha, respectively.

In the second scenario, the difference was made by the fact that the ecological barriers were weakened and permitted the inclusion of more lands, and that the area of hay meadows did not increase at all since the added area did not contain any hay meadow. This naturally caused that the area of pastures to increase by 44% as compared to the first scenario. The average productivity of pastures was 2.9 t/ha, slightly higher than average (above), which must be due to the fact that in this scenario hay meadows were not separately analysed, but mixed with pasture data. However, it does not reach the mean productivity of hay meadows (3.44 t/h). Despite the increase in pasture area and total yield (both double up) (Appendix 4), it should be understood that the use of steep slopes for intensive agricultural purposes is undesirable as such land use can destroy vegetation cover, and, as a consequence, increase the risk of landslides, soil erosion and loss of species diversity. Here vegetation restoration is associated with additional challenges and is often impossible (Wiesmair et al. 2016; Tedoradze et al. 2020). Despite the increased area of pastures in the second scenario, it is still almost three times less than the area indicated by Sakhokia for the subalpine belt (ca. 16606 h). Which can be attributed in part to the fact that our study did not fully cover all settlements of Khevi, although in our study the areas with a considerable presence of stones and rock outcrops were excluded from the analyses (Sakhokia 1983; Magiera et al. 2017).

Some settlements have more potential for hay production, which makes it possible to feed cattle in winter, while other hay meadows are small and less productive, making it almost impossible to feed cattle in winter. This was compensated during the Soviet period by the use of winter pastures in Dagestan and Azerbaijan, but now these opportunities are limited (Didebulidze and Plachter 2002). However, to cope with this challenge, according to Theissen et al. (2019), it is potentially possible to sow alfalfa on a significant part of arable lands and exchange the obtained resources between villages (Theissen et al. 2019). This is especially true if we are guided by the conditions set out in the first scenario. On the other hand, according to the National Statistics Agency in 2014, the number of cattle in Kazbegi municipality is 2593, and the number of sheep is 4315 (NSOG 2016). Considering that cattle require 942.6 kg / head for one season (Shavgulidze, Bedoshvili, and Aurbacher 2017), we can calculate the number of cattle heads that can be fed with natural food resources available during the winter season. This suggests that even under the first scenario productivity does not allow for an increase in livestock unless more alfalfa is used (Heiny, Mamniashvili, and Leonhaeuser 2017; Shavgulidze, Bedoshvili, and Aurbacher 2017; Theissen et al. 2019).

Conclusions

- The mean productivity of hay meadows for Khevi is 3.44 t/ha, and the mean productivity of pastures is 2.7 t/ha.
- The total area of pastures is 4.5 times larger than the area of hay meadows, and total expected yield is 3.7 times higher.
- Lands appropriate for hay production are disproportionately distributed among the villages, which is a challenge for cattle feeding in winter conditions.
- It is possible to increase the existing number of livestock under sustainable land use conditions by growing alfalfa in arable lands.

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Appendix 1: The quantitative characteristics of the soil seed bank of Kazbegi (Central Greater Caucasus, Georgia).

Family Name	Number of species per family	Number of genera per family	Genera	Number of species per genera
Compositae	11	10	*Bellis*	1
			Cota	1
			Lapsana	1
			Leucanthemum	1
			Gnaphalium	1
			Tripleurospermum	2
			Artemisia	1
			Pilosella	1
			Cirsium	1
			Leontodon	1
Poaceae	7	6	*Agrostis*	2
			Bromus	1
			Melica	1
			Festuca	1
			Phleum	1
			Poa	1
Lamiaceae	7	7	*Salvia*	1
			Origanum	1
			Stachys	1
			Teucrium	1
			Thymus	1
			Clinopodium	1
			Prunella	1
Plantaginaceae	6	3	*Plantago*	3
			Veronica	2
			Linaria	1

Cyperaceae	6	2	*Carex*	4
			Luzula	2
Caryophyllaceae	5	3	*Arenaria*	1
			Cerastium	1
			Silene	3
Leguminosae	5	3	*Trifolium*	3
			Medicago	1
			Anthyllis	1
Rosaceae	3	3	*Potentilla*	1
			Alchemilla	1
			Rubus	1
Brassicaceae	3	3	*Arabis*	1
			Cardamine	1
			Draba	1
Caprifoliaceae	2	2	*Lomelosia*	1
			Scabiosa	1
Boraginaceae	2	1	*Myosotis*	1
		1	*Echium*	1
Crassulaceae	2	1	*Sedum*	2
Scrophulariaceae	2	1	*Verbascum*	2
Violaceae	2	1	*Viola*	2
Urticaceae	1	1	*Urtica*	1
Polygonaceae	1	1	*Rumex*	1
Hypericaceae	1	1	*Hypericum*	1
Betulaceae	1	1	*Betula*	1
Primulaceae	1	1	*Primula*	1
Juncaceae	1	1	*Juncus*	1
Apiaceae	1	1	*Daucus*	1
.	**70**	**54**	**.**	**70**

Appendix 2: Table of species detected in the soil seedbank sorted by frequency. Bold species are common species between soil seed bank and aboveground vegetation. Red list status refers to the Caucasian ecoregion, Solomon et al. 2013 (NE = Not Evaluated; LC = Least Concern; NT = Near Threatened, DD = Data Deficient; EN = Endangered). Dots within the table indicate non available data. PC = *Polygonum carneum* grassland, RM = *Rhinanthus minor* grassland, AC = *Astragalus captiosus* grassland. N = number of plots.

				PC grassland (n=26)			**RM grassland (n=33)**			**AC grassland (n=15)**		
Species name	**Red List Status**	**Frequency soil seed bank (%)**	**Frequency aboveground vegetation (%)**	Number of seedlings (m^2)	Frequency (%)	Mean ± Std. error	Number of seedlings (m^2)	Frequency (%)	Mean ± Std. error	Number of seedlings (m^2)	Frequency (%)	Mean ± Std. error
Lomelosia caucasica	.	43	41	5624	15	216.3 ± 116.7	16092	46	487.6 ± 140.5	10757	73	717.2 ± 246.4
Potentilla crantzii	.	30	38	3175	12	122.1 ± 76.5	13524	36	409.8 ± 171.7	12490	40	832.7 ± 447.7
Agrostis vinealis subsp. planifolia	NE	29	72	15652	39	602 ± 209.5	5435	27	164.7 ± 60	399	7	26.6 ± 26.6

Arenaria serpyllifolia	.	26	1	1166	8	44.8 ± 31.2	6894	21	208.9 ± 88.2	5829	60	388.6 ± 112.2
Plantago atrata	.	24	46	3754	12	144.4 ± 111	9607	33	291.1 ± 85.2	1618	20	107.8 ± 68.2
Sedum hispanicum	.	20	1	280	4	10.8 ± 10.8	3583	12	108.6 ± 61	8885	60	592.3 ± 187.5
Trifolium pratense	.	19	58	4968	19	191.1 ± 94	3185	21	96.5 ± 36.8	591	7	39.4 ± 39.4
Urtica dioica	.	19	1	5182	31	199.3 ± 69.8	1154	12	35 ± 19.4	326	7	21.7 ± 21.7
Carex sp.	.	17	.	6458	23	248.4 ± 134.6	3410	18	103.3 ± 42.8	.	.	.
Trifolium repens	.	17	10	3432	19	132 ± 59.6	3182	18	96.4 ± 37.1	219	7	14.6 ± 14.6
Bellis perennis	.	14	.	922	8	35.4 ± 26.5	4697	24	142.3 ± 56.1	.	.	.
Cota triumfetti	.	13	1	1932	8	74.3 ± 51.9	3939	18	119.4 ± 48.6	555	7	37 ± 37
Luzula sp.	.	11	.	7752	19	298.2 ± 135.3	4043	9	122.5 ± 100.1	.	.	.

Agrostis capillaris	.	10	24	2719	15	104.6 ± 55.7	1599	6	48.4 ± 37.9	296	7	19.7 ± 19.7
Arabis sp.	.	10	.	966	4	37.2 ± 37.2	4569	15	138.5 ± 72.4	307	7	20.5 ± 20.5
Bromus variegatus	.	10	96	352	4	13.6 ± 13.6	4727	18	143.2 ± 59.6	.	.	.
Lapsana communis	.	10	.	1406	12	54.1 ± 31.1	2496	12	75.6 ± 40.7	.	.	.
Medicago lupulina	.	10	3	540	4	20.8 ± 20.8	735	3	22.3 ± 22.3	10319	33	688 ± 305.3
Melica uniflora	.	10	.	2693	12	103.6 ± 71.6	1101	3	33.4 ± 33.4	1021	20	68 ± 37.3
Rumex acetosella	.	10	18	531	4	20.4 ± 20.4	3262	18	98.8 ± 45.8	.	.	.
Hypericum perforatum	.	9	22	.	.	.	4164	12	126.2 ± 82.4	4286	13	285.7 ± 258.6
Sedum spurium	NE	9	26	.	.	.	2545	15	77.1 ± 34.4	399	7	26.6 ± 26.6
Betula litwinowii	.	7	1	.	.	.	2102	15	63.7 ± 27.3	.	.	.

Festuca pratensis	.	7	8	1793	15	69 ± 33.6	.	.	.	496	7	33.1 ± 33.1
Carex humilis	.	6	23	2141	12	82.3 ± 47.5	.	.	.	450	7	30 ± 30
Leucanthemum vulgare	.	6	31	2691	12	103.5 ± 61.3	229	3	6.9 ± 6.9	.	.	.
Primula algida	.	6	1	887	8	34.1 ± 24.1	1818	6	55.1 ± 46.1	.	.	.
Verbascum sp.	.	6	.	426	4	16.4 ± 16.4	.	.	.	1004	20	67 ± 36.1
Cerastium fontanum subsp. vulgare	.	4	.	3118	8	119.9 ± 91.1	292	3	8.9 ± 8.9	.	.	.
Gnaphalium supinum	.	4	.	.	.	.	.	.	.	759	20	50.6 ± 28.6
Phleum alpinum	.	4	12	483	4	18.6 ± 18.6	611	6	18.5 ± 13	.	.	.
Plantago major	.	4	1	1064	12	40.9 ± 23	.	.	.	.	.	.
Salvia verticillata	.	4	19	.	.	.	2394	6	72.5 ± 51	326	7	21.7 ± 21.7

Trifolium ambiguum	.	4	66	1110	8	42.7 ± 29.8	266	3	8.1 ± 8.1	.	.	.
Tripleurospermum inodorum	.	4	.	1117	4	43 ± 43	684	3	20.7 ± 20.7	307	7	20.5 ± 20.5
Veronica beccabunga	.	4	.	.	.	.	1123	6	34 ± 26.9	1699	7	113.3 ± 113.3
Artemisia absinthium	.	3	5	1283	4	49.4 ± 49.4	.	.	.	1149	7	76.6 ± 76.6
Cardamine sp.	.	3	.	5197	8	199.9 ± 182.5	.	.	.	.	.	.
Juncus tenuis	.	3	.	.	.	.	.	.	.	670	13	44.7 ± 30.5
Myosotis alpestris	.	3	57	.	.	.	.	.	.	954	13	63.6 ± 44.7
Origanum vulgare	.	3	.	1707	4	65.6 ± 65.6	.	.	.	1699	7	113.3 ± 113.3
Pilosella piloselloides	.	3	3	280	4	10.8 ± 10.8	373	3	11.3 ± 11.3	.	.	.
Scabiosa bipinnata	.	3	24	.	.	.	373	3	11.3 ± 11.3	399	7	26.6 ± 26.6

Silene wallichiana	.	3	15	.	.	.	507	6	15.4 ± 10.8	.	.	.
Stachys annua	.	3	3	.	.	.	1058	6	32 ± 23.3	.	.	.
Teucrium chamaedrys	LC	3	5	.	.	.	740	6	22.4 ± 15.6	.	.	.
Thymus collinus	NE	3	50	454	4	17.5 ± 17.5	.	.	.	363	7	24.2 ± 24.2
Viola arvensis	.	3	.	.	.	.	813	6	24.6 ± 17.3	.	.	.
Viola canina	.	3	.	1327	8	51 ± 37.5	.	.	.	.	.	.
Alchemilla sericata	NE	1	28	443	4	17 ± 17	.	.	.	.	.	.
Anthyllis variegata	NE	1	57	.	.	.	278	3	8.4 ± 8.4	.	.	.
Carex panicea	.	1	1	1782	4	68.5 ± 68.5	.	.	.	.	.	.
Carex tristis	.	1	12	3830	4	147.3 ± 147.3	.	.	.	.	.	.

