Institute of Landscape Ecology and Resources Management

Division of Landscape Ecology and Landscape Planning

Justus-Liebig-University Giessen

Assessment of species composition, productivity and functionality of grassland in the Greater Caucasus (Georgia, Kazbegi Region) by means of remote sensing

INAUGURAL DISSERTATION

for the degree of

Doctor agriculturae (Dr. agr.)

submitted to the

Faculty 09

Agricultural Science, Nutritional Science, and Environmental Management

Justus-Liebig-University Giessen

presented by

Anja Magiera M.Sc.

born in Uelzen

Giessen, 2017

With permission from

the Faculty 09

Agricultural Science, Nutritional Science, and Environmental Management

Justus-Liebig-University Giessen

Dean: Prof. Dr. Klaus Eder

Examining committee:

1. Supervisor:	Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte
2. Supervisor:	Prof. Dr. Bernd Honermeier
Examiner:	Prof. Dr. i. R. Ingrid-Ute Leonhäuser
Examiner:	Prof Dr. Rolf-Alexander Düring
Chair:	Prof. Dr. Joachim Aurbacher

Date of defence: 19.12.2017

Erklärung

gemäß der Promotionsordnung des Fachbereichs 09 vom 07. Juli 2004 § 17 (2):

„Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe. Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht.

Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" niedergelegt sind, eingehalten."

'Essentially, all models are wrong, but some are useful'

George Box, 1987

Contents

List of Publications[1]:

1. Magiera, A., Feilhauer, H., Waldhardt, R., Wiesmair, M., Otte, A. 2017: Modelling biomass of mountainous grasslands by including a species composition map. - Ecological Indicators 78: 8-18. DOI:10.1016/j.ecolind.2017.02.039.*

2. Magiera, A., Feilhauer, H., Waldhardt, R., Wiesmair, M., Otte, A.: Mapping plant functional groups in subalpine grassland of the Greater Caucasus. - Mountain Research and Development (submitted on 27.07.2017).

3. Magiera, A., Feilhauer, H., Tephnadze, N., Waldhardt, R., Otte, A. 2016: Separating reflectance signatures of shrub species – A case study in the Central Greater Caucasus. - Applied Vegetation Science 19: 304–315. DOI:10.1111/avsc.12205.**

Author`s contribution:

1. In the first publication I had the main responsibility, including fieldwork, statistical analysis and paper writing. Dr. Hannes Feilhauer contributed to the pre-processing of the satellite images and the random forest modelling. Prof. Dr. Rainer Waldhardt commented on the manuscript. Dr. Martin Wiesmair and I worked together on the application of the vegetation indices, he further commented on the manuscript. Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte initiated the study, significantly supported the field work, and gave valuable comments on the analysis of the vegetation data and the manuscript.

2. In the second publication I had the main responsibility, including fieldwork, statistical analysis and paper writing. Dr. Hannes Feilhauer commented on the statistical analysis as well as the manuscript. Prof. Dr. Rainer Waldhardt and Dr. Martin Wiesmair commented on the manuscript. Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte initiated the study, significantly supported the field work, and gave valuable comments on the analysis of the vegetation data and the manuscript.

* Reprinted with permission from Elsevier.
** Reprinted with permission from John Wiley and Sons.

---

[1] Citation styles and formatting in the dissertation follow the rules of the respective journal.

3. In the third publication I had the main responsibility, including fieldwork, statistical analysis and paper writing. Dr. Hannes Feilhauer contributed to the R Code and statistical analysis as well as the manuscript. Nato Tephnadze is the main author of the vegetation relevés taken from the Caucasus Vegetetation database. Prof. Dr. Rainer Waldhardt, commented on the manuscript. Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte initiated the study, significantly supported the field work, and gave valuable comments on the analysis of the vegetation data and the manuscript.

I contributed to the data analyses and manuscripts of the following studies, which supply further information about grassland patterns and processes in the Kazbegi region:

4. Hansen, W., Magiera, A., Theißen, T., Waldhardt, R., Otte, A.: Analyzing *Betula litwinowii* shrub encroachment and reforestation in the Kazbegi region, Greater Caucasus Georgia. - Journal of Vegetation Science (submitted).

5. Wiesmair, M., Feilhauer, H., Magiera, A., Otte, A., Waldhardt, R. 2016: Estimating Vegetation Cover from High-Resolution Satellite Data to Assess Grassland Degradation in the Georgian Caucasus. - Mountain Research and Development 36.1.

6. Magiera, A., Feilhauer, H., Otte, A., Waldhardt, R., Simmering, D. 2013: Relating canopy reflectance to the vegetation composition of mountainous grasslands in the Greater Caucasus. - Agriculture, Ecosystems & Environment 177: 101-112.

Moreover, I am the first author of a summarizing article in german language:

7. Magiera, A., Feilhauer, H., Waldhardt, R., Otte, A. 2017: Fernerkundungsbasierte Erfassung der Vegetationszusammensetzung und Produktivität von Grünlandbeständen im Großen Kaukasus. – Berichte der Reinhold-Tüxen-Gesellschaft (accepted).

List of Figures:

1. Synthesis:

2. Modelling biomass with species composition

3. Mapping plant functional groups

4. Reflectance signatures of shrub species

List of Tables:

1. Synthesis

2. Modelling biomass with species composition

3. Mapping Plant functional groups

4. Reflectance signatures of shrub species

1. Synthesis

1.1 High mountain grassland

High mountain ecosystems and their services are of global economic and ecologic importance (Gret-Regamey et al., 2012). Covering about 20 % of the terrestrial surface, high mountains provide habitat for 386 million people and supply freshwater to almost half of the human population (Körner, 2004; Körner et al., 2017; Messerli et al., 2004; Woodwell, 2004). At the same time they are unique sanctuaries for flora and fauna, with almost half of the global biodiversity hot-spots and one third of the terrestrial diversity being associated to high mountain ecosystems (Körner, 2004; Myers, 2003; Barthlott et al., 2005). Interactions of geographic isolation and fragmentation of habitats, the short succession of heterogeneous climatic zones and a high variability of microhabitats, caused by the terrain, lead to high species richness and a high number of endemic species in high mountain regions (Körner, 2004). A species-rich, undamaged vegetation layer is a prerequisite for the provision of multiple high mountain ecosystem functions, such as mitigation of erosion events, a high biodiversity and grassland yield, as the nutritional basis for local dairy and livestock production (Körner, 2004; O'Mara, 2012; Pohl et al., 2009).

High mountain ecosystems are sensitive to global change, which strongly affects their functioning through social change, land-use change and climatic change (Cocca et al., 2012; Klimek et al., 2007; Watson and Haeberli, 2004). Social changes, such as instability and rural migration, are leading to the economic marginalization of high mountain regions and are the main drivers of the abandonment of agricultural practices (Benayas et al., 2007; Gracheva et al., 2012). Since large parts of high mountain regions are embedded in low-income countries, with half of their population depending on regional food supply, high mountain agriculture is urgently needed for food security (Messerli et al., 2004). In the former member states of the Soviet Union the effects of rural migration and land abandonment are enhanced by the economic transformation process (Baumann et al., 2011). Substantial changes, with the economical and agricultural structure shifting from state-organized, intensive agriculture to private subsistence agriculture, are part of the transformation process and affect the land-use pattern and the functioning of the landscape itself (Heiny et al., 2017; Waldhardt et al., 2011).

Abandonment of traditional agricultural practices has been a major trend in Central European mountainous landscapes in the past decades (MacDonald et al., 2000), affecting the biodiversity, the productivity and the functionality of the grasslands of the mountainous landscape in complex ways (e.g. Marini et al., 2008; Peco et al., 2012; Tasser and Tappeiner, 2002), with strong impacts on low yielding and distant areas (Prishchepov et al., 2013). The abandonment of the traditional

mowing regime potentially leads to a loss of plant species richness in mountain hay meadows (Marini et al., 2007; Maurer et al., 2006; Tasser and Tappeiner, 2002). Moreover, traditionally used, species-rich meadows and pastures show a lower erodibility, because of their diversified root system (Tasser and Tappeiner, 2002).

Abandonment of high mountain grassland is often followed by shrub encroachment processes and reforestation (Cocca et al., 2012). Shrub encroachment is characterized by increasing shrub biomass, cover, and abundance and is expected to significantly alter high mountain ecosystems (Camarero and Gutiérrez, 2004; Holtmeier and Broll, 2007; Smith et al., 2009). An increase in shrub cover can strongly influence an ecosystem's surface energy exchange (Sturm et al., 2001), nutrient cycling (DeMarco et al., 2011), and carbon storage (Knapp et al., 2008), as well as the floristic composition and services provided (Wilson and Nilsson, 2009). In the Alps, experimental grazing enclosure results in a significant change in plant functional groups, especially an increase in tall, competitive grass species (Mayer et al., 2009), which might further enhance snow gliding and erosion (Tasser et al., 2003).

In order to counteract abandonment of high mountain grassland use and its consequences future-orientated land-use concepts, considering sociological and ecological relationships are needed in high mountain regions, especially in countries under transition (Gurung et al., 2012). Ecological data, including detailed spatial information of key ecosystem properties, such as species composition, productivity and plant functionality, as well as ecosystem processes, for instance shrub encroachment, are often scarce in remote high mountain regions and difficult to collect with resasonable efforts and expenses. Thus, remote sensing techniques could be beneficial for mapping and monitoring the highly diverse but also vulnerable grassland vegetation in mountainous regions (Peroni et al., 2000; Rocchini et al., 2010).

1.2 Remote sensing concepts

Optical remote sensing of grasslands is based on the reflectance signature of photosynthetically active vegetation (green vegetation), which is affected by the absorption of light by pigments, mainly chlorophyll a and b (Curran et al., 2001; Fillela and Penuelas, 1994; Horler et al., 1983; Thenkabail et al., 2000). The blue and red parts of the electromagnetic spectrum in the visible light are absorbed and used by the plant for photosynthesis, whereas the green light is reflected (green peak between 500-600 nm, see Fig. 1).

The strong increase of reflectance at approximately 700 nm, called the red edge, is strongly related to leaf chlorophyll content and a well-known indicator for stressed vegetation (Dawson and Curran, 1998; Mohd Shafr et al., 2006; Thenkabail et al., 2011). In the near-infrared (NIR, 700-1500 nm) reflectance is mainly influenced by the water content and leaf chemistry within the leaf and on canopy level by leaf structure, leaf area index and leaf position (Curran, 1983; Ustin and Gamon, 2010). The reflectance signal of vegetation types itself can be recorded by different sensors. Those are either multispectral, recording commonly between five to ten discrete bands over a certain range of wavelengths, or hyperspectral, recording reflectance almost continuously throughout the spectrum (see Fig. 1).
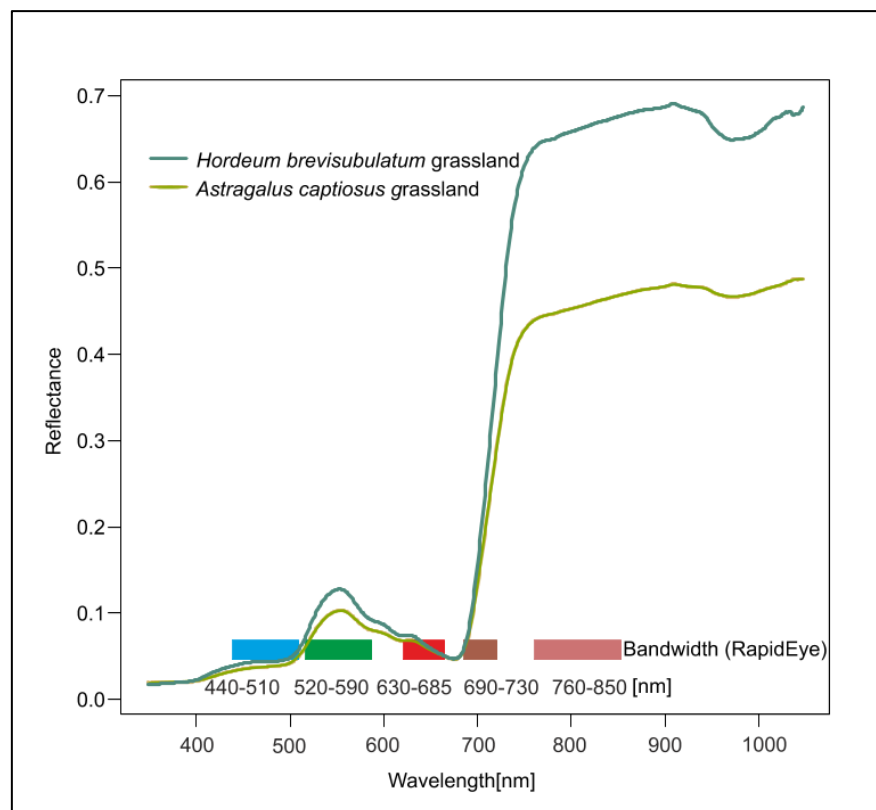
Fig. 1: Hyperspectral reflectance of *Hordeum brevisubulatum* and *Astragalus captiosus* grassland types compared to multispectral sensor bands (RapidEye).

The sensors can be attached to different carriers, such as satellites, airplanes or humans / tripods in the case of field spectrometers and cameras. To enhance the reflectance signal of vegetation, so called vegetation indices are calculated, by using the strong increase in reflection between the red and NIR. Vegetation indices are commonly used to assess biomass, vegetation cover, leaf area index, insufficient plant nutrient status or other signs of plant stress. leaf area index or vegetation cover (Biewer et al., 2009; Boschetti et al., 2007; Diker and Bausch, 2003; Huete et al., 1999; Jordan, 1969; Qi et al., 1994; Rouse et al., 1973). However, vegetation indices tend to saturate at high yields. Therefore, their relationship with biomass rich grassland, such as hay meadows is challenging. In a semi-natural landscape, with low farming intensity species composition and biomass are closely linked, so that species composition is a promising predictor for biomass.

In common vegetation mapping, discrete boundaries of vegetation types are depicted, even though standardized approaches defining vegetation types are rare (De Cáceres and Wiser, 2012) and consistency between classified vegetation maps is often low. In the last decades a quite new concept of vegetation maps, based on remotely sensed data, was introduced, emphasizing the continuous character of vegetation changes, examples for this method are given in Feilhauer et al., 2011, Schmidtlein et al., 2007, and Schmidtlein, 2005.

The common high mountain landscape is characterized by the absence of sharp boundaries like field- and meadow edges, typical for the fragmented, hessian agricultural landscape (Simmering et al., 2001; Waldhardt et al., 2011). Since discrete boundaries, or so called 'sharp edges' are mostly missing in grassland dominated high mountain regions, a non-classificatory approach, depicting the floristic composition, biomass and plant functional groups by means of remote sensing was chosen for the first and second study (chapter two and three).

As Schmidtlein, 2005 states: the challenge of classifying vegetation traces back to the long and ongoing discussion about the organization of vegetation and antagonism between perceiving vegetation types as interdependent species forming communities with homogeneous, discrete and recognizable units, following the community concept (Clements, 1916) or as individual species that simply co-occur in a certain area, individually following along environmental gradients (Gleason, 1926). The individualistic view is apprehended in the continuum concept and discussed in the light of niche-theory (Austin and Smith 1989). Vegetation boundaries change in space and time and are perceived either as sharp edges, the so called limes convergens or a smooth gradient, the limes divergens (van Leuwen, 1966).

Modelling gradual transitions is mostly technically implemented by relating either ordination axes or the gradient itself, such as biomass, or plant functional group coverage to a predictor dataset.

The gradual change of species composition of grasslands, Ellenberg indicator values, or plant strategy types (Feilhauer et al., 2011; Magiera et al., 2013; Schmidtlein et al., 2012), has already been successfully modelled. Plant functional groups were already successfully predicted by hyperspectral data, as pollination types (Feilhauer et al. 2016), and directly by MODIS data (Sun et al. 2008). Moreover, Lehnert et al. (2013) used hyperspectral data to discriminate grass from non-grass pixels, whereas studies using multispectral data to model plant functional types are rather scarce. Those techniques are mostly successful, since the growth forms of single plant species are adapted to local resource constraints and stress levels. These adaptive mechanisms are often linked to biochemistry and physiology as well as to the structure and phenology of a plant or vegetation type. Further, biophysical characteristics such as leaf inclination and canopy structure (especially the coverage of open soil, bare rock or biomass) determine a unique reflectance pattern (Tappeiner and Cernusca, 1989). The plants' characteristic growth forms, further result in a characteristic reflectance signature or 'optical type', which can be utilized for mapping based on remote sensing methods (Ustin and Gamon, 2010). However, only few studies have considered the potential to distinguish plant species by their reflectance signature (Buddenbaum et al., 2005; Cochrane, 2000) and the capability of different sensors for species separation, as well as the influence of acquisition date are still under discussion.

The rapid development in remote sensing technology in general, as well as the recent availability of open source remote sensing data facilitate grassland research on landscape level. Especially in the isolated high mountain regions with harsh terrain, remotely sensed data could be a useful tool to map and monitor species composition, biomass, plant functional groups or shrub encroachment.

1.3 Objectives

Since the unique species composition of high–mountain grassland and their related services, for example biomass productivity, are most likely to change with the ongoing abandonment in high mountain regions, mapping and monitoring of high mountain grassland properties and key ecosystem processes is highly needed. The assessment of species composition, productivity and functionality of grassland, as well as the separation of encroaching shrub species by means of remote sensing was thus the main focus of this study. The general objectives of this dissertation were:

i to analyse the species composition and main environmental gradients of the subalpine grassland,

ii to test the predictability of species composition, aboveground biomass and plant functional groups, as cover fractions of grass, herb, and legume by remotely sensed data and subsequently map them, and

iii to test the possibility of identifying encroaching shrub species in remotely sensed data, with respect to sensor characteristics and acquisition time.

Modelling biomass by including species composition (chapter two):

A spatially detailed yield assessment helps to identify possible meadows or, on the contrary, areas with a low carrying capacity in a region, making it easier to manage these sites. Consequently, the main objectives of this study were to model a spatially explicit grassland yield map and to test whether saturation issues, often occurring in high yielding grassland can be tackled by consideration of plant species composition in the modelling process. The aims of this study were:

i to describe the main vegetation and topographic gradients and their relationships to biomass yield,

ii to accurately and spatially explicit predict above ground biomass as continuous fields, and

iii to test, whether remotely sensed patterns of species composition are suitable predictor variables for a yield model.

Mapping plant functional groups (chapter three):

Plant functional groups (PFG), in our case grass, herbs and legumes and their spatial distribution hold information on key ecosystem functions such as species richness, nitrogen fixation and erosion control. The present study thus aims at describing and mapping the distribution of grass, herb, and legume coverage. To test the applicability of new sensors, the predictive power of simulated hyperspectral canopy reflectance, simulated multispectral reflectance, simulated vegetation indices and topographic variables for modelling PFGs was compared. The aims of this study were:

i to model and subsequently map grass, herb, and legume coverage, and

ii to test if the data of new hyperspectral sensors improve the model quality.

Reflectance signatures of shrub species (chapter four):

Shrub encroachment has been observed in many alpine and arctic environments and is expected to significantly alter these ecosystems. Mapping shrub encroachment on species level with remote sensing is a powerful tool for monitoring purposes. Thus, in this study the main objective was to test the distinctiveness of the reflectance signature of the target species: *Betula litwinowii, Hippophae rhamnoides, Rhododendron caucasicum,* and *Veratrum lobelianum*. Further aims of this study were:

i to test which multispectral sensor produces the best separability, and

ii to assess the influence of the timing of data acquisition in the vegetation period.

1.4 Study area

The study area, a part of the Kazbegi region (between 1.200 – 5.033 m a.s.l) is located on the northern slope of the central Greater Caucasus, Georgia and covers a total area of 155 km^2. The river Tergi drains the Kazbegi valley towards the north. In parallel run, the Georgian Military Highway, an old south north trade route. Many small villages are scattered along this transport corridor, often on alluvial fans of small side streams. The administrative center of the sparsely populated district (3.5 inhabitants per km^2 in 2016) is Stepantsminda (2016 approximately 1300 inhabitants, National Statistics Office of Georgia 2016a).

The parent rock in our study region is mainly of vulcanic origin and embraces tertiary and quarternary andesite and dacite (Ministry of Geology of the USSR, 1983, Hanauer et al., 2017). Moreover, terrigeneous flysch, clay shist and marl sandstone of the Jurrasic period as well as limestone from the lower Cretaceous period build up the parent material (Ministry of Geology of the USSR, 1983, Hanauer et al., 2017). Overall nutrient poor soils with a high content of humic acids in the top soil, originated out of the parent rock (Hanauer et al., 2017). The dominant soil types include shallow leptosols on south exposed steep slopes, stone rich regosols, and deep moderately nutrient rich cambisols and umbrisols (Hanauer et al., 2017). In the floodplain of the Tergi river and its tributaries fluvisols and gleysols prevail.

Because of its central location in the Greater Caucasus the climate in the study area is relatively continental (Lichtenegger et al., 2006). The mean annual temperature is about 4.7°C, and the mean annual rainfall amounts to 806 mm (mainly between July and August). The short vegetation period is a challenge even for a moderate intensification of the local agriculture (Kikvidze et al., 2011; Nakhutsrishvili, 1999; Nakhutsrishvili et al., 2006). However, the microclimate of north and south exposed slopes varies strongly, even influencing the sequence of the elevational belts. The overshadowed and therefore cooler, north facing slopes exhibit a shorter vegetation period than the sun exposed, south facing slopes of more than three weeks. The subalpine belt thus starts at 1800 m a.s.l. and 1900 m a.s.l., respectively and extends to the alpine belt starting at 2400 / 2500 m a.s.l. and reaching up to 2960 / 3000 m a.s.l. (Nakhusrishvili, 2013). The alpine belt is followed by the subnival belt up to 3600 / 3740 m a.s.l. and the nival belt, which includes the elevations above 3740 m a.s.l. (Nakhusrishvili, 2013).

Due to the presence of a research station (Kazbegi High-Mountain Research Station), the flora of the Kazbegi region has been thoroughly studied during the last decades (Akhalkatsi et al., 2006; Kikvidze, 1996; Nakhutsrishvili and Gagnidze, 1999; Nakhutsrishvili, 1976; Pyšek and Šrutek, 1989; Tephnadze et al., 2014). The whole Caucasus ecoregion is one of the global biodiversity hot spots because of its species richness and high content of endemic plants and animals (Myers, 2003).

About 1100 plant species can be found in the study area, 595 in the subalpine belt, 33% of them are counted as endemic (Nakhutsrishvili et al., 2006).

The landscape is dominated by grassland, covering about 50% of the study area. Remnants of birch forests (*Betula litwinowii*), which are part of the potential natural vegetation in the subalpine belt, grow on steep, north-facing slopes (Akhalkatsi et al., 2006). In the vicinity of forest patches young birches encroach and form dense stands of birch shrubbery. During the Soviet times Scotts pine (*Pinus sylvestris*) was planted in close proximity to the villages, as a supply for firewood (Nakhutsrishvili et al., 2006).

Up until today agriculture, especially dairy cattle, is an important factor for the livelihoods of the local people (Heiny et al., 2017). However, since the independence of the Republic of Georgia in 1991 the pasturing system changed rapidly. The overuse of the pastured grasslands, mainly in the upper subalpine to alpine belt, by intensive sheep grazing in the Kazbegi region ceased (Didebulidze and Plachter, 2002). Until the 1980s it was a common pasturing practice to move large flocks of sheep from Azerbaidjan, along the Georgian Military Highway to summer pastures in the high mountains (transnational transhumance). From central villages like Stepantsminda or Gudauri herdsmen on horseback herded the sheep (up to 1000 animals per herd) to their subalpine and alpine pastures (up to 3000 m a.s.l., Didebulidze and Plachter, 2002). After the collapse of the Soviet Union, the sheep numbers dramatically declined in Georgia (Fig. 2). The traditional transhumance system of shepherding was abandoned. In the Kazbegi region, until today small herds of cattle pasture the slopes of the mountains (Nakhutsrishvili et al., 2005). However, they are often linked to overgrazing, deforestation and thus erosion. Even though the influence of pastured animals is often discussed, very little is known about the exact locations of pastures and the pathways of the cattle.
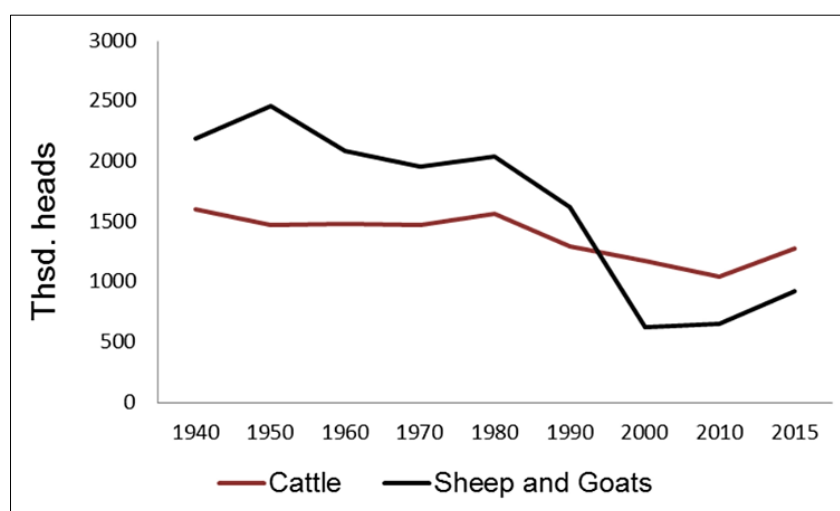
Fig. 2: Cattle and sheep numbers in Georgia between 1940 and 2015 in thousands, National Statistics Office of Georgia 2016b.

The pastures in the subalpine belt are of poor soil quality with a high stone content, signs of erosion and low nutritive value (Sakhokhia, 1983). Moreover, pasturing early in the year when the vegetation cover is still low, stands for the ongoing land degradation (Sakhokhia, 1983). Caused by strong trampling, gaps appear in the vegetation cover, which foster erosion. This becomes highly visible along the pasturing trails (Wiesmair et al., 2017).

The meadows in the subalpine belt are mown once or partly twice per year. The first cut generally happens late in the vegetation period mainly towards the end of July. Some farmers integrate arable land use (potato fields) and grassland use (meadows) in a form of crop rotation. Moreover, most of the productive hay meadows are pastured in early spring and autumn (Sakhokhia, 1983, Tephnadze et al., 2014).

The traditional management of the local pastures and meadows in the vicinity of villages is an important factor for the dairy production and consequently helps to assure food security. Only small areas are suitable for hay making, even though hay is the main winter fodder. Consequently hay is a tradeable and scarce good in the region, limiting the amount of pastured cattle (Nakhutsrishili et al., 2005). Dairy farming as well as horticulture practiced in home and field gardens in the Kazbegi region are within the limits of subsistence farming (Heiny et al., 2017). Therefore, traditional grassland management ceases and large areas distant to the settlements were abandoned recently. The abandonment of agricultural practices combined with a strong migration of the younger generation, hits mostly remote high mountain villages, which were part of the transnational transhumance system.

1.5 Material and methods

1.5.1 Sampling design of the subalpine grasslands (chapter two and three)

For mapping biomass (chapter two) and plant functional types (chapter three) of the subalpine grasslands (1800 – 2100 m a.s.l.) in the Kazbegi region the same vegetation dataset, including 90 relevés on 5 x 5 m plots sampled by Anja Magiera, Natalia Tephnadze and Prof. Dr. Dr. habil. Dr. h. c. (TSU) Otte, was analyzed. The subalpine grassland around the villages Stepantsminda, Gergeti, Pansheti, Sioni, Phkelsche and Goristhikhe was sampled in a stratified random design, covering a large productivity gradient in summer 2014 (see Fig 3).
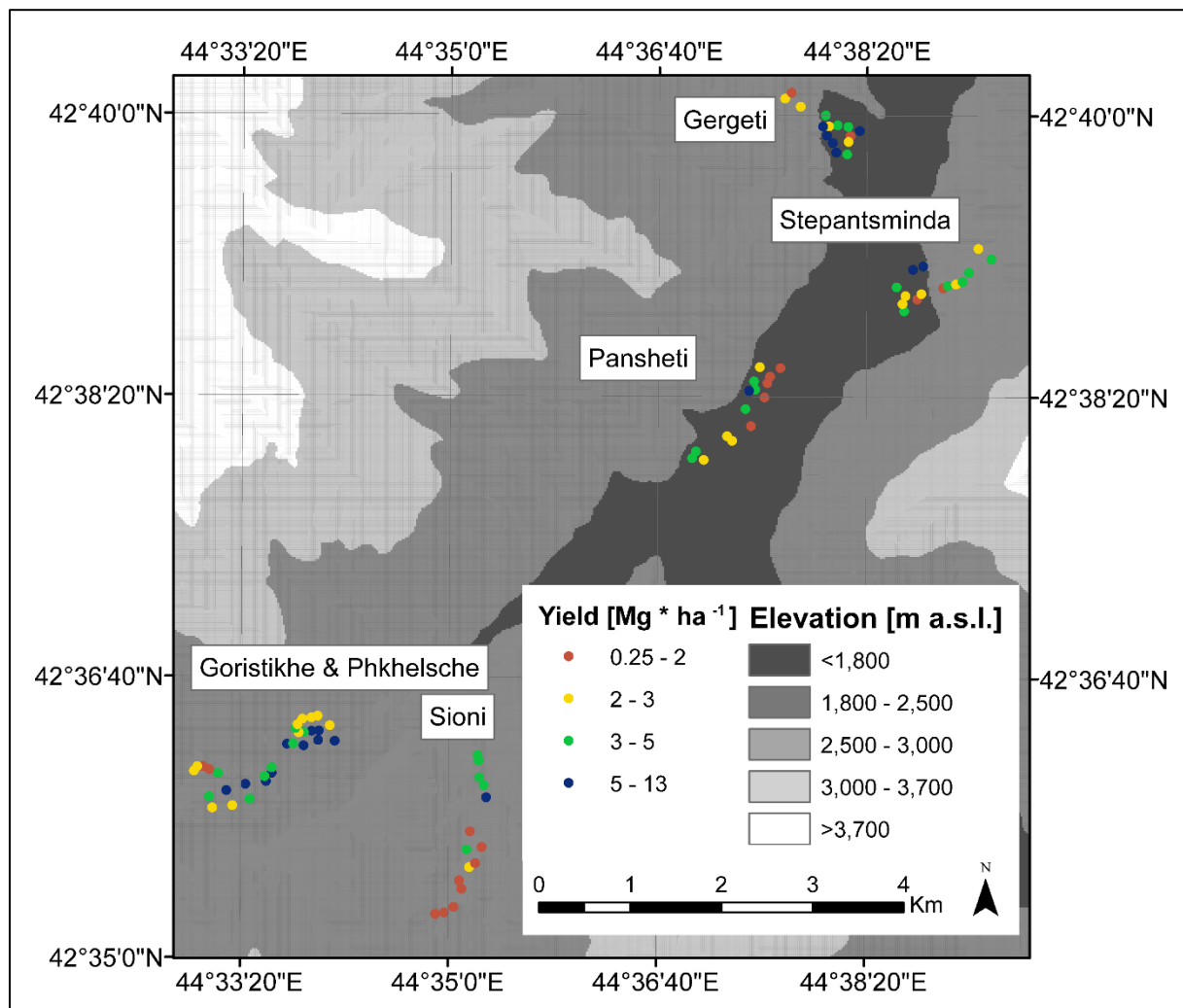
Fig. 3: Map of the study area, Magiera et al. 2017.

Only widely homogeneous grassland areas were sampled in order to avoid edge effects, mixtures of vegetation types, and problems with positional errors. Next to each village, 15 plots were sampled for vegetation composition, reflectance and biomass.

Besides proportions of plant species coverage (according to the modified Braun-Blanquet scale), total vegetation cover, coverage of open soil, bare rock, and the upper and lower vegetation layer were estimated. Additionally, the cover fraction of the functional groups of broad-leafed herbs and

grasses were estimated and the average height of the upper and lower herb layer were measured. Nomenclature was generally based on The Plant List 1.1 (The Plantlist, 2010) and Gagnidze 2005 (chapter four), though *Hordeum violaceum,* named according to the taxonomy of (Gagnidze, 2005) in chapter two, is regarded as *Hordeum brevisubulatum* in chapter three, since the nomenclature changed. Shortly before mowing at the end of July we recorded canopy reflectance with a HandHeld ASD field spectrometer and clipped biomass out of four regularly placed squares. To determine dry-matter yield the biomass was oven dried at 60 °C for 48 hours and weighed.