Cirsium obvallatum	.	1	41	.	.	.	.	.	.	181	7	12.1 ± 12.1
Clinopodium acinos	.	1	.	.	.	.	684	3	20.7 ± 20.7	.	.	.
Daucus carota	.	1	.	.	.	.	231	3	7 ± 7	.	.	.
Draba hispida	NE	1	1	.	.	.	.	.	.	326	7	21.7 ± 21.7
Echium rubrum	.	1	11	.	.	.	229	3	6.9 ± 6.9	.	.	.
Leontodon hispidus	.	1	39	.	.	.	505	3	15.3 ± 15.3	.	.	.
Linaria genistifolia	VU B1abi	1	.	.	.	.	.	.	.	296	7	19.7 ± 19.7
Luzula spicata	.	1	4	3348	4	128.8 ± 128.8	.	.	.	.	.	.
Plantago media	.	1	7	531	4	20.4 ± 20.4	.	.	.	.	.	.
Poa alpina	.	1	12	.	.	.	684	3	20.7 ± 20.7	.	.	.

Prunella vulgaris	.	1	1	1116	4	42.9 ± 42.9	.	.	.	.	.	.
Rubus idaeus	.	1	.	.	.	.	269	3	8.1 ± 8.1	.	.	.
Silene otites	.	1	.	.	.	.	498	3	15.1 ± 15.1	.	.	.
Silene ruprechtii	.	1	45	.	.	.	256	3	7.8 ± 7.8	.	.	.
Tripleurospermum transcaucasicum	.	1	.	.	.	.	.	.	.	363	7	24.2 ± 24.2
Verbascum pyramidatum	.	1	3	.	.	.	.	.	.	363	7	24.2 ± 24.2
Veronica peduncularis	.	1	.	.	.	.	735	3	22.3 ± 22.3	.	.	.

Appendix 3: Environmental features of the three grassland types *Polygonum carneum* grassland (PC), *Rhinanthus minor* grassland (RM), and *Astragalus captiosus* grassland (AC). Superscript letters indicate homogeneous groups in mean rank multiple comparison tests (Nemeneyi Test) after Kruskal–Wallis ANOVA ($p < 0.05$).

Environmental Features	PC grassland (n=26)	RM grassland (n=33)	AC grassland (n=15)
Physical landscape data	Mean ± St error	Mean ± St error	Mean ± St error
Altitude (m)	1986 ± 24.4	2006.4 ± 24.6	1938.9 ± 22.7
Slope (^{0})	25.2 ± 1.6	27.2 ± 1.7	27.8 ± 1.4
Northness	0.4 ± 0.1 ^{a}	-0.2 ± 0.1 ^{b}	-0.5 ± 0.1 ^{b}
Eastness	0.3 ± 0.1	0.3 ± 0.1	-0.2 ± 0.2
NDVI	0.7 ± 0.01 ^{a}	0.7 ± 0.01 ^{a}	0.6 ± 0.02 ^{b}
Vegetation			
Total vegetation cover (%)	88.5 ± 2.5	82.3 ± 2.8	70.3 ± 5.5
Cover cryptogams (%)	50.6 ± 3.6 ^{a}	33.4 ± 3.3 ^{b}	26.9 ± 3.5 ^{b}
Cover litter (%)	51.7 ± 4.8 ^{a}	29 ± 3 ^{b}	21.6 ± 2.5 ^{b}
Cover bare rock (%)	7 ± 2	6.2 ± 1.6	8.4 ± 2.8
Cover open soil (%)	2.8 ± 1.1 ^{a}	9.9 ± 1.8 ^{b}	15.6 ± 3.7 ^{b}
Min height (cm)	11.1 ± 1.4 ^{a}	7.5 ± 0.6 ^{b}	5.6 ± 0.6 ^{b}
Mean height (cm)	47.8 ± 2.8 ^{b}	44.9 ± 2.2 ^{b}	30.9 ± 2.6 ^{a}
Maximum height (cm)	97.6 ± 5.5 ^{b}	85.9 ± 3.5 ^{b}	67.5 ± 3.3 ^{a}
Cryptogams height (cm)	7.4 ± 0.7 ^{a}	5.2 ± 0.5 ^{b}	5.1 ± 0.5 ^{b}

Litter height (cm)	6.6 ± 0.6 [a]	5.1 ± 0.3 [b]	4 ± 0.3 [b]
Biomass			
Grass biomass (%)	34.1 ± 2.7 [b]	41.6 ± 2.2 [a]	33.6 ± 4.3 [b]
Herbs biomass (%)	45.5 ± 2.8 [a]	27.7 ± 2.5 [b]	29.5 ± 4.1[b]
Legumes biomass (%)	11.2 ± 1.5 [a]	20.8 ± 2.3 [b]	21.6 ± 3.3 [b]
Species number & Eveness			
Aboveground species number	34.2 ± 0.8	34.9 ± 0.8	30.9 ± 1.3
Aboveground Evenness	1 ± 0.0017	1 ± 0.0015	1 ± 0.0021
Belowground Species number	4 ± 0.4	5 ± 0.6	5.1 ± 0.6
Belowground Evenness	0.9 ± 0.038	0.9 ± 0.041	0.8 ± 0.064
Seed density	3935.7 ± 616.4	3599.8 ± 544.4	4412.3 ± 883.1
Soil			
Roots weight (%)	4 ± 0.4 [a]	2.7 ± 0.2 [b]	1.8 ± 0.2 [b]
Soil depth (cm)	14.3 ± 1.2 [a]	10.8 ± 0.8 [b]	7.9 ± 1 [b]
Skeleton content (%)	14.9 ± 1.9 [a]	22.3 ± 2 [b]	20.9 ± 1.9 [b]
pH H_2O	5.8 ± 0.113 [a]	6.2 ± 0.067 [b]	6.4 ± 0.071 [b]
Corg (%)	8.8 ± 0.6 [a]	5.6 ± 0.5 [b]	3.5 ± 0.5 [b]
Norg (%)	0.8 ± 0.1[a]	0.5 ± 0.04 [b]	0.4 ± 0.04 [b]
C/N	10.8 ± 0.2 [b]	10.2 ± 0.2 [b]	8.7 ± 0.4 [a]
Kcal (mg/kg)	93.3 ± 18.7 [b]	75.9 ± 7.3 [b]	37.3 ± 5.3 [a]
Pcal (mg/kg)	19.1 ± 2.1 [b]	13.3 ± 2.4 [b]	6.1 ± 1.2 [a]
Mgcal (mg/k)	377.7 ± 44	372.4 ± 30.3	282.1 ± 20.3

Appendix 4: Area (ha) and DM biomass (t * a^{-1}) for different land cover and land use (LCLU) types in 2015 and for scenarios PROT-REG, PROT-MAX and LIM-MAX, for the 17 study settlements. The area calculation was based on the LCLU pattern and the defined scenario maps. The biomass yield calculation for meadow and pasture were derived from the biomass model. Theissen et al. 2019.

Context	Size & Quantity	Land cover & land use	Settlement									
			Gergeti, Stepantsminda	Pansheti	Koseli, Sno, Akhaltsikhe	Tsdo	Sioni, Vardisubani	Pkhelshe, Goristsikhe	Kanobi	Kobi[a], Almasiani[a], Nogkau[a], Ukhati[b]	Juta	Total
			1765 m a.s.l.	1770 m a.s.l.	1770 m a.s.l.	1780 m a.s.l.	1875 m a.s.l.	1900 m a.s.l.	1985 m a.s.l.	[a]2,010 m a.s.l.; [b]2,190 m a.s.l.	2160 m a.s.l.	
Condition 2015	Area [ha]	Forest & shrubland	371	2	239	80	43	16	8	262	128	1149
		Arable land	10	1	4	1	4	5	4	18	1	48
		Orchard	48	10	31	2	49	17	4	7	4	172
		Meadow	114	20	138	31	91	113	92	69	103	771
		Pasture	1214	348	955	172	187	414	302	1064	719	5375
		Sparsely to non vegetated	400	132	408	33	60	102	82	183	73	1473
		Settlement	117	12	42	2	58	28	6	12	6	284
		Road	34	3	13	4	15	3	9	20	3	109
		Total	2308	528	1835	325	507	698	507	1635	1037	9381
Scenarios PROT-REG & PROT-MAX	Area [ha]	Meadow (< 30°)	106	20	127	24	89	54	77	56	46	599

		Pasture (< 30°)	614	178	379	118	127	223	123	643	308	2713
		Total	720	198	506	142	216	277	200	699	354	3312
	Biomass [t DM * a-1]	Meadow	336	75	416	102	280	200	271	145	142	1967
		Pasture	1661	437	1041	385	315	576	299	1721	874	7309
		Total	1997	512	1457	487	595	776	570	1866	1016	9276
		Meadow for one ha (< 30°)	3.17	3.75	3.28	4.25	3.15	3.7	3.52	2.59	3.09	30.5
		Pasture for one ha (< 30°)	2.71	2.46	2.75	3.26	2.48	2.58	2.43	2.68	2.84	24.19
Scenario LIM-MAX	**Area [ha]**	Pasture (< 40°)	960	328	965	170	160	358	257	958	688	4844
		Total	960	328	965	170	160	358	257	958	688	4844
	Biomass [t DM * a-1]	Pasture	2904	861	2837	567	442	972	792	2749	1932	14056
		Pasture for one ha (< 40°)	3.03	2.63	2.94	3.34	2.76	2.72	3.08	2.87	2.81	26.18
		Total	2904	861	2837	567	442	972	792	2749	1932	14056

[a] indicates settlements at 2,010 meter above see level.

[b] indicates the settlement at 2,190 m a.s.l.