The research design aims at the quantification of the standing crop as an approximation of the hay yield. Since the subalpine grassland in the Kazbegi region is intensively grazed in early spring and contains almost no tussock grass, only the standing biomass of the recent year was harvested.

1.5.2 Statistical analysis of subalpine grassland vegetation

Ordination is a frequently used means in vegetation science to reduce the dimensionality of a vegetation data set towards an analysis of gradual changes in species composition, the so-called floristic gradients. By employing two different ordination methods, isomap (isometric-feature mapping, chapter two) and NMDS (non-metric multidimensional scaling, chapter three), the *n*-dimensional vegetation dataset was reduced to lower dimensional floristic gradients.

Isomap is a powerful but rarely tested ordination technique for non-linear reduction of vegetation datasets with a high variability in species composition, such as high mountain grasslands (Tenenbaum et al., 2000). It has already been applied for gradient mapping in peatlands (Harris et al., 2003) and heathlands (Feilhauer et al., 2011). The benefit of isomap lies in the maintenance of the intrinsic geometry of the data. Isomap takes the longer geodesic distances for k nearest neighbours of each data point into account. Other common multidimensional scaling algorithms consider only the pairwise linear distances between data points. To avoid noise in the dataset species with less than three occurrences were excluded from the isomap analysis, using $k = 87$ neighbours based on Bray Curtis distances for the final solution.

NMDS was chosen as an ordination method in chapter two, since it is a robust and frequently used technique, which is known to display the ordinal scaled vegetation data accurately, without being dependent on an optimal k. A three dimensional solution, based on Bray-Curtis distances, was calculated, using the monoMDS function of the R package vegan 2.4-1 (Bray and Curtis, 1957; Oksanen, 2015). The NMDS axes were rotated by Principal component–rotation, so that the new axis one points to the direction of the largest variance (Clarke, 1993).

For interpretative purposes, the vegetation dataset was clustered, using the isopam clustering algorithm (Schmidtlein et al. 2010) to group the vegetation relevés by their plant species

composition. The vegetation clusters were used as a grouping variable in chapter two and three to test for significant differences by using a Kruskal Wallis ANOVA with subsequent Nemenyi test for pairwise multiple comparisons in yield, as well as for grass, herb and legume coverage and connected properties. Isopam is a brute-force approach to detect patterns in noisy vegetation data based on the partitioning of an optimized isomap ordination space (Schmidtlein et al., 2010). Its main purpose is to overcome the differences between phytosociological vegetation tables, which are based on expert knowledge, and numerical analysis, in order to find species with a high fidelity to groups in a data driven way (Schmidtlein et al., 2010).

1.5.3 Spatial data as co-variables for yield and plant functional group modelling

For the purpose of modelling species composition (chapter two) and plant functional groups (chapter three) remotely sensed imagery in combination with topographical data as predictors was used.

Space borne imagery was acquired on the 21st of June 2014 by the Rapid Eye sensor with five multispectral bands at a spatial resolution of 5 m x 5 m. The data were delivered with orthorectification in the product level 3-A and converted to top-of-atmosphere reflectance. Moreover, we accounted for differences in illumination caused by the exposition of the surface by using a cosine topographical correction (Teillet et al., 1982). Besides the original sensor bands vegetation indices (see chapter two Tab. 1) were included in the analysis. The topographical parameters were extracted from a Digital Elevation Model with 20 m resolution. Eastness, northness, slope as well as plan curvature, mean curvature, profile curvature and solar radiation were calculated with the Arc Map 10.2.1 tool box. CTI (Compound Topographic Index), TRI (Topographic Ruggedness Index), HLI (Heat Load Index) and SRR (Surface Relief Ratio) were calculated with the Geomorphometry and Gradient Metrics Toolbox version 1.1 (Evans et al. 2014).

1.5.4 Modelling of main floristic gradients and biomass

Instead of a discrete classification our approach was based on the continuous change of species composition, which was represented by a three dimensional ordination space with the plot scores as the three main floristic gradients. These gradients were used as the three response variables in three random forest models to be related to multispectral and topographic information to gain three separate floristic gradient maps (Fig. 5a). The resulting scores on the metrically scaled ordination axes were then related to aboveground biomass with a second random forest model, resulting in a grassland yield map.

In order to compare the species composition based model to a model relating multispectral reflectance, vegetation indices and topographical parameters directly to biomass, without including species composition as a proxy variable, a random forest model with biomass as a response variable and the multispectral bands, vegegtation indices, and topographic parameters as predictors was calculated (see Fig. 4b).
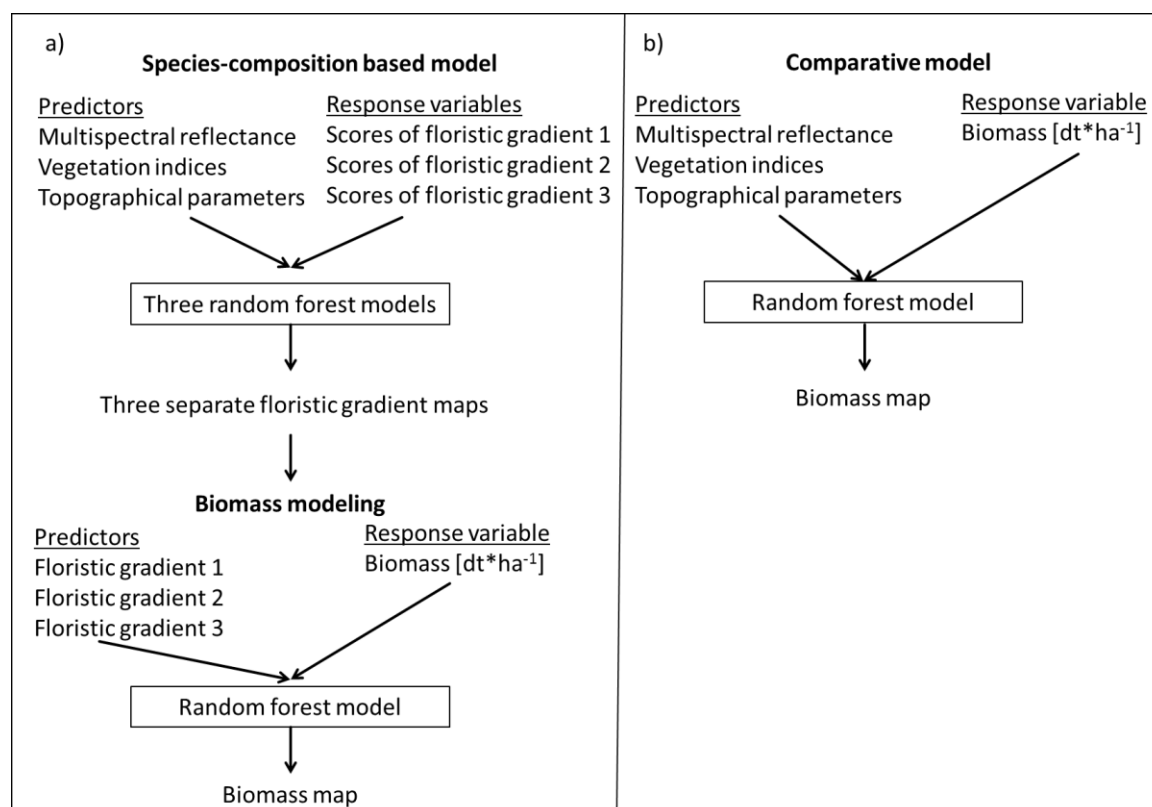
Fig. 4: Flow-chart of our modelling approach. The biomass modelling includes a) a species-composition based model and b) a bootstrapped comparative common model.

As a modelling technique random forest regression models were used (Breiman, 2001). Random forests belong to the bagged machine learning algorithms of ensemble modelling (a forest contains many classification or regression trees) and can be used for classification and regression. Being a non-parametric technique, random forest is able to cope with skewed data distributions as present in our study (Liaw and Wiener, 2002). As described by Liaw and Wiener 2002, a bootstrapped training sample of about one third of the data is first drawn from the input data, which resulted in 500 unpruned regression trees for our case. At every node of every tree, a subset of the ten predictor variables is tested for the best split. An average vote of all trees is then generated for the regression. The model out of bag error is calculated for every tree and finally aggregated for the forest.

In order to compare the biomass model based on species composition to a comparative common model based on vegetation indices and topographic variables, the full dataset was used to calculate

the predicted versus observed R² and the root mean square error of prediction (RMSEP) for a 100 time, bootstrapped dataset.

In order to derive the yield map, the whole data-set was then randomly stratified and equally separated into a calibration (with 7 samples in the low and high yield ranges) and a validation dataset. The predicted versus observed R² and root mean square error of prediction were calculated. The random forest model was used to predict the biomass map, by using the three isomap axes maps as predictors. Validation was performed with the validation dataset by correlating the observed ground truth with the predicted biomass values.

From the biomass map, areas with a low NDVI (<0.2) were masked out to exclude bare rocks as well as elevations above 2100 m a.s.l. in order to limit the spatial prediction to areas covered by the field sampling. All analyses were performed in the R statistical environment using the packages vegan (version 2.2.1, Oksanen, 2015), isopam (version 0.9-13, Schmidtlein et al., 2010), randomForest (version 4.6-10, Liaw and Wiener, 2002) and PMCMR (version 4.1, Pohlert 2014).

1.5.5 Mapping of plant functional groups

Hyperspectral field spectrometric data and multispectral satellite imagery, including vegetation indices and topographic data were tested as predictors for the modelling of grass, herb, and legume coverage. Compared to the coarse spectral resolution of multispectral data, commonly including three to ten discrete bands, the high spectral resolution of hyperspectral data, in our case including 118 discrete bands, allows for a higher flexibility in the selection of spectral features (Feilhauer et al., 2013). Vegetation indices are either ratios or linear combinations of sensor bands that aim to enhance the vegetation signal and allow to draw conclusions on the status and condition of vegetation (Jackson and Huete, 1991).

In mid-July 2014, at the time of the highest biomass, we acquired hyperspectral field spectrometric canopy reflectance using a hand-held field spectrometer (ASD HH2), covering the range between 325-1075 nm (750 wavelengths) of the solar electromagnetic spectrum. The measurements were taken from the same 5 m x 5 m plots as the vegetation relevés. To cover the entire plot, four measurements per plot were recorded with five repetitions (each measurement with an internal averaging of 50 spectra), totaling up to 20 spectra per plot. The measurements were collected close to the solar noon, on days with clear sky and low wind speed. Atmospheric changes were accounted for by measuring relative to a white standard panel (Spectralon®, Labsphere Inc.), with a recalibration at least every five minutes. During pre-processing, the 20 spectra sampled per plot were averaged and filtered. A Savitzky-Golay filter with a quartic polynom and a filter length of 51 nm was used to smooth the spectra (Savitzky and Golay, 1964). The filtered field spectrometric

reflectance measurements were used to test the applicability of hyperspectral sensors compared to multispectral sensors for modelling PFGs by simulating the bands of the sensors AISA Eagle (hyperspectral, 400-970 nm) and RapidEye (multispectral, 440-840 nm).

Both sensors were chosen because they cover a similar spectral range and offer a high spatial resolution. In order to calculate the spectral signal of the AISA Eagle sensor, the specific wavelengths were cut out, whereas the function simulatoR (Feilhauer et al., 2013) and the spectral response curve were used to simulate RapidEye reflectance.

1.5.6 Separation of shrub reflectance

In order to assess the separation of reflectance signatures of shrub species (chapter four), which are currently expanding in the Kazbegi region, the floristic composition was analyzed for similarities. Field spectrometric data was used for sensor comparison and assessment of the influence of accession date, whereas, satellite imagery was analyzed to test separability under real conditions (see Fig. 5).
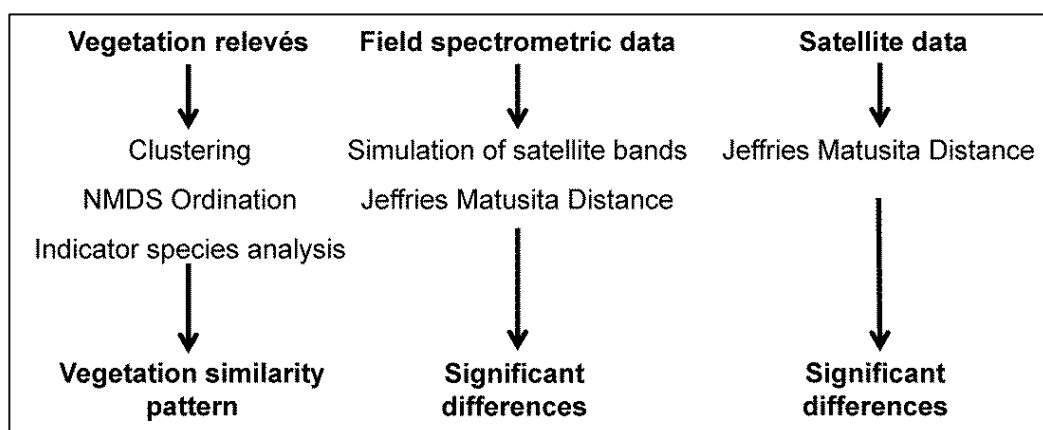
 Fig. 5: Flow chart of the statistical analysis.

Altogether, the floristic composition of 52 relevés either containing *Betula litwinowii*, *Rhododendron caucasicum*, *Hippophae rhamnoides* or *Veratrum lobelianum* on plot sizes ranging from 5 x 5 m to 10 x 10 m, sampled in 2009, 2010, and 2011 by Erich Hübl, Annette Otte, Georg Nakhutsrishvili, and Nato Tephnadze, was analyzed. The vegetation data originate from the Caucasus Vegetation Database, registered as AS-GE-001 under the Global Index of Vegetation-Plot Databases (Dengler et al. 2011). It was analyzed using clustering, NMDS ordination and Indicator Species Analysis.

Hyperspectral field spectrometric measurements were conducted at research sites located between 1,600 m and 2,600 m above sea level, from mid-June to mid-July 2011, using an ASD Hand Held 2 Field Spec ® portable spectrometer (325 - 1075 nm). Altogether, on 48 plots reflectance

measurements were taken. For each target species 12 plots of approximately 1 m² were measured with five regularly placed repetitions. The total number of spectra hence amounted to 240, including five repetitions per plot with 12 plots per species and the four target species *Betula litwinowii*, *Hippophae rhamnoides*, *Rhododendron caucasicum*, and *Veratrum lobelianum*. From the field spectrometric data multispectral sensor bands (IKONOS, Quickbird 2, RapidEye, WorldView-2), directly taken from the target species, were simulated using the simulatoR function and the respective response curves (Feilhauer et al., 2013).

The sites of the hyperspectral reflectance measurements are mostly in proximity to the vegetation relevés but are not the exact locations. The vegetation relevés were selected as a proxy of the vegetation types and species occurrences on a larger scale. The coordinates of the vegetation relevés were used to extract the reflectance signatures of the corresponding pixels from two multispectral RapidEye images taken on 27.06.2011 and 08.09.2011. The images were delivered with orthorectification and radiometric correction (product level 3-A). The size of a pixel after resampling was 5 x 5 m. At sensor reflectance was calculated from the images to roughly account for the solar angle and a cosine topographical correction was used (Teillet et al. 1982). For all datasets the Jeffries-Matusita Distance (JMD), a separability measure commonly used in remote sensing (Adam and Mutanga, 2009; Schmidt and Skidmore, 2003) was calculated. The reflectance signature of the single bands was tested for differences, using a Kruskall-Wallis ANOVA and post hoc pairwise testing for homogeneous groups using Bonferroni corrected pairwise Wilcox Rank test comparisons (see chapter four).

1.6 Main results and discussion

1.6.1 Floristic composition and structure of the subalpine grassland

The analysed grassland vegetation was grouped in three main types (chapter two): *Hordeum brevisubulatum*-meadow, *Gentianella caucasea*-grassland and *Astragalus captiosus*-grassland (see Fig. 6).

Fig. 6: a) *Hordeum brevisubulatum* **meadow, b)** *Gentianellea caucasea* **grassland and c)** *Astragalus captiosus* **grassland.**

Their distribution in the high mountain study area is mainly determined by the slope exposition to the east, curvature and elevation. A strong gradient in yield and related properties, such as the height of the upper and lower herb layer, and vegetation cover characterizes the vegetation structure. Generally, all tested grassland was species-rich but differed in grass, herb, and legume content (chapter three Tab. 1).

The grassland types can be floristically described by typical species (see Tab. 1), as well as by Indicator Species (see Appendices Tab. 1).

Tab. 1: Typical species of the grassland types according to the isopam analysis.

Vegetation type	Typical species
Hordeum brevisubulatum meadow	*Phleum pratense, Hordeum violaceum, Silene vulgaris, Rumex acetosa, Carum caucasicum, Festuca pratensis, Bunias orientalis, Poa trivialis, Vicia tenuifolia* subsp. *variabilis, Poa pratensis, Rumex obtusifolius*
Gentianella caucasea grassland	*Alchemilla sericata, Gentianella caucasea, Primula algida, Seseli alpinum*
Astragalus captiosus grassland	*Astragalus captiosus, Potentilla crantzii, Silene linearifolia*

The typical grass-rich, productive *Hordeum brevisubulatum* meadow belongs to the mesophilous grassland with many typical species forming the Central European grassland, too. But the distribution of the main characteristic species *Hordeum brevisubulatum* does not reach Central Europe. It ranges from temperate Asia to India, Nepal and Pakistan, as well as to European Russia (The IUCN Red List of Threatened Species, 2017). It further shows a strong bond to young mountain hay meadows (habitat type 6520), listed under the European Habitats Directive Annex I. It is fertilized only by spring pastured cattle and scythed once per year. According to

phytosociological units it could be associated with the *Molinio-Arrhenaretalia*, however Caucasian high mountain meadows with *Hordeum brevisubulatum* are up to now not described in the European Vegetation Survey (Dengler et al., 2013), which covers parts of the Greater Caucasus. But the French system eVeg opens up a possibility to group them in a class *Hordeeta brevisubulati* with different associations as described by Mirkin et al. 1992.

The species and herb rich *Gentianella caucasea* grassland can be classified as semi-natural dry grassland as described in the European Habitats directive. This type needs to be further partitioned in subalpine to alpine calcareous grasslands (6170) and the siliceous alpine and boreal grasslands (6150) with *Nardus stricta* occurring in few plots. There further is a strong correspondence between the semi-natural dry grasslands (*Festuco-Brometalia*, 6210), which includes different subtypes belonging to the Mesobromion and the subalpine to alpine calcareous grassland. The *Astragalus captiosus* grassland due to its low vegetation cover and distribution on steep slopes with shallow soil can be associated to vegetation types of rock and scree. Nakhutsrishvili 2012 classifies this type under the *Astragaleta captiosus*. All three vegetation types are characterized by broad, gradual transitions, which become apparent in the isomap analysis (chapter two) and are also inherent to the vegetation classification systems, where a clear classification in types and communities, as in the case of the *Gentianella caucasea* grassland is often a challenge. In the Kazbegi region the gradual transition, as well as grassland floristic diversity is partially caused by the alternating land use as meadow, spring pasture and pasture.

Abandonment, succession, afforestation, as well as severe grazing are identified as main threats for semi-natural dry grasslands in Central Europe (García-González et al., 2008). Maintaining the local, extensive livestock practice of spring pasturing is thus highly recommended to counteract those main threads. Moreover, the *Hordeum brevisubulatum* meadows, similar to the Central European mountain meadows depend on the light fertilization by cattle manure and regular cuttings (Calaciura and Spinelli, 2008). The highest species diversity, caused by the presence of many herb species, was found in the *Gentianella caucasea* grassland. Due to its moderate biomass, the *Gentianella caucasea* grassland has been mown whenever winter fodder was scarce and was pastured in spring. This low-intensive grassland use probably has significantly contributed to its high species diversity (Maccherini et al., 2011; Peco et al., 2012; Tasser and Tappeiner, 2002). An abandonment of this management practice would lead to a considerable loss of high mountain plant diversity (Maurer et al., 2006). The legume dominated, relatively species poor *Astragalus captiosus* grassland, characterized by typically low vegetation coverage, occurs mostly on south-east exposed slopes and indicates areas potentially prone to erosion (Wiesmair et al., 2016). Due to selective conditions, such as nutrient-poor soil conditions and desiccation at the erosion edges, only few species are able

to establish and keep the vegetation cover (Caprez et al., 2011). This highlights the importance of single species, especially the dominant, deep-rooting *Astragalus captiosus* (approximately 90 cm root length), to mitigate erosion processes (Caprez et al., 2011). Mineral fertilization of legume-rich swards slopes could thus lead to a decline in legume coverage, followed by a lower vegetation cover, enabling erosion on steep slopes. Management of the legume dominated *Astragalus captiosus* grassland, with its typically low vegetation coverage should be adapted to its erosion sensivity, especially on the drier south-east exposed slopes, which are characterized by low vegetation cover (Wiesmair et al., 2016).

1.6.2 Modelling floristic composition, biomass and plant functional groups

Chapter two and three was aimed at modelling and subsequently mapping species composition, biomass and plant functional groups. Species composition, in the form of three isomap ordination axes was successfully predicted by random forest regression. Relating multispectral satellite imagery, vegetation indices and topographical parameters to floristic composition resulted in an R^2 of 0.64, 0.32 and 0.46, respectively, indicating a good representability of floristic composition (for further references of the applicability of this method see chapter two).

Biomass was modelled by multispectral satellite imagery, vegetation indices and topographical parameters, as a benchmark model with an $R^2 = 0.42$ in validation. The model based on species composition, using the three modelled scores along the ordination axes as predictors, resulted in a $R^2 = 0.55$ in validation. However, high yields were generally difficult to predict with both models at yields above 6 Mg *ha^{-1}. The saturation effect and other non-linear relationships between vegetation indices and canopy properties, especially biomass are known to decrease model accuracy (Glenn et al., 2008).

However, index saturation depends on the grassland under study, modelling techniques and the indices used (Hancock and Dougherty, 2007; Vescovo and Gianelle, 2008). Vescovo and Gianelle (2008) noticed the saturation effect of NIR based vegetation indices for yields above 1.5 Mg*ha^{-1}, whereas Hancock and Dougherty (2007) detected the saturation point in blue and red based NDVI and wide range indices above 3.74 Mg*ha^{-1}. Moreover, the upper limit of the predicted range of the yield map (0.43 - 8.68 Mg *ha^{-1}) is comparable to the yields reported in literature for *Hordeum brevisubulatum* meadows (7.5 Mg*ha^{-1}) on a test site above shallow soil. A minor advantage of using species composition to model the biomass distribution lies in the close connection of species composition and yield. Ecological patterns such as the clear appearance of the high standing *Hordeum brevisubulatum* meadows, were sustained within the yield map and can be easily interpreted.
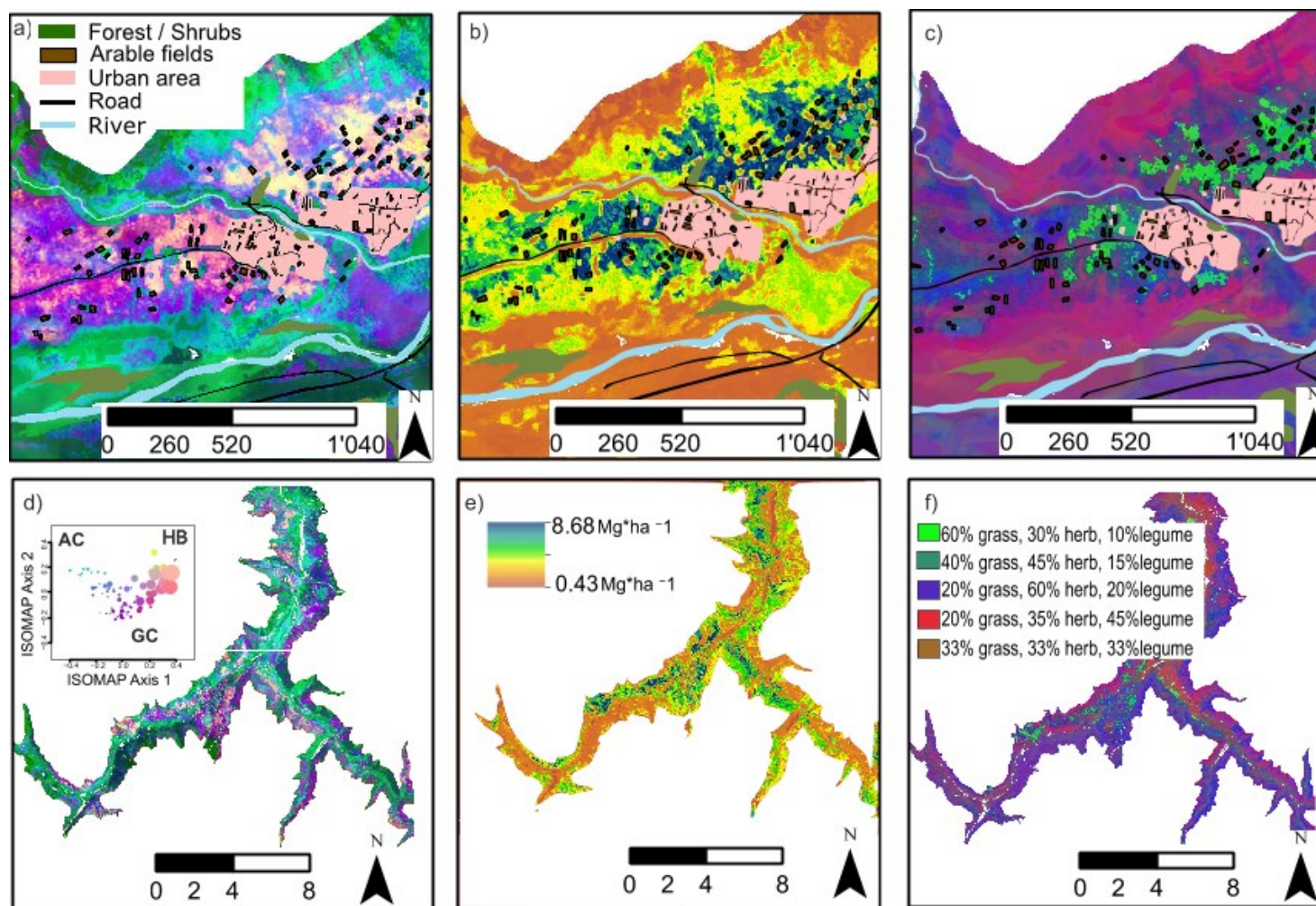
Fig. 7: Insert map of the village Phkelsche for a) Species composition in isomap Axis scores, b) yield in Mg*ha⁻¹, and c) cover of plant functional groups in %, and d), e), f) the respective maps of the research area (HB = *Hordeum brevisubulatum* meadow, GC = *Gentianella caucasea* grassland, AC = *Astragalus captiosus* grassland).

Models for plant functional groups i.e. grass, herb and legume coverage explained 36%, 25%, 37% of the respective variance and their root mean square errors varied between 12% - 15% (chapter three). When comparing simulated multispectral and hyperspectral data, the best model fits were achieved with a combination of multispectral reflectance, vegetation indices and topographic variables as predictors, indicating that a finer spectral resolution does not necessarily produces better model fits. In particular, the topographic parameters showed a strong predictive power, since they are the main influential factors for species composition (Tephnadze et al., 2014). Open source multispectral imagery as delivered by Sentinel 2 could improve the model quality since it offers three red edge, two NIR and two SWIR bands and a high revisiting rate between five to ten days, allowing for phenological observations (Drusch et al., 2012). The capability of multispectral reflectance to model floristic composition (Feilhauer et al., 2013), as well as aboveground biomass and vegetation cover, is generally high (Meyer et al., 2017; Wiesmair et al., 2016). In the high mountain context topographical parameters can significantly improve model fits. The results further indicate, that biomass, as well as species composition, are easier to model than plant functional groups, probably because of the low variance inherent to the distribution of grass, herb and legume coverage.

1.6.3 Spectral separability of encroaching shrub species

The great importance to separate birch encroachment, from other shrubs becomes highly apparent in Hansen et al. n.d., stating that *Betula litwinowii* forest increased between 2005 and 2010 by approximately 25%, possibly triggered by reduced grazing pressure and to a minor extend climate change. *Betula litwinowii* is the only shrub tested, that can develop the life-form of a tree and thus lead to reforestation in the Kazbegi region.

The analysis of the floristic composition mainly revealed that the three targeted shrub species revealed a strong co-occurrence of the shrub species. The highest abundance of *Betula litwinowii* was found in birch shrubbery but *Betula litwinowii* also appeared in *Rhododendron* shrubbery along the treeline and in *Hippophae rhamnoides* shrubbery at lower abundances. In contrast, *Hippophae rhamnoides* only emerged in its own habitat near rivers and in depressions with rock and scree. *Rhododenron caucasicum* and *Veratrum lobelianum* also typically grow in the understory of *Betula litwinowii* forest.

Fig. 8: Shrub encrachment in the Kazbegi region. Photo by Anja Magiera.

The distances (JMD) calculated for simulated satellite bands (IKONOS, Quickbird 2, RapidEye, WorldView-2) showed a good to moderate spectral separability with distances varying from 1.58 to 2 between the different species. The shortest distances (1.58, 1.59) were observed for the satellites IKONOS and Quickbird 2, which only comprise four spectral bands. The red edge band of the RapidEye sensor and the NIR II of WorldView-2 add additional information, increasing the overall separability between the classes. This is especially the case for the separation between *Rhododendron caucasicum* and *Veratrum lobelianum,* which increased with the increasing number of bands. Besides these findings, the distances between *Betula litwinowii* and *Rhododenron caucasicum* as well as between *Betula litwinowii* and *Veratrum lobelianum* generally featured a similar spectral signal across all tested satellites, indicating difficulties in spectrally separating these species. The JMDs for the vegetation clusters indicated a moderate separability of the classes with JMD ranging between 1.24 - 1.55 in June. The image taken in September produced an improved overall separability of JMD 1.56 - 1.9. The largest spectral differences were observed between the *Betula* and *Hippophae* clusters, and the least pronounced ones between the *Betula* and *Rhododendron* clusters.

Separating reflectance signatures of plant species assumes a classificatory approach, with sharp vegetation boundaries and a high homogeneity in species composition. In the tree line ecotone, where most of the research was located, this is only partly applicable. Even though forest and large shrubberies exhibit sharp boundaries, smaller shrubs such as *Rhododendron caucasium* do not. A possibility to map the above mentioned gradually expanding shrub types (excluding *Hippophae rhamnoides*, since it shows a good seperability from *Betula litwinowii*) is shown in Hansen et al., n.d. Here, structural vegetation types were derived from vegetation relevés, closely related to shrub coverage, which was subsequently mapped using the random forest algorithm and

topographical parameters as well as satellite imagery as predictors. Further, a quite distinct, species-rich floristic composition in birch shrubs and forests, closely related to site conditions, as well as tree and shrub coverage is described.

Due to the ceasing impact of land use, mainly reduced grazing pressure, further encroachment of shrubs is expected and will greatly alter the high mountain ecosystem in the Kazbegi region (Hansen et al., n.d.). The impacts of shrub encroachment and possible forest regeneration on species composition, productivity and functionality of high mountain grassland are widely unknown. Mapping and monitoring of shrub encroachment in a timely and cost-effective manner is thus urgently needed.

1.6.4 Implications for mapping and monitoring

A central question of this dissertation was to test if species composition, aboveground biomass and plant functional groups, as well as shrub encroachment can be assessed by remotely sensed data with reasonable errors to supply base maps in a cost-effective way. It could be shown in chapter two, that species composition and aboveground biomass (yield) in high mountainous regions can be mapped accurately with acceptable errors. Both parameters are under consideration for global monitoring approaches of biodiversity and ecosystem functions (Pereira et al., 2013). Recently, a set of remotely sensed Essential Biodiversity Variables has been developed to globally monitor changes in biodiversity and ecosystem functioning, including net primary productivity and community composition (Pettorelli et al., 2016). The selected variables allow for a global, periodic and standardized monitoring system (Paganini et al., 2016), even though in high yielding ecosystems challenges of the saturation effect might prevail.

Plant functional groups, were difficult to assess compared to species composition and biomass (see discussion in chapter three). Even though up until today remote sensing based studies on plant functional groups in grassland are scarce, discriminant analysis as in Lehnert et al., 2013 and Paganini et al., 2016 is proposed as a promising tool. Moreover, sensor characteristics, especially the inclusion of the shortwave infrared, play an important role (Paganini et al., 2016). However, close cooperation between vegetation ecology and the remote sensing community is necessary in order to express satellite observation requirements to detect meaningful changes (Paganini et al., 2016).

Even though the obtained results (chapter four) indicate that shrub encroachment can be separated and mapped on species level based on remotely sensed data, plant species composition and diversity is largely related to structural types, especially in the tree line cotone (Hansen et al., n.d.). In order to monitor changes in forest and shrub expansion and their effects on the ecosystem,

structural parameters are recommended, which can be modelled using connectivity analysis, as well as texture and radar data (Petrou et al., 2015).

Global and large scale monitoring approaches in biodiversity and ecosystem functioning become more and more likely with new sensor development, the construction of freely-available biodiversity databases and consistent classification schemes, such as the European Vegetation Survey (Dengler et al., 2013). In Europe the availability of remotely sensed data, for the whole globe has significantly risen with the Sentinel satellites in the Copernicus - programme of the European Comission and the European Space Agency. Already operating sensors are Sentinel 1a and b (radar imaging) and the twin optical sensors, Sentinel 2a and Sentinel 2b, with a revisiting rate between five to ten days (Drusch et al., 2012). However, influences of the fast phenological development in high mountain regions challenge the transferability of models in time, thus development of regional algorithms for different phenological stages is needed (Magiera et al., 2013).

This highlights both the importance and the possibility for future global monitoring schemes including biomass and species composition as remotely sensed Essential Biodiversity Variables. This opens up the possibility to monitor changes in biodiversity, as well as key ecosystem functions in remote high mountain regions on a regular basis. Transitional countries, like Georgia, and especially the Kazbegi region could benefit from this large scale monitoring approach.

1.7 General conclusions

The grassland in the high mountainous Kazbegi region was under low-intensity and continuous use in the past, it is therfore species and herb rich and characterized by a unique structure. The high biodiversity of the high mountain grassland is amongst other factors caused by the traditional practice of pasturing. Thus, the conservation of floristic diversity is intrinsically linked to the conservation of the traditional land use. Shrub encroachment, as a consequence of reduced land use intensity, has already been observed in considerable quantity in the Kazbegi region and is expected to significantly alter ecosystem functions.

Mapping and monitoring of species composition, biomass, plant functional groups or shrub encroachment is thus of high importance. Remote sensing based techniques for the assessment of diversity, productivity and functionality of grassland supply important information on multiple scales. For remote areas, where data availability is particularly scarce, easily obtainable remotely sensed data such as multispectral satellite imagery and digital elevation models can be beneficial as a basis for modelling, even though the calibration data, such as biomass clippings and vegetation relevés still have to be acquired, the workload compared to common mapping approaches is considerably less. Throughout this thesis it has been demonstrated, that species composition, biomass and to a minor degree plant functional groups can be mapped with the aid of remotely sensed data. Based on the results of separating shrub reflectance signatures it can be concluded that remote sensing, with high spatial resolution sensors, is capable of providing the necessary information to differentiate, classify and in return monitor the encroachment in subalpine and alpine environments, which is identified as a major thread to species diversity in Central European mountainous grassland. Even though, saturation effects, as well as the fast phenological development in the study region remain challenging for remote sensing applications.

The obtained data and base maps offer important information for the development of sustainable land use concepts in remote high mountain regions, where innovative approaches, including sociological, economical and ecologial aspects, to sustain the agricultural practice are urgently needed.

References

Adam, E., Mutanga, O., 2009. Spectral discrimination of papyrus vegetation (*Cyperus papyrus* L.) in swamp wetlands using field spectrometry. ISPRS J. Photogramm. Remote Sens. 64 (6), 612–620.

Akhalkatsi, M., Abdaladze, O., Nakhutsrishvili, G., Smith, W.K., 2006. Facilitation of seedling microsites by Rhododendron caucasicum extends the Betula litwinowii Alpine treeline, Caucasus Mountains, Republic of Georgia. Arct. Antarct. Alp. Res. 38 (4), 481–488.

Austin, M.P., Smith, T.M., 1989. A New Model for the Continuum Concept. Vegetatio 83 (1-2), 35–47.

Barthlott, W., Rafiqpoor, D., Mutke, J.,Kier, G., Kreft, H., 2005. Global centers of vascular plant diversity. Nova Acta Leopoldina 92 (342), 61–83.

Baumann, M., Kuemmerle, T., Elbakidze, M., Ozdogan, M., Radeloff, V.C., Keuler, N.S., Prishchepov, A.V., Kruhlov, I., Hostert, P., 2011. Patterns and drivers of post-socialist farmland abandonment in Western Ukraine. Land Use Policy 28 (3), 552–562.

Benayas, R. M.J., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 2 (57).

Biewer, S., Fricke, T., Wachendorf, M., 2009. Development of Canopy Reflectance Models to Predict Forage Quality of Legume-Grass Mixtures. Crop Sci. 49 (5), 1917–1926.

Boschetti, M., Bocchi, S., Brivio, P.A., 2007. Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information. Agric. Ecosyst. Environ. 118 (1-4), 267–272.

Bray, J.R., Curtis, J.T., 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecol. Monogr., 27 (4), 325–349.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.

Buddenbaum, H., Schlerf, M., Hill, J., 2005. Classification of coniferous tree species and age classes using hyperspectral data and geostatistical methods. Int. J. Remote Sens. 26 (24), 5453–5465.

Calaciura, B., Spinelli, O., 2008. Management of Natura 2000 habitats. Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco Brometalia). European Commission. http://ec.europa.eu/environment/nature/natura2000/management/habitats/pdf/6210_Seminatural_dry_grasslands.pdf (accessed 11.08.2017).

Camarero, J.J., Gutiérrez, E., 2004. Pace and Pattern of Recent Treeline Dynamics: Response of Ecotones to Climatic Variability in the Spanish Pyrenees. Clim. Change 63 (1-2), 181–200.

Caprez, R., Spehn, E., Nakhutsrishvili, G., Körner, C., 2011. Drought at erosion edges selects for a "hidden" keystone species. Plant Ecol. Divers. 4 (4), 303–311.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 18 (1), 117–143.

Clements, F.E., 1916. Plant succession; an analysis of the development of vegetation, Carnegie Institution of Washington, Washington.

Cocca, G., Sturaro, E., Gallo, L., Ramanzin, M., 2012. Is the abandonment of traditional livestock farming systems the main driver of mountain landscape change in Alpine areas? Land Use Policy 29 (4), 878–886.

Cochrane, M.A., 2000. Using vegetation reflectance variability for species level classification of hyperspectral data. Int. J. Remote Sens. 21 (10), 2075–2087.

Curran, P.J., 1983. Multispectral remote sensing for the estimation of green leaf-area index. Philos. Trans. R. Soc. Lond. Ser. -Math. Phys. Eng. Sci. 309 (1508), 257–270.

Curran, P.J., Dungan, J.L., Peterson, D.L., 2001. Estimating the foliar biochemical concentration of leaves with reflectance spectrometry: Testing the Kokaly and Clark methodologies. Remote Sens. Environ. 76 (3), 349–359.

Dawson, T.P., Curran, P.J., 1998. A new technique for interpolating the reflectance red edge position. Int. J. Remote Sens., 9 (11), 2133-2139,

De Cáceres, M., Wiser, S.K., 2012. Towards consistency in vegetation classification. J. Veg. Sci. 23 (2), 387–393.

DeMarco, J., Mack, M.C., Bret-Harte, M.S., 2011. The Effects of Snow, Soil Microenvironment, and Soil Organic Matter Quality on N Availability in Three Alaskan Arctic Plant Communities. Ecosystems 14 (5), 804–817.

Dengler, J., Jansen, F., Glöckler, F., Peet, R. K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., Mucina, L., Rodwell, J.S., Schaminée, J. H. J., Spencer, N, 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. J. Veg. Sci. 22 (4), 582–597.

Dengler, J., Bergmeier, E., Willner, W., Chytrý, M., 2013. Towards a consistent classification of European grasslands. Appl. Veg. Sci. 16, 518–520.

Didebulidze, A., Plachter, H., 2002. Nature conservation aspects of pastoral farming in Georgia, in: Redecker, B., Fink, B., Härdtle, W., Riecken, U., Schröder, E. (Eds.), Pasture Landscapes and Nature Conservation. Springer, Berlin, pp. 87–105.

Diker, K., Bausch, W.C., 2003. Potential Use of Nitrogen Reflectance Index to estimate Plant Parameters and Yield of Maize. Biosyst. Eng. 85 (4), 437–447.

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., Meygret, A., Spoto, F., Sy, O., Marchese, F., Bargellini, P., 2012. Sentinel-2: ESA's Optical High-Resolution Mission for GMES Operational Services. Remote Sens. Environ. 120, 25–36.

Evans J.S., Oakleaf J., Cushman S.A., Theobald D., 2014. An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, Version 2.0-0. http://evansmurphy.wix.com/evansspatial (accessed 02.10.14).

Feilhauer, H., Faude, U., Schmidtlein, S., 2011. Combining Isomap ordination and imaging spectroscopy to map continuous floristic gradients in a heterogeneous landscape. Remote Sens. Environ. 115 (10), 2513–2524.

Feilhauer, H., Thonfeld, F., Faude, U., He, K.S., Rocchini, D., Schmidtlein, S., 2013. Assessing floristic composition with multispectral sensors—A comparison based on monotemporal and multiseasonal field spectra. Int. J. Appl. Earth Obs. Geoinformation 21, 218–229.

Feilhauer H, Doktor D, Schmidtlein, S, Skidmore AK. 2016. Mapping pollination types with remote sensing. J. Veg. Sci. 27 (5), 999-1011.

Fillela, I., Penuelas, J., 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass and hydric status. Int. J. Remote Sens. 15 (7), 1459–1470.

Gagnidze, R., 2005. Vascular Plants of Georgia – A Nomenclatural Checklist. Georgian Academy of Sciences, N. Ketskhoveli Institute of Botany, I. Javakhishvili Tbilisi State University, Department of Botany, Tbilisi.

García-González, R., 2008. Management of Natura 2000 habitats. Alpine and subalpine calcareous grasslands. European Comission. http://ec.europa.eu/environment /nature/natura2000/management/habitats/pdf/6170_Alpine_calcareous_grasslands.pdf. (accessed 13.08.2017).

Gleason, H.A., 1926. The individualistic concept of plant association. Bull. Torrey Bot. Club 53, 7–26.

Glenn, E.P., Huete, A.R., Nagler, P.L., Nelson, S.G., 2008. Relationship Between Remotely-sensed Vegetation Indices, Canopy Attributes and Plant Physiological Processes: What Vegetation Indices Can and Cannot Tell Us About the Landscape. Sensors 8 (4), 2136–2160.

Gracheva, R., Kohler, T., Stadelbauer, J., Meessen, H., 2012. Population dynamics, changes in land management, and the future of mountain areas in Northern Caucasus: the example of North Ossetia. Erdkunde 66 (3), 197–219.

Gret-Regamey, A., Brunner, S.H., Kienast, F., 2012. Mountain ecosystem services: Who cares? Mt. Res. Dev. 32, 23–S34.

Gurung, A.B., von Dach, S.W., Price, M.F., Aspinall, R., Balsiger, J., Baron, J.S., Sharma, E., Greenwood, G., Kohler, T., 2012. Global Change and the World's Mountains— Research Needs and Emerging Themes for Sustainable Development. Mt. Res. Dev. 32, 47–S54.

Hanauer, T., Pohlenz, C., Kalandadze, B., Urushadze, T., Felix-Henningsen, P., 2017. Soil distribution and soil properties in the subalpine region of Kazbegi; Greater Caucasus; Georgia: Soil quality rating of agricultural soils. Ann. Agrar. Sci. 15 (1). 1-10.

Hancock, D.W., Dougherty, C.T., 2007. Relationships between Blue- and Red-based Vegetation Indices and Leaf Area and Yield of Alfalfa. Crop Sci. 47, 2547–2556.

Hansen, W., Magiera, A. Theißen, T., Waldhardt, R., Otte, A.: Analyzing *Betula litwinowii* shrub encroachment and reforestation in the Kazbegi region, Greater Caucasus Georgia. - Journal of Vegetation Science (submitted).

Harris, A.T., Asner, G.P., Miller, M.E., 2003. Changes in vegetation structure after long-term grazing in pinyon-juniper ecosystems: Integrating imaging spectroscopy and field studies. Ecosystems 6 84), 368–383.

Heiny, J., Mamniashvili, G., Leonhaeuser, I.-U., 2017. The socioeconomic situation of private households in the Kazbegi region – First insights based on quantitative data. Ann. Agrar. 15 (1), 31-39.

Holtmeier, F.-K., Broll, G., 2007. Treeline advance–driving processes and adverse factors. Landsc. Online 1 (1–33), 61-83.

Horler, D.N.H., Dockray, M., Barber, J., 1983. The red edge of plant leaf reflectance. Int. J. Remote Sens. 4 82), 273–288.

Huete, A., Justice, C., Van Leeuwen, W., 1999. MODIS vegetation index (MOD13). Algorithm Theor. Basis Doc. 3, 213.

Jackson, R.D., Huete, A.R., 1991. Interpreting vegetation indices. Prev. Vet. Med. 11 (3), 185–200.

Jordan, C.F., 1969. Derivation of Leaf-Area Index from Quality of Light on the Forest Floor. Ecology 50 (4), 663–666.

Kikvidze, Z., 1996. Neighbour interaction and stability in subalpine meadow communities. J. Veg. Sci. 7 (1), 41–44.

Kikvidze, Z., Michalet, R., Brooker, R.W., Cavieres, L.A., Lortie, C.J., Pugnaire, F.I., Callaway, R.M., 2011. Climatic drivers of plant-plant interactions and diversity in alpine communities. Alp. Bot. 121 (1), 63–70.

Klimek, S., Richter gen. Kemmermann, A., Hofmann, M., Isselstein, J., 2007. Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. Biol. Conserv. 134 (4), 559–570.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., Peters, D.P., Young, D.R., Shaver, G.R., Pendall, E., Cleary, M.B., 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Glob. Change Biol. 14 (3), 615–623.

Körner, C., 2004. Mountain biodiversity, its causes and function. Ambio Spec. No.13. 11–17.

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K., M. Spehn, E., 2017. A global inventory of mountains for bio-geographical applications. Alp. Bot. 127 (1), 1–15.

Lehnert L.W., Meyer H., Meyer N., Reudenbach C., Bendix J. 2013. Assessing pasture quality and degradation status using hyperspectral imaging: a case study from western Tibet. Remote Sensing for Agriculture, Ecosystems, and Hydrology XV, 88870I.

Lehnert L.W., Meyer H., Meyer N., Reudenbach C., Bendix J. 2014. A hyperspectral indicator system for rangeland degradation on the Tibetan Plateau: A case study towards spaceborne monitoring. Ecol. Ind. 39: 54–64.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R News 2, 18–22.

Lichtenegger, E., Bedoschwili, D., Hübl, E., Scharf, E., 2006. Höhenstufengliederung der Grünlandvegetation im Zentralkaukasus. Verhandlungen Zool.-Bot. Ges. Österr. 143, 43–81.

Maccherini, S., Marignani, M., Gioria, M., Renzi, M., Rocchini, D., Santi, E., Torri, D., Tundo, J., Honnay, O., 2011. Determinants of plant community composition of remnant biancane badlands: a hierarchical approach to quantify species-environment relationships. Appl. Veg. Sci. 14 (3), 378–387.

MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J.G., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. J. Environ. Manage. 59 (1), 47–69.

Magiera, A., Feilhauer, H., Otte, A., Waldhardt, R., Simmering, D., 2013. Relating canopy reflectance to the vegetation composition of mountainous grasslands in the Greater Caucasus. Agric. Ecosyst. Environ. 177 (1), 101–112.

Magiera, A., Feilhauer, H., Waldhardt, R., Wiesmair, M., Otte, A., 2017. Modelling biomass of mountainous grasslands by including a species composition map. – Ecol. Ind. 78, 8-18.

Marini, L., Scotton, M., Klimek, S., Isselstein, J., Pecile, A., 2007. Effects of local factors on plant species richness and composition of Alpine meadows. Agric. Ecosyst. Environ. 119 (3-4), 281–288.

Marini, L., Scotton, M., Klimek, S., Pecile, A., 2008. Patterns of plant species richness in Alpine hay meadows: Local vs. landscape controls. Basic Appl. Ecol. 9 (4), 365–372.

Maurer, K., Weyand, A., Fischer, M., Stocklin, J., 2006. Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. Biol. Conserv. 130 (3), 438–446.

Mayer, R., Kaufmann, R., Vorhauser, K., Erschbamer, B., 2009. Effects of grazing exclusion on species composition in high-altitude grasslands of the Central Alps. Basic Appl. Ecol. 10 (5), 447–455.

Messerli, B., Viviroli, D., Weingartner, R., 2004. Mountains of the World: Vulnerable Water Towers for the 21st Century. Ambio Spec. No. 13, 29–34.

Meyer, H., Lehnert, L.W., Wang, Y., Reudenbach, C., Nauss, T., Bendix, J., 2017. From local spectral measurements to maps of vegetation cover and biomass on the Qinghai-Tibet-Plateau: Do we need hyperspectral information? Int. J. Appl. Earth Obs. Geoinformation 55, 21–31.

Ministry of Geology of the USSR (1983): K38-54-Geological Map M 1:50.000. (in Russian).

Mirkin, B.M., Kononov, K.E., Gogoleva, P.A., Burtseva, E.I., Naumova, L.G., 1992. The Floodplain Grasslands of the Middle Lena-River II Classification. Folia Geobot. Phytotax. 27, 247-300

Mohd Shafr, H.Z., Mohd Sall, M.A., Ghiyamat, A., 2006. Hyperspectral Remote Sensing of Vegetation Using Red Edge Position Techniques. Am. J. Appl. Sci. 3, 1864–1871.

Myers, N., 2003. Biodiversity hotspots revisited. Bioscience 53, 916–917.

Nakhutsrishvili, G., 1999. The vegetation of Georgia (Caucasus). Braun-Blanquetia 15, 5–74.

Nakhutsrishvili, G., Abdaladze, O., Akhalkatsi, M., 2006. Biotope types of the treeline of the Central Greater Caucasus, in: Gafta, D., Akeroyd, J. (Eds.), Nature Conservation: Concepts and Practice, Environmental Science and Engineering. Springer, Berlin, pp. 211–225.

Nakhutsrishvili, G., Abdaladze, O., Kikodze, A., 2005. Khevi - Kazbegi region. Institute of Botany, Tbilisi, pp. 54.

Nakhutsrishvili, G., Gagnidze, R., 1999. Die subnivale und nivale Hochgebirgsvegetation des Kaukasus. Phytocoen. - Suppl. Cartogr. Geobot. 11, 173–183.

Nakhutsrishvili, G.S., 1976. Ecological Investigations at Kazbeg high-mountain station. Sov. J. Ecol. 7, 256–260. (in Russian).

Nakhutsrishvili, G. 2012. The Vegetation of Georgia (South Caucasus). Springer-Verlag, Vienna, pp. 235.

National Statistics Office of Georgia 2016a: Demographic Situation in Georgia. http://www.geostat.ge/cms/site_images/_files/georgian/population/Demografiuli%20 Vitareba%20SaqartveloSi%20Krebuli%202016.pdf. (accessed 17.05.2017).

National Statistics Office of Georgia 2016b:Agriculture in Georgia. http://www.geostat.ge/cms/site_images/_files/english/calendar/agriculture/Agriculture%20of%20Georgia%202010.pdf. (accessed 17.05.2017).

Oksanen, J. 2015. Multivariate Analysis of Ecological Communities in R: vegan tutorial. http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf. (accessed 25.07.2017).

O'Mara, F.P., 2012. The role of grasslands in food security and climate change. Ann. Bot. 110 (3), 1263–1270.

Paganini, M., Leidner, A.K., Geller, G., Turner, W., Wegmann, M., 2016. The role of space agencies in remotely sensed essential biodiversity variables. Remote Sens. Ecol. Conserv. 2 (3), 132–140.

Peco, B., Carmona, C.P., de Pablos, I., Azcarate, F.M., 2012. Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. Agric. Ecosyst. Environ. 152, 27–32.

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Hoft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. Essential Biodiversity Variables. Science 339 (18), 277–278.

Peroni, P., Ferri, F., Avena, G.C., 2000. Temporal and spatial changes in a mountainous area of central Italy. J. Veg. Sci. 11 (4), 505–514.

Petrou, Z.I., Manakos, I., Stathaki, T., 2015. Remote sensing for biodiversity monitoring: a review of methods for biodiversity indicator extraction and assessment of progress towards international targets. Biodivers. Conserv. 24 (10), 2333–2363.

Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T.P., Fernandez, M., Lucas, R., Schaepman, M.E., Wang, T., O'Connor, B., Jongman, R.H.G., Kempeneers, P., Sonnenschein, R., Leidner, A.K., Böhm, M., He, K.S., Nagendra, H., Dubois, G., Fatoyinbo, T., Hansen, M.C., Paganini, M., de Klerk, H.M., Asner, G.P., Kerr, J.T., Estes, A.B., Schmeller, D.S., Heiden, U., Rocchini, D., Pereira, H.M., Turak, E., Fernandez, N., Lausch, A., Cho, M.A., Alcaraz-Segura, D., McGeoch, M.A., Turner, W., Mueller, A., St-Louis, V., Penner, J., Vihervaara, P., Belward, A., Reyers, B., Geller, G.N., 2016. Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. Remote Sens. Ecol. Conserv. 2 (3), 122–131.

Pohl, M., Alig, D., Körner, C., Rixen, C., 2009. Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant Soil 324 (1-2), 91–102.

Pohlert, T., 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). R package. http://CRAN.R-project.org/package=PMCMR. (accessed 09.08.2017).

Prishchepov, A.V., Müller, D., Dubinin, M., Baumann, M., Radeloff, V.C., 2013. Determinants of agricultural land abandonment in post-Soviet European Russia. Land Use Policy 30 (1), 873–884.

Pyšek, P., Šrutek, M., 1989. Numerical Phytosociology of the subalpine belt of the Kazbegi region, Caucasus, USSR. Vegetatio 81 (1-2), 199–208.

Qi, J., Chehbouni, A., Huete, A.R., Kerr, Y.H., Sorooshian, S., 1994. A modified soil adjusted vegetation index. Remote Sens. Environ. 48 (2), 119–126.

Rhodes, L., Bradley, I., Zair, W. Maxted, N., 2016. Hordeum brevisubulatum. The IUCN Red List of Threatened Species 2016. http://dx.doi.org/10.2305/IUCN.UK.20163.RLTS.T172229A19410689.en. (accessed 01.08.2017).

Rocchini, D., He, K.S., Oldeland, J., Wesuls, D., Neteler, M., 2010. Spectral variation versus species beta-diversity at different spatial scales: a test in African highland savannas. J. Environ. Monit. 12 (4), 825–831.

Rouse, J.W., Haas, R.H., Schell, J.A., Deering, D.W., 1973. Monitoring vegetation systems in the Great Plains with ERTS. NASA. Goddard Space Flight Center 3d ERST-1 Symp., Vol. 1, Sect. A, p. 309-317.

Sakhokia, M., 1983. Agrobotanical review of Khevi (Kazbegi region) pastures and hay meadows and optimization ways, Metsniereba, Tbilisi. (in Georgian).

Savitzky A, Golay MJE: 1964. Smoothing and Differentiation of Data by Simplified Least Squares Procedures. Anal. Chem. 36, 1627–1639.

Schmidt, K., Skidmore, A., 2003. Spectral discrimination of vegetation types in a coastal wetland. Remote Sens. Environ. 85 (1), 92–108.

Schmidtlein, S., 2005. Imaging spectroscopy as a tool for mapping Ellenberg indicator values. J. Appl. Ecol. 42 (5), 966–974.

Schmidtlein, S., Feilhauer, H., Bruelheide, H., 2012. Mapping plant strategy types using remote sensing. J. Veg. Sci. 23 (3), 395–405.

Schmidtlein, S., Tichy, L., Feilhauer, H., Faude, U., 2010. A brute-force approach to vegetation classification. J. Veg. Sci. 21 (6), 1162–1171.

Schmidtlein, S., Zimmermann, P., Schüpferling, R., Weiss, C., 2007. Mapping the floristic continuum: Ordination space position estimated from imaging spectroscopy. J. Veg. Sci. 18 (1), 131–140.

Simmering, D., Waldhardt, R., Otte, A., 2001. Zur vegetationsökologischen Bedeutung scharfer Grenzlinien in Agrarlandschaften-Beispiele aus einer kleinstrukturierten Mittelgebirgslandschaft. Peckiana 1, 79–87.

Smith, W., Germino, M., Johnson, D., Reinhardt, K., 2009. The Altitude of Alpine Treeline: A Bellwether of Climate Change Effects. Bot. Rev. 75 (2), 163–190.

Sturm, M., Holmgren, J., McFadden, J.P., Liston, G.E., Chapin, F.S., Racine, C.H., 2001. Snow–Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic Implications. J. Clim. 14, 336–344.

Sun W, Liang S, Xu G, Fang H, Dickinson R. 2008. Mapping plant functional types from MODIS data using multi-source evidential reasoning. Remote Sensing of Environment 112:1010–1024.

Tappeiner, U., Cernusca, A., 1989. Canopy structure and light climate of different alpine plant communities: Analysis by means of a model. Theor. Appl. Climatol. 40 (1-2), 81–92.

Tasser, E., Mader, M., Tappeiner, U., 2003. Effects of land use in alpine grasslands on the probability of landslides. Basic Appl. Ecol. 4 (3), 271–280.

Tasser, E., Tappeiner, U., 2002. Impact of land use changes on mountain vegetation. Appl. Veg. Sci. 5 (2), 173–184.

Teillet, P.M., Guindon, B., Goodenough, D.G., 1982. On the Slope-Aspect Correction of Multispectral Scanner Data. Can. J. Remote Sens. 8 (2), 84–106.

Tenenbaum, J.B., Silva, V. de, Langford, J.C., 2000. A Global Geometric Framework for Nonlinear Dimensionality Reduction. Science 290, 2319–2323.

Tephnadze, N., Abdaladze, O., Nakhutsrishvili, G., Simmering, D., Waldhardt, R., Otte, A., 2014. The impacts of management and site conditions on the phytodiversity of the upper montane and subalpine belts in the Central Greater Caucasus. Phytocoenologia 44, 255–291.

The IUCN Red List of Endangered Species, 2017. The IUCN Red List of Endangered Species. Version 2017-1. http://www.iucnredlist.org/details/172229/0 (accessed 11.08.2017).

The Plantlist, 2013. The Plantlist. Version 1.1. http://www.theplantlist.org (accessed 16.02.2016).

Thenkabail, P.S., Smith, R.B., Pauwde, E., 2000. Hyperspectral Vegetation Indices and Their Relationships with Agricultural Crop Characteristics. Remote Sens. Environ. 71 (3-4), 158–182.

Thenkabail, P.S., Lyon, J.G., Huete, A., 2011. Hyperspectral Remote Sensing of Vegetation, New Edition. CRC Press Inc., Boca Raton.

Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. New Phytol. 186 (4), 795–816.

van Leeuwen, C. G., 1966. A relation theoretical approach to pattern and process in vegetation. Wentia. 15 (S1), 25–46.

Vescovo, L., Gianelle, D., 2008. Using the MIR bands in vegetation indices for the estimation of grassland biophysical parameters from satellite remote sensing in the Alps region of Trentino (Italy). Adv. Space Res. 41 (11), 1764–1772.

Waldhardt, R., Abdaladze, O., Otte, A., Simmering, D., 2011. Landschaftswandel im Kaukasus Georgiens. Interdisziplinäre Forschung für eine nachhaltigere Zukunft. Spieg. Forsch. 28, 4–15.

Watson, R.T., Haeberli, W., 2004. Environmental Threats, Mitigation Strategies and High-Mountain Areas. Ambio Spec. No. 13, 2–10.

Wiesmair, M., Feilhauer, H., Magiera, A., Otte, A., Waldhardt, R., 2016. Estimating Vegetation Cover from High-Resolution Satellite Data to Assess Grassland Degradation in the Georgian Caucasus. Mt. Res. Dev. 36 (1), 56–65.

Wiesmair, M., Otte, A., Waldhardt, R., 2017. Relationships between plant diversity, vegetation cover, and site conditions: implications for grassland conservation in the Greater Caucasus. Biodivers. Conserv. 26 (2), 273–291.

Wilson, S.D., Nilsson, C., 2009. Arctic alpine vegetation change over 20 years. Glob. Change Biol. 15 (7), 1676–1684.

Woodwell, G.M., 2004. Mountains: top down. Ambio Spec. No. 13, 35–38.

2. Modelling biomass of mountainous grasslands by including a species composition map

Anja Magiera [1], Hannes Feilhauer [2], Rainer Waldhardt [1], Martin Wiesmair[3], Annette Otte [1]

[1, 3]*Division of Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resources Management, Justus-Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany*[+]

[2] *Institute of Geography, Friedrich-Alexander University, Wetterkreuz 15, 91058 Erlangen, Germany*

[3] *Center for International Development and Environmental Research (ZEU), Senckenbergstrasse 3, 35390 Giessen, Germany*

Key words: Yield, standing biomass, hay meadows, Isomap, Random Forest, gradient modelling, remote sensing, Greater Caucasus

Abstract

High mountain grasslands offer multiple goods and services to society but are severely threatened by improper land use practices such as abandonment or rapid intensification. In order to reduce abandonment and strengthen the common extensive agricultural practice a sustainable land use management of high mountain grasslands is needed. A spatially detailed yield assessment helps to identify possible meadows or, on the contrary, areas with a low carrying capacity in a region, making it easier to manage these sites. Such assessments are rarely available for remote and inaccessible areas. Remotely sensed vegetation indices are able to provide valuable information on grassland properties. These indices tend, however, to saturate for high biomass. This affects their applicability to assessments of high-yield grasslands.

The main aim of this study was to model a spatially explicit grassland yield map and to test whether saturation issues can be tackled by consideration of plant species composition in the modelling process. The high mountain grassland of the subalpine belt (1,800 - 2,500 m a.s.l.) in the Kazbegi region, Greater Caucasus, Georgia, was chosen as test site for its strong species composition and yield gradients.

We first modelled the species composition of the grassland described as metrically scaled gradients in the form of ordination axes by random forest regression. We then derived vegetation indices from Rapid Eye imagery, and topographic variables from a digital elevation model as predictive variables. For comparison, we performed two yield models, one excluding the species composition maps and one including the species composition map as predictors. Moreover, we performed a third individual model, with species composition as predictors and a split dataset, to produce the final yield map.

Three main grassland types were found in the vegetation analysis: *Hordeum violaceum*-meadows, *Gentianella caucasea*-grassland and *Astragalus captiosus*-grassland. The three random forest regression models for the ordination axes explained 64%, 33% and 46% of the variance in species composition. Independent validation of modelled ordination scores against a validation data set resulted in an R^2 of 0.64, 0.32 and 0.46 for the first, second and third axes, respectively. The model based on species composition resulted in a $R^2 = 0.55$, whereas the benchmark model showed weaker relationships between yield and the multispectral reflectance, vegetation indices, and topographical parameters ($R^2 = 0.42$). The final random forest yield model used to derive the yield map resulted in 62% variance explained and an $R^2 = 0.64$ between predicted and observed biomass. The results further indicate that high yields are generally difficult to predict with both models.

The benefit of including a species composition map as a predictor variable for grassland yield lies in the preservation of ecologically meaningful features, especially the occurrence of high yielding vegetation type of *Hordeum violaceum* meadows is depicted accurately in the map. Even though we used a gradient based design, sharp boundaries or immediate changes in productivity were visible, especially in small structures such as arable fields or roads (Fig. 6b), making it a valuable tool for sustainable land use management. The saturation effect however, was mitigated by using species composition as predictor variables but is still present at high yields.