Annex 1: The list of recorded 269 species in the pasture and hay meadow communities of Khevi. Species names are given according to Vascular Plants of Georgia - A Nomenclatural Checklist (first and second editions) (Gagnidze 2005, Davlianidze et al. 2018) and have been harmonized with online international plant databases ("Euro+Med" 2006; "The Plant List" 2013; "GBIF.Org" 2020; "IPNI" 2021). Chorotypes are defined according to the use of flora of the different countries and regions (Komarov 1934-1960; Takhtajan 1954-2011, 2003-2012; Tutin et al. 1964-1993; Davis 1965-2001; Ketskhoveli, Kharadze, and Gagnidze 1971-2011) and online international plant databases ("GBIF.org" 2020; "Euro+Med" 2006; "World Flora Online" 2021). Plant life formes are defined by using LEDA Traitbase (Klotz et al. 2002). Dots within the table indicate non available data. Caucasian Endemic - CE, Georgian Endemic - GE, Hemicryptophyte - H, Cryptophyte - Cr, Chamaephyte - Ch, Therophyte - Th, Geophyte - G, Phanerophyte - Ph, Liana - L, Vascular semi-parasite - Vsp, Euras. step. - Eurasian steppe, Med. - Mediterranean, Cauc. - Caucasian, Tur. - Turanian, Anat. - Anatolian, E. - East, N. - North, S. - South, W. - West, As. - Asian.

N	Family	Species	Chorotypes	Solomon et al. 2013	Life form	Gagnidze (2005)	Davlianidze et al. 2018
1	Amaranthaceae	*Chenopodium album* L.	*Cosmopolitan*	.	Th	.	.
2	Apiaceae	*Astrantia trifida* Hoffm.	Caucasian	NE	H	CE	CE
3	Apiaceae	*Astrodaucus orientalis* (L.) Drude	Caucaso-SW Asian (conditionally)	.	Th	.	.
4	Apiaceae	*Bupleurum falcatum* subsp. *polyphyllum* (Ledeb.) H.Wolff	Caucasian (with E. Anat. irradiation)	.	H	.	.
5	Apiaceae	*Carum carvi* L.	Palearctic	.	H	.	.
6	Apiaceae	*Carum caucasicum* (M. Bieb.) Boiss.	Caucaso-SW Asian	.	H	.	.
7	Apiaceae	*Chaerophyllum roseum* M.Bieb.	Caucasian	NE	H	CE	CE
8	Apiaceae	*Chamaesciadium acaule* (M.Bieb.) Boiss.	Caucasian (with irradiation)	.	Ch	.	.
9	Apiaceae	*Heracleum asperum* (Hoffm.) M. Bieb.	Caucasian	NE	H	CE	CE
10	Apiaceae	*Pastinaca armena* Fisch. & C.A.Mey.	Caucasian	NE	H	.	.
11	Apiaceae	*Pimpinella rhodantha* Boiss.	Caucasian (with Anat. irradiation)	.	H	.	.
12	Apiaceae	*Pimpinella saxifraga* L.	Palearctic (West Palearctic)	.	H	.	.

13	Apiaceae	*Seseli transcaucasicum* (Schischk.) Pimenov & Sdobnina	Euro-SW Asian	.	H	.	.
14	Asparagaceae	*Muscari armeniacum* Leichtlin ex Baker	Caucaso-East Mediterranean	.	G (Cr)	.	.
15	Asteraceae	*Hieracium laevigatum* Willd.	Euro-Mediterranean	.	H	.	.
16	Asteraceae	*Lactuca racemosa* Willd.	Caucasian	NE	H	.	.
17	Asteraceae	*Achillea arabica* Kotschy	Med.-S.W. As.-Tur. (E. Med.-S.W. As.-Tur.)	.	H	.	.
18	Asteraceae	*Achillea millefolium* L.	Holarctic	.	H	.	.
19	Asteraceae	*Antennaria caucasica* Boriss.	Caucaso-Anatolian	.	Ch	.	.
20	Asteraceae	*Artemisia absinthium* L.	Palearctic	.	Ch	.	.
21	Asteraceae	*Artemisia vulgaris* L.	Palearctic	.	H	.	.
22	Asteraceae	*Aster alpinus* L.	Holarctic	.	H	.	.
23	Asteraceae	*Aster amellus subsp. ibericus* (Steven) V.E.Avet.	Caucasian	.	H	.	.
24	Asteraceae	*Centaurea phrygia subsp. abbreviata* (K.Koch) Dostál	Caucaso-Euxinian	.	H	.	.
25	Asteraceae	*Centaurea phrygia subsp. salicifolia* (M.Bieb. ex Willd.) Mikheev	Caucaso-Euxinian	.	H	.	.
26	Asteraceae	*Cirsium caucasicum* (Adams) Petr.	Caucaso-Anatolian	NE	H	.	.
27	Asteraceae	*Cirsium echinus* (M.Bieb.) Hand.-Mazz.	Caucaso-SW Asian	.	H	.	.
28	Asteraceae	*Cirsium obvallatum* (M.Bieb.) Fisch.	Caucasian (with irradiation)	NE	H	.	.
29	Asteraceae	*Cirsium pugnax* Sommier & Levier	Caucasian	LC	H	CE	.
30	Asteraceae	*Cirsium simplex* C.A.Mey.	Caucasian	NE	H	.	.
31	Asteraceae	*Cota triumfetti* (L.) J.Gay	Euro-Mediterranean-SW Asian	.	H	.	.
32	Asteraceae	*Cyanus cheiranthifolius* (Willd.) Soják	Caucasian (with irradiation)		H	.	.
33	Asteraceae	*Doronicum macrophyllum* Fisch.	Caucasian	.	H	.	.
34	Asteraceae	*Erigeron acris* L.	Holarctic	.	H	.	.
35	Asteraceae	*Erigeron alpinus* L.	Euro-Mediterranean	.	H	.	.
36	Asteraceae	*Erigeron caucasicus* Steven	Caucasian	.	H	.	.
37	Asteraceae	*Hieracium umbellatum* L.	Holarctic	.	H	.	.
38	Asteraceae	*Inula orientalis* Lam.	Caucaso-Anatolian	.	H	.	.
39	Asteraceae	*Leontodon caucasicus* (M.Bieb.) Fisch.	Caucaso-Euxinian	.	H	CE	.
40	Asteraceae	*Leontodon hispidus* L.	Euro-Mediterranean	.	H	.	.
41	Asteraceae	*Leucanthemum vulgare* Lam.	Palearctic	.	H	.	.
42	Asteraceae	*Pilosella officinarum* Vaill.	Euro-Mediterranean	.	H	.	.

43	Asteraceae	*Pilosella piloselloides* (Vill.) Soják	Euro-SW Asian (conditionally)	.	H	.	.
44	Asteraceae	*Psephellus dealbatus* (Willd.) K.Koch	Caucasian	NE	H	.	.
45	Asteraceae	*Solidago virgaurea* L.	Palearctic	.	H	.	.
46	Asteraceae	*Tanacetum coccineum* (Willd.) Grierson	Caucasian	.	H	.	.
47	Asteraceae	*Tanacetum macrophyllum* (Waldst. & Kit.) Sch.Bip.	Caucaso-Euxinian	.	H	.	.
48	Asteraceae	*Tanacetum vulgare* L.	Palearctic	.	H	.	.
49	Asteraceae	*Taraxacum confusum* Schischk.	Caucasian	NE	H	CE	CE
50	Asteraceae	*Taraxacum campylodes* G.E.Haglund (Taraxacum officinale Weber ex Wiggins)	Palearctic	.	H	.	.
51	Asteraceae	*Taraxacum stevenii* (Spreng.) DC.	Caucaso-SW Asian	.	H	.	.
52	Asteraceae	*Tragopogon filifolius* Rehmann ex Boiss.	Caucasian	LC	H	CE	CE
53	Asteraceae	*Tragopogon reticulatus* Boiss. & A.Huet	Caucaso-SW Asian	.	H	.	.
54	Betulaceae	*Betula litwinowii* Doluch.	Hyrcano-Euxine	.	Ph	.	.
55	Boraginaceae	*Echium rubrum* Forssk.	Euro-Mediterranean	.	H	.	.
56	Boraginaceae	*Echium vulgare* L.	Holarctic	.	H	.	.
57	Boraginaceae	*Eritrichium caucasicum* (Albov) Grossh.	Caucasian	NT	H	CE	CE
58	Boraginaceae	*Myosotis alpestris* F.W.Schmidt	Euro-SW Asian	.	H	.	.
59	Boraginaceae	*Myosotis arvensis* (L.) Hill	Palearctic	.	Th	.	.
60	Boraginaceae	*Onosma caucasica* Levin ex Popov	Caucasian	NE	H	.	.
61	Brassicaceae	*Alyssum murale* Waldst. & Kit.	Med.-S.W. As.-Euras.step.	.	H	.	.
62	Brassicaceae	*Bunias orientalis* L.	Palearctic (conditionally)	.	H	.	.
63	Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.	Cosmopolitan	.	Th, H	.	.
64	Brassicaceae	*Descurainia sophia* (L.) Webb ex Prantl	Palearctic	.	Th	.	.
65	Brassicaceae	*Draba hispida* Willd.	Caucaso-Anatolian	NE	Ch	.	CE
66	Brassicaceae	*Draba siliquosa* M.Bieb.	Euro-Mediterranean-SW Asian	NE	Ch	.	CE
67	Brassicaceae	*Thlaspi perfoliatum* L.	Euro-Ancient Mediterranean	.	Th	.	.
68	Campanulaceae	*Asyneuma campanuloides* (M.Bieb. ex Sims) Bornm.	Caucasian	NE	H	CE	CE
69	Campanulaceae	*Campanula bellidifolia* Adams	Caucasian	NT	H	CE	CE
70	Campanulaceae	*Campanula collina* Sims	Caucasian	NE	H	.	CE
71	Campanulaceae	*Campanula glomerata subsp. caucasica* (Trautv.) Ogan.	Caucasian	NE	H	.	CE
72	Campanulaceae	*Campanula rapunculoides* L.	Palearctic	.	H	.	.

73	Campanulaceae	*Campanula sibirica subsp. hohenackeri* (Fisch. & C.A.Mey.) Damboldt	Caucaso-SW Asian	NE	Th	.	CE
74	Campanulaceae	*Campanula stevenii* M.Bieb.	Palearctic (conditionally)	.	H	.	.
75	Campanulaceae	*Campanula tridentata* Schreb.	Caucaso-Anatolian		H or Ch	.	CE
76	Caprifoliaceae	*Cephalaria gigantea* (Ledeb.) Bobrov	Caucasian	NE	H	CE	CE
77	Caprifoliaceae	*Lomelosia caucasica* (M.Bieb.) Greuter & Burdet	Caucasian	NE	H	.	CE
78	Caprifoliaceae	*Scabiosa bipinnata* K. Koch	Caucasian	.	H	.	.
79	Caprifoliaceae	*Valeriana officinalis* L.	Palearctic	.	H	.	.
80	Caryophyllaceae	*Arenaria serpyllifolia* L.	Palearctic	.	Th	.	.
81	Caryophyllaceae	*Cerastium arvense* L.	Holarctic	.	Ch	.	.
82	Caryophyllaceae	*Cerastium purpurascens* Adams	Caucaso-SW Asian	.	Ch	.	.
83	Caryophyllaceae	*Dianthus caucaseus* Sims	Caucasian	LC	H	CE	CE
84	Caryophyllaceae	*Dianthus cretaceus* Adams	Caucasian	.	H	.	.
85	Caryophyllaceae	*Dianthus ruprechtii* Schischk. ex Grossh.	Caucasian	NE	H	.	CE
86	Caryophyllaceae	*Minuartia circassica* (Albov) Woronow ex Grossh.	Caucasian	NE	Ch	.	.
87	Caryophyllaceae	*Minuartia oreina* Schischk.	Euro-SW Asian	.	Ch	.	.
88	Caryophyllaceae	*Silene italica* (L.) Pers.	Euro-Mediterranean-SW Asian	.	H	.	.
89	Caryophyllaceae	*Silene latifolia subsp. alba* (Mill.) Greuter & Burdet	Palearctic	.	H	.	.
90	Caryophyllaceae	*Silene linearifolia* Otth	Caucasian	.	H	CE	CE
91	Caryophyllaceae	*Silene ruprechtii* Schischk.	Caucaso-SW Asian	.	H	.	.
92	Caryophyllaceae	*Silene wallichiana Klotzsch* (Silene vulgaris (Moench) Garcke)	Palearctic	.	H or Ch	.	.
93	Caryophyllaceae	*Silene compacta* Fisch.	Mediterranean-SW Asian	.	H or Ch	.	.
94	Celastraceae	*Parnassia palustris* L.	Holarctic	.	H	.	.
95	Cistaceae	*Helianthemum nummularium* (L.) Mill.	Euro-Mediterranean	.	Ch	.	.
96	Cistaceae	*Helianthemum nummularium subsp. grandiflorum* (Scop.) Schinz & Thell.	Euro-Mediterranean	.	Ch	.	.
97	Crassulaceae	*Sedum acre* L.	Euro-Mediterranean	.	Ch	.	.
98	Crassulaceae	*Sedum hispanicum* L.	Mediterranean-SW Asian	.	Ch	.	.
99	Crassulaceae	*Sedum spurium* M.Bieb.	Caucaso-SW Asian	NE	Ch	.	CE
100	Crassulaceae	*Sempervivum caucasicum* Rupr. ex Boiss.	Caucasian	NE	Ch	CE	CE
101	Crassulaceae	*Sempervivum pumilum* M.Bieb.	Caucasian	NE	Ch	CE	CE
102	Cyperaceae	*Carex humilis* Leyss.	Euro-Siberian	.	H	.	.