2.1 Introduction

High mountain grasslands offer multiple ecosystem services to society (Gret-Regamey et al., 2008). The high mountain grassland vegetation regulates water flows and prevents erosion events with its root system (Körner, 2004; Pohl et al., 2009), whereas the grassland yield supplies the nutritional basis for local dairy and livestock production (O'Mara, 2012). High mountain grasslands further provide important cultural services, such as recreation or scenic beauty (Schirpke et al., 2013). As a result of a long term agricultural use as meadow or pasture, the high mountain grassland features a high biodiversity and unique plant species composition, significantly influencing the functioning of the mountainous ecosystem (Körner et al., 2006).

The species diversity of high mountain grassland and thus the functioning of the mountainous ecosystem with its provision of services is strongly affected by land-use changes, such as the abandonment of low-intensity agricultural practices (Cocca et al., 2012; Klimek et al., 2007). In order to prevent farmers from abandoning agricultural practices, the mode of production needs to be economically viable. Including spatially explicit information about the productivity or yield of the grassland into the land use management can help to determine the carrying capacity, livestock stocking rates and the amount of available fodder in a region, aiding in avoiding over use or abandonment.

The estimation of aboveground biomass or related variables, such as leaf area index, is a key topic in many remote sensing studies that is addressed with either multispectral (Anderson et al., 1993; Liu et al., 2007; Wu et al., 2007) or hyperspectral vegetation indices (Boschetti et al., 2007; Cho and Skidmore, 2009; Fillela and Penuelas, 1994; Psomas et al., 2011). Vegetation indices use the strong contrast between the absorption features of chlorophyll in the visible light and the high reflectance in the near–infrared region (NIR) to quantify the vegetation condition (Jackson and Huete, 1991). However, vegetation indices in general tend to saturate in areas of a high biomass or leaf area, even though the exact saturation point varies between the indices. In the past, vegetation indices were used to model pasture yields, which cover a gradient from low to moderate standing biomass

(Boschetti et al. 2007; Hancock and Dougherty, 2007; Vescovo and Gianelle, 2008; Chen et al., 2009). These studies are limited by the fact that saturation of vegetation indices mainly occurs at high yields. Therefore, their relationship with high yield grassland, such as hay meadows still remains challenging. Moreover, Dusseux et al. (2015) found that biophysical variables (leaf area index and fractional vegetation cover) derived from remotely sensed imagery showed better correlations to biomass than the tested vegetation indices.

High mountain grasslands are an ideal research object, providing strong gradients of grassland productivity within gradually transitioning grassland types, offering a good example of the gradual change of species composition along topographic, and especially altitudinal gradients (Gleason, 1926). Modelling the gradual change of species composition of grasslands was already successfully performed (Feilhauer and Schmidtlein, 2011; Magiera et al., 2013; Schmidtlein and Sassin 2004). Although the relationship between biomass productivity and species richness is controversially discussed (Adler et al., 2011; Grace et al., 2012), both are clearly linked to each other (Guo, 2007). In a semi-natural landscape, with low farming intensity, the environmental conditions such as nutrient availability, soil depth or water content determine both species composition and the yield.

The primary aim of this study was to derive a spatially explicit grassland yield using remotely sensed data, in order to obtain a base map for sustainable land–use management. Our main objectives were:

i) to describe the main vegetation and topographic gradients and their relationships to biomass yield;

ii) to accurately and spatially explicitly predict above ground biomass as continuous fields;

iii) to test, whether remotely sensed patterns of species composition are suitable predictor variables for a yield model.

In order to meet these objectives, we first modelled the species composition of the diverse subalpine grassland by employing a random forest model between species composition and vegetation indices together with topographical parameters. We then related these gradients to biomass data and generated a yield map. We compared the yield model based on the species composition maps to a model, which only related multispectral reflectance, vegetation indices and topographical parameters to yield. The high mountain region of Kazbegi, Greater Caucasus, Georgia, was chosen as our test site since it offered ideal research opportunities with species-rich and structurally diverse subalpine grassland types.

2.2. Material and methods

2.2.1 Study area

The study area (Fig. 1) is located in the Kazbegi district in the Republic of Georgia, which lies in the central part of the Greater Caucasus, a high mountain range that is characterized by high elevations, steep slopes, as well as harsh and continental climatic conditions (Akhalkatsi et al. 2006).
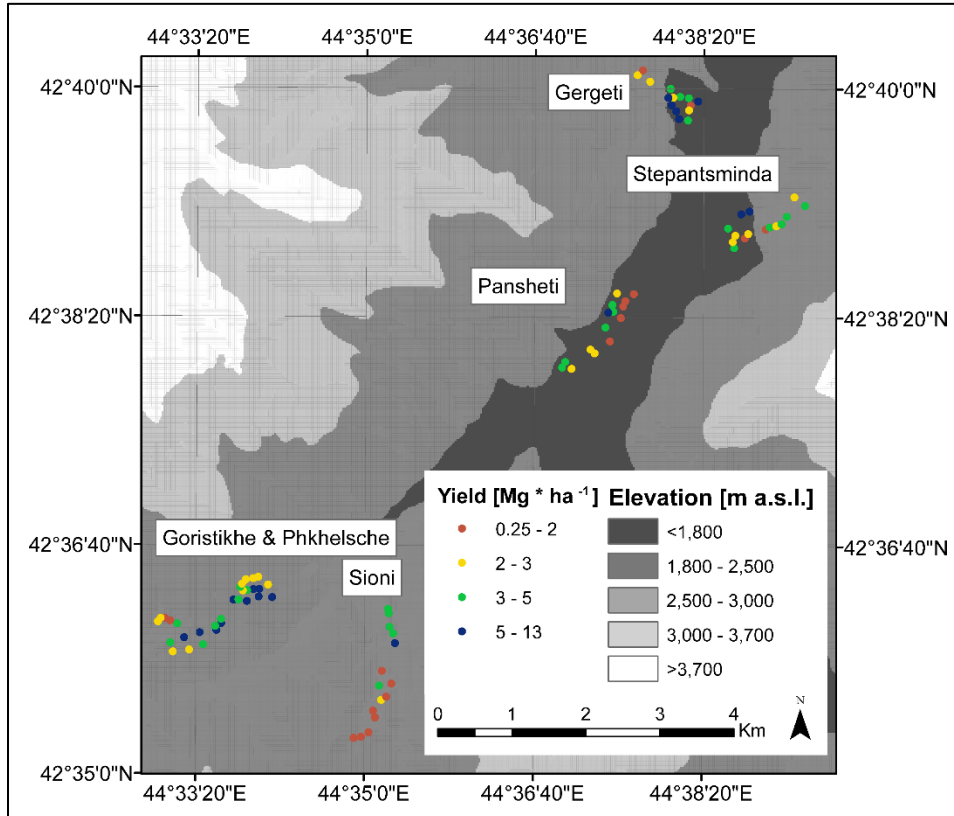
Fig. 1: Map of the study area with yields observed in the sampling plots.

The main village Stepantsminda (1800 m a.s.l.) stretches next to the banks of the river Tergi, which flows in a northern direction. The land cover of the Kazbegi region is dominated by different grassland types, which are used as meadow or pasture with low-intensity (Waldhardt et al., 2011). In spring, from the snow melt until the mid of May, the first shoots of the productive hay meadows of the valley bottom are grazed by cattle. There is no application of fertilizer on the meadows, besides the cow dung from the spring pasturing. A high proportion of the actual hay meadows were used as arable land decades ago. After May, the cattle are moved to either higher elevations or less productive low land pastures (1700 m a.s.l.). A system of fences is then installed to protect the subalpine meadows from free ranging cattle. In the summer these meadows are mown once between the end of July and the end of August, which is late in the vegetation period but precipitation poor (Sakokhia, 1983). For a detailed description of the study region we refer to Magiera et al. (2013) and Tephnadze et al. (2014).

2.2.2. Data sampling and analysis

In order to model the grassland yield, we related species composition, in the form of three Isomap axes to multispectral reflectance, vegetation indices and topographic information. The general approach is visualized in Fig 2.
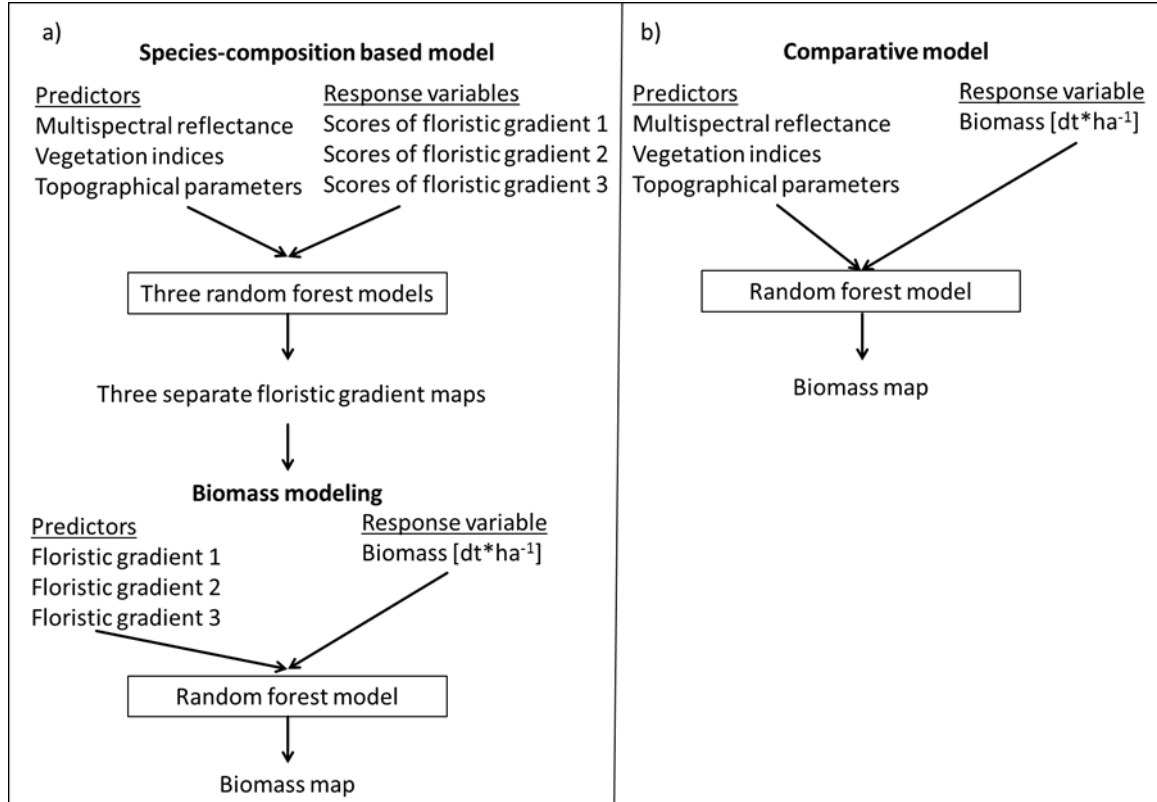
Fig. 2: Flow-chart of our modelling approach. The biomass modelling includes a) a species-composition based model and b) a bootstrapped comparative common model.

Instead of a discrete classification our approach was based on the continuous change of species composition, which was represented by a three dimensional ordination space with the plot scores as the three main floristic gradients. Ordination is a frequently used means in vegetation science to reduce the dimensionality of a vegetation data set towards an analysis of gradual changes in species composition, the so-called floristic gradients. These gradients were used as the three dependent variables in three random forest models to be further related to topographical and multispectral information to gain a species composition map. The resulting scores on the metrically scaled ordination axes were then related to aboveground biomass with a second random forest model, resulting in a grassland yield map. In order to compare our species composition based model to a model relating multispectral reflectance, vegetation indices and topographical parameters directly to biomass, without including species composition as a proxy variable, we further calculated a random forest model with biomass as a response variable and the topographic parameters as predictors (see Fig. 2 b).

2.2.2.1 Assessment of species composition and biomass sampling

In order to cover the whole biomass gradient of grassland in the valley bottom and on the lower slopes, we sampled the surrounding grassland of six villages (Stepantsminda, Gergeti, Pansheti, Sioni, Phkelsche and Goristhikhe) in the Kazbegi region. These grasslands are in use either as hay meadow or pasture. The exact locations of sampling plots were chosen in a stratified random design and covered a productivity gradient. Only large homogeneous grassland areas were sampled in order to avoid edge effects, mixed pixels, and problems with positional errors. Moreover, a minimum distance of approximately 50 m between the plots was kept. The position was recorded with a common GPS (Garmin 64s) with a positioning accuracy of approximately 3 m. Next to each village, 15 plots of 25 m² each (90 plots in total) were sampled for vegetation composition analysis and biomass clippings. In June and July 2014, at peak biomass, vascular plant species composition and cover were visually estimated by using the modified Braun Blanquet scale and were later transformed into ordinal values for the statistical analysis (Braun-Blanquet, 1964; van der Maarel, 1979). Nomenclature was generally based on The Plant List 1.1 (The Plantlist, 2010) in chapter two and three, only in the case of *Hordeum violaceum* the taxonomy of Gagnidze et al. 2005 was kept. The nomenclature of chapter four is based on Gagnidze et al. 2005. As explanatory variables we further recorded the total vegetation cover, as well as the cover of open soil and bare rocks. For the upper and lower herb layers we separately assessed their cover percentage and height. Additionally, we estimated the cover fraction of the functional groups of broad-leafed herbs and grasses. In the last week of July 2014 at the time of regular mowing we clipped the aboveground biomass in four regularly placed squares with a size of 0.1 m², 2 cm above ground on the same plots. To determine dry-matter yield the biomass was oven dried at 60 °C for 48 hours and weighed. Our research design aims at the quantification of the standing crop as an approximation of the hay yield. Since, the subalpine grassland in the Kazbegi region is severely grazed in early spring and contains almost no tussock grass, only the standing biomass of the recent year was harvested.

To reduce the multidimensional vegetation dataset to three main floristic gradients we used isomap ordination (Tenenbaum et al., 2000). Isomap is a powerful ordination technique for non-linear reduction of vegetation datasets with a high variability in species composition, such as high mountain grasslands. It has already been applied for gradient mapping in peatlands (Harris et al. 2015) and heathlands (Feilhauer et al. 2011). The benefit of isomap lies in the maintenance of the intrinsic geometry of the data. Isomap takes the "longer" geodesic distances for k nearest neighbours of each data point into account. Other common multidimensional scaling algorithms consider only the pairwise linear distances between data points. To avoid noise in the dataset we excluded species with less than three occurrences from the isomap analysis using $k = 87$ neighbours based on Bray Curtis distances for the final solution.

For interpretative purposes, the vegetation dataset was clustered, using the isopam clustering algorithm (Schmidtlein et al. 2010) to group the vegetation relevés by their plant species composition. The vegetation clusters were used as a grouping variable in the Isomap analysis and for box plotting the average yield per type, in order to give some general overview of yields and typical species. Isopam is a brute-force approach to detect patterns in noisy vegetation data based on the partitioning of an optimized isomap ordination space. Its main purpose is to overcome the differences between phytosociological vegetation tables, based on expert knowledge and numerical analysis, in order to find species with a high fidelity to groups in a data driven way (Schmidtlein et al. 2010). As a distance metric we used the Bray Curtis distances (Bray and Curtis, 1957). The cluster tree was pruned after visual inspection at the first level resulting in three main grassland types. Every plot was then assigned to a cluster. The dry matter yield, in the respective clusters, was tested for significant differences by using a Kruskal Wallis ANOVA with subsequent Nemeneyi test for pairwise multiple comparisons.

2.2.2.2 Spatial data as co-variables for modelling

For the purpose of modelling species composition we used the three isomap axis scores of each plot as dependent variables and remotely sensed imagery in combination with topographical data as predictors. Space borne imagery was acquired on the 21st of June 2014 by the Rapid Eye sensor with five multispectral bands at a spatial resolution of 5 m x 5 m (see Tab. 1). The data were delivered with orthorectification in the product level 3-A and converted to top-of-atmosphere reflectance. Moreover, we accounted for differences in illumination caused by the exposition of the surface by using a cosine topographical correction (Teillet et al., 1982). Besides the original sensor bands we further included vegetation indices (see Tab. 1) into the analysis.

The topographical parameters were extracted from a Digital Elevation Model with 20 m resolution. Eastness, northness, slope as well as plan curvature, mean curvature, profile curvature and solar radiation were calculated with the Arc Map 10.2.1 tool box. CTI (Compound Topographic Index), TRI (Topographic Ruggedness Index), HLI (Heat Load Index) and SRR (Surface Relief Ratio) were calculated with the Geomorphometry and Gradient Metrics Toolbox version 1.01 (Evans et al. 2014). All predictors were standardized prior to analysis.

Tab. 1: Vegetation indices and topographical parameters used in the random forest vegetation modelling.

Abbreviation	Full name	Definition	Reference
Vegetation Indices			
Blue band		440-510 nm	(Weichelt et al., 2011)
Green band		520-590 nm	(Weichelt et al., 2011)
Red band		630-685 nm	(Weichelt et al., 2011)
Red edge band		690-730 nm	(Weichelt et al., 2011)
NIR band		760-850 nm	(Weichelt et al., 2011)
Red edge / red	Ratio 695/670 Carter5	$\dfrac{Red\ edge}{Red}$	(Carter, 1994; Carter et al., 2005; le Maire et al., 2004)
NIR / red edge	Simple Ratio 760/695	$\dfrac{NIR}{Red\ edge}$	(Carter, 1994)
Red edge / NIR	Simple Ratio 695/760 Carter2	$\dfrac{Red\ edge}{NIR}$	(Carter, 1994; Carter et al., 2005; le Maire et al., 2004)
NIR / red	Simple Ratio 801/670 NIR/Red	$\dfrac{NIR}{Red}$	(Daughtry et al., 2000)
NIR /green	Simple Ratio 800/550	$\dfrac{NIR}{Green}$	(Buschmann and Nagel, 1993)
NDVI	Normalized Difference Vegetation Index	$\dfrac{NIR - Red}{NIR + Red}$	Kriegler et al., 1969, Rouse et al. 1973).
Red edge NDVI	Normalized difference red edge index	$\dfrac{NIR - Red\ edge}{NIR + Red\ edge}$	(Herrmann et al., 2010)
EVI	Enhanced Vegetation Index	$2.5\,\dfrac{NIR - Red}{(NIR + 6\ Red - 7.5\ Blue) + 1}$	(Huete et al., 1999)
ARVI 2	Atmospherically Resistant Vegetation Index 2	$-0.18 + 1.17\left(\dfrac{NIR - Red\ edge}{NIR + Red\ edge}\right)$	(Kaufman and Tanre, 1992)
BWDRVI	Blue-wide dynamic range vegetation index	$\dfrac{0.1\ NIR - Blue}{0.1\ NIR + Red\ edge}$	(Gitelson, 2004)
WDRVI	Wide Dynamic Range Vegetation Index	$\dfrac{0.1\ NIR - Red}{0.1\ NIR + Red}$	(Ahamed et al., 2011; Gitelson, 2004; Hancock and Dougherty, 2007)
SAVI05	Soil Adjusted Vegetation Index	$\dfrac{NIR - Red}{NIR + Red + 0.5}\,(1 + 0.5)$	(Huete, 1988)
MSAVI	Modified Soil Adjusted Vegetation Index	$\dfrac{2\ NIR + 1 - \sqrt{(2\ NIR + 1)^2 8(\ NIR - Red)}}{2}$	(Qi et al., 1994)

Topographical Parameters

Abbreviation	Full name	Definition	Reference
EAST	Eastness	$sin(aspect)$	(Zar, 1999)
NORTH	Northness	$cos(aspect)$	(Zar, 1999)
ELEVATION	Elevation [m a.s.l.]		
PRO CURV	Profile curvature		Arc Map 10.2.1
PLA CURV	Planform curvature		Arc Map 10.2.1
CURV	Mean curvature		Arc Map 10.2.1
TRI	Topographic Ruggedness Index		(Riley et al. 1999)
HLI	Heat Load Index		(Mc Cune and Keon, 2002)
CTI	Compound Topographic Index		(Gessler et al., 1995)
SRR	Surface Relief Ratio		(Pike and Wilson, 1971)
SOLRAD	Solar radiation [Wh/m²]		Arc Map 10.2.1

2.2.3 Modelling of main floristic gradients and biomass

In order to model the main floristic gradients as represented by the three isomap axes we used three random forest regression models. Random Forests (Breiman, 2001) belong to the bagged machine learning algorithms of ensemble modelling and can be used for classification and regression. Being a non-parametric technique, random forest is able to cope with skewed data distributions as present in our study. The random forest algorithm is described by Liaw and Wiener (2002). A bootstrapped training sample of about one third of the data is first drawn from the input data, which resulted in 500 unpruned regression trees for our case. At every node of every tree, a subset of the ten predictor variables is tested for the best split. An average vote of all trees is then generated for the regression. The model out of bag error is calculated for every tree and finally aggregated for the forest. All three floristic gradients were predicted by the models and three separate maps were produced. The measured biomass values were transformed by taking the 4th root in order to achieve a Gaussian distribution.

In order to compare the biomass model based on species composition to a comparative common model based on vegetation indices and topographic variables, we used the full dataset and calculated the predicted versus observed R² and the root mean square error of prediction (RMSEP) for a 100 time, bootstrapped dataset.

The root mean square error of prediction (RMSEP) was calculated using the following equation:

$$RMSEP = \sqrt{\sum_{i=0}^{n}((X_i - Y_i)^2/n)}$$

with X being the predicted yield, Y the observed yield, and n the number of predictions.

In order to derive the yield map, the whole data-set was then randomly stratified and equally separated into a calibration (with 7 samples in the low and high yield ranges) and a validation

dataset. We calculated the predicted versus observed R² and root mean square error of prediction. The random forest model was used to predict the biomass map, by using the three isomap axes maps as predictors. Validation was performed with the validation dataset by correlating the observed ground truth with the predicted biomass values. For a better understanding, the results were later reconverted from transformed values to Mg per ha.

From the biomass map we masked out areas with a low NDVI (<0.2) to exclude bare rocks as well as elevations above 2100 m a.s.l. in order to limit the spatial prediction to areas covered by the field sampling. All analyses were performed in the R statistical environment using the packages vegan (version 2.2.1), isopam (version 0.9-13), stats (version 2.3-40), randomForest (version 4.6-10) and PMCMR (version 4.1).

2.3. Results

2.3.1 Analysis of the vegetation data

The sampled data set included a total of 177 plant species. 125 species had three or more occurrences and were included in the isomap ordination. Species richness ranged from 15 to 45 species per plot with an average of 28 species per plot (25 m²). The analysis of the vegetation data revealed typical species for the main grassland vegetation communities; as well as species occurrence along the main topographic gradients. The ordination diagram shows the three main grassland types derived by the isopam clustering (see Fig. 3).

We found *Hordeum violaceum* hay meadows, characterized by the typical species *Phleum pratense*, *Hordeum violaceum*, *Silene vulgaris*, *Rumex acetosa*, *Carum caucasicum*, *Festuca pratensis*, *Bunias orientalis*, *Poa trivialis*, *Vicia tenuifolia* subsp. *variabilis*, *Poa pratensis*, and *Rumex obtusifolius*. These meadows are mown once per year and are highly productive. We also found a second vegetation community used as a meadow or pasture with the typical species *Alchemilla sericata, Gentianella caucasea, Primula algida* and *Seseli alpinum*. The third grassland type detected by the clustering algorithm is characterized by the typical species *Astragalus captiosus*, *Potentilla crantzii*, and *Silene linearifolia*. On the first axis of the isomap ordination diagram the *Astragalus* pastures transition gradually to the *Hordeum violaceum* meadows. The second axis, however, depicts the change from *Gentianella caucasea* meadows to either *Astragalus pastures* or *Hordeum violaceum* meadows.
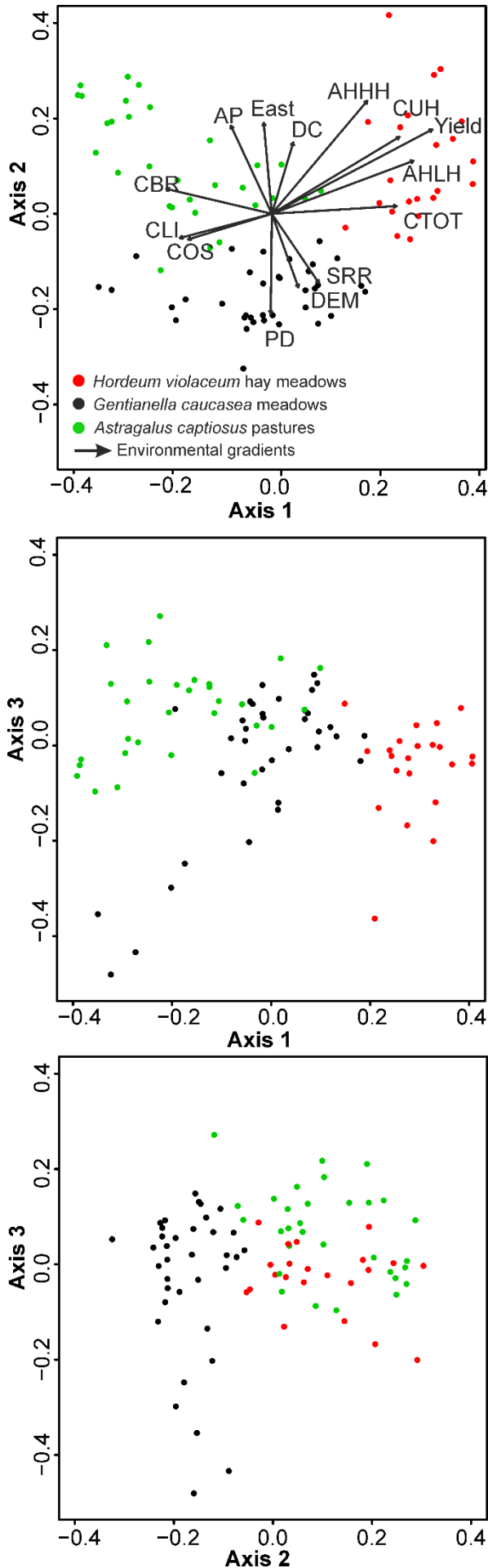
Fig. 3: Isometric feature mapping of the three main grassland types: where
AHH = Average Height High Herbs,
AHLH = Average Height Lower Herbs, AP = Alluvial Deposit,
CBR = Cover Bare Rocks,
CLI =Cover Litter,
COS = Cover Open Soil,
CTOT = Total Cover,
CUH = Cover Upper Herbs,
DC = Dilluvial Deposit,
DEM = Elevation,
East = Eastness,
SRR = Surface Relief Ratio,
PD = Proluvial Deposit, and
YIELD = Dry Matter, p<0.01.

The isomap ordination transferred 79% variation in the vegetation data to the ordination space. The first ordination axis explained 53% of the initial variation. Along the first axis, we found a separation by yield ($R^2 = 0.54$), average height of the lower herb layer ($R^2 = 0.4$), cover of the upper herb layer ($R^2 = 0.35$) and total vegetation cover ($R^2 = 0.29$). The second axis correlated with $R^2 = 0.22$ to the initial variation and showed a differentiation of the plots by average height of the upper herb layer ($R^2 = 0.2$), eastness ($R^2 = 0.17$), and elevation ($R^2 = 0.1$). The third axis did not cover much of the initial variation with $R^2 = 0.13$, with only little relation to northness ($R^2 = 0.12$). The average yield was highest in the *Hordeum violaceum* stands, followed by the *Gentianella caucasea* grassland and the *Astragalus captiosus* grassland.
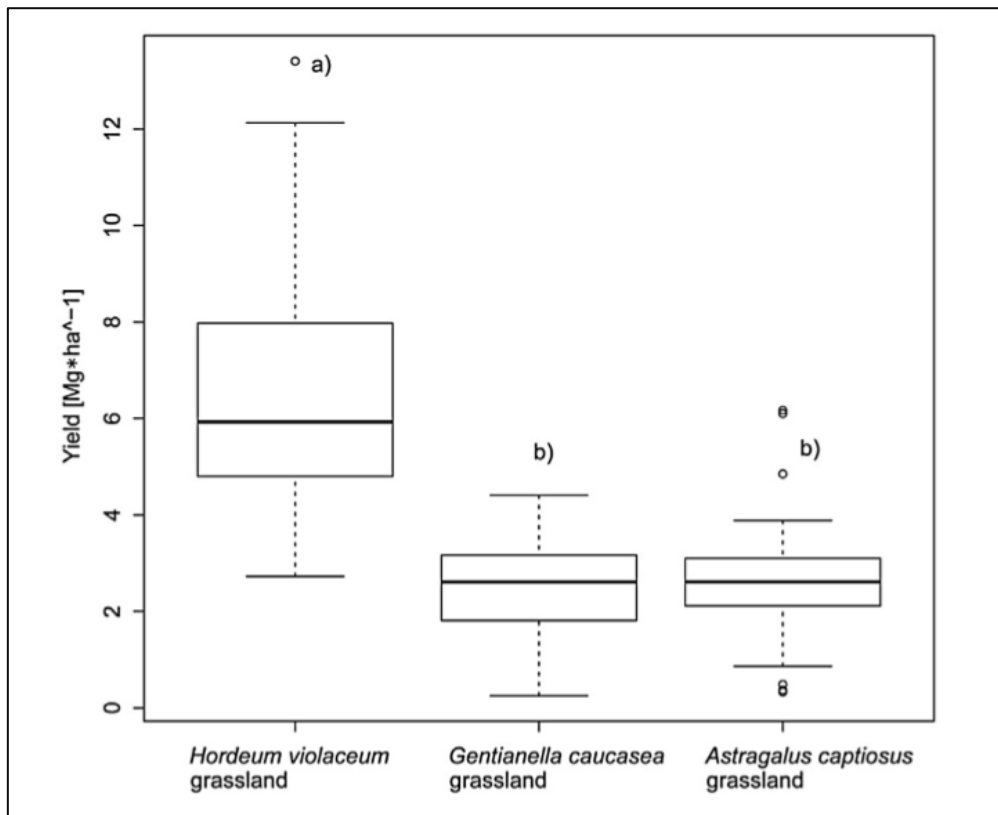
Fig. 4: Box whisker plots of the three vegetation types, with dots representing outliers, which are 1.5 times outside of the interquartile range. Whiskers represent minimum and maximum of the data except from the outliers, the box boundaries upper and lower quartiles, and the black line the median value. Letters indicate homogeneous groups in pairwise comparisons using the Nemenyi test, with Chi-squared approximation, after a Kruskall Wallis test.

The biomass yield differed significantly between the *Hordeum violaceum* meadows and *Gentianella caucasea* and *Astragalus captiosus* grassland, however no significant yield differences were found between *Gentianella caucasea* and *Astragalus captiosus* grassland (see Fig. 4.).

2.3.2 Vegetation and yield modelling

Modelling the three isomap axes with a random forest resulted in 64% of variance explained by the first axis model, 33% of the variance explained by the second axis model and 46% variance explained by the third axis model. Table 2 illustrates the variable importance for the random forest models, depicting the main predictor variables, with a variable importance higher than 0.1. SAVI 05, the NIR band and the MSAVI were decisive predictors to model the vegetation change between *Astragalus captiosus* grassland and *Hordeum violaceum* meadows (axis one). To model the vegetation change on the second isomap axis, besides the red edge band, eastness and elevation played a crucial role. As predictors for the third isomap axis, elevation and northness were most important.

Tab. 2: Variable importance as Increment Node Impurity > 0.1 for the three random forest models.

Axis one		Axis two		Axis three	
SAVI 05	0.91	Red edge band	0.31	ELEVATION	0.25
NIR band	0.60	EASTNESS	0.17	NORTHNESS	0.10
MSAVI	0.57	ELEVATION	0.16		
NIR/red	0.28	GREEN band	0.14		
NDVI	0.27	SRR	0.10		
NIR/green	0.25				
BWDRVI	0.21				
rededge_NIR2	0.15				
NIR/red edge	0.11				
Red edge NDVI	0.11				
Sol Rad	0.11				

The model based on species composition (Fig. 5a) showed a higher R^2 of 0.55 and a lower RMSEP (1.76 Mg*ha^{-1}) than the comparative model, including only multispectral reflectance, vegetation indices, and topographical parameters as predictors (see Fig. 5b) (R^2 = 0.42, RMSEP = 1.91 Mg*ha^{-1}). Moreover, when the observed biomass exceeds 6 Mg*ha-1 both models exhibit high residuals. This indicates that high yields are generally difficult to predict with both models. However, the model based on multispectral reflectance, vegetation indices and topographic variables showed high residuals even for biomass values below 6 Mg*ha^{-1} and had thus a weaker performance. The final random forest model combined the modelled isomap scores of the three axes as predictor variables resulting in the biomass map (see Fig. 6). A moderate relationship (variance explained = 62.32%) between isomap scores and yield, was found in the calibration of the model, whereas the external validation, comparing the observed yield of the validation dataset to the modelled one exhibited an R^2 = 0.64 with a RMSEP of 1.6 Mg*ha^{-1}. The yield covered by our model ranged from 0.43 to 8.68 Mg*ha^{-1} (see Fig. 6).
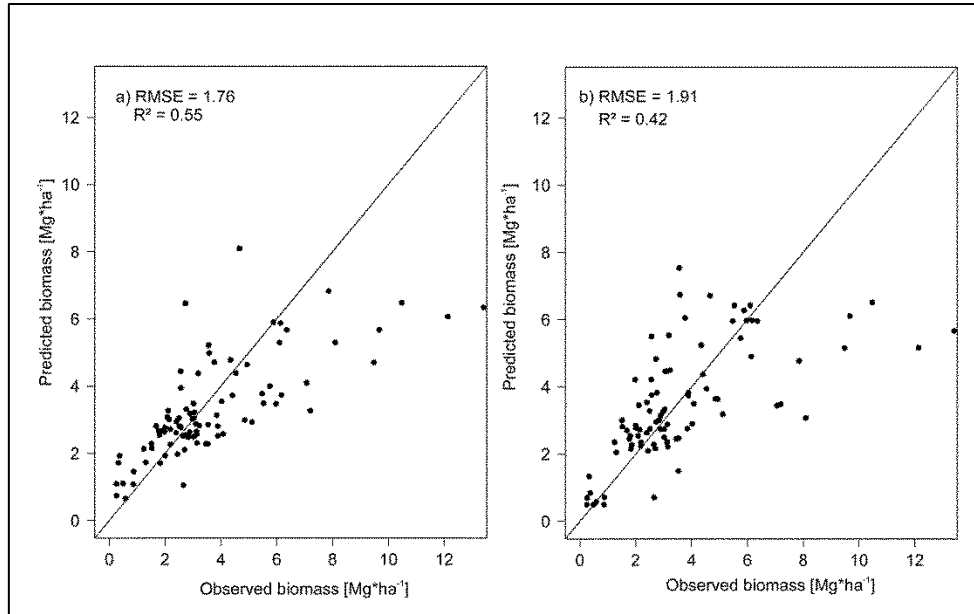
Fig. 5: a) Predicted versus observed biomass yields of the subalpine grassland in the Kazbegi region of a) the yield model, including species composition and b) the common comparative model.
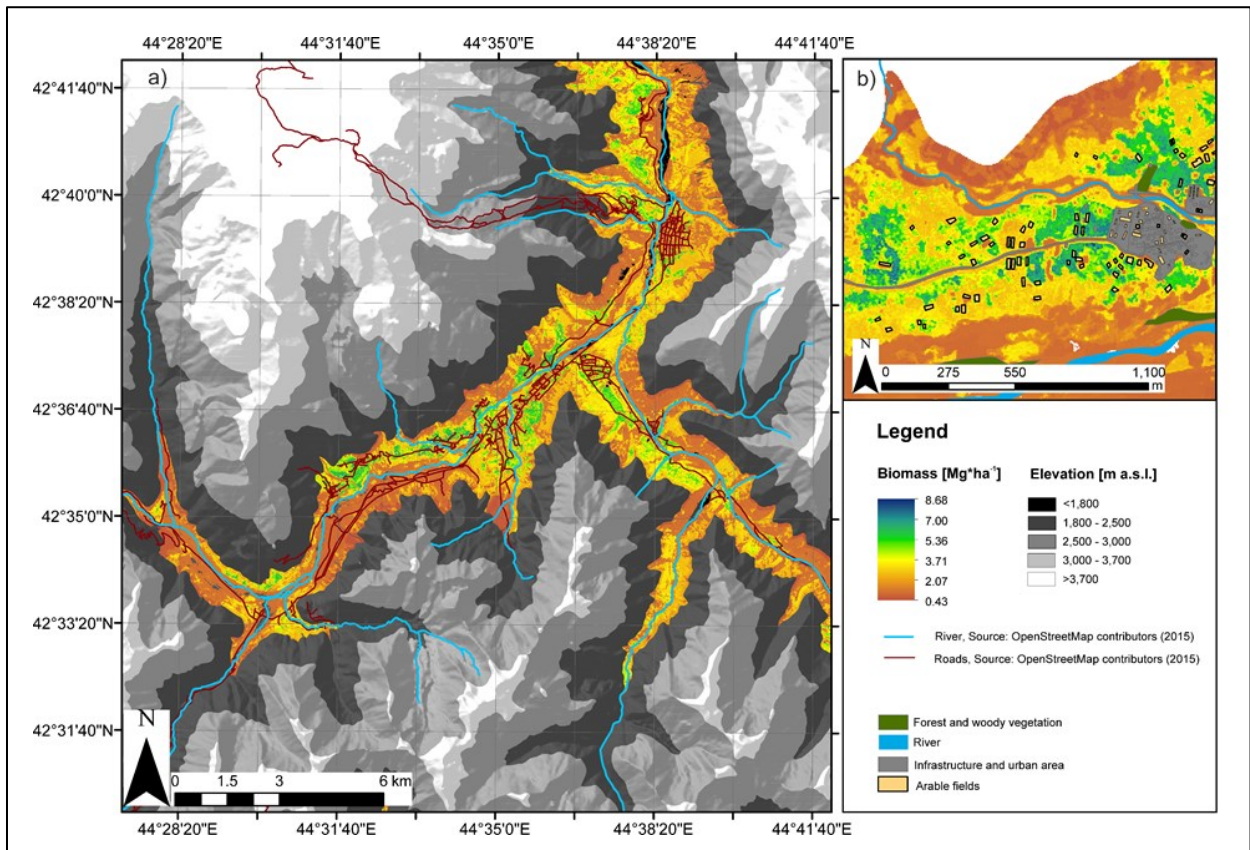
Fig. 6: a) Yield map in Mg*ha⁻¹, resulting from modelled isopam axis scores, which represent the species composition of the high mountainous grassland in the Kazbegi region and b) an insert map of the village Pkhelsche.

2.4. Discussion

2.4.1 Grassland types and main predictor variables

The main objective of our study was to model a spatially explicit, gradual representation of the above ground biomass of the subalpine grassland of the Kazbegi region by including species composition to test whether remotely sensed patterns of species composition are suitable predictor variables for a yield model.

Since the vegetation composition of high mountain grassland is closely related to topography and, thus, environmental conditions, strong vegetation gradients are present in our study area (Körner, 2004; Tephnadze et al., 2014). This relationship between yield, vegetation composition and the topographic factors was employed to model the yield map.

In our analysis the grassland was classified into three main grassland types, *Hordeum violaceum* meadows, *Gentianella caucasea* grasslands, and *Astragalus captiosus* pastures, which transition gradually to each other. Since the grassland of the Kazbegi region has been under study for decades, descriptions of the subalpine grassland already exist (Lichtenegger et al., 2006; Nakhutsrishvili, 1999; Tephnadze et al., 2014). However exact statements for grassland yield are rare and, if available relate to higher elevations.

Lichtenegger et al. (2006) reported for the *Hordeum violaceum* grassland a yield of 7.5 Mg*ha^{-1} on a test site above shallow soil. In general, *Hordeum violaceum* prefers humid and moderately deep soils (Lichtenegger et al., 2006). Such conditions can be found on the dilluvial deposits, where villages are established. Moreover, in early spring cattle and horse grazing fertilizes the meadows near the villages, additionally increasing plant productivity (Lichtenegger et al. 2006, Sakhokia, 1983). Parts of theses meadows may have been used as arable land and potentially fertilized with dung in former times (Seifriz, 1931; Tephnadze et al., 2014). These nutrient sources explain the comparably high productivity of the *Hordeum violaceum* grassland, in rare cases even above 8 Mg*ha^{-1}, where tall-herb stands develop.

The *Gentianella caucasea* grassland is often dominated by *Agrostis vinealis / capillaris* and *Bromus variegatus*, which can be related to the nutrient rich pastures of the high-montane belt (Lichtenegger et al., 2006). This grassland type occurs on the skeleton rich soils of proluvial deposits up to 2700 m a.s.l. (Nakhutsrishvili, 1999). The yield in our dataset did not exceed **5 Mg*ha^{-1}**, whereas Nakhutsrishvili et al. (1980) found up to 6 Mg*ha^{-1} for a similar vegetation type in late summer. The discrepancy might have arisen from the different research design used in Nakhutsrishvili et al. (1980), with smaller plots sizes at different elevations as well as the fact that the *Gentianella caucasea* grassland might have reached even higher yields under more growth enhancing weather conditions. Moreover, our datasets included few plots of the *Gentianella caucasea*

vegetation type, which were dominated by *Nardus stricta,* a species with very low yield, explaining a low average yield. *Nardus stricta* indicates in our case the influence of the acidic dacite base rock (Lichtenegger et al., 2006).

The *Astragalus captiosus* grassland was largely used as pasture, except for a few plots, which exhibited moderate yields and were used for hay making as well. This vegetation type is characterized by high herb content, low vegetation cover and a habitat preference on shallow soils with high stone content on flat to steep, south exposed slopes (Magiera et al., 2013; Nakhutsrishvili, 2012; Tephnadze et al., 2014).

The vegetation composition of the above discussed grassland types could be explained by the vegetation structural gradients, which were represented by the multispectral vegetation indices and the topographic gradients by using random forest models. The good performance of those models related to the strong connection between species composition, reflectance and topographic conditions, has been successful in other modelling approaches (Feilhauer and Schmidtlein, 2011; Magiera et al., 2013). However, the relationship between species composition and reflectance in a semi natural landscape is enhanced by co-factors contributing to the spectral signal, such as a high stone content or soil moisture (Feilhauer et al. 2011, Harris et al. 2015, Verrelst et al. 2009). Our dataset shows a moderate relation of biomass to the topographic gradients elevation and eastness, which are consequently important predictor variables in the random forest models (see Fig. 3). Tephnadze et al. (2014) found similar relationships, especially for eastness. This can be explained by the different soil conditions on eastern and western slopes. The high importance of elevation is not surprising, since it is the dominant gradient in high mountain systems (Körner, 2004). However, structural vegetation factors, such as total vegetation cover and vegetation height formed equally strong gradients in our dataset. This is further confirmed by the strong influence of the single bands (NIR, red edge) and the vegetation indices on the random forest models. The influence of the spectral predictors even outperformed the topographic gradients in the random forest models. This can be caused by the strong relationship between canopy reflectance and canopy structure (Ustin and Gamon, 2010). The high importance of SAVI and MSAVI for the isomap model of the first axis supports this finding. The first isomap axis displayed the gradient of total vegetation cover and vegetation composition between the *Astragalus captiosus* grassland and the *Hordeum violaceum* grassland. SAVI 05 and MSAVI were both designed to correct for soil brightness, which was beneficial for the influence of low vegetation cover. The second isomap axis, covered a shorter vegetation structural gradient based on the transition between the *Gentianella caucasea*-grassland and both *Hordeum violaceum*- and *Astragalus captiosus*-grassland. This gradient was mainly related to eastness, which was further confirmed by the high importance of eastness and elevation in the

random forest model. The influence can be explained by the micro climatic conditions of the slightly warmer slopes, exposed to the east, as well as the different soil conditions east and west to the valley. A prior study in the Kazbegi region, Greater Caucasus, using hyperspectral field spectrometric data to relate canopy reflectance to vegetation composition resulted in R^2 values ranging from 0.6 to 0.83 in validation (Magiera et al. 2013). However, it needs to be considered, that the strength of the model coefficients is dependent on the length of the floristic gradient (Schmidtlein et al. 2007). In our study the floristic gradient is comparably short. Enlarging the floristic gradient by considering the vegetation of steep slopes as in Magiera et al. (2013) would presumably enhance the quality of the species composition model and allow an application of the yield model to steep slopes.

2.4.2 Applicability of the yield map

The high spatial resolution of the Rapid Eye Imagery (5 m x 5 m) resulted in a very detailed yield map, depicting small scale yield heterogeneity and its gradual transition along topographic conditions. Whereas in a mosaic landscape grassland yield is often assessed on a patch scale, our grassland dominated high mountain study region lacked sharp vegetation or anthropogenic boundaries, making the yield assessment even more challenging. However, a further advantage of the high spatial resolution of the yield map is an increased visibility of small features such as shrubbery, dirt paths or small arable lands (<100 m²) (Fig. 6). The biomass distribution indirectly followed the species composition, so that ecological patterns such as the clear appearance of the high standing *Hordeum violaceum* meadows, were sustained within the map. It is important to note for interpretation and usage of the resulting map that the model was only trained for grassland. Post processing procedures such as masking out areas not covered by the field sampling is needed for a fine scale assessment of the grassland potential. Further, we only included training data from moderately steep terrain and below 2100 m a.s.l., we thus restricted the prediction areas. For our purposes the yield map, assessing the yield of meadows near the villages is highly sufficient.

2.4.3 Mitigating effects of index saturation through maps of species composition

In the present study, yield was estimated by modelled species composition showing a generally good agreement with the validation data. We were able to depict gradual changes in yield estimates, with R^2 of 0.64 in validation, which is comparable to other studies. Todd et al. (1998) tested multispectral vegetation indices (Landsat TM Tasseled Cap green vegetation index, brightness index, wetness index, the normalized difference vegetation index and the red waveband) on a biomass gradient between 0.8-1.5 Mg*ha^{-1} in the Rocky Mountains. They found good correlations between reflectance and biomass with an R^2 ranging between 0.62-0.67 for pastured sites. However,

if test sites within grazing exclosures (high biomass) were included into the analysis the R^2 values declined.

For the yield assessment of alpine pastures Boschetti et al. (2007) covered a yield range between 0.61 Mg*ha^{-1} for *Nardus stricta*-grassland and 2.797 Mg*ha^{-1} for *Deschampsia caespitosa*- grassland. The authors used multispectral vegetation indices with log transformed regression analysis, resulting in a model for soil adjusted vegetation indices with an $R^2 > 0.6$. Another study of alpine meadows shrubs in the Tibetan Plateau, dominated by sedges and dwarf shrubs with a yield gradient between 1.5841 Mg*ha^{-1} and 3.5675 Mg*ha^{-1} (mean vegetation height 12 cm) showed moderate correlations with an $R^2 = 0.27$ in regression analysis with vegetation indices (Chen et al., 2009). Hyperspectral vegetation indices tested by Fava et al. (2009) on a gradient between 3.95 – 13.37 Mg*ha^{-1}, with the best models including the NIR and red edge, resulted in an $R^2 = 0.73$ (Fava et al., 2009). However, Vescovo and Gianelle (2008) noticed the saturation effect of NIR based vegetation indices for yields above 1.5 Mg*ha^{-1}, whereas Hancock and Dougherty (2007) detected the saturation point in blue and red based NDVI and wide range indices above 3.74 Mg*ha^{-1}. All quoted studies focus on moderate yields, even though full canopy cover was reported in most cases.

The saturation effect and other non-linear relationships between vegetation indices and canopy properties, especially biomass may decrease model accuracy (Glenn et al., 2008). This problem is highly relevant for the biomass rich meadows. However, including the intermediate step of calculating a species composition map, proved to be successful for our dataset. In a bootstrapped comparative model we directly related the vegetation indices and topographic variables to yield and noticed a higher RMSE, as well as higher residuals even below an observed biomass of 6 Mg*ha^{-1}. We were able to accurately model a quite long yield gradient, even though the highest residuals were observed for high yields. A possible alternative to estimate the residuals would be to project the final model directly into the ordination space (Neumann et al. 2015, Luft et al. 2016). Since vegetation composition is closely related to the biophysical vegetation variables, using an intermediate step of species composition maps might help to improve the model quality.

2.5 Conclusions and outlook

Yield maps give additional information beside species composition for sustainable land use planning and nature conservation, since they can help to estimate yields over a larger area giving local farmers and authorities a tool in hand to plan an economically viable and ecologically meaningful grassland management. The resulting yield map further allows to generate integrative land-use scenarios in the Kazbegi region and to give practical recommendations to the local farmers for a sustainable land-use management. We could show that floristic gradients serve well as

predictors for grassland yield modelling by including easily obtainable, remotely sensed data. The question of how to enhance the quality of models estimating the yield of productive grasslands is still under discussion. For remote areas where data availability is particularly scarce, easily obtainable remotely sensed data such as multispectral satellite imagery and digital elevation models can be beneficial as a basis for modelling, even though the calibration data such as biomass clippings and vegetation relevés still have to be acquired, the workload compared to common mapping approaches is considerably less. It is, however, based on the close relationship between topographic conditions and species composition which is typical for a high mountain region. Future studies with larger datasets in different habitat types, such as agricultural landscapes are needed to get better knowledge and understanding of this observation.

References

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., others 2011. Productivity is a poor predictor of plant species richness. Sci. 333, 1750–1753.

Ahamed, T., Tian, L., Zhang, Y., Ting, K.C. 2011. A review of remote sensing methods for biomass feedstock production. Biomass Bioenerg. 35, 2455–2469.

Akhalkatsi, M., Abdaladze, O., Nakhutsrishvili, G., Smith, W.K., 2006. Facilitation of seedling microsites by Rhododendron caucasicum extends the Betula litwinowii Alpine treeline, Caucasus Mountains, Republic of Georgia. Arct. Antarct. Alp. Res. 38, 481–488.

Anderson, G., Hanson, J., Haas, R., 1993. Evaluating landsat thematic mapper derived vegetation indices for estimating above-ground biomass on semiarid rangelands. Remote Sens. Environ. 45, 165–175.

Boschetti, M., Bocchi, S., Brivio, P.A., 2007. Assessment of pasture production in the Italian Alps using spectrometric and remote sensing information. Agric. Ecosyst. Environ., 118, 267–272.

Braun-Blanquet, J., 1964. Pflanzensoziologie: Grundzüge der Vegetationskunde, Springer-Verlag, Munich. (in German)

Bray, J. R., Curtis, J.T., 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecol. Monogr., 4 (27), 325-349.

Breiman, L., 2001. Random forests. J. Mach. Learn. 45(1), 5–32.

Buschmann, C., Nagel, E., 1993. In vivo spectroscopy and internal optics of leaves as basis for remote sensing of vegetation. Int. J. Remote Sens., 14 (4), 711–722.

Carter, G.A., 1994. Ratios of leaf reflectances in narrow wavebands as indicators of plant stress. Int. J. Remote Sens., 15 (3), 697–703.

Carter, G.A., Knapp, A.K., Anderson, J.E., Hoch, G.A., Smith, M.D., 2005. Indicators of plant species richness in AVIRIS spectra of a mesic grassland. Remote Sens. Environ. 98 (2-3), 304–316.

Chen, J., Gu, S., Shen, M.G., Tang, Y.H., Matsushita, B., 2009. Estimating aboveground biomass of grassland having a high canopy cover: An exploratory analysis of in situ hyperspectral data. Int. J. Remote Sens. 30 (24), 6497–6517.

Cho, M.A., Skidmore, A.K., 2009. Hyperspectral predictors for monitoring biomass production in Mediterranean mountain grasslands: Majella National Park, Italy. Int. J. Remote Sens. 30, 499–515.

Cocca, G., Sturaro, E., Gallo, L., Ramanzin, M., 2012. Is the abandonment of traditional livestock farming systems the main driver of mountain landscape change in Alpine areas? Land Use Policy. 29 (4), 878–886.

Daughtry, C.S.T., Walthall, C.L., Kim, M.S., De Colstoun, E.B., McMurtrey, J.E., 2000. Estimating corn leaf chlorophyll concentration from leaf and canopy reflectance. Remote Sens. Environ. 74 (2), 229–239.

Dusseux, P., Hubert-Moy, L., Corpetti, T., Vertès, F., 2015. Evaluation of SPOT imagery for the estimation of grassland biomass. Int. J. Appl. Earth Obs. Geoinf. 38, 72–77.

Evans J.S., Oakleaf J., Cushman S.A., Theobald D., 2014. An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, Version 2.0-0. http://evansmurphy.wix.com/evansspatial (accessed 02.10.14).

Fava, F., Colombo, R., Bocchi, S., Meroni, M., Sitzia, M., Fois, N., Zucca, C., 2009. Identification of hyperspectral vegetation indices for Mediterranean pasture characterization, Int. J. Appl. Earth. Obs. Geoinf. 11, 233–243.

Feilhauer, H., Faude, U., Schmidtlein, S., 2011. Combining Isomap ordination and imagingspectroscopy to map continuous floristic gradients in a heterogeneous landscape. Remote Sens. Environ. 115, 2513–2524.

Feilhauer, H., Schmidtlein, S., 2011. On variable relations between vegetation patterns and canopy reflectance. Ecol. Inform. 6 (2), 83–92.

Fillela, I., Penuelas, J., 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass and hydric status. Int. J. Remote Sens. 15 (7), 1459–1470.

Gagnidze, R., 2005. Vascular Plants of Georgia – A Nomenclatural Checklist. Georgian Academy of Sciences, N. Ketskhoveli Institute of Botany, I. Javakhishvili Tbilisi State University, Department of Botany, Tbilisi.

Gessler, P.E., Moore, I.D., Mc Kenzie, N.J., Ryan, P.J., 1995. Soil-landscape modelling and spatial prediction of soil attributes. Int. J. Geogr. Inf. Syst. 9 (4), 421–432.

Gitelson, A.A., 2004. Wide Dynamic Range Vegetation Index for Remote Quantification of Biophysical Characteristics of Vegetation. Plant. Physiol. 161 (2), 165–173.

Gleason, H.A., 1926. The individualistic concept of plant association. Bull. Torrey Bot. Club. 53, 7–26.

Glenn, E.P., Huete, A.R., Nagler, P.L., Nelson, S.G., 2008. Relationship Between Remotely-sensed Vegetation Indices, Canopy Attributes and Plant Physiological Processes: What Vegetation Indices Can and Cannot Tell Us About the Landscape. Sensors. 8 (4), 2136–2160.

Grace, J.B., Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Anderson, T.M., Bakker, J.D., Brown, C.S., Buckley,

Y.M., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Gruner, D.S., Hagenah, N., Jin, V.L., Kirkman, K.P., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Orrock, J.L., Prober, S.M., Stevens, C.J., Wragg, P.D., Yang, L.H., 2012. Response to Comments on "Productivity Is a Poor Predictor of Plant Species Richness.". Sci. 335 (6075), 1441–1441.

Gret-Regamey, A., Walz, A., Bebi, P., 2008. Valuing ecosystem services for sustainable landscape planning in Alpine regions. Mt. Res. Dev. 28 (2), 156–165.

Guo, Q., 2007. The diversity–biomass–productivity relationships in grassland management and restoration. Basic Appl. Ecol. 8 (3), 199–208.

Hancock, D.W., Dougherty, C.T., 2007. Relationships between Blue- and Red-based Vegetation Indices and Leaf Area and Yield of Alfalfa. Crop Sci. 47 (6), 2547–2556.

Harris, A., Charnock, R., Lucas, R. M., 2015. Hyperspectral remote sensing of peatland floristic gradients. Remote Sens. Environ. 162 (1), 99-111.

Herrmann, I., Karnieli, A., Bonfil, D.J., Cohen, Y., Alchanatis, V., 2010. SWIR-based spectral indices for assessing nitrogen content in potato fields. Int. J. Remote Sens., 31 (19), 5127–5143.

Horn, B.K.P., 1981. Hill shading and the reflectance map. Proc. IEEE. 69 (1), 14–47.

Huete, A., Justice, C., Van Leeuwen, W., 1999. MODIS vegetation index (MOD13). Algorithm theoretical basis document. 3, 213.

Huete, A.R., 1988. A Soil Adjusted Vegetation Index (SAVI). Remote Sens. Environ. 25 (3), 295–309.

Jackson, R.D., Huete, A.R., 1991. Interpreting vegetation indices. Prev. Vet. Med. 11 (3), 185–200.

Kaufman, Y.J., Tanre, D., 1992. Atmospherically resistant vegetation index (ARVI) for EOS-MODIS, IEEE Trans. Geosci. Remote Sens. 30 (2), 261–270.

Klimek, S., Richter gen. Kemmermann, A., Hofmann, M., Isselstein, J., 2007. Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. Biol. Cons. 134 (4), 559–570.

Körner, C., 2004. Mountain biodiversity, its causes and function. Ambio. 13, 11–17.

Körner, C., Spehn, E., Nakhutsrishvili, G.. 2006. High-Elevation Land Use, Biodiversity, and Ecosystem Functioning, in: Spehn, E, Libermann, M., Körner, C. (Eds.), Land Use Change and Mountain Biodiversity. CRC Press, Boca Raton, Florida, pp. 2–21.

Kriegler F.J., Malila W.A., Nalepka R.F. and Richardson W., 1969. Preprocessing transformations and their effects on multispectral recognition, in: Proceedings of the Sixth International

Symposium on Remote Sensing of Environment, University of Michigan, Ann Arbor, Michigan, p. 97-131.

Le Maire, G., François, C., Dufrêne, E., 2004. Towards universal broad leaf chlorophyll indices using PROSPECT simulated database and hyperspectral reflectance measurements. Remote Sens. Environ, 89 (1), 1–28.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R News, 2, 18–22.

Lichtenegger, E., Bedoschwili, D., Hübl, E., Scharf, E., 2006. Höhenstufengliederung der Grünlandvegetation im Zentralkaukasus. Verhandlungen der Zoologisch-Botanischen Gesellschaft Österreich, 143, 43–81.

Liu, Z.Y., Huang, J.F., Wu, X.H., Dong, Y.P., 2007. Comparison of vegetation indices and red-edge parameters for estimating grassland cover from canopy reflectance data. J. Integr. Plant. Biol. 49 (3), 299–306.

Luft, L., Neumann, C., Itzerott, S., Lausch, A., Doktor, D., Freude, M., Blaum, N., Jeltsch, F., 2016. Digital and real-habitat modeling of Hipparchia statilinus based on hyper spectral remote sensing data. Int. J. Environ. Sci. Technol. 13, 187-200.

van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio. 39 (2), 97–114.

Magiera, A., Feilhauer, H., Otte, A., Waldhardt, R., Simmering, D., 2013. Relating canopy reflectance to the vegetation composition of mountainous grasslands in the Greater Caucasus. Agric. Ecosyst. Environ. 177, 101–112.

Mc Cune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13(4), 603–606.

Nakhutsrishvili, G., Chikwadze, A.K., Hezuriani, L.D., 1980. Productivity of High Mountain Grassland in the Central Caucasus, Metsniereba, Tbilisi, (in Russian).

Nakhutsrishvili, G.,1999. The vegetation of Georgia (Caucasus). Braun-Blanquetia. 15, 5–74.

Nakhutsrishvili, G., 2012. The Vegetation of Georgia (South Caucasus), Springer Verlag, Berlin, Heidelberg.

Neumann, C., Weiss, G., Schmidtlein, S., Itzerott, S., Lausch, A., Doktor, D., Brell, M., 2015. Gradient-Based Assessment of Habitat Quality for Spectral Ecosystem Monitoring. Remote Sens. 7, 2871-2898.

O'Mara, F.P., 2012. The role of grasslands in food security and climate change. Ann. Bot. 110, 1263–1270.

Pike, R.J., Wilson, S.E. 1971. Elevation-Relief Ratio, Hypsometric Integral, and Geomorphic Area-Altitude Analysis. Geol. Soc. Am. Bull. 82 (2), 1079–1084.

Pohl, M., Alig, D., Körner, C., Rixen, C., 2009. Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant Soil. 324, (1-2), 91–102.

Psomas, A., Kneubühler, M., Huber, S., Itten, K., Zimmermann, N.E., 2011. Hyperspectral remote sensing for estimating aboveground biomass and for exploring species richness patterns of grassland habitats. Int. J. Remote Sens. 32 (24), 9007-9031.

Qi, J., Chehbouni, A., Huete, A.R., Kerr, Y.H., Sorooshian, S.,1994. A modified soil adjusted vegetation index. Remote Sens. Environ. 48 (2), 119–126.

Riley, S. J., De Gloria, S. D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermt. J. Sci. 5 (1-4), 23–27.

Rouse, J. W., Haas, R. H., Schell, J. A., and Deering, D. W., 1973. Monitoring vegetation systems in the Great Plains with ERTS. Third ERTS Symposium, NASA SP-351, I, 309–317.

Sakhokia, M., 1983. Agrobotanical review of Khevi (Kazbegi region) pastures and hay meadows and optimization ways, Metsniereba, Tbilisi. (in Georgian).

Schirpke, U., Tasser, E., Tappeiner, U., 2013. Predicting scenic beauty of mountain regions. Landsc. Urban. Plan. 111, 1–12.

Schmidtlein, S., Sassin, J., 2004. Mapping continuous floristic gradients in grasslands using hyperspectral imagery. Remote Sens. Environ. 92, 126-138.

Schmidtlein, S., Tichý, L., Faude, U., Feilhauer, H., 2010. A brute force approach to vegetation classification. J. Veg. Sci. 21, 1162-1171.

Schmidtlein, S., Zimmermann, P., Schüpferling, R., Weiss, C., 2007. Mapping the floristic continuum: Ordination space position estimated from imaging spectroscopy. J. Veg. Sci. 18 (1), 131–140.

Seifriz, W. 1931. Sketches of the vegetation of some southern provinces of Soviet Russia: II. Plant life along the Georgian military way, North Caucasus. J. Ecol. 19 (2), 372–382.

Teillet, P.M., Guindon, B., Goodenough, D.G. 1982. On the Slope-Aspect Correction of Multispectral Scanner Data. Can. J. Remote Sens. 8 (2), 84–106.

Tenenbaum, J.B., Silva, V. de, Langford, J.C., 2000. A Global Geometric Framework for Nonlinear Dimensionality Reduction. Sci. 290 (5500), 2319–2323.

Tephnadze, N., Abdaladze, O., Nakhutsrishvili, G., Simmering, D., Waldhardt, R., Otte, A., 2014. The impacts of management and site conditions on the phytodiversity of the upper montane and subalpine belts in the Central Greater Caucasus. Phytocoenologia. 44(3-4), 255–291.

The Plantlist, 2013. The Plantlist. Version 1.1. http://www.theplantlist.org (accessed 16.02.2016).

Todd, S.W., Hoffer, R.M., Milchunas, D.G., 1998. Biomass estimation on grazed and ungrazed rangelands using spectral indices. Int. J. Remote Sens. 19 (3), 427–438.

Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. New Phytol. 186 (4), 795–816.

Verrelst, J., Geerling, G.W., Sykora, K.V., Clevers, J.G.P.W., 2009. Mapping of aggregated floodplain plant communities using image fusion of CASI and Lidar data. Int. J. Appl. Earth Obs. Geoinf. 11, 83-94.

Vescovo, L., Gianelle, D., 2008. Using the MIR bands in vegetation indices for the estimation of grassland biophysical parameters from satellite remote sensing in the Alps region of Trentino (Italy). Adv. Space Res. 41 (11), 1764–1772.

Waldhardt, R., Abdaladze, O., Otte, A., Simmering, D. 2011. Landschaftswandel im Kaukasus Georgiens. Interdisziplinäre Forschung für eine nachhaltigere Zukunft. Spiegel der Forschung. 28, 4–15. (in German).

Weichelt, H., Rosso, P., Marx, A., Reigber, S., Douglass, K., Heynen, M., 2011. White Paper - The RapidEye Red Edge Band. RapidEye White Papers. https://resa.blackbridge.com/files/2014-06/Red_Edge_White_Paper (accessed 09.07.16)

Wu, J., Wang, D., Bauer, M.E., 2007. Assessing broadband vegetation indices and QuickBird data in estimating leaf area index of corn and potato canopies. Field Crop. Res. 102 (1), 33–42.