103	Cyperaceae	*Carex medwedewii* Leskov	Caucaso-SW Asian	.	G (Cr) or H	.	.
104	Cyperaceae	*Carex panicea* L.	Euro-Siberian	.	G (Cr) or H	.	.
105	Cyperaceae	*Carex tristis* M.Bieb.	Caucaso-Anatolian	.	G (Cr) or H	.	.
106	Cyperaceae	*Kobresia macrolepis* Meinsh.	Caucasian	.	H	.	.
107	Ericaceae	*Vaccinium myrtillus* L.	Holarctic	.	Ch	.	.
108	Euphorbiaceae	*Euphorbia iberica* Boiss.	Caucaso-SW Asian	NE	H or Ch	.	.
109	Euphorbiaceae	*Euphorbia macroceras* Fisch. & C.A.Mey.	Caucasian	LC	H or Ch	CE	CE
110	Euphorbiaceae	*Euphorbia oblongifolia* (K.Koch) K.Koch	Hyrcano-Euxine	.	H	.	.
111	Euphorbiaceae	*Euphorbia squamosa* Willd.	Hyrcano-Euxine	.	H	.	.
112	Fabaceae	*Anthyllis variegata* Grossh.	Caucasian	NE	H	.	.
113	Fabaceae	*Anthyllis vulneraria subsp. boissieri* (Sagorski) Bornm.	Caucaso-Euxinian	.	H	CE	CE
114	Fabaceae	*Astracantha denudata* (Steven) Podlech	Caucasian	NE	Ph (nano)	.	.
115	Fabaceae	*Astragalus captiosus* Boriss.	Caucasian	NE	H	CE	CE
116	Fabaceae	*Lathyrus pratensis* L.	Palearctic	.	H	.	.
117	Fabaceae	*Lotus corniculatus* L.	Palearctic	.	H	.	.
118	Fabaceae	*Medicago glomerata* Balb.	Mediterranean-SW Asian (conditionally)		H	CE	CE
119	Fabaceae	*Medicago lupulina* L.	Palearctic	.	Th	.	.
120	Fabaceae	*Melilotus officinalis* (L.) Pall.	Palearctic	.	H	.	.
121	Fabaceae	*Onobrychis biebersteinii* Širj.	Caucasian	NE	H	CE	CE
122	Fabaceae	*Securigera varia* (L.) Lassen	Euro-Mediterranean-SW Asian	.	H	.	.
123	Fabaceae	*Trifolium alpestre* L.	Euro-SW Asian	.	G (Cr)	.	.
124	Fabaceae	*Trifolium ambiguum* M.Bieb.	Euro-SW Asian	.	H	.	.
125	Fabaceae	*Trifolium arvense* L.	Palearctic	.	Th	.	.
126	Fabaceae	*Trifolium aureum* Pollich	Palearctic	.	Th	.	.
127	Fabaceae	*Trifolium canescens* Willd.	Caucaso-SW Asian	.	H	.	.
128	Fabaceae	*Trifolium fontanum* Bobrov	Caucasian	NE	H	CE	CE
129	Fabaceae	*Trifolium pratense* L.	Palearctic	.	H	.	.
130	Fabaceae	*Trifolium repens* L.	Palearctic	.	H	.	.
131	Fabaceae	*Trifolium spadiceum* L.	Euro-Siberian	.	Th, H	.	.
132	Fabaceae	*Trifolium trichocephalum* M.Bieb.	Caucasian (with irradiation)	.	H	.	.

133	Fabaceae	*Vicia alpestris* Steven	Caucaso-Anatolian	NE	L	.	.
134	Fabaceae	*Vicia tenuifolia subsp. variabilis* (Freyn & Sint.) Dinsm.	Caucaso-SW Asian	.	L	.	.
135	Gentianaceae	*Gentiana aquatica* L.	Holarctic	.	Th	.	.
136	Gentianaceae	*Gentiana cruciata* L.	Euro-Siberian	.	H	.	.
137	Gentianaceae	*Gentiana septemfida* Pall.	Caucaso-Anatolian	.	H	.	.
138	Gentianaceae	*Gentianella caucasea* (Lodd. ex Sims) Holub	Caucaso-Anatolian	.	H	.	.
139	Gentianaceae	*Swertia iberica* Fisch. & C.A. Mey.	Caucasian	NE	H	CE	.
140	Geraniaceae	*Geranium ibericum* Cav.	Hyrcano-Euxine	NE	H	.	.
141	Geraniaceae	*Geranium platypetalum* Fisch. & C.A.Mey.	Caucasian	NE	H	.	.
142	Geraniaceae	*Geranium sanguineum* L.	Euro-Mediterranean	.	G (Cr)	.	.
143	Hypericaceae	*Hypericum caucasicum* (Woronow) Gorschk.	Caucaso-Euxinian	.	H	.	.
144	Hypericaceae	*Hypericum linarioides* Bosse	Mediterranean-SW Asian	.	H	.	.
145	Hypericaceae	*Hypericum perforatum* L.	Palearctic	.	H	.	.
146	Iridaceae	*Gladiolus tenuis* M.Bieb.	Caucaso-Euxinian (conditionally)	.	G (Cr)	.	.
147	Juncaceae	*Luzula multiflora* (Ehrh.) Lej.	Holarctic	.	H	.	.
148	Juncaceae	*Luzula spicata* (L.) DC.	Holarctic	.	H	.	.
149	Juncaceae	*Luzula stenophylla* Steud.	Caucaso-SW Asian	NE	H	.	.
150	Lamiaceae	*Betonica macrantha* k. Koch	Caucasian	.	H	.	.
151	Lamiaceae	*Origanum vulgare* L.	Palearctic	.	H	.	.
152	Lamiaceae	*Prunella vulgaris* L.	Holarctic	.	H	.	.
153	Lamiaceae	*Salvia verticillata* L.	Euro-Mediterranean-SW Asian	.	H	.	.
154	Lamiaceae	*Scutellaria oreophila* Grossh.	Caucasian	NE	H	CE	CE
155	Lamiaceae	*Stachys annua* (L.) L.	Palearctic (West Palearctic)	.	Th	.	.
156	Lamiaceae	*Teucrium chamaedrys subsp. nuchense* (K.Koch) Rech.f.	Caucasian	NE	H or Ch	CE	CE
157	Lamiaceae	*Teucrium orientale* L.	Caucaso-SW Asian	.	H	.	.
158	Lamiaceae	*Thymus collinus* M.Bieb.	Caucasian	NE	Ch	CE	CE
159	Lamiaceae	*Thymus nummularius* M.Bieb.	Caucasian	NE	Ch	.	CE
160	Lamiaceae	*Ziziphora puschkinii* Adams	Caucasian	NE	Ch	CE	CE
161	Liliaceae	*Fritillaria collina* Adams	Caucasian	NE	G (Cr)	.	.
162	Linaceae	*Linum austriacum* L.	Med.-S.W. As.-Euras.step.	.	Ch	.	.

163	Linaceae	*Linum hypericifolium* Salisb.	Caucasian	NE	H	.	.
164	Melanthiaceae	*Veratrum lobelianum* Bernh.	Palearctic	.	G (Cr)	.	.
165	Onagraceae	*Epilobium colchicum* Albov	Caucasian	.	H	.	.
166	Onagraceae	*Epilobium dodonaei* Vill.	Euro-Mediterranean-SW Asian	.	H or Ch	.	.
167	Orchidaceae	*Gymnadenia conopsea* (L.) R.Br.	Palearctic	.	G (Cr)	.	.
168	Orchidaceae	*Herminium monorchis* (L.) R.Br.	Palearctic	.	G (Cr)	.	.
169	Orchidaceae	*Platanthera bifolia* (L.) Rich.	Euro-Siberian	.	G (Cr)	.	.
170	Orchidaceae	*Platanthera chlorantha* (Custer) Rchb.	Euro-Mediterranean	.	G (Cr)	.	.
171	Orobanchaceae	*Euphrasia caucasica* Juz.	Caucasian	NE	Vsp	CE	CE
172	Orobanchaceae	*Euphrasia hirtella* Jord. ex Reut.	Palearctic	.	Th	.	.
173	Orobanchaceae	*Orobanche alba* Stephan ex Willd.	Euro-Mediterranean-SW Asian	.	Th	.	.
174	Orobanchaceae	*Orobanche lutea* Baumg.	Euro-Mediterranean-SW Asian	.	Th	.	.
175	Orobanchaceae	*Pedicularis armena* Boiss. et Huet	Caucasian	.	Vsp	.	.
176	Orobanchaceae	*Pedicularis eriantha* (Boiss. & Buhse) T.N. Popova	Caucasian	.	Vsp	.	.
177	Orobanchaceae	*Pedicularis condensata* M.Bieb.	Caucaso-SW Asian	.	Vsp	.	.
178	Orobanchaceae	*Pedicularis sibthorpii* Boiss.	Caucaso-SW Asian	.	Vsp	.	.
179	Orobanchaceae	*Pedicularis wilhelmsiana* Fisch. ex M.Bieb.	Caucaso-SW Asian	NE	Vsp	.	.
180	Orobanchaceae	*Rhinanthus minor* L.	Euro-Siberian	.	Vsp	.	.
181	Orobanchaceae	*Rhinanthus vernalis* (N.W.Zinger) Schischk. & Serg.	Holarctic	.	Vsp	.	.
182	Orobanchaceae	*Rhynchocorys elephas* (L.) Griseb.	Mediterranean-SW Asian	.	H	.	.
183	Plantaginaceae	*Plantago atrata* Hoppe	Euro-Mediterranean	.	H	.	.
184	Plantaginaceae	*Plantago lanceolata* L.	Palearctic	.	H	.	.
185	Plantaginaceae	*Plantago major* L.	Holarctic	.	H	.	.
186	Plantaginaceae	*Plantago media* L.	Palearctic	.	H	.	.
187	Plantaginaceae	*Veronica arvensis* L.	Palearctic	.	Th	.	.
188	Plantaginaceae	*Veronica gentianoides* Vahl	Caucaso-SW Asian	.	H	.	.
189	Plantaginaceae	*Veronica petraea* (M. Bieb.) Steven	Caucasian	NE	Ch	CE	CE
190	Poaceae	*Agrostis capillaris* L.	Palearctic	.	H	.	.
191	Poaceae	*Agrostis vinealis subsp. planifolia* (K. Koch) Tzvelev	Caucaso-Anatolian	NE	H	.	.
192	Poaceae	*Alopecurus glacialis* K.Koch	Caucasian	.	H	.	.