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall, Upper Saddle River, New York.

3. Mapping plant functional groups in subalpine grassland of the Greater Caucasus

Magiera, Anja[1,3] ; Feilhauer, Hannes[2]; Waldhardt, Rainer[1]; Wiesmair, Martin[1,3]; Otte, Annette[1,3]

[1] *Division of Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resources Management, Justus-Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany;*

[2] *Institute of Geography, Friedrich-Alexander University Erlangen-Nürnberg, Wetterkreuz 15, 91058 Erlangen, Germany*

[3] *Center for International Development and Environmental Research (ZEU), Senckenbergstrasse 3, 35390 Giessen, Germany*

Abstract

Plant functional groups (PFG), in our case grass, herbs and legumes and their spatial distribution hold information on key ecosystem functions such as species richness, nitrogen fixation and erosion control. Spatial knowledge about the distribution of PFGs provide valuable information for grassland monitoring and management. The present study thus aims at describing and mapping the distribution of grass, herb and legume coverage of the subalpine grassland in the high mountain region Kazbegi, Greater Caucasus, Georgia. To test the applicability of new sensors, we compared the predictive power of simulated hyperspectral canopy reflectance, simulated multispectral reflectance, simulated vegetation indices and topographic variables for modelling PFGs.

Generally, all tested grassland was species-rich but differed in grass, herb and legume content and connected properties, such as yield. Dominance of grass (*Hordeum brevisubulatum*) was found in biomass-rich hay meadows. Herb-rich grassland featured the highest species richness and evenness, whereas legume-rich grassland was accompanied by a high coverage of open soil and showed dominance of species such as *Astragalus captiosus*. Models for grass, herb and legume coverage explained 36%, 25%, 37% of the respective variance and their root mean square errors were between 12-15%. The best model fits were achieved with a combination of multispectral reflectance, vegetation indices and topographic variables as predictors. Hyperspectral and multispectral reflectance as predictors resulted in similar models. We thus conclude that the combination of multispectral and topographical parameters suits best for modelling grass, herb and legume coverage. However, overall model fits were merely moderate and further testing, including stronger gradients and the addition of shortwave infrared wavelengths, is needed.

3.1. Introduction

Worldwide, high mountain grassland is a species-rich habitat, which includes numerous endemic species (Körner, 2004), but is commonly highly affected by natural and land-use supported erosion, land-degradation and land-use changes (e. g. Lehnert et al., 2014; Tasser and Tappeiner, 2002; Wiesmair et al., 2016).

The high species richness of subalpine to alpine grassland results from and is affected by its long term agricultural use. During the last decades, the central European mountain grassland communities were altered by the introduction of modern farming practices in grassland management on the one side and the abandonment of agricultural use on the other (Tasser and Tappeiner, 2002). Traditional high mountain land use systems with low input of system-specific organic fertilizers have greatly contributed to a distinct floristic pattern up to the introduction of mineral fertilizers and more effective agricultural techniques. Consequently, more intensive management regimes became applicable to large grassland sites and thus modified the traditional mowing and grazing regimes by homogenization of the floristic pattern (Homburger and Hofer, 2012). The introduction of mineral nitrogen and phosphorus fertilizers caused the greatest change in the floristic composition of grassland and resulted in an increased abundance of grass species.

In contrast, the subalpine grassland in our study region, the Kazbegi region, Greater Caucasus, Georgia, has up to now been traditionally managed without any mineral fertilizer application (Tephnadze et al., 2014). Thus, near-natural, species-rich and quite distinct grassland types with a strong relation to topography and land-use type dominate the subalpine and alpine landscape of the Kazbegi region (Nakhutsrishvili, 1999; Pyšek and Šrutek, 1989; Tephnadze et al., 2014). Species-rich grassland, characterized by a dense and vertical structured vegetation layer and a diverse, deep root system, contribute to the functioning of the high mountain ecosystem, especially to erosion control (Körner, 2003, Pohl et al., 2009). Both, species richness and erosion control – the latter being mainly determined by the root system – are interrelated and indicated by grass, herb and legume coverage (Lehnert et al., 2014; Tasser and Tappeiner, 2002; Wiesmair et al., 2017). Plant functional group (PFG, i.e. grass, herb, and legume) proportions shift if land-use management is intensified (e.g. through mineral fertilization, irrigation or the establishment of sown grassland), which in return destabilizes ecosystem functions (Voigtlaender et al., 1987). Therefore, detailed spatial knowledge about the distribution of grass, herb and legume coverage provides valuable information for grassland monitoring and management.

Previous studies indicate the feasibility to use remotely sensed imagery as well as topographic information to model grass, herb and legume content (Biewer et al., 2009a, 2009b; Himstedt et al., 2009; Psomas et al., 2011; Zha et al., 2003). However, studies using grass, herb and legume content

as a target variable are so far limited to controlled systems achieving best results at a homogenous yield. In contrast, our study is based on semi-natural mountain grassland with varying yields and cover.

In our study, we briefly characterize the grassland composition with respect to PFGs and dominant species of the researched grassland types and, subsequently, model and map their spatial distribution. We further test if hyperspectral reflectance, in our case from field spectrometric data, enhances the model quality. We thus aim:

i)   to model and map grass, herb and legume coverage and

ii)   to test if simulated hyperspectral reflectance improves the model quality.

3.2 Study area

Steep slopes and a harsh continental climate characterize the high mountain range of the Central Greater Caucasus, Georgia and especially the environmental conditions of the isolated Kazbegi region (Fig.1).
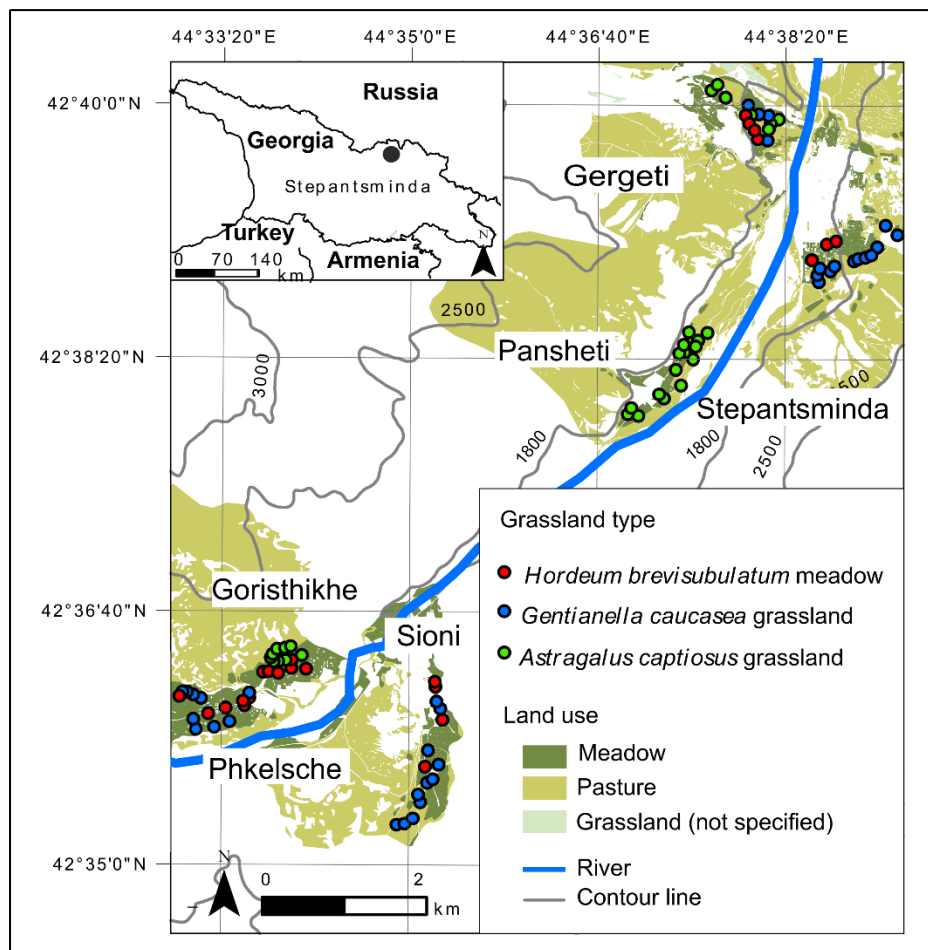
Fig. 1: The study area in the Kazbegi region, Greater Caucasus, Georgia.

The Tergi river runs in northern direction, at its banks, the main village Stepantsminda stretches (1700 m above sea level (a. s. l.)). West of the river, the Mount Kazbeg elevates (5033 m a. s .l) as the highest summit in the region (Ketskhoveli et al., 1975). The climate of the valley is relatively continental with long, cool summers and winters with low snow cover. The mean annual temperature is 4.7 °C with a vegetation period of five to six months. The mean annual precipitation at 1850 m a. s. l. amounts to 806 mm (Lichtenegger et al., 2006; Nakhutsrishvili, 1999). The bedrock of the study area comprises Jurassic sediments (clay shists), quaternary volcanic rocks (andesite and dacite) as well as quaternary pyroclastic deposits and fluvial sediments. Younger, pleistocenic glacial sediments as well as holocenic peats can also be found (Akhalkatsi et al., 2006). The main soil types of the top slopes are shallow leptosols, mainly used as pastures, whereas on the lower slopes and accumulation areas, depending on the bedrock, moderately deep cambisols can be found in the surroundings of the villages, which are used as meadows or even potato fields (Tephnadze et al., 2014).

The landscape is characterized by large, low-productive, pastured grassland alternating with small remnants of birch forests (*Betula litwinowii*) and shrubberies. The latter are dominated by *Elaeagnus rhamnoides* in the lowlands and *Betula litwinowii and Rhododendron caucasicum* in the northern-exposed tree-line ecotone (Magiera et al., 2013, 2016). In contrast, grassland of north-facing slopes exhibits a relatively high biomass, but is often characterized by unpalatable plant species such as *Veratrum lobelianum* or *Festuca varia* (Nakhutsrishvili, 2012). On alluvial fans and in close vicinity to the villages, young hay meadows occur on former organicly fertilized arable fields characterized by *Hordeum brevisubulatum* (Tephnadze et al., 2014). Old, non-fertilized and species-richer hay meadows grow at steeper slopes and further away from the villages. However, we found no indication for the application of mineral fertilizers in our study region. For a detailed description of the study area, we refer to Magiera et al., 2013; Nakhutsrishvili, 1999; Tephnadze et al., 2014.

3.3. Material and Methods

3.3.1 Vegetation data

In summer 2014, the grassland vegetation within walking distance of six selected villages in the Kazbegi valley (Stepantsminda, Gergeti, Pansheti, Sioni, Phkehlshe and Goristhikhe) was sampled in a stratified random design including low, medium and high productivity sites (strata). Exact locations of the plots, however, were chosen randomly. In order to avoid edge effects, we sampled only large homogeneous grassland patches at a minimum inter-distance of 50 m to each other. The vegetation composition of 90 plots, each covering 25 m², was assessed using the modified Braun-Blanquet scale and including all vascular plant species.

The nomenclature follows The Plant List 1.1. Furthermore, we recorded the total vegetation cover as well as the cover of open soil and bare rocks. The cover percentage and height of the upper and lower herb layers were assessed separately. In order to estimate the cover fractions of the functional plant groups (grass *(Poaceae, Juncaceae, Cyperaceae)*, legume *(Fabaceae),* herb (all other species)), the Braun-Blanquet scale was transformed to cover percentages (r = 0.6%, + = 1.2%, 1 = 2.5%, 2m = 5%, 2a = 10%, 2b = 20%, 3 = 40%, 4 =80%, 5 = 160%). We summarized the coverage of all species belonging to each functional group and used this as 100% coverage for comparison (van der Maarel, 2007). We further identified the most dominant and frequent species for the three grassland types. Those include all species with a mean coverage of 5% per vegetation type and a presence in at least 30% of the vegetation relevés.

To depict the main floristic gradients, we performed a non-metric multidimensional scaling (NMDS, Kruskal, 1964) ordination. Ordination is a commonly used tool to reduce the *n*-dimensional vegetation dataset to lower dimensional floristic gradients. NMDS was chosen as an ordination method since it is a robust, distance-based method, which displays the ordinal-scaled vegetation data accurately. We calculated two NMDS ordinations with three dimensions using the monoMDS function of the R package vegan 2.4-1 (Oksanen, 2011). A NMDS was calculated for the plant species composition of the plots based on Bray-Curtis distances as a distance measure (Bray and Curtis, 1957). The NMDS axes were rotated by principal component-rotation, so that the new axis one points to the direction of the largest variance (Clarke, 1993).

Moreover, we tested structural vegetation parameters for significant differences between the three grassland vegetation types (*Hordeum brevisubulatum* meadow, *Gentianella caucasea* grassland and *Astragalus captiosus* grassland*)*, using a Kruskal-Wallis ANOVA and Nemenyi-tests for multiple comparisons of rank sums implemented in the R package PMCMR 4.1.

3.3.2 Pre-processing of hyperspectral field spectrometric data, satellite imagery and topographic data

We tested hyperspectral field spectrometric data and multispectral satellite imagery, including vegetation indices and topographic data for the modelling of grass, herb, and legume coverage. Compared to the coarse spectral resolution of multispectral data, commonly including three to ten discrete bands, the high spectral resolution of hyperspectral data, in our case including 118 discrete bands, allows for a higher flexibility in the selection of spectral features (Feilhauer et al., 2013). Vegetation indices are either ratios or linear combinations of sensor bands that aim to enhance the vegetation signal and allow to draw conclusions on the status and condition of vegetation (Jackson and Huete, 1991).

In mid-July 2014, at the time of the highest biomass, we acquired hyperspectral field spectrometric canopy reflectance using a hand-held field spectrometer (ASD HH2), covering the range between 325-1075 nm (750 wavelengths) of the solar electromagnetic spectrum. The measurements were taken from the same 5 m x 5 m plots as the vegetation relevés. To cover the entire plot, we took four measurements per plot with five repetitions (each measurement with an internal averaging of 50 spectra), totaling up to 20 spectra per plot. The measurements were collected close to the solar noon, on days with clear sky and low wind speed. Atmospheric changes were accounted for by measuring relative to a white standard panel (Spectralon®, Labsphere Inc., North Sutton, NH), with a recalibration at least every five minutes. During pre-processing, the 20 spectra sampled per plot were averaged and filtered. A Savitzky-Golay filter with a quartic polynom and a filter length of 51 nm was used to smooth the spectra (Savitzky and Golay, 1964). The filtered field spectrometric reflectance measurements were used to test the applicability of hyperspectral sensors compared to multispectral sensors for modelling PFGs by simulating the bands of the sensors AISA Eagle (hyperspectral, 400-970 nm) and RapidEye (multispectral, 440-840 nm). Plant functional groups were already successfully predicted by AISA dual as pollination types (Feilhauer et al. 2016) and by MODIS data (Sun et al. 2008). Moreover, Lehnert et al. (2013) used hyperspectral data to discriminate grass from non-grass, whereas studies using multispectral data to model plant functional types are rather scarce. Both sensors were chosen because they cover a similar spectral range and offer a high spatial resolution. In order to calculate the spectral signal of the AISA Eagle sensor, we cut out the specific wavelengths, whereas the function simulatoR (Feilhauer et al. 2013) and the spectral response curve were used to simulate RapidEye reflectance.

Multispectral, space borne imagery was acquired on the 21st of June 2014 by the RapidEye sensor. The sensor provides information on the canopy reflectance in five bands (blue $440 - 510$ nm, green $520 - 590$ nm, red $630 - 685$ nm, red edge 690 -730 nm and NIR $760 - 850$ nm, Weichelt et al., 2011). The imagery was orthorectified (product level 3-A) and converted to top-of-atmosphere reflectance. Differences in illumination due to the topography were corrected by a cosine topographical correction (Teillet et al., 1982). Besides the five original bands, we included a set of previously published vegetation indices in the analysis (Magiera et al., 2017). We used simple ratios including red edge / red, NIR / red edge, red edge / NIR, NIR / red, NIR /green. Moreover, we included the Atmospherically Resistant Vegetation Index 2 (ARVI, Kaufman and Tanre, 1992), the Blue-wide dynamic range vegetation index (BWDRVI, Gitelson, 2004), the Modified Soil Adjusted Vegetation Index (MSAVI, Qi et al., 1994), the Enhanced Vegetation Index (EVI, Huete et al., 1999), the Normalized Difference Vegetation Index (NDVI) and the red edge NDVI (Herrmann et al., 2010). All indices were calculated by using the R raster package Version 2.5-8.

Topographic data were included from a digital elevation model (DEM) with a 20 m x 20 m resolution. Derivatives from that DEM, eastness, northness (Zar, 1998), slope (Horn, 1981) as well as plan curvature, mean curvature, profile curvature, solar radiation, CTI (Compound Topographic Index, Gessler et al., 1995), HLI (Heat Load Index, Mc Cune and Keon, 2002) and SRR (Surface Relief Ratio, Pike and Wilson, 1971) were calculated with the Arc Map 10.2.1 tool box and the Geomorphometry and Gradient Metrics Toolbox version 1.0. The topographic data were used to estimate the impact of the environmental conditions, mostly the roughness of the terrain on the vegetation structure. We extracted the vegetation indices and topographic variables for the positions of the vegetation relevés.

3.3.3 Modelling the vegetation structure

We tested the predictive power of hyperspectral canopy reflectance, multispectral reflectance, vegetation indices and topographic variables for modelling plant functional groups.

As modelling technique, we chose random forest regression (Breiman, 2001), an ensemble method belonging to the bagged machine learning as implemented in the R package randomForest version 4.6-12 (Liaw and Wiener, 2002). The random forest regression algorithm requires no assumptions on data distributions, thus transformations are not necessarily needed (Breiman, 2001; Liaw and Wiener, 2002). It can capture non-linear data structures, which are often inherent when it comes to analyzing vegetation data. Moreover, it is robust towards outliers and can handle 'noise' introduced by many predictor variables. The error rate of a random forest is assessed by out-of-bag estimation. The importance of a variable is assessed as % **Increment MSE** by permuting the out-of-bag data and the resulting error increase when one variable is left out (Liaw and Wiener, 2002). Models were validated by a 100 times bootstrapping procedure, because of the relatively small sample size. All three resulting maps were stacked and plotted in the red green blue (rgb) - colour code with r = legume coverage, g = grass coverage, and b = herb coverage.

3.4. Results

3.4.1 Grassland

The 90 vegetation relevés contained 177 plant species belonging to 35 families (26 graminoid species, 125 herbaceous species, 22 fabaceous species and 4 sedge species).
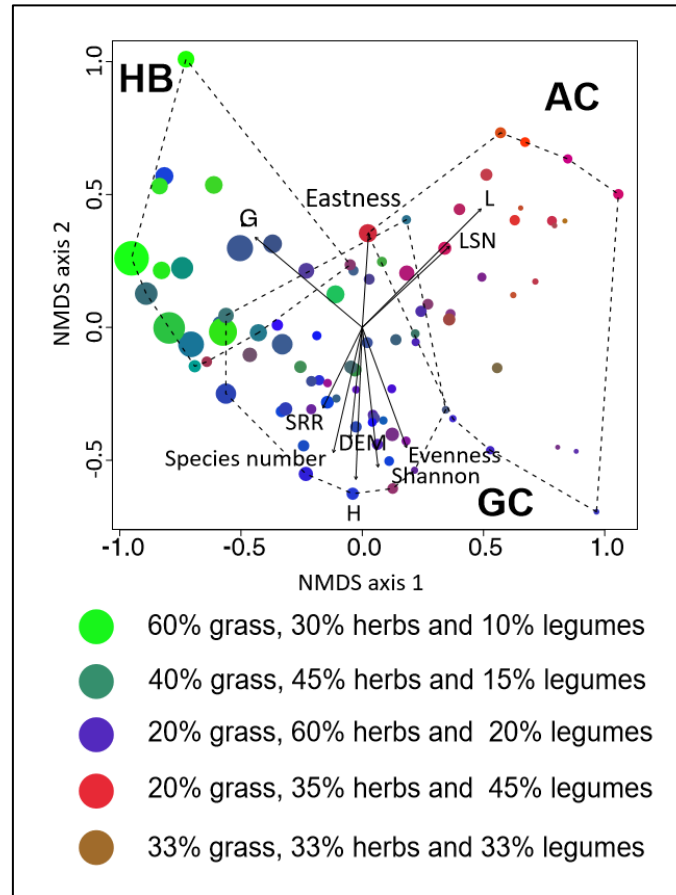
Fig. 1: NMDS ordination diagram of the two main floristic gradients. The arrows point in the direction of the strongest change in topographical gradients (eastness, surface relief ratio (SRR) and elevation (DEM)) as well as vegetation based gradients (grass (G), herb (H), legume (L), legume species number (LSN), species number, Shannon Index and Evenness). The length of the arrow represents the relation between ordination and gradient with a significance level of $p \leq 0.01$. Point size is fitted to grassland biomass (maximum biomass = 13.4 t*ha^{-1}, minimum biomass = 0.25 t*ha^{-1}).

The NMDS ordination accurately depicts the two main floristic gradients with a stress level of 0.14 (see Fig. 2). Most of the original variation in the data (61%) is explained by the first NMDS axis, the second and third axis represent 26% and 0.5%, respectively. The colour scheme represents the distribution of grass, herb, and legume in the rgb colour space, i.e. greenish points represent a high grass content. The grassland vegetation is characterized by broad transitions, which explains the high species richness but makes it difficult to delineate grassland vegetation types.

The high grass coverage of the *Hordeum brevisubulatum* meadow is accompanied by a significantly higher total cover and yield (see Tab. 1). Dominated by *Hordeum brevisubulatum* and in the drier and stonier parts by *Agrostis vinealis, Trifolium repens*, *Ranunculus caucasicu*s and *Ranunculus ampelophyllus*, they occur on deep soils. The high herb coverage as detected in the *Gentianella caucasea* grassland is caused by species richness – mainly of herb species – and a coverage more evenly distributed among single species, i.e. many species exhibit an average coverage below 15%. In contrast, dominance is mainly established by grassland matrix species, shared with the *Astragalus captiosus* grassland, such as *Trifolium repens*, *Trifolium ambiguum*, *Bromus variegatus* and *Poa alpina*. A high number of legume species and coverage (e.g. *Medicago glutinosa* as a dominant species) characterize the *Astragalus captiosus* grassland connected to open soil, bare rock, and litter.

Tab. 1: Structural variables of the grassland types. Letters indicate homogeneous groups after a Kruskal Wallis ANOVA and Nemenyi-tests for multiple comparisons of rank sums p ≤ 0.01.

	Hordeum brevisubulatum meadow			*Gentianella caucasea* grassland			*Astragalus captiosus* grassland		
	n=23			n=36			n=31		
	Median	25 Perc.	75 Perc.	Median	25 Perc.	75 Perc.	Median	25 Perc.	75 Perc.
Yield [Mg*ha^{-1}]	5.97	4.80	7.98	2.61[a]	1.81	3.17	2.66[a]	2.13	3.16
Cover total [%]	100	98	100	95.5[a]	93.5	98	95[a]	90	96
Coverage litter [%]	0	0	0	0.5[a]	0	2	0[a]	0	2.5
Open soil [%]	0	0	2	2.5[a]	1	5	4[a]	2	5
Bare rock [%]	0[a]	0	0	0[a] [b]	0	0	1[b]	0	4.5
Grass coverage	39[a]	31	54	21[b]	15	29	22[b]	19	29
Herb coverage [%]	43[a]	32	54	59	50	68	43[a]	32	50
Legume coverage [%]	12[a]	8	16	16[a]	9	23	35	18	43
Species number	28[a][b]	25	32	31[a]	28	35	27[b]	21	32
Shannon index	2.78[a]	2.49	2.92	2.99	2.82	3.18	2.69[a]	2.62	3.02
Evenness	0.83[a]	0.76	0.86	0.88[a][b]	0.86	0.91	0.84[b]	0.81	0.89

3.4.2 Modelling PFGs

The random forest models explained 36% of the variance in the data and had an root mean square error (RMSE) = 13% for grass coverage, a 25% explained variance with an root mean square error RMSE = 12% for herb coverage and a 37% explained variance and a RMSE = 11% for legume coverage in calibration, using multispectral reflectance and -vegetation indices and topographic parameters as predictors. The most important predictor variables include the red edge / NIR ratio, the ARVI and the WDRVI for grass coverage, the elevation a.s.l., the red edge band and the profile curvature for herb coverage as well as the elevation a.s.l., the NIR band and the MSAVI for legume coverage.
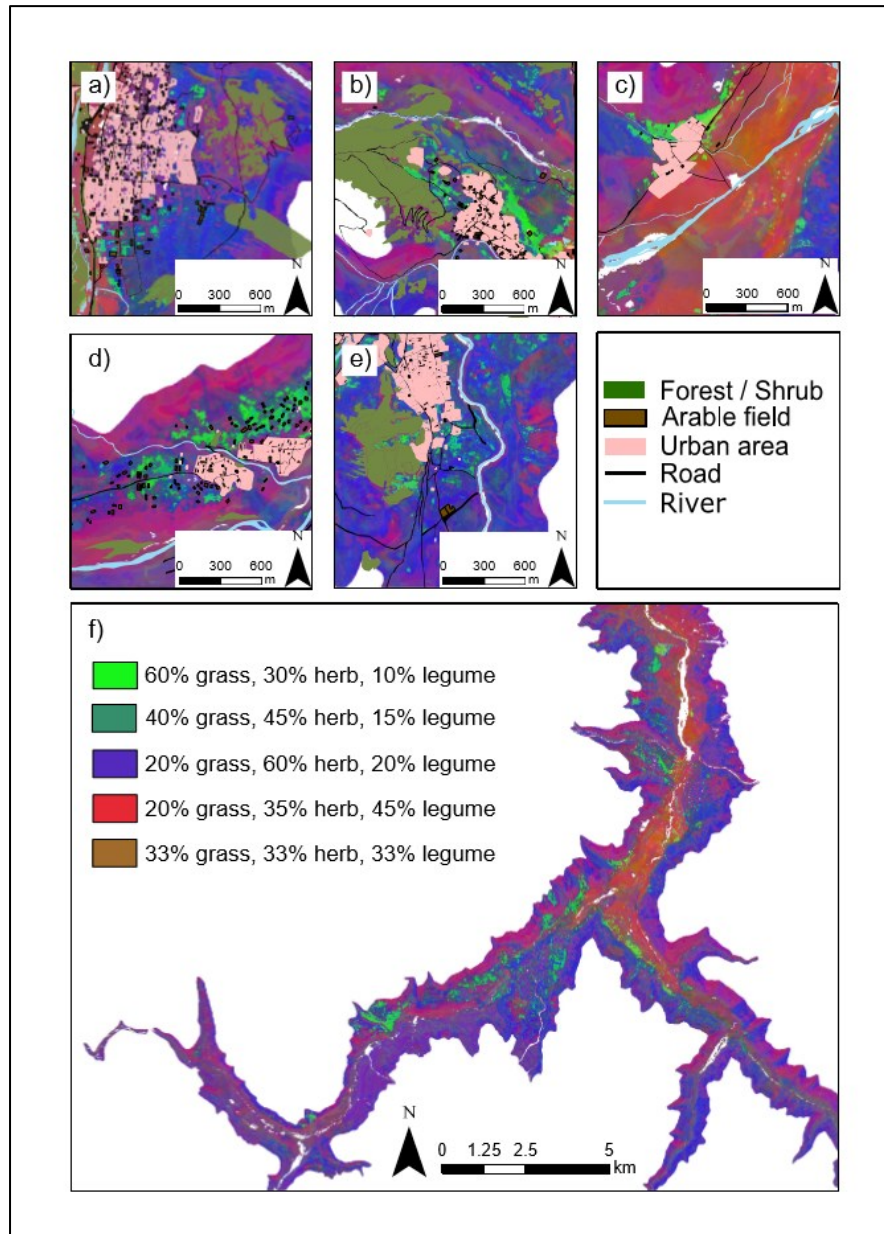
Fig. 2: Modelled grass, herb and legume content in the villages a) Stepantsminda, b) Gergeti, c) Pansheti, d) Goristhikhe and Phkelsche and e) Sioni as well as for f) the whole Kazbegi region.

The grassland matrix is characterized by a high herb content, whereas grass and legume content differ in the vegetation types. Grass dominated patches are only small and established in close proximity to the settlements (Fig. 3 see b, c, d). In contrast, those dominated by legumes (mainly *Astragalus captiosus*) cover larger areas mainly in the floodplains or on steep, south exposed slopes, which are characterized by open soil and bare rock (Fig. 3 see c).

We further tested if simulated hyperspectral field spectrometric reflectance, which matches the spectral characteristics of the AISA sensor, enhances the model quality compared to simulated multispectral reflectance (RapidEye) or a mix of simulated multispectral reflectance, simulated vegetation indices and topographic variables as predictor variables.

Tab. 2: Adjusted R² of the random forest models as determined by correlation between predicted and observed values in calibration and validation (bootstrapping) for simulated hyperspectral reflectance (HR, AISA), simulated multispectral reflectance (MR, RapidEye) and simulated vegetation indices (VI), topographic parameters (TP) and the PFGs.

	HR in cal.		HR in val.	
	Adj. R²	RMSE [%]	Adj. R²	RMSE [%]
Grass coverage [%]	0.07	14.16	0.05	14.39
Herb coverage [%]	0.17	14.06	0.18	13.90
Legume coverage [%]	0.30	11.71	0.28	11.84
	MR in cal.		MR in val.	
	Adj. R²	RMSE [%]	Adj. R²	RMSE [%]
Grass coverage [%]	0.04	14.36	0.03	14.48
Herb coverage [%]	0.15	14.18	0.15	14.14
Legume coverage [%]	0.25	12.16	0.25	12.10
	MR, VI, TP in cal.		MR, VI, TP in val.	
	Adj. R²	RMSE [%]	Adj. R²	RMSE [%]
Grass coverage [%]	0.18	13.19	0.19	13.20
Herb coverage [%]	0.21	13.69	0.24	13.51
Legume coverage [%]	0.32	11.52	0.33	11.48

The best fitting models resulted from a mixed set of simulated multispectral reflectance, vegetation indices and topographic variables, whereas simulated hyperspectral reflectance performed equally well to the simulated multispectral reflectance (see Tab. 2).
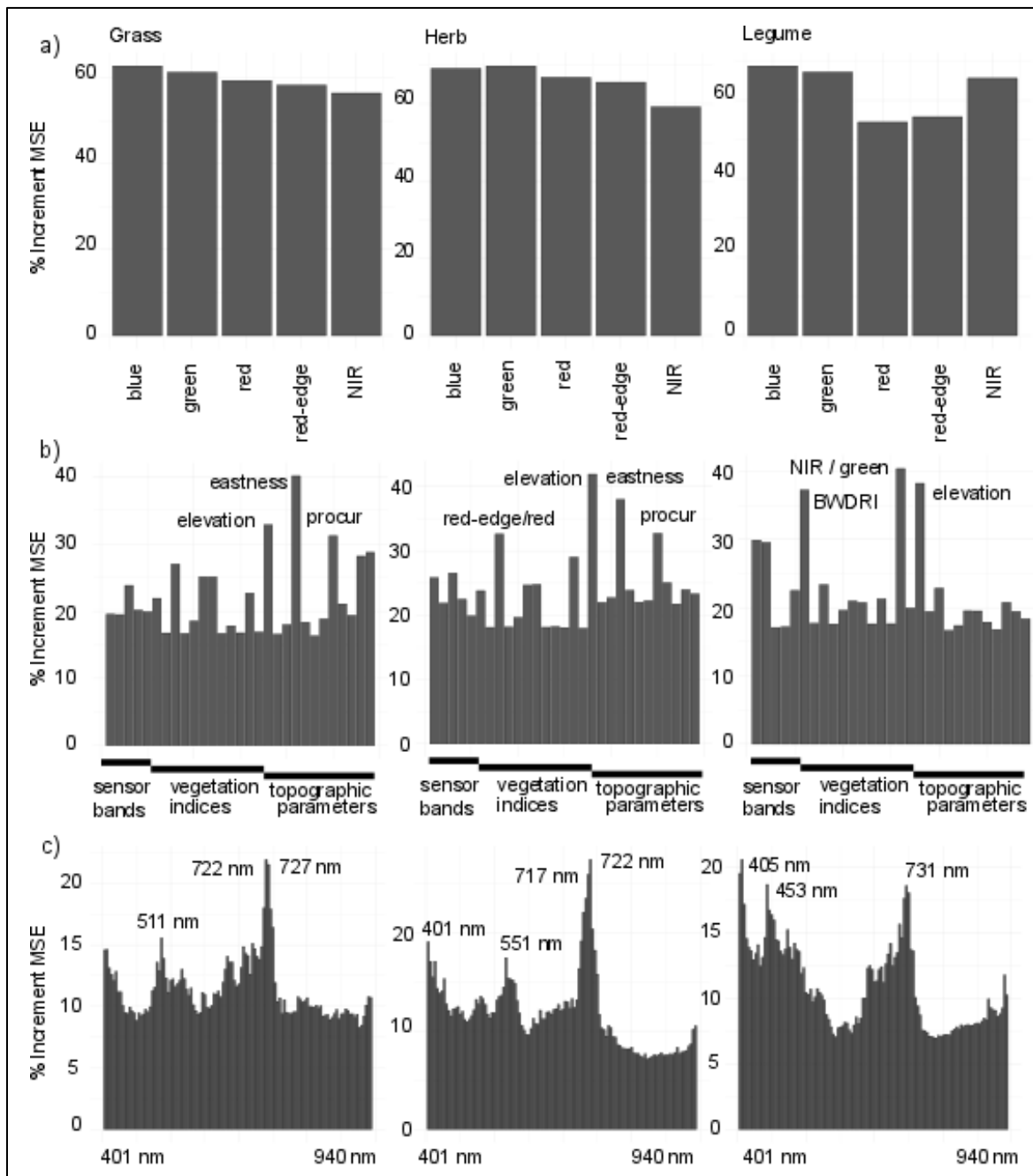
Fig. 3: Variable importance calculated as % Increment MSE using a) simulated multispectral reflectance (RapidEye), b) simulated multispectral reflectance (RapidEye, MR), simulated vegetation indices and topographic parameters (MR, VI, TP) and c) simulated hyperspectral reflectance (HR, AISA) as predictors for grass, herb and legume cover.