193	Poaceae	*Anthoxanthum odoratum* L.	Euro-Mediterranean	.	H	.	.
194	Poaceae	*Briza media* L.	Palearctic (West Palearctic)	.	H	.	.
195	Poaceae	*Bromus riparius* Rehmann	Euro-Mediterranean	.	H	.	.
196	Poaceae	*Bromus variegatus* M.Bieb.	Caucaso-SW Asian	.	H	.	.
197	Poaceae	*Calamagrostis arundinacea* (L.) Roth	Palearctic	.	H	.	.
198	Poaceae	*Deschampsia cespitosa* (L.) P.Beauv.	Holarctic		H	.	.
199	Poaceae	*Deschampsia flexuosa* (L.) Trin.	Holarctic	.	H	.	.
200	Poaceae	*Festuca arundinacea* Schreb.	Palearctic	.	H	.	.
201	Poaceae	*Festuca ovina* L.	Holarctic	.	H	.	.
202	Poaceae	*Festuca pratensis* Huds.	Palearctic	.	H	.	.
203	Poaceae	*Festuca rubra* L.	Holarctic	.	H	.	.
204	Poaceae	*Festuca valesiaca* Schleich. ex Gaudin	S.W. As.-Cauc.-Euras. step.	.	H	.	.
205	Poaceae	*Festuca varia* Haenke	Euro-Mediterranean	.	H	.	.
206	Poaceae	*Helictotrichon adzharicum* (Albov) Grossh.	Caucasian	NE	H	GE	CE
207	Poaceae	*Helictotrichon pubescens* (Huds.) Schult. & Schult.f.	Palearctic (West Palearctic)	.	H	.	.
208	Poaceae	*Hordeum brevisubulatum* (Trin.) Link	Palearctic (conditionally)	.	H	.	.
209	Poaceae	*Koeleria pyramidata* (Lam.) P.Beauv. (*Koeleria cristata* (L.) Pers.)	Palearctic	.	Th	.	.
210	Poaceae	*Koeleria eriostachya* Pancic (*Koeleria caucasica* (Domin) B. Fedtsch.)	Mediterranean-SW Asian		H	.	.
211	Poaceae	*Koeleria luerssenii* (Domin) Domin	Caucasian	NE	H	CE	CE
212	Poaceae	*Lolium rigidum* Gaudin	Mediterranean-SW Asian	.	Th	.	.
213	Poaceae	*Nardus stricta* L.	Holarctic	.	H	.	.
214	Poaceae	*Phleum alpinum* L.	Holarctic	.	H	.	.
215	Poaceae	*Phleum montanum* K.Koch	Mediterranean-SW Asian	.	H	.	.
216	Poaceae	*Phleum phleoides* (L.) H.Karst.	Palearctic	.	H	.	.
217	Poaceae	*Phleum pratense* L.	Palearctic	.	H	.	.
218	Poaceae	*Poa alpina* L.	Holarctic	.	H	.	.
219	Poaceae	*Poa pratensis* L.	Palearctic	.	G (Cr) or H	.	.
220	Poaceae	*Poa trivialis* L.	Palearctic	.	G (Cr) or H	.	.
221	Polygalaceae	*Polygala alpicola* Rupr.	Caucasian	NE	Ch	.	.
222	Polygalaceae	*Polygala anatolica* Boiss. & Heldr.	Caucaso-Euxinian	.	Ch	.	.

223	Polygonaceae	*Persicaria alpina* (All.) H.Gross	Palearctic	.	H	.	.
224	Polygonaceae	*Persicaria vivipara* (L.) Ronse Decr.	Holarctic	.	H	.	.
225	Polygonaceae	*Polygonum carneum* K. Koch	Caucaso-Anatolian	.	G (Cr)	.	.
226	Polygonaceae	*Polygonum cognatum* Meisn.	Caucaso-SW Asian	.	H	.	.
227	Polygonaceae	*Rumex acetosa* L.	Holarctic	.	H	.	.
228	Polygonaceae	*Rumex acetosella* L.	Palearctic	.	H	.	.
229	Primulaceae	*Androsace villosa* L.	Euro-Mediterranean-SW Asian	.	H	.	.
230	Primulaceae	*Primula algida* Adams	Caucaso-SW Asian (conditionally)	.	G (Cr)	.	.
231	Primulaceae	*Primula veris subsp. macrocalyx* (Bunge) Lüdi	Euro-Siberian	.	H	.	.
232	Ranunculaceae	*Anemone narcissiflora subsp. fasciculata* (L.) Ziman & Fedor.	Caucaso-Anatolian		Cr	.	.
233	Ranunculaceae	*Pulsatilla violacea* Rupr.	Caucasian (with irradiation)	NE	H	CE	CE
234	Ranunculaceae	*Ranunculus caucasicus* M.Bieb.	Caucasian	.	H	CE	CE
235	Ranunculaceae	*Ranunculus breyninus* Crantz	Euro-Mediterranean-SW Asian	.	H	.	.
236	Ranunculaceae	*Thalictrum minus* L.	Palearctic	.	G (Cr)	.	.
237	Ranunculaceae	*Thalictrum simplex* L.	Palearctic	.	G (Cr)	.	.
238	Ranunculaceae	*Thalictrum foetidum* L.	Palearctic	.	H	.	.
239	Ranunculaceae	*Aconitum nasutum* Fisch. ex Rchb.	Caucaso-Euxinian	.	H/G (Cr)	.	.
240	Rosaceae	*Alchemilla caucasica* Buser	Caucaso-Anatolian	NE	H	.	.
241	Rosaceae	*Alchemilla debilis* Juz.	Caucasian	DD	H	CE	CE
242	Rosaceae	*Alchemilla dura* Buser	Caucasian	NE	H	.	.
243	Rosaceae	*Alchemilla retinervis* Buser	Caucaso-Anatolian	.	H	.	.
244	Rosaceae	*Alchemilla rigida* Buser	Caucasian	NE	H	.	.
245	Rosaceae	*Alchemilla sericata* Rchb. ex Buser	Caucasian	NE	H	.	.
246	Rosaceae	*Alchemilla sericea* Willd.	Caucasian	.	H	.	.
247	Rosaceae	*Filipendula vulgaris* Moench	Palearctic (West Palearctic)	.	H	.	.
248	Rosaceae	*Potentilla crantzii* (Crantz) Beck ex Fritsch	Holarctic	.	H	.	.
249	Rosaceae	*Potentilla recta* L.	Palearctic	.	H	.	.
250	Rosaceae	*Potentilla reptans* L.	Palearctic	.	H	.	.
251	Rosaceae	*Rosa corymbifera* Borkh.	Euro-Mediterranean-SW Asian	.	Ph	.	.
252	Rosaceae	*Rosa boissieri* Crép.	Caucaso-SW Asian	.	Ph	.	.

253	Rosaceae	*Sibbaldia parviflora* Willd.	Caucaso-SW Asian (Balkan irradiation)	.	Ch	.	.
254	Rubiaceae	*Asperula glomerata* (M.Bieb.) Griseb.	Caucaso-SW Asian (conditionally)	.	H	.	.
255	Rubiaceae	*Asperula molluginoides* (M.Bieb.) Rchb.	Caucasian (with irradiation)	.	H	.	.
256	Rubiaceae	*Cruciata glabra* (L.) Ehrend.	Euro-Siberian	.	H	.	.
257	Rubiaceae	*Cruciata laevipes* Opiz	Euro-Mediterranean	.	H	.	.
258	Rubiaceae	*Galium album* Mill.	Palearctic (West Palearctic)	.	H	.	.
259	Rubiaceae	*Galium verum* L.	Palearctic	.	H	.	.
260	Salicaceae	*Salix caprea* L.	Euro-Siberian	.	Ph	.	.
261	Santalaceae	*Thesium alpinum* L.	Euro-Mediterranean	.	H	.	.
262	Scrophulariaceae	*Verbascum gossypinum* M.Bieb.	Caucasian	.	H	.	.
263	Scrophulariaceae	*Verbascum pyramidatum* M.Bieb.	Caucaso-Euxinian	.	H	.	.
264	Thymelaeaceae	*Daphne glomerata* Lam.	Caucasian	LC	Ph (nano)	.	.
265	Urticaceae	*Urtica dioica* L.	Palearctic	.	H	.	.
266	Rubiaceae	*Galium valantioides* M. Bieb.	Caucasian	NE	H	CE	CE
267	Lamiaceae	*Salvia glutinosa* L.	Caucaso-SW Asian	.	H	.	.
268	Campanulaceae	*Campanula alliariifolia* Willd.	Caucaso-Anatolian	NE	H	.	.
269	Polygonaceae	*Polygonum aviculare* L.	Holarctic	.	Th	.	.

Annex 2. Releve´ table containing five phytosociological groups of the subalpine pasture and hay meadow communities of Khevi. For 69 (from 269) species and 74 (seven discarded because don't fitted in any established gropes) relevés of subalpine and high-montane vegetation; Species in gropes ordered by the constancy values. Blocks of diagnostic species are shaded. Within blocks, diagnostic species are ranked by decreasing constancy, which measured with the percentage proportion of releve´s in which the species is presented. Species with _ > 0.20 were considered as diagnostic. The name of the group is represented by the species, which is characterised by the maximum level of fidelity (it shows how often a species is found in an established group) value and constancy degree. Companion species as well, are ranked by decreasing constancy within the entire table. Species occurring in a single releve´are not shown.

Consecutive number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Running number	56	1	7	4	6	3	5	2	26	25	24	8	32	67	22	27	80	28	33	34	15	16	17	18	14	29	23	21	20	50	49	51	46	52	54	48	47
Relevé	Kan8	PKE7	k2	Sno6	Sio8	PKE6	AKH7	PKE5	AKH4	AKH5	Sno8	Sno7	k15	K4	CDO4	AKH6	Sno3	AKH2	k12	k13	JUT9	JUT6	JUT7	JUT8	JUT10	AKH3	CDO5	CDO3	CDO1	Kan2	Kan3	Kob5	Sio5	Kob4	Kob8	Kan5	Kan4
Original number from Turboveg	41	56	2	23	33	55	65	54	62	63	25	24	14	4	71	64	20	60	12	13	81	78	79	80	82	61	72	70	68	35	36	46	30	45	49	38	37
Physical landscape data																																					
Altitude (masl)	2121	2040	1842	1886	2025	2026	1922	2021	1908	1911	1956	1893	2046	1791	1961	1904	1794	1825	1944	1967	2224	2165	2257	2262	2130	1859	1924	1947	1866	2150	2172	2101	2135	2069	2021	2159	2168
Longitude	44.5217	44.55558	44.63587	44.64437	44.59395	44.55521	44.66892	44.55424	44.66576	44.6656	44.64591	44.64587	44.61666	44.63328	44.62732	44.66826	44.63219	44.66652	44.6202	44.62087	44.74257	44.74454	44.7438	44.74251	44.73991	44.66757	44.62817	44.6255	44.62807	44.52078	44.51824	44.52551	44.57851	44.51358	44.51242	44.51828	44.51756
Latitude	42.59024	42.60424	42.65726	42.60571	42.59359	42.60371	42.58879	42.6033	42.59274	42.59434	42.6063	42.60463	42.67219	42.65459	42.69069	42.59033	42.60499	42.58388	42.67237	42.6712	42.58083	42.58147	42.58177	42.58131	42.57741	42.59144	42.69191	42.68868	42.68933	42.59666	42.59675	42.55599	42.58564	42.55359	42.55504	42.59339	42.59552
Slope (°)	20	35	45	15	30	25	15	15	15	15	15	15	30	30	25	30	20	20	25	20	20	20	25	20	15	35	25	18	15	45	35	25	45	30	15	40	50
Slope position	3	3	4	3	3	3	3	3	3	4	1	3	3	1	4	3	3	3	3	3	3	3	4	4	3	4	4	4	3	4	3	3	3	3	3	3	3
Aspect	NE	SE	S	S	S	SE	S	S	SE	SE	S	S	SE	NE	SE	S	N	NW	SE	SE	NE	SE	SE	NE	SE	NW	NE	SE	SE	SE	SE	S	SE	S	NW	SE	SE
Vegetation coverage (%)																																					
Open soil Abundance [%]	0	20	50	5	40	20	30	15	20	10	5	10	10	0	10	20	5	5	20	0	10	8	20	8	10	20	12	5	5	20	30	10	20	0	5	20	25
Cover bare rock [%]	20	0	40	10	10	5	5	0	0	10	10	5	20	0	0	0	5	0	20	0	0	5	5	0	0	20	0	10	0	0	0	20	10	0	30	0	30
Total herb layer [%]	80	80	10	85	50	75	65	85	80	80	85	85	70	100	90	80	90	95	60	100	90	87	75	92	90	60	88	85	95	80	70	70	70	100	65	80	45
Vegetation composition																																					
Cover herb layer (%)	70	40	20	60	40	60	40	40	40	70	60	60	70	95	50	60	70	60	70	95	70	70	60	70	60	70	40	60	70	70	80	80	60	80	50	70	60
Grasses Abundance [%]	40	30	30	40	30	30	40	50	40	40	40	40	30	80	70	40	40	60	70	60	50	40	50	75	65	50	65	40	25	50	50	40	50	60	40	30	60
Fabaceae Abundance [%]	60	60	40	30	50	40	60	60	50	60	50	50	50	70	30	40	50	40	30	40	10	60	30	60	40	60	50	20	40	70	75	70	50	70	60	60	50
Cryptogams Abundance [%]	50	20	30	10	30	20	20	20	30	20	30	10	40	60	30	20	20	40	30	60	5	20	5	10	5	40	40	10	30	20	15	50	40	40	30	40	20
Cover litter layer (%)	30	20	20	20	20	20	30	30	20	10	40	10	40	15	10	30	15	30	60	40	5	10	20	10	5	20	30	45	3	20	20	40	40	30	20	20	10
Vegetation structure (cm)																																					
Min height herbs (cm) 2015	5	5	3	10	8	5	5	5	3	5	6	5	8	10	5	4	5	5	7	15	10	5	6	10	20	5	8	8	10	5	10	4	5	5	5	6	10
Mean height herbs (cm) 2015	40	30	15	30	40	30	40	40	15	25	40	35	40	50	30	20	35	30	40	50	75	50	60	40	55	40	35	30	50	50	50	35	30	40	35	40	40
Maximum height herbs (cm) 2015	80	70	40	70	70	70	90	70	60	60	80	60	70	90	60	70	70	60	70	70	110	80	125	80	85	75	70	60	90	80	100	75	55	80	80	100	110
Herbs Hight (cm)	40	20	30	40	30	20	30	30	30	40	30	20	90	90	30	30	30	20	40	50	60	40	40	75	20	40	40	25	40	40	40	40	40	40	2	80	40
Grasses Hight [cm]	60	60	15	60	70	60	80	70	60	70	80	70	70	120	65	90	60	50	60	60	60	70	70	40	70	110	80	100	70	120	90	70	70	80	50	60	50
Fabaceae Hight [cm]	30	20	10	20	20	15	20	25	15	30	20	15	20	50	50	30	30	20	20	30	40	30	20	30	40	40	40	25	20	30	50	30	20	20	20	50	30
Cryptogams Hight [cm]	8	5	7	4	5	8	3	8	4	5	3	3	5	8	6	4	5	5	5	5	2	3	3	2	1	3	5	5	2	5	5	5	5	5	5	8	5
Litter Hight [cm]	5	5	2	3	3	5	5	5	3	3	4	3	5	6	5	5	5	5	5	4	4	4	5	5	3	5	4	7	3	5	5	5	5	8	3	5	5
Biomass																																					
Grass [%]	48	44	23	18	23	32	56	21	30	34	9	78	35	37	34	28	43	54	24	28	39	57	54	32	57	48	6	29	41	41	32	58	32	53	54	45	56
Herbs [%]	26	18	51	36	58	23	20	33	33	18	23	5	35	49	54	18	23	21	30	26	47	23	17	26	6	29	88	51	38	30	41	22	22	17	19	28	26
Legumes[%]	16	27	17	32	19	35	13	38	13	35	50	17	23	3	6	37	19	9	40	41	9	15	22	34	29	7	2	14	16	22	20	6	45	21	18	19	12
Rest[%]	10	11	8	13	0	9	10	8	24	13	17	0	8	11	6	17	15	17	6	5	5	6	7	7	8	16	4	7	5	7	7	13	0	10	8	8	6
Biomass [T/Ha]	5.49	4.45	1.27	2.32	2.67	2.71	2.26	3.59	1.89	2.83	2.85	2.89	4.07	3.21	4.04	1.48	2.7	2.52	3.99	5.02	4.2	4.31	4.33	4.28	4.71	2.8	5.62	4.6	6.91	4.35	3.54	2.03	3.52	3.84	3.33	4.3	3.72
Modeled biomass [T/Ha]	4.52	4.42	2.28	2.47	3.29	3.38	2.35	3.67	2.56	3.42	2.91	2.76	4.46	3.1	3.42	2.33	3.25	3.29	3.88	4.36	.	3.84	.	.	3.72	2.51	4.07	4.16	5.39	3.87	4.27	2.75	3.81	3.77	3.74	4.03	3.13
Soil																																					
Soil depth (cm)	8	8	5	8	5	10	5	20	5	7	10	5	10	20	10	5	8	5	5	15	15	10	5	10	15	8	10	10	15	15	10	10	15	25	5	15	8
Skeleton (%)	23	21	29	17	32	24	29	26	18	27	22	21	24	1	18	27	22	44	19	15	32	33	33	36	29	34	4	4	5	26	25	28	18	14	15	21	25
Roots (%)	3	2	1	2	1	1	1	3	2	1	3	2	3	2	2	1	3	2	3	3	2	3	2	2	2	3	3	3	4	2	2	2	4	2	2	2	1
pH H2O	6.11	6.63	6.38	6.33	6.83	6.55	6.74	6.78	6.36	6.16	6.44	6.57	5.84	6	6.58	6.48	6.09	5.57	5.9	5.85	6.53	6.45	6.29	6.4	6.29	5.82	6.29	6.34	6.38	6.49	6.42	6.53	6.36	6.81	6.07	5.86	7.05
pH KCl	5.73	5.77	5.57	5.53	5.81	5.62	5.75	6.12	5.85	5.45	5.55	5.8	5.23	5.4	6.01	5.57	5.42	4.98	5.47	5.42	5.9	5.86	5.59	5.83	5.64	5.35	5.61	5.84	5.85	5.77	5.75	6.01	5.61	6.28	5.45	5.22	6.41
Corg (%)	8.21	2.45	3.27	2.93	1.41	2.42	1.23	3.99	2.93	3.6	3.24	3.73	5.02	6.43	5.98	2.19	9.93	6.25	5.82	5.3	5.02	5.31	4.34	4.04	3.98	7.54	7.48	7.49	5.22	4.26	4.37	2.73	3.46	3.91	6.36	6.33	2.57
Norg (%)	0.86	0.34	0.35	0.34	0.24	0.33	0.2	0.47	0.31	0.36	0.34	0.38	0.46	0.67	0.53	0.25	0.87	0.58	0.56	0.47	0.49	0.49	0.43	0.41	0.42	0.67	0.63	0.67	0.47	0.51	0.54	0.27	0.3	0.39	0.58	0.7	0.35
C/N	9.6	7.23	9.36	8.71	5.92	7.39	6.05	8.44	9.39	9.9	9.46	9.76	10.93	9.65	11.36	8.64	11.47	10.76	10.49	11.3	10.3	10.78	10.21	9.79	9.54	11.31	11.82	11.23	11.09	8.3	8.11	10.2	11.36	10.04	10.9	9.09	7.39
Kcal (mg/kg soil)	81	22	40	34	10	23	9	45	35	28	48	59	55	59	59	26	60	48	113	153	70	109	116	94	58	55	95	186	72	30	25	81	70	46	120	49	16
Pcal (mg/kg soil)	12	2	5	6	2	1	2	4	6	5	4	7	10	16	14	4	22	14	17	15	7	7	8	5	3	20	17	17	15	6	6	6	2	6	5	12	1
Mgcal (mg/kg soil)	327	287	242	249	277	244	159	175	220	392	279	279	320	340	492	247	551	356	330	350	352	324	275	298	393	449	513	585	411	500	516	112	190	114	149	514	384
Seed density (m-2)	1350.48	4536.81	5947.22	2456.26	2902.27	2248.06	1915.33	.	7224.36	5211.9	11568.9	2213.25	9995.12	496.073	2872.04	9162.25	4273.08	2028.86	8082.71	10076.7	3630.4	2805.8	6214.65	5048.06	2752.08	4561.03	432.754	2254.07	1792.97	4281.99	9568.79	2818.37	.	590.431	584.346	1373.71	1154.65
Land use																																					
Habtype	NE.M	SE.P	S.P	S.P	S.P	SE.P	S.P	S.P	SE.P	SE.P	S.P	S.P	SE.P	NE.M	SE.P	S.P	N.P	NW.P	SE.P	SE.P	NE.M	SE.M	SE.M	NE.M	SE.M	NW.P	NE.P	SE.P	SE.M	SE.M	SE.M	S.P	SE.P	S.P	NW.P	SE.M	SE.M
Landuse (Pas meadow, Med pature)	Med	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Med	Pas	Pas	Pas	Pas	Pas	Pas	Med	Med	Med	Med	Med	Pas	Pas	Pas	Med	Med	Med	Pas	Pas	Pas	Pas	Med	Med
Grazing	M.Un	P.He	P.He	P.He	P.He	P.He	P.He	P.He	P.He	P.Mo	P.Li	P.He	P.Li	M.Li	P.He	P.He	P.Mo	P.Mo	P.Li	P.Li	M.Un	M.Un	M.Un	M.Un	M.Un	P.He	P.Mo	P.Mo	M.Li	M.Un	M.Li	P.Mo	P.He	P.Mo	P.He	M.Un	M.Un
Species ID																																					
AC group	Kan8	PKE7	k2	Sno6	Sio8	PKE6	AKH7	PKE5	AKH4	AKH5	Sno8	Sno7	k15	K4	CDO4	AKH6	Sno3	AKH2	k12	k13	JUT9	JUT6	JUT7	JUT8	JUT10	AKH3	CDO5	CDO3	CDO1	Kan2	Kan3	Kob5	Sio5	Kob4	Kob8	Kan5	Kan4
1 *Astragalus captiosus* Boriss.	3	2a	2a	2b	3	2a	3	1	3	3	3	2b	2b	2a	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2 *Dianthus cretaceus* Adams	.	.	+	+	r	+	1	+	2a	1	+	1	.	.	1	1	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
3 *Sempervivum pumilum* M.Bieb.	+	+	+	+	+	r	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.
4 *Sedum acre* L.	.	.	+	1	.	.	.	.	+	+	+	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
PA group	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5 *Plantago atrata* Hoppe	.	.	.	+	.	.	.	.	+	+	2b	2b	+	.	1	+	2b	1	+	+	1	2a	1	2a	2a	2b	1	1	+	.	.	.	.	+	.	.	.
6 *Potentilla crantzii* (Crantz) Beck ex Fritsch	.	.	.	.	.	.	.	.	+	+	1	+	.	1	1	.	.	.	+	1	1	1	+	1	1	+	+	+	+	.	.	+	+	+	.	.	.
7 *Scabiosa bipinnata* K. Koch	.	.	.	.	.	r	.	+	.	+	2b	+	1	.	.	+	.	.	.	+	+	+	1	1	+	.	.	.	.	+	.	r	.	.	.	.	.
8 *Bupleurum falcatum subsp. polyphyllum* (Ledeb.) H.Wolff	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	+	.	1	1	.	+	1	+	.	.	.	.	.	.	.	.
9 *Campanula rapunculoides* L.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	+	+	+	.	.	.	+	.	.	+	.	.	.	.	+
10 *Phleum pratense* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	1	.	.	.	.	.	.	.	.