For the prediction of grass coverage, the blue and green band played a key role when only MR was used as predictor. Eastness, elevation and profile curvature were most successful predictors in MR, VI and TP. Considering simulated AISA reflectance, wavelengths of 722-727 nm (red edge) resulted in the strongest increase in MSE. Wavelengths in the green part of the electromagnetic spectrum of the light (511 nm) were strong predictors, too. Herb coverage was mostly predicted

by the MR blue, green and red band, whereas elevation, eastness, profile curvature and the red edge/red ratio contributed most to the MR, VI and TP model. The variable importance for predicting legume coverage shows a high predictability of the blue band, the green band and the NIR band in MR. Strong predictors in MR, VI and TV were elevation, BWDRVI and the NIR/green ratio. In HR, strong predictors were found in the blue (405 nm) region of the spectrum and the red edge (731 nm).

3.5 Discussion

3.5.1 Composition of grassland swards and management implications

The tested high mountain grassland exhibited a vegetation structure which is common for unfertilized high mountain grassland (Rudmann-Maurer et al., 2008). Within all vegetation types, herbs and legumes achieve comparably high coverages with special regard to farmed grassland that typically is composed of 45% grass, 10% legume and 45% herb coverage (Voigtlaender et al., 1987). Grass coverage is significantly higher in *Hordeum brevisubulatum* meadows, but is still within the range of unfertilized farmland, which are almost lost in central Europe due to intensive farming practices, but is in parts conserved in high mountain systems. Moreover, many central European grassland species with a deep growing root system such as *Rumex obtusifolius, Festuca pratense* and *Geranium sylvaticum* are frequent.

A higher herb coverage characterizes the species-rich *Gentianella caucasea* grassland (Ø species number: 31), which is mostly influenced by the environmental factors soil type, geology, topography and land use (Tephnadze et al., 2014). Even due to its moderate biomass, the *Gentianella caucasea* grassland has been mown whenever winter fodder was scarce and was pastured in spring. This low-intensive grassland land use has contributed to its high species diversity. An abandonment of this management practice would lead to a considerable loss of high mountain plant diversity (Maurer et al., 2006). Due to its species richness, the *Gentianella caucasea* grassland is regarded to supply an erosion mitigating vegetation cover on shallow, nutrient-poor soils, even though many shallow rooting species are typical for its composition (*Leontodon hispidus, Anthoxanthum odoratum* and *Lotus corniculatus*).

Low species diversity, as analyzed for the legume dominated *Astragalus captiosus* grassland, and the typically low vegetation coverage indicate potential areas prone to erosion mostly on south-east exposed slopes (Wiesmair et al., 2016). Due to nutrient-poor soil conditions and drought at the erosion initials, only few species are able to establish and keep the vegetation cover. This highlights the importance of single species, especially the dominant *Astragalus captiosus* with its immense (90 cm) root length, to mitigate erosion processes (Caprez et al., 2011). Mineral fertilization of legume-

rich swards could thus lead to a decline in legume coverage, followed by a lower vegetation cover, enabling erosion on steep slopes.

3.5.2 Modelling and mapping of PFGs

Even though overall model quality was moderate, compared to the results of Biewer (2009a) in sown swards, errors (11-15 %) compared to the errors of visual field estimations. Moreover, the resulting map depicts clear patterns of grass, herb and legume coverage. The moderate model fits could be explained by the overall low variability in the dataset with a standard deviation for grass coverage of 14.74, for herb coverage of 15.05 and for legume coverage of 14.15. The mixed set of multispectral reflectance, vegetation indices and topographic variables resulted in the most accurate predictions, with elevation and profile curvature being the most important topographic variables since near-natural vegetation mainly follows topographic gradients. The characteristic biophysical features of grass, herb and legume-species such as leaf angle and orientation, stems, stalks and litter content further add to a characteristic reflectance pattern (Pfitzner et al., 2006).

We compared modelling results for predicting PFGs with hyperspectral reflectance and simulated multispectral data to test the potential of hyperspectral imagery for modelling PFGs. Using the resampled field spectrometric data minimizes the effects of illumination differences in multi-date comparisons (Nilson and Peterson, 1994). Moreover, both datasets originate from the same spectra unlike in a comparison of real satellite imagery, where images are often recorded weeks apart. Therefore, we avoided inaccuracies introduced by the fast phenological development in high mountain regions (Körner, 2003). However, spatial scale as a crucial sensor characteristic is not taken into account. The field of view of the spectrometer covers areas below 1 m², depending on the average height above ground, whereas the rescalable, airborne AISA Eagle imagery has varying pixel sizes (< 5 m x 5m) and the spaceborne RapidEye sensor delivers imagery with a pixel size of 5 m x 5m. The number of species in a pixel size increases with pixel size, even though we counteracted this problem by averaging spectra on 5 m x 5 m plots. Using actual imagery might result in different model qualities (Magiera et al., 2016; Meyer et al., 2017).

Hyperspectral reflectance outperformed the multispectral reflectance by only 2-3%, whereas vegetation indices and topographic parameters explained another 10% of variance. In particular, the topographic parameters showed a strong predictive power. The capability of multispectral reflectance to model floristic composition (Feilhauer et al., 2013) as well as aboveground biomass and vegetation cover (Meyer et al., 2017) is generally high. It may, however, be enhanced by including topographic variables, especially in a high mountain study area. In addition, spectral information from the short-wave infrared range, which is sensitive to the water and dry matter content of the leaves, may add valuable information to the models (Feilhauer et al. 2013). Such

information is, however, only available for few sensors with a high spatial resolution (e.g., the commercial WorldView-3). Free multispectral imagery as delivered by Sentinel 2 could improve the model quality since it offers three red edge, two NIR and two SWIR bands. However, the main pitfall of Sentinel 2a data is the rather coarse spatial resolution (20 m x 20 m pixel size) compared to RapidEye (5 m x 5 m pixel size). Further testing while using a broader spectral range, as delivered by Sentinel 2, is thus needed.

3.6. Conclusions

The high mountain grassland of the Kazbegi region displays a unique species diversity with a high coverage of herbs and legumes, resulting in a typical structure and vegetation cover. Mapping grass, herb and legume content revealed the spatial limitation of grass-rich swards for agricultural grassland use and the erosion vulnerability of large areas currently dominated by legumes. Sustainable, economically and ecologically viable case sensitive grassland management, which is highly needed in remote high mountain regions, can be enhanced by implementing grass, herb and legume cover maps derived from multispectral imagery and topographic parameters. In order to enhance model fits, further testing, including even stronger vegetation gradients and the addition of shortwave infrared wavelengths, is needed.

References

Akhalkatsi M, Abdaladze O, Nakhutsrishvili G, Smith WK. 2006. Facilitation of seedling microsites by Rhododendron caucasicum extends the Betula litwinowii Alpine treeline, Caucasus Mountains, Republic of Georgia. Arctic Antarctic and Alpine Research 38: 481–488.

Biewer S, Erasmi S, Fricke T, Wachendorf M. 2009a. Prediction of yield and the contribution of legumes in legume-grass mixtures using field spectrometry. Precision Agriculture 10: 128–144.

Biewer S, Fricke T, Wachendorf M. 2009b. Determination of Dry Matter Yield from Legume-Grass Swards by Field Spectroscopy. Crop Science 49: 1927–1936.

Bray JR, Curtis JT. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecological Monographs 27: 325-349.

Breiman L. 2001. Random forests. Machine learning 45: 5–32.

Caprez R, Spehn E, Nakhutsrishvili G, Körner C. 2011. Drought at erosion edges selects for a "hidden" keystone species. Plant Ecology & Diversity 4: 303–311.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18: 117–143.

Feilhauer H, Thonfeld F, Faude, U, He, KS, Rocchini D, Schmidtlein S. 2013. Assessing floristic composition with multispectral sensors—A comparison based on monotemporal and multiseasonal field spectra. International Journal of Applied Earth Observation and Geoinformation 21: 218–229.

Feilhauer H, Doktor D, Schmidtlein, S, Skidmore AK. 2016. Mapping pollination types with remote sensing. Journal of Vegetation Science 27: 999-1011.

Gessler PE, Moore, ID, Mc Kenzie NJ, Ryan PJ. 1995. Soil-landscape modelling and spatial prediction of soil attributes. International Journal of Geographical Information Systems 9: 421–432.

Gitelson AA. 2004. Wide Dynamic Range Vegetation Index for Remote Quantification of Biophysical Characteristics of Vegetation. Journal of Plant Physiology 161: 165–173.

Herrmann I, Karnieli A, Bonfil DJ, Cohen Y, Alchanatis V. 2010. SWIR-based spectral indices for assessing nitrogen content in potato fields. International Journal of Remote Sensing 31: 5127–5143.

Himstedt M, Fricke T, Wachendorf M. 2009. Determining the Contribution of Legumes in Legume-Grass Mixtures Using Digital Image Analysis. Crop Science 49: 1910–1916.

Homburger H, Hofer G. 2012. Diversity change of mountain hay meadows in the Swiss Alps. Basic and Applied Ecology 13: 132–138.

Horn, BKP. 1981. Hill shading and the reflectance map. Proceedings of the IEEE 69: 14–47.

Huete A, Justice C, Van Leeuwen W. 1999. MODIS vegetation index (MOD13). Algorithm theoretical basis document 3: 213.

Jackson RD, Huete AR., 1991. Interpreting vegetation indices. Preventive Veterinary Medicine 11: 185–200.

Kaufman, YJ, Tanre D. 1992. Atmospherically resistant vegetation index (ARVI) for EOS-MODIS. IEEE Transactions on Geoscience and Remote Sensing 30: 261–270.

Ketskhoveli N, Kharadze, AL, Ivanishvili MA, Gagnidze, RI. 1975. Botanical description of the Georgian military road. (Tbillisi-Kazbegi-Ordjonikidze). Presented at the XII. International Botanical Congress, The Academy of Sciences of the Georgian SSR, The Institute of Botany, Tbillisi, p. 95.

Körner C. 2003. Alpine Plant Life. Berlin Heidelberg, Springer.

Körner C. 2004. Mountain biodiversity, its causes and function. Ambio 3:11–17.

Kruskal JB. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–129.

Lehnert LW, Meyer H, Meyer N, Reudenbach C, Bendix J. 2014. A hyperspectral indicator system for rangeland degradation on the Tibetan Plateau: A case study towards spaceborne monitoring. Ecological Indicators 39: 54–64.

Lehnert LW, Meyer, H., Meyer, N., Reudenbach, C., Bendix, J. 2013. Assessing pasture quality and degradation status using hyperspectral imaging: a case study from western Tibet. Remote Sensing for Agriculture, Ecosystems, and Hydrology XV, 88870I.

Liaw A, Wiener M. 2002. Classification and regression by randomForest. R news 2: 18–22.

Lichtenegger E, Bedoschwili D, Hübl E, Scharf E. 2006. Höhenstufengliederung der Grünlandvegetation im Zentralkaukasus. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich: 43–81.

Magiera A, Feilhauer H, Otte A, Waldhardt R, Simmering D. 2013. Relating canopy reflectance to the vegetation composition of mountainous grasslands in the Greater Caucasus. Agriculture, Ecosystems & Environment 177, 101–112.

Magiera A, Feilhauer H, Tephnadze N, Waldhardt R, Otte A. 2016. Separating reflectance signatures of shrub species - a case study in the Central Greater Caucasus. Applied Vegetation Science 19 : 304–315.

Magiera A, Feilhauer H, Waldhardt R, Wiesmair M, Otte A. 2017: Modelling biomass of mountainous grasslands by including a species composition map. Ecological Indicators 78: 8-18.

Maurer K, Weyand A, Fischer M, Stocklin J. 2006. Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. Biological Conservation 130: 438–446.

Mc Cune B. Keon D. 2002. Equations for potential annual direct incident radiation and heat load. Journal of vegetation science 13: 603–606.

Meyer H, Lehnert LW, Wang Y, Reudenbach C, Nauss T, Bendix J. 2017. From local spectral measurements to maps of vegetation cover and biomass on the Qinghai-Tibet-Plateau: Do we need hyperspectral information? International Journal of Applied Earth Observation and Geoinformation 55: 21–31.

Nakhutsrishvili G. 1999. The vegetation of Georgia (Caucasus). Braun-Blanquetia 15: 5–74.

Nakhutsrishvili G. 2012. The Vegetation of Georgia (South Caucasus). Springer, Dordrecht.

Nilson T, Peterson U. 1994. Age dependence of forest reflectance: Analysis of main driving factors. Remote Sensing of Environment 48: 319–331.

Oksanen, J. 2015. Multivariate Analysis of Ecological Communities in R: vegan tutorial. http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf; accessed on 25.07.2017.

Pfitzner K, Bollhöfer A, Carr G. 2006. A Standard Design for Collecting Vegetation Reference Spectra: Implementation and Implications for Data Sharing. Spatial Science 52: 79–92.

Pike RJ, Wilson SE. 1971. Elevation-Relief Ratio, Hypsometric Integral, and Geomorphic Area-Altitude Analysis. Geological Society of America Bulletin 82: 1079–1084.

Pohl M, Alig D, Körner C, Rixen C. 2009. Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant and Soil 324: 91–102.

Psomas A, Kneubühler M, Huber S, Itten K, Zimmermann NE. 2011. Hyperspectral remote sensing for estimating aboveground biomass and for exploring species richness patterns of grassland habitats. International Journal of Remote Sensing 32: 9007–9031.

Pyšek P, Šrutek, M. 1989. Numerical Phytosociology of the subalpine belt of the Kazbegi region, Caucasus, USSR. Vegetatio 81: 199–208.

Qi J, Chehbouni A, Huete AR, Kerr YH, Sorooshian S, 1994. A modified soil adjusted vegetation index. Remote Sensing of Environment 48: 119–126.

Rudmann-Maurer K, Weyand A, Fischer M, Stöcklin J. 2008. The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps. Basic and Applied Ecology 9: 494–503.

Savitzky A, Golay MJE: 1964. Smoothing and Differentiation of Data by Simplified Least Squares Procedures. Analytical Chemistry 36: 1627–1639.

Sun W, Liang S, Xu G, Fang H, Dickinson R. 2008. Mapping plant functional types from MODIS data using multi-source evidential reasoning. Remote Sensing of Environment 112:1010–1024.

Tasser E, Tappeiner U. 2002. Impact of land use changes on mountain vegetation. Applied Vegetation Science 5: 173–184.

Teillet PM, Guindon B, Goodenough DG. 1982. On the Slope-Aspect Correction of Multispectral Scanner Data. Canadian Journal of Remote Sensing 8: 84–106.

Tephnadze N, Abdaladze O, Nakhutsrishvili G, Simmering D, Waldhardt R, Otte A. 2014. The impacts of management and site conditions on the phytodiversity of the upper montane and subalpine belts in the Central Greater Caucasus. Phytocoenologia 44: 255–291

van der Maarel E. 2007. Transformation of cover-abundance values for appropriate numerical treatment - Alternatives to the proposals by Podani. Journal of Vegetation Science 18: 767–770.

Voigtlaender G, Jacob H, Boeker P. 1987. Grünlandwirtschaft und Futterbau. Stuttgart, Ulmer.

Weichelt H, Rosso P, Marx A, Reigber S, Douglass K, Heynen M. 2011. White Paper - The RapidEye Red Edge Band. RapidEye White Papers 1–6.

Wiesmair M, Feilhauer H, Magiera A, Otte A, Waldhardt R. 2016. Estimating Vegetation Cover from High-Resolution Satellite Data to Assess Grassland Degradation in the Georgian Caucasus. Mountain Research and Development 36: 56–65.

Wiesmair M, Otte A, Waldhardt R. 2017. Relationships between plant diversity, vegetation cover, and site conditions: implications for grassland conservation in the Greater Caucasus. Biodiversity and Conservation 26, 273–291.

Wold H. 1966. Estimation of Principal Components and Related Models by Iterative Least Squares. *In:* Krishnaiah, PR. Editor. *Multivariate Analysis*. Academic Press, New York, pp. 391–420.

Zar JH. 1998. *Biostatistical Analysis*, 4 edition. Upper Saddle River, New York, Prentice Hall.

Zha Y, Gao J, Ni SX, Liu YS, Jiang JJ, Wei YC. 2003. A spectral reflectance-based approach to quantification of grassland cover from Landsat TM imagery. Remote Sensing of the Environment 87: 371–375.

4. Separating reflectance signatures of shrub species – A case study in the Central Greater Caucasus

Anja Magiera [1], Hannes Feilhauer [2], Nato Tephnadze [3], Rainer Waldhardt [1], Annette Otte [1]

[1] *Division of Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resources Management, Justus-Liebig University, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany*

[2] *Institute of Geography, Friedrich-Alexander University Erlangen-Nürnberg, Wetterkreuz 15, 91058 Erlangen, Germany*

[3] *Institute of Ecology, Ilia State University, 3/5 Kakutsa Cholokashvili str., 0162 Tbilisi, Georgia*

Key words: Field spectroscopy; remote sensing; woody encroachment; multispectral; spectral discrimination; alpine vegetation

Abstract

Questions: Shrub encroachment has been observed in many alpine and arctic environments and is expected to significantly alter these ecosystems. Mapping these processes with remote sensing is a powerful tool for monitoring purposes. Thus, we aim to test the distinctiveness of the reflectance signature of target species relative to their co-occurring shrub species using uni- and multivariate analyses for an alpine ecosystem. We ask: i) Is it possible to differentiate shrub species with a unique growth form by their reflectance signature? ii) Which of the tested multispectral sensors produces the best separability? and iii) How are the results affected by the timing of data acquisition in the vegetation period?

Location: We analyzed three shrub (*Betula litwinowii, Rhododendron caucasicum,-Hippophae rhamnoides)* and one tall forb species *(Veratrum lobelianum)* occurring in the subalpine to alpine belt of the Kazbegi district, Central Greater Caucasus, Georgia.

Method: The vegetation of 52 relevés was analyzed using Non-Metric Multidimensional Scaling (NMDS) and Indicator Species Analysis (ISA). From field spectrometric data we simulated multispectral sensor bands (IKONOS, Quickbird 2, RapidEye, WorldView-2) directly taken from the target species. We analyzed the reflectance signature in RapidEye data from June and September. For all datasets we calculated the Jeffries-Matusita Distance (JMD) as a separability measure and tested the reflectance signature of the single bands for differences.

Results: *Betula litwinowii* and *Veratrum lobelianum* always co-occured in our data. A high abundance of *Betula litwinowii* could also be found in the *Rhododendron* cluster and vice versa; whereas the *Hippophae* cluster was more homogeneous. Simulated bands showed a good overall separability (JMD 1.58 - 2) of the target species. The separability increased with the increase of the number of bands and the inclusion of the red edge band. There was a general trend in which the reflectance from satellite images produced a lower separability (JMD 1.2 - 1.55) than the simulations, with the best separability in the late vegetation period.

Conclusion: Our results showed the possibility to spectrally separate encroaching shrub species with a unique growth form in a high mountain environment by using simulated multispectral data and satellite imagery.

4.1. Introduction

Shrub encroachment processes such as increasing shrub biomass, cover and abundance are currently being reported from many alpine (Camarero & Gutiérrez 2004, Holtmeier & Broll 2007) and arctic environments (Jia et al. 2003, Tape et al. 2006). Moreover, the arctic and alpine tree lines, conventionally defined as the lines connecting the highest forest patches within a given slope or series of slopes, are expanding (Körner 1998). These changes are expected to significantly alter the structure and functioning of alpine and arctic ecosystems (Myers-Smith et al. 2011). An increase in shrub cover can strongly influence an ecosystem's surface energy exchange (Sturm et al. 2001), nutrient cycling (DeMarco et al. 2011), and carbon storage (Knapp et al. 2008), as well as the floristic composition and the services provided (Wilson & Nilsson 2009).

Three main trends can be observed regarding shrub encroachment. First, shrub recruitment or recolonization seems to increase over the years. Second, single shrubs are spreading, leading to a denser canopy cover. Third, gaps within stands are filled (Tape et al. 2006). Climatic and land use changes are often mentioned as drivers for these processes. Generally, milder winters and springs increase the chances of survival for seedlings and saplings. De-intensified land use with reduced grazing intensities and abandonment of remote pastures lead to initial successional stages of shrub encroachment (Holtmeier & Broll 2007).

As an example of shrub encroachment in a high montane to alpine region, the present study aims to analyze the phenomenon of shrub encroachment in Kazbegi, Georgia. In this study region, forests are limited to steep, north facing and inaccessible slopes and the landscape is mainly characterized by grassland communities (Ketskhoveli et al. 1975). Up to the 1990s, a very strong grazing pressure and illegal cutting of firewood were hampering any establishment of woody species (Akhalkatsi et al. 2006). However, a visual comparison of aerial images of the region from 1975, 1980, and 2005 based on expert knowledge and field visits already revealed a trend towards reforestation and initial succession of birch (*Betula litwinowii*) in the Kazbegi district (Waldhardt et al. 2011).

Besides *Betula litwinowii (B. litwinowii)*, the dominant shrub species in this region, *Hippophae rhamnoides (H. rhamnoides)*, *Rhododendron (R. caucasicum)* and a representative of a tall herb *Veratrum (V. lobelianum)* are forming larger thickets. The latter was chosen based on its shrub-like growth form as it was expected to be easily confused with a low shrub (< 100 cm) in remote sensing data. All four species, chosen as the target species of this study, exhibit very unique growth forms. *B. litwinowii,* forms small stands, which are commonly located at high altitudes, as well as on very steep and remote slopes. It often grows as crook-stemmed form due to heavy snow load (> 2000 m a.s.l.). Individual trees form the tree line at about 2500 m a.s.l. (Akhalkatsi et al. 2006). In contrast, the thorny *H.*

rhamnoides with its silvery lanceolate leaves forms dense shrubs (up to 350 cm height), which occur mainly on disturbed sites such as areas of landslide or fluvial deposits of the small streams and rivers in the valley (Tephnadze et al. 2014). *R. caucasicum* grows to a lower height (< 100 cm) but develops a closed canopy with its evergreen, planophile leaves. It is typically distributed in the upper subalpine belt around 2200 m above sea level (Nakhutsrishvili & Gagnidze 1999). *V. lobelianum* is a tall herb with large leaves, and grows patchy with a low cover. The growth forms of these plant species are adapted to the local resource constraints and stress levels. These adaptive mechanisms are often linked to biochemistry and physiology as well as to the structure and phenology of a plant or vegetation type. Further, biophysical characteristics such as leaf inclination and canopy structure may determine a unique reflectance pattern (Tappeiner & Cernusca 1989). The plants' characteristic growth forms, thus, result in a characteristic reflectance signature or 'optical type', which can be utilized for mapping based on remote sensing methods (Ustin & Gamon 2010).

A remote sensing based mapping and monitoring of shrub encroachment, in which encroaching species can be readily separated, is important for various questions related to land use management, policy, and decision-making processes. However, a clear distinction of plant species based on remote sensing is difficult since the reflectance signal of vegetation itself is influenced by multiple factors such as the water content of the vegetation, which is influenced by phenology and seasonality, the atmospheric influences, and the illumination geometry, all of which must be considered for a long term monitoring (Nilson & Peterson 1994, Pottier et al. 2014).

The multispectral signal in satellite images commonly includes five to ten discrete spectral bands covering a broad range of the solar electromagnetic spectrum. Multispectral satellite imagery is easy to obtain and globally available. Moreover, it is already applied in combination with various modeling techniques for vegetation type mapping. Feilhauer et al. (2013) showed that multispectral data provide sufficient information for detailed vegetation mapping. Univariate testing was successfully applied to hyperspectral field spectrometric data, aiming to distinguish maquis tree species from shrubs (Manevski et al. 2012). However, only few studies have considered the potential of remote sensing to assess encroaching shrubs in arctic or alpine environments (e.g. Gould et al. 2002).

We aim to test the distinctiveness of the multispectral response of the target species relative to their co-occurring shrub species using uni- and multivariate analyses. We simulated the signal measured by the multispectral satellite sensors IKONOS, Quickbird 2, RapidEye, and WorldView-2 to test the applicability of different sensors for this purpose. The tested sensors all offer a high spatial resolution required for shrub detection. This was enabled by simulating the data based on hyperspectral field spectrometric data directly taken from the target species. Further, we used

already existing vegetation relevés and RapidEye data of two different dates in the vegetation period to determine the reflectance signature of the vegetation types and to assess the importance of timing in data acquisition.

4.2. Material and Methods

4.2.1 Study area

The study area is located in the Republic of Georgia in the northern part of the Central Greater Caucasus close to the Russian border (see Fig. 1). The high mountain study area belongs to the rural Kazbegi district (1082 km², 1200 - 5033 m a.s.l., 4.5 inhabitants per km² in 2013), which is part of the administrative region Mtskheta-Mtianeti (www.geostat.ge). The largest settlement is the small town Stepantsminda (1700 m a.s.l.; 1,800 inhabitants in 2013). The Georgian Military Road connects the remote valley to Tbilisi via the Cross pass in the south and to Vladikavkas (Russia) via the Dariali Gorge in the north. Parallel to the Georgian Military Road, the river Tergi runs through the valley from south to north, bordered by Mount Kazbeg (5035 m a.s.l.) on the west and Mount Elia on the east.

The study site comprises of young quaternary glacial and fluvial sediments, clay slate sedimentary rocks from the Lower Jurassic period, as well as quaternary rocks of volcanic (andesit / dacit) and pyroclastic (tuff and lava) origin (Nakhutsrishvili 2012). The soil types are closely related to the geology and topography of the region. On the upper slopes shallow, stone rich regosols prevail, followed by shallow to moderately deep cambisols on the mid to lower slopes. The fluvial sediments of the floodplains are characterized by fluvisols and gleysols. The related soil chemical parameters show acidic conditions with a moderate to low level of soil nutrients (Tephnadze et al. 2014). Mud and debris flows occur frequently in this area (Keggenhoff et al. 2014).

The climate in this high mountain region is comparably harsh. The mean annual temperature is 4.7 °C and the mean annual precipitation reaches not more than 800 mm in the subalpine (1800 / 1900 – 2400 / 2500 m a.s.l) zone (Lichtenegger et al. 2006). A snow cover of 20-40 cm in average persists from November to May (Akhalkatsi et al. 2006). The microclimatic conditions vary with the exposition of the slopes and the altitudinal belts. Under the relatively continental climatic conditions of the study area, the subalpine belt ranges from 1800 / 1900 to 2400 / 2500 m a.s.l., (see Fig. 1) followed by the alpine belt from 2400 / 2500 to 2960 / 3000 m a.s.l., the subnival belt from 2900 / 3000 to 3600 / 3750 m a.s.l., and the nival belt above 3700 m a.s.l. (Nakhutsrishvili 2012).
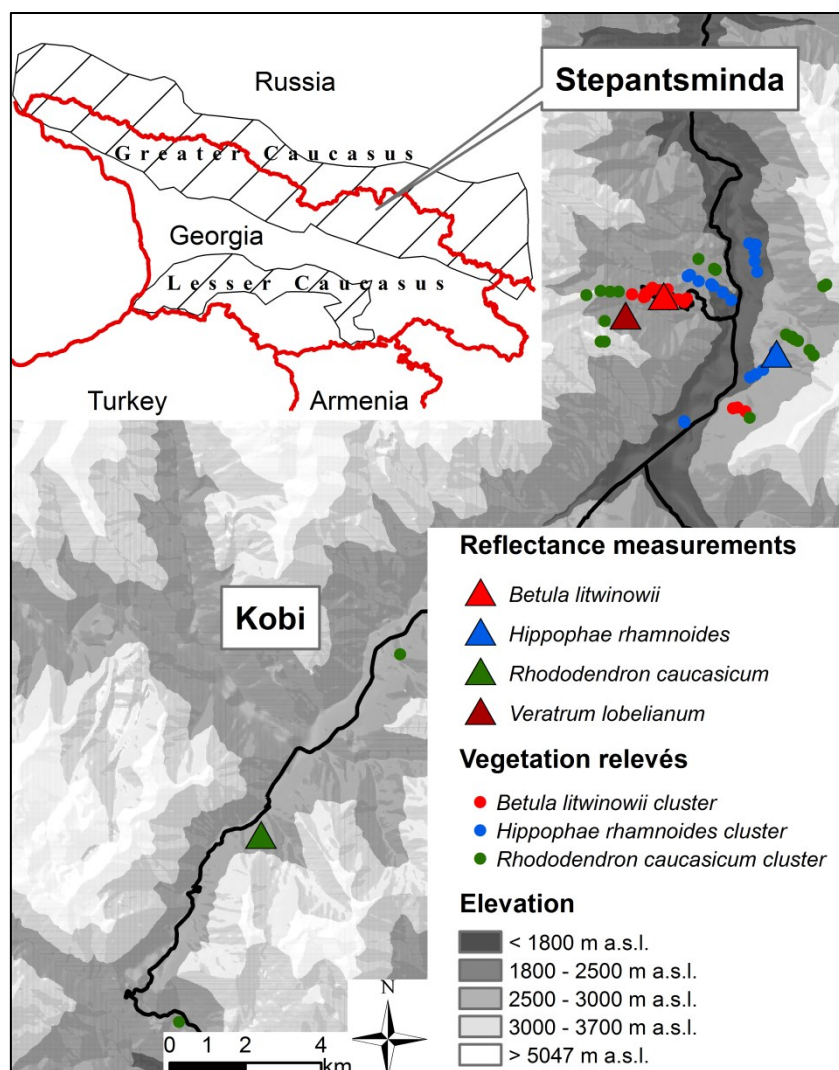
Fig. 1: Map of the study area with the altitudinal boundaries according to Nakhutsrishvili 2012 and the research sites, based on the positions of the reflectance measurements and the vegetation relevés.

The flora of the study area is known for its high percentage of endemic species. Altogether 1100 vascular plants have been recorded, 26% of which are endemic (Nakhutsrishvili 1999, Gagnidze 2005). The subalpine to alpine belt of the study area is dominated by open grasslands, which have been extensively researched for decades (Nakhutsrishvili 1976, 1990, 1999, Pyšek and Šrutek 1989, Nakhutsrishvili & Gagnidze 1999, Kikvidze et al. 2005, Lichtenegger et al. 2006, Tephnadze et al. 2014). In the valley bottom herb-rich hay meadows with *Hordeum violaceum* are typical. On the mid slopes, stony, and species poor pastures with characteristic species such as *Bromopsis variegata* and *Astragalus captiosus* occur. In the upper subalpine to alpine belt, grasslands dominated by *Festuca varia* occur on northerly exposed slopes and rock and scree vegetation on southerly exposed steep slopes.