Consecutive number	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	Total frequency	Frequency in group	Fidelity value	Constancy values	Species ID
Running number	82	55	53	79	81	76	42	35	39	36	63	64	74	40	38	41	31	75	37	62	65	69	30	43	72	61	68	70	71	57	9	12	13	10	11	19	77					
Relevé	Sno4	Sio1	Kob3	Sno5	Sno1	PKE1	Sio3	k5E	Kob7	k6E	k8E	k9E	k16	Kan6	Kob6	AKH1	AKH9	k17	Kob1	k11	Sno2	Kob2	AKH8	Sio6	PKE3	Sio7	k3	Kan7	Kan1	k1	JUT4	JUT1	JUT2	JUT5	JUT3	CDO2	PKE2					
Original number from Turboveg	21	26	44	22	18	50	28	5	48	6	8	9	15	39	47	59	67	16	42	11	19	43	66	31	53	32	3	40	34	1	76	73	74	77	75	69	51					
Physical landscape data																																										
Altitude (masl)	1795	1959	2038	1806	1750	1998	2033	2040	1989	2076	1943	1934	2077	2134	2001	1853	1797	2129	1957	1918	1795	2017	1804	2119	2068	2012	1848	2125	2130	1822	2317	2217	2262	2316	2281	1935	2020					
Longitude	44.6349	44.58376	44.50863	44.64032	44.62502	44.54411	44.58172	44.66442	44.51528	44.66455	44.65783	44.65685	44.61634	44.5185	44.51988	44.66468	44.65388	44.61603	44.49622	44.6209	44.62772	44.5073	44.65771	44.57847	44.54903	44.59076	44.63606	44.52068	44.52123	44.63367	44.75299	44.74787	44.74899	44.75227	44.75017	44.62663	44.54585					
Latitude	42.60217	42.59428	42.555	42.60086	42.61032	42.60095	42.59014	42.65735	42.56244	42.65677	42.65559	42.65351	42.67272	42.5918	42.56498	42.58527	42.59413	42.67348	42.55678	42.67183	42.60826	42.55495	42.59219	42.58442	42.60372	42.58998	42.65766	42.59152	42.59701	42.65976	42.58247	42.58002	42.58077	42.58213	42.58165	42.68917	42.60054					
Slope (°)	20	30	30	40	20	20	20	30	35	35	40	40	40	20	40	35	25	40	40	30	30	40	30	30	30	20	35	35	40	40	25	15	18	10	20	10	20					
Slope position	3	3	3	4	3	1	3	1	3	3	1	1	3	4	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	3	4	3	3	3					
Aspect	N	NE	NE	N	N	S	N	N	NW	N	NW	SW	SE	N	NW	N	N	SE	NW	SE	N	N	NW	N	N	NW	NE	N	N	N	NW	NW	NW	NW	NW	NW	S					
Vegetation coverage (%)																																										
Open soil Abundance [%]	0	0	0	0	0	0	0	10	0	5	0	10	0	0	0	0	0	0	20	0	0	0	0	0	0	5	0	0	0	20	0	20	5	0	15	5	0					
Cover bare rock [%]	0	0	0	0	0	0	0	5	40	25	5	10	20	0	10	5	0	10	0	5	0	0	0	0	5	50	0	0	0	25	0	0	0	5	0	15	10					
Total herb layer [%]	100	100	100	100	100	100	100	85	60	70	95	80	80	100	90	95	100	90	80	95	100	100	100	100	95	45	100	100	100	55	100	80	95	95	85	80	90					
Vegetation composition																																										
Cover herb layer (%)	70	90	80	80	60	60	10	40	80	50	80	80	50	60	70	70	10	90	60	70	85	95	60	80	70	80	60	80	80	70	90	80	95	75	80	80	70					
Grasses Abundance [%]	40	70	60	40	40	25	80	50	60	70	40	60	90	50	80	70	60	90	50	80	60	80	40	70	40	80	100	90	90	70	70	40	60	50	70	60	40					
Fabaceae Abundance [%]	60	30	70	70	50	70	50	60	40	40	50	40	40	40	50	20	30	40	40	40	50	60	20	60	60	50	70	60	60	50	40	40	40	40	50	15	60					
Cryptogams Abundance [%]	60	30	70	50	30	50	70	30	70	40	60	40	50	80	50	80	70	80	20	70	30	40	50	60	60	50	30	60	30	30	60	40	40	30	40	35	70					
Cover litter layer (%)	30	30	60	40	20	50	70	40	60	70	80	60	80	70	70	40	40	90	20	70	20	35	30	90	50	70	10	80	50	10	60	50	70	80	60	20	60					
Vegetation structure (cm)																																										
Min height herbs (cm) 2015	8	8	10	8	8	5	10	10	5	15	15	10	7	10	5	10	15	15	5	15	40	8	10	15	10	20	15	5	10	5	10	10	15	10	15	5	10					
Mean height herbs (cm) 2015	60	35	65	60	50	50	40	40	20	50	50	40	45	40	40	50	70	70	30	70	80	40	40	40	70	70	60	40	45	40	55	25	60	60	60	40	60					
Maximum height herbs (cm) 2015	100	70	120	120	90	70	70	80	80	100	100	80	70	70	150	70	120	150	60	150	130	120	60	90	110	120	100	75	100	80	100	80	120	120	100	110	130					
Herbs Hight (cm)	50	40	40	40	30	30	30	90	40	90	60	70	70	40	40	40	20	70	20	80	60	30	30	50	40	60	110	30	50	70	60	1	40	40	55	60	40					
Grasses Hight [cm]	90	60	80	80	80	60	60	70	80	120	110	50	60	70	70	90	110	100	60	70	80	70	60	70	70	70	90	70	70	60	110	40	120	110	70	120	80					
Fabaceae Hight [cm]	40	30	20	90	25	25	30	20	30	50	50	30	20	30	40	30	40	30	10	50	30	40	30	20	30	20	50	30	30	15	20	5	15	15	15	25	30					
Cryptogams Hight [cm]	8	5	8	8	5	5	10	5	8	10	15	10	10	8	5	10	5	15	3	10	3	5	5	10	5	10	8	8	8	5	5	3	3	4	3	4	10					
Litter Hight [cm]	5	5	5	8	5	8	10	5	8	10	10	5	5	10	5	8	4	10	4	5	3	5	3	15	8	8	5	10	5	5	7	5	3	10	5	5	10					
Biomass																																										
Grass [%]	47	19	49	52	48	50	26	24	44	2	47	49	33	38	23	50	44	33	19	34	34	57	57	31	64	95	28	24	45	36	40	51	34	53	46	19	25					
Herbs [%]	20	8	18	22	26	23	56	54	40	86	43	32	44	40	61	44	46	55	61	47	52	31	20	49	28	1	52	40	31	26	53	22	50	42	45	69	51					
Legumes[%]	19	73	24	17	18	19	18	11	3	6	7	14	18	9	8	2	6	9	5	13	12	6	9	20	4	4	13	36	17	24	2	8	5	1	3	7	19					
Rest[%]	14	0	9	9	8	8	0	10	13	6	3	4	6	14	8	4	5	2	15	6	3	5	14	0	5	0	7	0	8	13	5	19	11	4	6	6	6					
Biomass [T/Ha]	3.58	12.44	4.75	4.68	4.65	4.25	3.81	3.57	1.31	6.08	4.7	4.41	5.44	3.86	1.96	4.15	4.1	9.47	1.5	3.89	5.03	3.8	2.77	3.01	6.93	4.02	9.37	6.47	4.83	2.25	4.11	3.24	4.02	4.41	4.19	6.22	6.55					
Modeled biomass [T/Ha]	3.59	7.24	4.31	4.13	4.61	4.06	3.6	3.52	1.65	4.58	4.38	4.06	5.04	3.31	1.88	3.77	3.66	6.52	2.29	4.62	4.82	4.47	3.07	3.25	5.56	3.6	2.28	4.98	4.91	2.53	.	.	.	.	.	5.11	5.11					
Soil																																										
Soil depth (cm)	10	15	15	20	7	10	25	10	5	20	15	10	10	10	10	15	10	10	25	10	10	30	10	15	15	2	15	15	20	10	20	20	20	15	20	20	15					
Skeleton (%)	20	21	10	10	19	12	19	26	22	15	6	22	4	9	14	8	15	7	6	23	36	6	19	14	22	72	13	15	26	37	15	2	3	22	4	6	5					
Roots (%)	4	4	2	5	3	4	6	3	4	4	4	3	3	5	4	2	4	5	3	3	2	3	4	6	5	3	2	4	3	2	5	5	11	7	4	5	5					
pH H2O	5.97	5.93	7.5	6.01	5.81	6.22	5.5	5.96	5.98	6.21	6.31	6.45	6.37	5	5.83	5.18	6.42	6.23	5.72	5.94	6.43	5.46	5.77	5.11	5.92	6.36	6.6	5.42	5.16	6.47	5.57	4.63	4.66	5.72	4.55	6.22	6.23					
pH KCl	5.28	5.37	7.04	5.48	5.28	5.58	4.91	5.37	5.4	5.71	5.81	6.04	5.9	5	5.31	4.62	5.24	5.83	4.93	5.44	5.79	4.55	5.29	4.46	5.29	6.03	6.15	4.67	4.46	5.74	4.87	4.12	4.09	5.09	3.95	5.74	5.48					
Corg (%)	6.55	4.62	10.8	12.59	7.64	5.34	8.11	5.19	8.15	6.96	14.32	10.55	10.18	5	8.18	10.82	9.87	12.81	6.44	6.27	5.41	6.08	12.09	9.87	6.68	6.49	8.37	7.31	5.89	4.71	9.08	16.27	18.27	9.1	14.94	7.65	8.21					
Norg (%)	0.63	0.43	0.96	1.06	0.76	0.53	0.63	0.49	0.68	0.61	1.26	0.96	0.91	5	0.71	0.95	0.89	1.17	0.63	0.59	0.56	0.6	1.19	0.78	0.61	0.63	0.89	0.74	0.67	0.45	0.79	1.41	1.53	0.78	1.28	0.68	0.71					
C/N	10.34	10.75	11.29	11.86	10.1	10.18	12.78	10.66	12.01	11.49	11.39	10.98	11.19	5	11.56	11.35	11.05	10.94	10.25	10.71	9.61	10.08	10.18	12.59	10.92	10.3	9.35	9.9	8.81	10.46	11.48	11.54	11.95	11.7	11.67	11.18	11.62					
Kcal (mg/kg soil)	62	92	117	110	57	68	132	34	103	61	52	54	115	5	67	91	48	126	39	65	50	38	61	90	91	84	43	76	50	44	79	196	226	74	125	517	104					
Pcal (mg/kg soil)	20	11	79	38	24	12	23	7	8	9	13	14	21	5	13	20	31	32	6	18	25	9	35	17	28	16	16	16	18	5	18	38	50	25	35	20	21					
Mgcal (mg/kg soil)	710	260	335	839	479	308	194	299	191	446	812	716	704	5	197	354	614	832	120	366	569	58	625	109	410	202	491	224	254	275	382	253	231	494	201	461	418					
Seed density (m-2)	2909.73	3455.28	3156.44	5482.03	1568.74	6123.01	11161.4	6466.97	758.472	908.945	1675.72	5699.71	5395.11	5	1329.29	2180.24	5310.92	7680.94	584.346	8340.39	2415.21	1424.45	4385.58	1064.92	2062.77	.	629.581	9361.82	2941.21	4039.79	.	.	9801.23	.	.	1762.03	5320.61		Species			
Land use																																										
Habtype	N.M	NE.M	NE.M	N.M	N.M	S.M	N.P	N.P	NW.P	N.M	NW.P	SW.M	SE.P	N.P	NW.P	N.M	N.M	SE.P	NW.P	SE.P	N.M	N.M	NW.P	N.P	N.M	NW.P	NE.M	N.M	N.M	N.P	NW.P	NW.P	NW.P	NW.P	NW.P	NW.P	S.M					
Landuse (Pas meadow, Med pature)	Med	Med	Med	Med	Med	Med	Pas	Pas	Pas	Med	Pas	Med	Pas	Pas	Pas	Med	Med	Pas	Pas	Pas	Med	Med	Pas	Pas	Med	Pas	Med	Med	Med	Pas	Pas	Pas	Pas	Pas	Pas	Pas	Med					
Grazing	M.Un	M.Un	M.Un	M.Un	M.Un	M.Un	P.Li	P.Mo	P.He	M.Li	P.Mo	M.Li	P.Li	P.Li	P.He	M.Un	M.Un	P.Li	P.Mo	P.Li	M.Un	M.Un	P.Mo	P.Mo	M.Un	P.Mo	M.Un	M.Un	M.Un	P.Mo	P.Li	P.Mo	P.Mo	P.Li	P.Mo	P.Mo	M.Un					
Species ID																																										
AC group	Sno4	Sio1	Kob3	Sno5	Sno1	PKE1	Sio3	k5E	Kob7	k6E	k8E	k9E	k16	Kan6	Kob6	AKH1	AKH9	k17	Kob1	k11	Sno2	Kob2	AKH8	Sio6	PKE3	Sio7	k3	Kan7	Kan1	k1	JUT4	JUT1	JUT2	JUT5	JUT3	CDO2	PKE2					
1 *Astragalus captiosus* Boriss.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	19	16	84.2	25.7	1
2 *Dianthus cretaceus* Adams	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	18	12	66.7	24.3	2
3 *Sempervivum pumilum* M.Bieb.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	7	70	13.5	3
4 *Sedum acre* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	7	100	9.5	4
PA group	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5 *Plantago atrata* Hoppe	1	.	.	+	1	.	r	.	.	r	.	+	.	.	.	+	+	.	.	.	.	.	+	.	.	.	+	.	.	+	.	+	.	.	+	1	.	36	20	55.6	48.6	5
6 *Potentilla crantzii* (Crantz) Beck ex Fritsch	1	+	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	+	.	.	.	1	+	.	+	.	1	.	.	.	.	.	.	.	.	.	29	17	58.6	39.2	6
7 *Scabiosa bipinnata* K. Koch	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	19	11	57.9	25.7	7
8 *Bupleurum falcatum subsp. polyphyllum* (Ledeb.) H.Wolff	.	+	.	.	+	+	.	.	.	.	+	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	17	8	47.1	23	8
9 *Campanula rapunculoides* L.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	5	41.7	16.2	9
10 *Phleum pratense* L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	+	.	8	4	50	10.8	10

11	*Leontodon caucasicus* (M.Bieb.) Fisch.	[illegible]	6	3	50	8.1	**11**
	LC group						
12	*Lomelosia caucasica* (M.Bieb.) Greuter & Burdet	[illegible]	29	11	37.9	39.2	**12**
13	*Polygala anatolica* Boiss. & Heldr.	[illegible]	23	12	52.2	31.1	**13**
14	*Salvia verticillata* L.	[illegible]	17	11	64.7	23	**14**
	PC group						
15	*Cirsium obvallatum* (M.Bieb.) Fisch.	[illegible]	31	20	64.5	41.9	**15**
16	*Pimpinella rhodantha* Boiss.	[illegible]	26	19	73.1	35.1	**16**
17	*Cyanus cheiranthifolius* (Willd.) Soják	[illegible]	27	19	70.4	36.5	**17**
18	*Polygonum carneum* K. Koch.	[illegible]	23	21	91.3	31.1	**18**
19	*Betonica macrantha* K. Koch.	[illegible]	21	19	90.5	28.4	**19**
20	*Carex humilis* Leyss.	[illegible]	18	15	83.3	24.3	**20**
21	*Anthoxanthum odoratum* L.	[illegible]	18	11	61.1	24.3	**21**
	CA group						
22	*Calamagrostis arundinacea* (L.) Roth	[illegible]	11	5	45.5	14.9	**22**
23	*Silene linearifolia* Otth	[illegible]	8	5	62.5	10.8	**23**
24	*Helictotrichon adzharicum* (Albov) Grossh.	[illegible]	9	5	55.6	12.2	**24**
25	*Deschampsia cespitosa* (L.) P.Beauv.	[illegible]	5	5	100	6.8	**25**
26	*Veratrum lobelianum* Bernh.	[illegible]	4	4	100	5.4	**26**
27	*Anemone narcissiflora subsp. fasciculata* (L.) Ziman & Fedor.	[illegible]	4	4	100	5.4	**27**
28	*Fritillaria collina* Adam	[illegible]	4	4	100	5.4	**28**
29	*Potentilla reptans* L.	[illegible]	4	3	75	5.4	**29**
30	*Chaerophyllum roseum* M.Bieb.	[illegible]	3	3	100	4.1	**30**
31	*Carex panicea* L.	[illegible]	3	3	100	4.1	**31**
	RM group						
32	*Rhinanthus minor* L.	[illegible]	49	46	93.9	66.2	**32**
33	*Ranunculus breyninus* Crantz	[illegible]	42	38	90.5	56.8	**33**
34	*Rumex acetosa* L.	[illegible]	31	28	90.3	41.9	**34**
35	*Vicia alpestris* Steven	[illegible]	27	24	88.9	36.5	**35**
36	*Hieracium umbellatum* L.	[illegible]	24	22	91.7	32.4	**36**
37	*Cruciata glabra* (L.) Ehrend.	[illegible]	24	22	91.7	32.4	**37**
38	*Trifolium trichocephalum* M.Bieb.	[illegible]	21	19	90.5	28.4	**38**
39	*Leucanthemum vulgare* Lam.	[illegible]	20	17	85	27	**39**
40	*Alchemilla sericata* Rchb. ex Buser	[illegible]	20	18	90	27	**40**
41	*Agrostis capillaris* L.	[illegible]	20	20	100	27	**41**
42	*Polygala alpicola* Rupr.	[illegible]	16	15	93.8	21.6	**42**
43	*Gentianella caucasea* (Lodd. ex Sims) Holub	[illegible]	16	16	100	21.6	**43**
44	*Pedicularis armena* Boiss. & Huet	[illegible]	15	14	93.3	20.3	**44**
45	*Carum caucasicum* (M.Bieb.) Boiss.	[illegible]	15	15	100	20.3	**45**
	Companion species						
46	*Bromus variegatus* M.Bieb.	[illegible]	69	.	.	93.2	**46**
47	*Phleum phleoides* (L.) H.Karst.	[illegible]	52	.	.	70.3	**47**
48	*Medicago glomerata* Balb.	[illegible]	54	.	.	73	**48**
49	*Campanula collina* Sims	[illegible]	53	.	.	71.6	**49**
50	*Agrostis vinealis subsp. planifolia* (K. Koch) Tzvelev	[illegible]	51	.	.	68.9	**50**
51	*Trifolium ambiguum* M.Bieb.	[illegible]	49	.	.	66.2	**51**
52	*Lotus corniculatus* L.	[illegible]	47	.	.	63.5	**52**
53	*Veronica gentianoides* Vahl	[illegible]	48	.	.	64.9	**53**
54	*Pastinaca armena* Fisch.& C.A.Mey.	[illegible]	39	.	.	52.7	**54**
55	*Myosotis alpestris* F.W.Schmidt	[illegible]	39	.	.	52.7	**55**
56	*Anthyllis variegata* Grossh.	[illegible]	40	.	.	54.1	**56**
57	*Trifolium pratense* L.	[illegible]	42	.	.	56.8	**57**
58	*Trifolium alpestre* L.	[illegible]	37	.	.	50	**58**
59	*Alchemilla rigida* Buser	[illegible]	39	.	.	52.7	**59**
60	*Festuca ovina* L.	[illegible]	39	.	.	52.7	**60**
61	*Euphrasia hirtella* Jord. ex Reut.	[illegible]	34	.	.	45.9	**61**
62	*Koeleria luerssenii* (Domin) Domin	[illegible]	33	.	.	44.6	**62**
63	*Thymus collinus* M.Bieb.	[illegible]	36	.	.	48.6	**63**
64	*Silene ruprechtii* Schischk.	[illegible]	33	.	.	44.6	**64**
65	*Leontodon hispidus* L.	[illegible]	30	.	.	40.5	**65**
66	*Galium verum* L.	[illegible]	28	.	.	37.8	**66**
67	*Festuca varia* Haenke	[illegible]	27	.	.	36.5	**67**
68	*Sedum spurium* M.Bieb.	[illegible]	22	.	.	29.7	**68**
69	*Trifolium canescens* Willd.	[illegible]	23	.	.	31.1	**69**