4.2.2 Data acquisition and research design

The existing vegetation data were taken from the Caucasus Vegetation Database, registered as AS-GE-001 under the Global Index of Vegetation-Plot Databases (Dengler et al. 2011, http://www.givd.info). From this database a total of 52 vegetation relevés, which included the target species *B. litwinowii* (occurrences 34), *H. rhamnoides* (occurrences 20), *R. caucasicum* (occurrences 8) and *V. lobelianum* (occurrences 15), were selected (see Fig. 2).
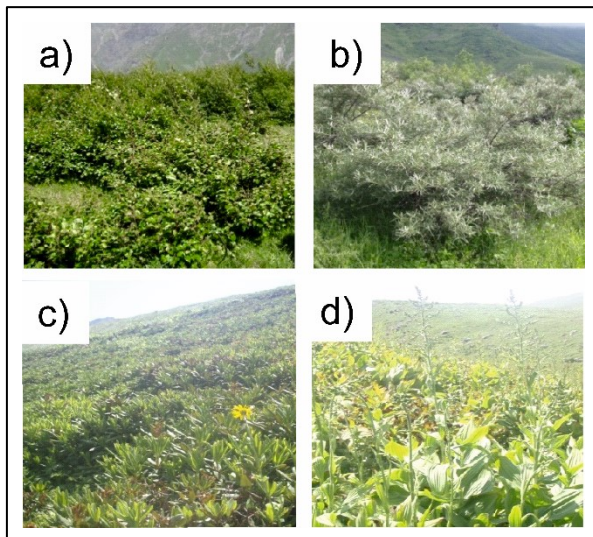
Fig. 2: Photographs of the four target species (a) *Betula litwinowii*, (b) *Hippophae rhamnoides*, (c) *Rhododendron caucasicum*, (d) *Veratrum lobelianum* in summer 2011.

All relevés were recorded in the years 2009, 2010, and 2011 by Erich Hübl, Annette Otte, Georg Nakhutsrishvili, and Nato Tephnadze, using the Braun-Blanquet Scale (Braun-Blanquet 1964). The different relevés had plot sizes of 25 m², 50 m², and 100 m².

The geographic coordinates of the vegetation relevés were used to extract the reflectance signatures of the corresponding pixels from two multispectral RapidEye images taken on June 27th, 2011 and September 8th, 2011. These images were delivered with orthorectification and radiometric correction (product level 3A). The size of a pixel after resampling was 5 m x 5 m on the ground. The RapidEye sensor, a multispectral pushbroom imager, provides spectral information in the blue, green, red, red edge, and NIR spectral region in five broad bands. The red edge band particularly provides valuable information on the status of vegetation (Weichelt et al. 2011). The pixel values were converted into at-sensor-reflectance and a cosine topographical correction was used to mitigate illumination differences due to the steep terrain (Teillet et al. 1982).

Hyperspectral field spectrometric measurements were conducted at research sites located between 1600 m and 2600 m a.s.l., from mid-June to mid-July 2011, using an ASD Hand Held 2 Field Spec ® portable spectrometer (325 - 1075 nm, ASD Inc. Boulder, CO). Canopy reflectance was measured relative to a white reference panel (Spectralon). To account for atmospheric and

illumination changes, a white reference was taken at every plot and at least every five minutes. Internal averaging of the spectrometer was set to 100 measurements for reflectance, dark current and white reference. The spectrometer was positioned in nadir view 110 cm above the target species aiming to get pure spectra of the target species.

Altogether, 48 reflectance samples were taken. For each target species 12 plots of approximately 1 m² were measured with five regularly placed repetitions. The total number of spectra, hence, amounted to 240, including five repetitions per plot with 12 plots per species and the four target species *B. litwinowii*, *H. rhamnoides*, *R. caucasicum*, and *V. lobelianum* (see Fig. 2.). The sites of the hyperspectral reflectance measurements were mostly in proximity to the vegetation relevés, but were not identical. The vegetation relevés were selected as a proxy of the vegetation types and species occurrences on a larger scale.

4.2.3 Statistical analyses

The statistical analyses consisted of two parts. First, with the analysis of the vegetation data we aimed to describe the floristic composition of the tested shrub types, in order to assess their floristic homogeneity by using ordination and ISA, as a detailed description of the ground truth. Second, we aimed to test the spectral separability of the shrub species based on reflectance signatures of different sensors derived from field spectrometric data as well as from real Rapid Eye imagery by using the Jeffries-Matusita distance (JMD) and significance testing (see Fig. 3). All statistical analysis were performed in the R statistical environment using the packages vegan version 2.2-1 for ordination and clustering techniques, labdsv version 1.6-1 for Indicator Species Analysis (ISA), as well as the package stats 2.15.3 for the multivariate analysis. As a first step, we transformed the original cover values of the Braun-Blanquet scale into ordinal values ranging from 1-7 (Braun-Blanquet 1964, van der Maarel 1979).
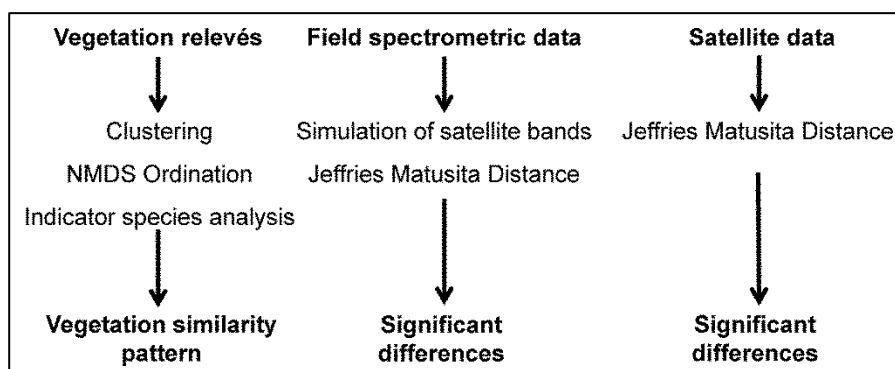
Fig. 3: Flowchart of the statistical analysis.

This plot based vegetation data was then used to calculate a Bray - Curtis distance matrix (Bray & Curtis 1957) using the vegan package. Subsequently, this distance matrix was subjected to Ward

Clustering in order to recover the shrub species (Ward 1963). The clusters were further used in an ISA (Dufrene & Legendre 1997) as vegetation types, in order to characterize the vegetation patterns. For the ordination Non-Metric Multidimensional Scaling (NMDS, Kruskal 1964) was chosen, since it is a distance based technique, which is known to be able to cope with the ordinal scaled vegetation data (Oksanen 2015).

To test the applicability of different sensors for the separation of the shrub species we derived simulated spectral bands of the sensors IKONOS, Quickbird 2, RapidEye and WorldView-2 from the unfiltered field spectrometric reflectance measurements (see Tab. 1). These multispectral sensors were chosen because they offer a high spatial resolution and cover the visible and NIR region of the light spectrum. In order to calculate the corresponding spectral signal we used the function simulatoR (Feilhauer et al. 2013) and the spectral response curves of the respective sensors. The simulated signals were log transformed in order to achieve a normal distribution of the reflectance values. To assess the separability of the target species we derived the JMD (Davis et al. 1978) with the package fpc version 2.1-9 (Hennig 2014), first calculating the Bhattaryachrya distance (BD, equation (1)) with i and j as the two normal distributions, m_i and $m_{j,}$ as the average reflectance values and the covariance matrixes $\sum_i , \sum_j$. The BD was the converted to the JMD using the equation (2):

$$BD = \frac{1}{8} * \left(m_i * m_j\right)^t \left\{\frac{\Sigma_i + \Sigma_j}{2}\right\}^{-1} * \left(m_i * m_j\right) + \frac{1}{2}\ln\left\{\frac{|\Sigma_i + \Sigma_j|}{|\Sigma_i|^{\frac{1}{2}}|\Sigma_j|^{\frac{1}{2}}}\right\} \tag{1}$$

$$JMD = 2 * (1 - e^{-BD}) \tag{2}$$

The JMD is scaled from $0 - 2$, with 2 representing perfectly separable classes (Richards 1993). Significance between the target species within the bands was tested with a Kruskall-Wallis ANOVA and post hoc pairwise testing for homogeneous groups using Bonferroni corrected pairwise Wilcox Rank test comparisons at p = 0.001.

From the corrected RapidEye images we extracted the reflectance values at the position of the vegetation relevés. The JMD was calculated and the test for significance described above was applied. The analysis was performed for both acquisition dates in June and September.

Tab. 1: Specifications of the four tested satellites with ground sampling distance (GSD), band names, band width and quotation.

| Satellite	GSD at nadir	Band names	Band width	Quotation
IKONOS	3.28 m	blue	445 - 516 nm	(Dial et al. 2003)
		green	506 - 595 nm	
		red	632 - 698 nm	
		NIR	757 - 853 nm	
Quickbird 2	2.8 m	blue	450 - 520 nm	https://www.digitalglobe.com/sites/default/files/QuickBird-DS-QB-Prod.pdf
		green	520 - 600 nm	
		red	630 - 690 nm	
		NIR	760 - 900 nm	
RapidEye	6.5 m	blue	440 - 510 nm	(Weichelt et al. 2011)
		green	520 - 590 nm	
		red	630 - 685 nm	
		red edge	690 - 730 nm	
		NIR	760 - 850 nm	
WorldView-2	1.85 m	coastal	400 - 450 nm	https://www.digitalglobe.com/sites/default/files/DG_WorldView2_DS_PROD.pdf
		blue	450 - 510 nm	
		green	510 - 580 nm	
		yellow	585 - 625 nm	
		red	630 -690 nm	
		red edge	705 - 745 nm	
		NIR I	770 - 895 nm	
		NIR II	860 - 1040 nm	

4.3. Results

4.3.1 Vegetation data

In this study, we analyzed 52 vegetation relevés of the Caucasus Vegetation database, including a total of 136 species with more than three occurrences. The Ward clustering revealed three different clusters of vegetation named after their most abundant species as *Betula* cluster (n = 22), *Hippophae* cluster (n = 20), and *Rhododendron* (n = 10) cluster. Vegetation relevés with *V. lobelianum* formed a cluster together with the *B. litwinowii* relevés, because they shared many species. The analysis of the similarity pattern by NMDS ordination (Fig. 4) showed that the first NMDS axis separated the *Hippophae* cluster (with NMDS axis scores from -2 to -0.5) from the *Betula* and *Rhododendron* clusters (NMDS axis scores ranging from -0.5 to 1.5). Along the second NMDS -axis, a differentiation between the *Betula* cluster (second NMDS axis scores ranging from -1.5 to -0.5), and *Rhododendron* cluster (second NMDS axis scores ranging from -0.5 to 1) was determined. Interpreting compositional similarity in combination with the abundance of the target species (*B. litwinowii*, *H. rhamnoides*, *R. caucasicum,* and *V. lobelianum*) revealed that the vegetation clusters were not discrete. Figure 4 shows the abundance of the target species in the clusters. Most surprisingly, the highest

abundance of *B. litwinowii* was found in the *Betula* cluster (red). *B. litwinowii* also appeared in the *Rhododendron* and *Hippophae* clusters at lower abundances. In contrast, *H. rhamnoides* was only present in its own cluster at high abundance. *R. caucasicum* and *V. lobelianum* also typically grow in the understory of *B. litwinowii* forest, which was the reason for their presence in the *Betula* cluster.

The results of the ISA revealed a more differentiated pattern. Altogether 29 species were identified as significant indicator species (Tab. 2). The *Betula* cluster contained eight indicator species. Some of the indicator species such as *Rubus saxatilis*, *Sorbus aucuparia,* and *Polygonatum verticilliatum* or tall herb communities (*V. lobelianum*) indicated a late succession stage and can be linked to forest. The eleven indicator species of the *Hippophae* cluster are associated with ruderal habitats of debris and scree (*Cerastium arvense*, *Phleum phleoides*, *Galium spurium*) and base-rich, xeric grasslands (*Galium verum*, *Trisetum flavescens*, *Trifolium campestre*). The eleven indicator species, of the *Rhododendron* cluster were mostly dwarf shrubs (e.g., *Vaccinium vitis- idaea*, *Daphne glomerata*, *Empetrum caucasicum*) and are adapted to the harsh conditions of the upper belt of the tree line ecotone.
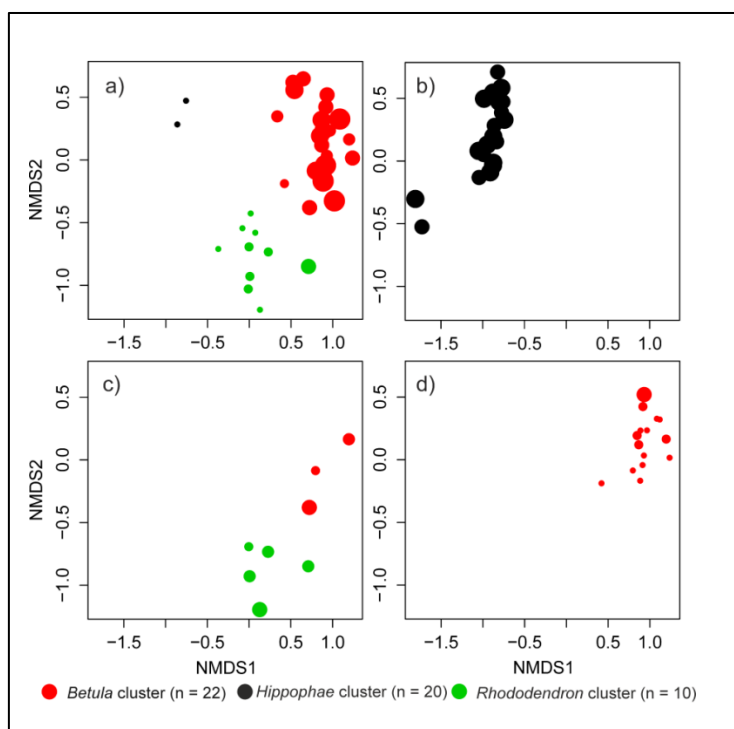
Fig. 4: NMDS Ordination of 52 vegetation releves with a stress level of 0.12 and a non-metric fit of R^2 = 0.98. A priori derived clusters: red = *Betula* cluster (n = 22), black = *Hippophae* cluster (n = 20), green = *Rhododendron* cluster (n = 10). Point size was fitted to the cover abundance of (a) *Betula litwinowii*, (b) *Hippophae rhamnoides*, (c) *Rhododendron caucasicum*, (d) *Veratrum lobelianum*.

Tab. 2: Indicator species analysis with relative abundance values, a species was considered an indicator species if the indicator value was ≥ 0.40 and p ≤ 0.001.

Species name	Indicator value	Relative Abundance			p value
		B	H	R	
Betula cluster (B)					
Rubus saxatilis	0.85	0.94	0.00	0.06	0.0001
Sorbus aucuparia	0.77	1.00	0.00	0.00	0.0001
Veratrum lobelianum	0.68	1.00	0.00	0.00	0.0001
Betula litwinowii	0.65	0.65	0.02	0.33	0.0001
Alchemilla laeta	0.55	1.00	0.00	0.00	0.0001
Polygonatum verticilliatum	0.64	1.00	0.00	0.00	0.0002
Calamagrostis arundinacea	0.51	0.81	0.00	0.19	0.0005
Hippophae cluster (H)					
Hippophae rhamnoides	1.00	0.00	1.00	0.00	0.0001
Poa pratensis	0.69	0.08	0.92	0.00	0.0001
Galium album	0.55	0.00	1.00	0.00	0.0001
Cerastium arvense	0.58	0.08	0.83	0.09	0.0002
Galium verum	0.55	0.00	1.00	0.00	0.0002
Phleum phleoides	0.50	0.00	1.00	0.00	0.0002
Achillea millefolium	0.55	0.00	1.00	0.00	0.0003
Galium spurium	0.50	0.00	1.00	0.00	0.0003
Trisetum flavescens	0.50	0.00	0.90	0.10	0.0006
Pastinaca armena	0.48	0.12	0.88	0.00	0.0009
Trifolium campestre	0.40	0.00	1.00	0.00	0.0010
Rhododendron cluster (R)					
Vaccinium vitis-idaea	0.84	0.00	0.07	0.93	0.0001
Daphne glomerata	0.75	0.00	0.16	0.84	0.0001
Trifolium canescens	0.70	0.00	0.00	1.00	0.0001
Anthoxanthum alpinum	0.63	0.00	0.09	0.91	0.0001
Helictotrichon adzharicum	0.60	0.00	0.00	1.00	0.0001
Polygonum viviparum	0.60	0.00	0.00	1.00	0.0001
Empetrum caucasicum	0.50	0.00	0.00	1.00	0.0001
Scabiosa caucasica	0.46	0.00	0.07	0.93	0.0002
Carex tristis	0.50	0.00	0.00	1.00	0.0003
Carex caucasica	0.40	0.00	0.00	1.00	0.0010
Gentiana pyrenaica	0.40	0.00	0.00	1.00	0.0010
Rhododendron caucasicum	**0.39**	**0**	**0.21**	**0.79**	**0.0026**

Even though the indicator species analysis focused on finding typical species for each cluster, there are many shared species amongst the vegetation clusters due to their spatial proximity.

4.3.2 Spectral separability

The JMDs calculated for simulated satellite bands (IKONOS, Quickbird 2, RapidEye, WorldView-2) showed a good to moderate spectral separability with distances varying from 1.58 to 2 between the different species. The shortest distances (1.58, 1.59) were observed for the satellites IKONOS and Quickbird 2, which only comprise four spectral bands. The red edge band of the RapidEye sensor and the NIR II of WorldView-2 add additional information, increasing the overall separability between the classes. This is especially the case for the separation between *R. caucasicum* and *V. lobelianum,* which increased with the increasing number of bands. Besides these findings, the distances between *B. litwinowii* and *R. caucasicum* as well as between *B. litwinowii* and *V. lobelianum* generally featured a similar spectral signal across all tested satellites, indicating difficulties in spectrally separating these species.
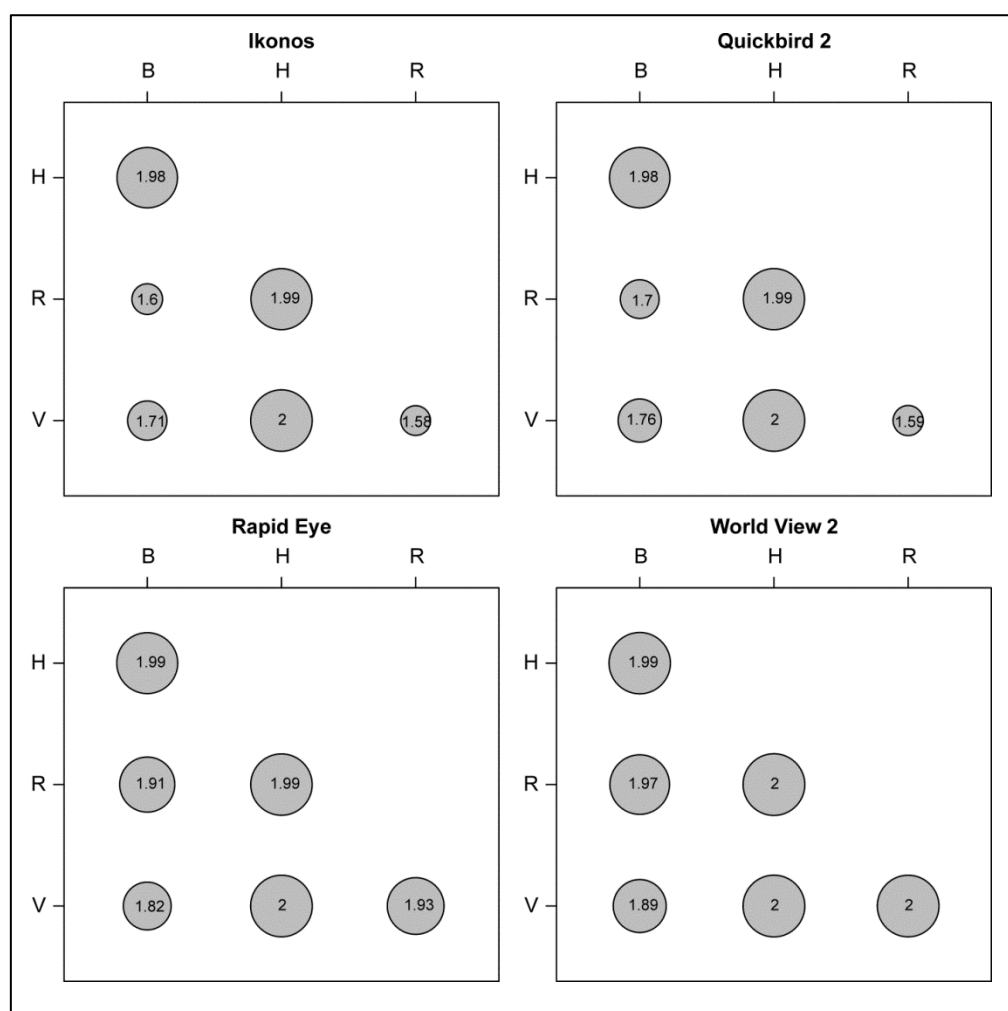

Fig. 5: Jeffries Matusita distances for simulated multispectral bands. JMD = 2 indicates perfect separability. B = *Betula litwinowii*,H= *Hippophae rhamnoides*,R= *Rhododendron caucasicum*, V= *Veratrum lobelianum*.

The simulated reflectance in Fig. 5 shows that significant differences between the species occur in all bands and in all tested satellites.

The significance pattern was very similar across the tested sensors. *B. litwinowii* and *H. rhamnoides,* which exhibited a good separability in Fig. 5 also exhibited significant differences in the blue and green bands (Fig. 6). *B. litwinowii* and *R. caucasicum*, as well as *B. litwinowii* and *V. lobelianum*, featured a moderate separability, exhibiting significant differences especially in the red to NIR region.
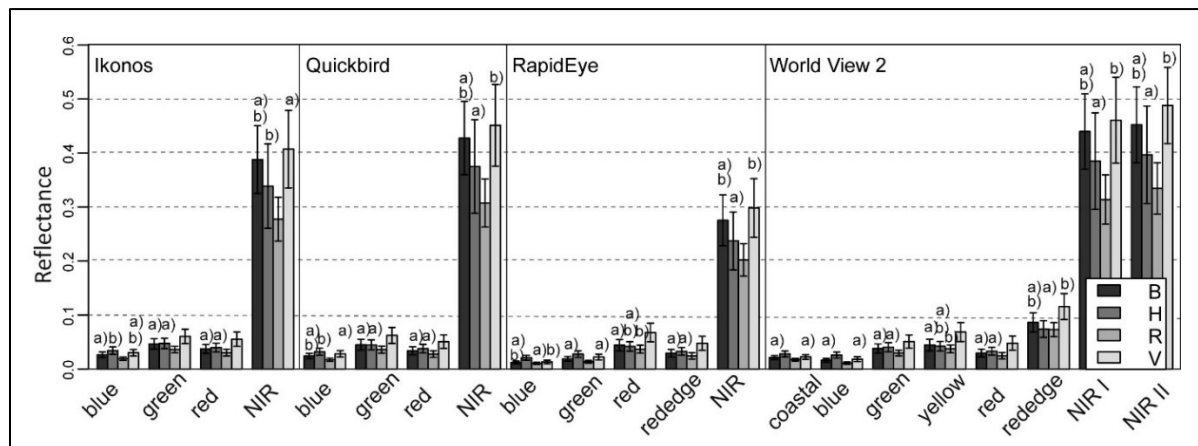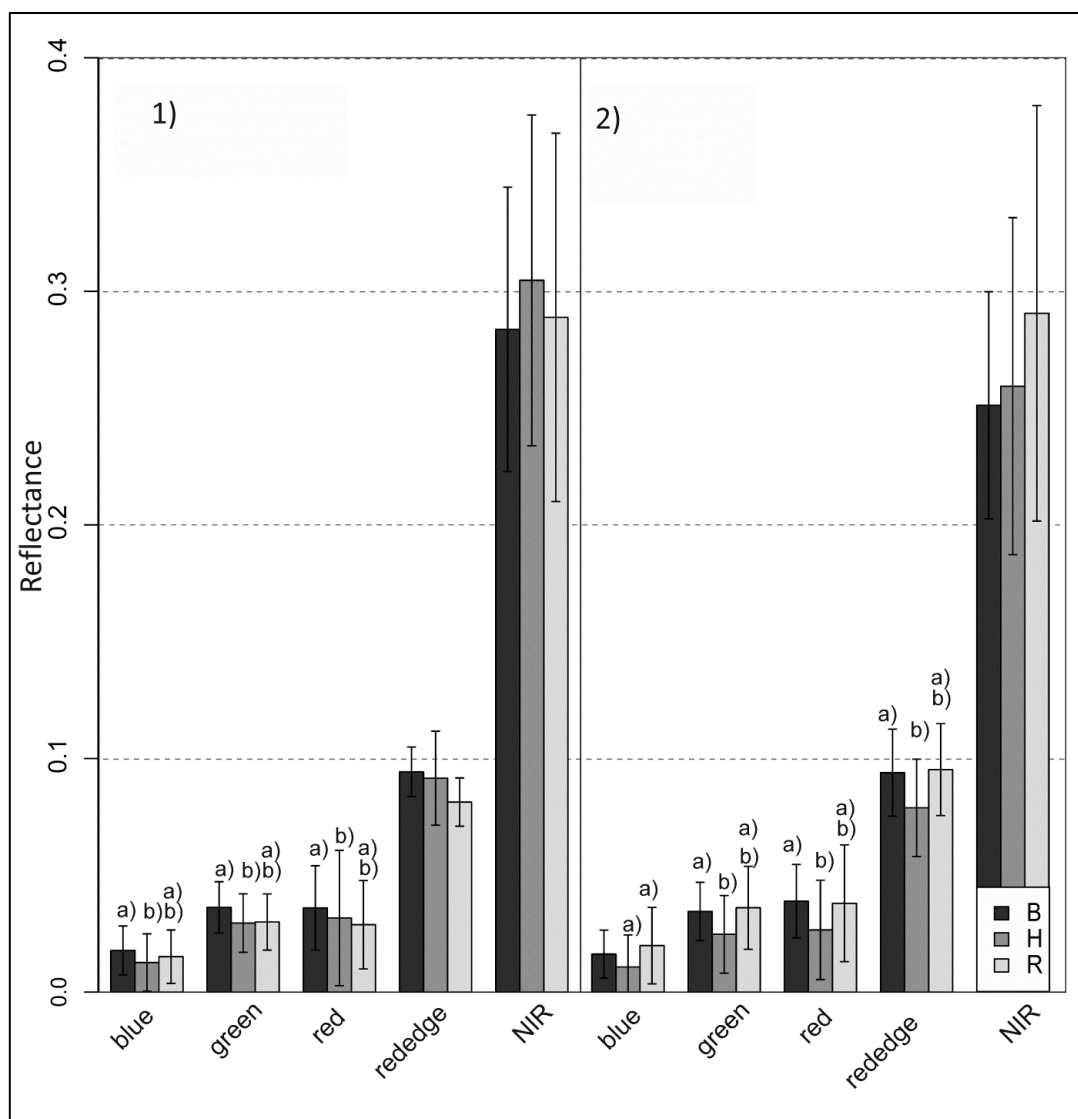

Fig. 6: Simulated reflectance of the satellites IKONOS. Quickbird 2, RapidEye and WorldView-2 subjected to Kruskall–Wallis ANOVA and post hoc significance testing for homogeneous groups using Bonferroni corrected pairwise Wilcox Rank Sum tests. P = 0.001. Homogeneous groups per band are indicated by letters (a) and (b).

The JMDs for the vegetation clusters indicated a moderate separability of the classes with JMD ranging between 1.24 - 1.55 in June (see Fig. 7). The image taken in September produced an improved overall separability of JMD 1.56 - 1.9. The largest spectral differences were observed between the *Betula* and *Hippophae* clusters, and the least pronounced ones between the *Betula* and *Rhododendron* clusters.
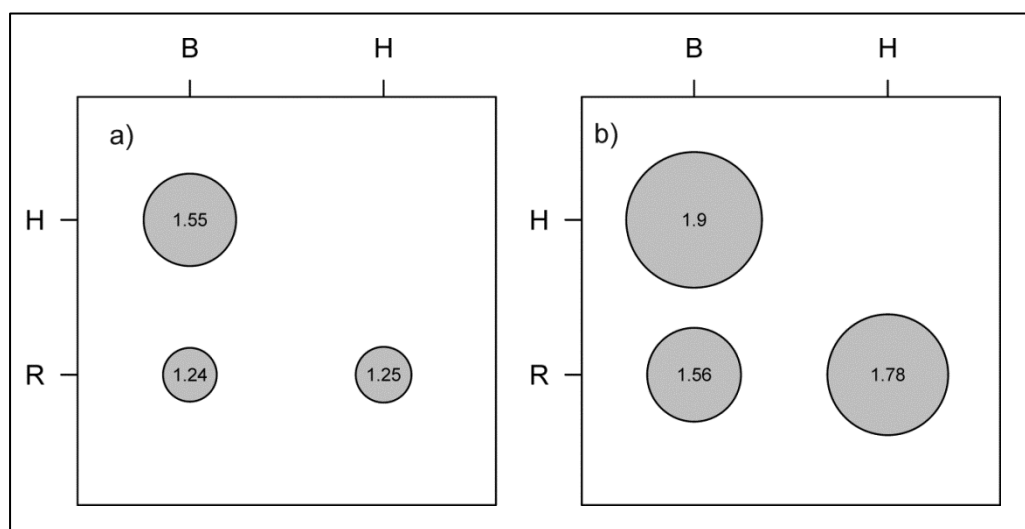
Fig. 7: Jeffries Matusita distances for the vegetation clusters derived in the vegetation analysis, dominated by *Betula, Rhododendron, Hippophae* in (a) June and (b) September for original Rapid Eye satellite imagery.

Fig. 8: Reflectance from the RapidEye satellite for the vegetation clusters derived in the vegetation analysis, dominated by *Betula*, *Rhododendron*, *Hippophae* in (1) June and (2) September, subjected to Kruskall–Wallis ANOVA and post hoc significance testing for homogeneous groups using Bonferroni corrected pairwise Wilcox Rank Sum tests. P = 0.001. Homogeneous groups per band are indicated by letters (a) and (b).

The reflectance pattern for the vegetation clusters showed no significant differences in the red edge band and the NIR band of the June image. Furthermore, no significant differences were found in the NIR band of the September image. The *Betula* cluster differed significantly from the *Hippophae* cluster in the blue, green and red bands of the June image, as well as in the blue, green, red and red edge bands of the September image, resulting in the strongest JMD (see Fig. 8). The *Betula* and *Rhododendron* clusters, however, formed homogeneous groups except in the blue band of the September image, resulting in a weak separability.

4.4 Discussion

4.4.1 Implications and limitations of evaluating spectral separability

The aim of our study was to test the spectral separability of four encroaching shrub species, each with a unique growth form in the high mountain environment of the Greater Caucasus. A species based spatial analysis of shrub encroachment is applicable for monitoring and evaluating the ecosystem functions of arctic and alpine treelines as well as for landuse planning purposes. Even though our tested species are not the same as in the arctic treeline, our results highlight the importance of the plant species growth form for spectral separability. In this study, simulated bands resulted in a much better separability than the original RapidEye image data. This can partly be explained by various disturbances, such as atmospheric influences and the illumination geometry, which affect the original RapidEye images (Nilson & Peterson 1994, Pottier et al. 2014). Despite the applied cosine topographical correction, the reflectance pattern might still be influenced by those factors. Furthermore, with increasing pixel size the species number included in the pixel increases, leading to mixed pixels. The floristic homogeneity of the encroaching species' stands should be considered a crucial factor. This is even more important when the spatial resolution of the image increases.

Our methods (JMD and significance testing) were already successfully applied for assessing spectral separability (Feilhauer et al. 2013, Manevski et al. 2012). We thus assumed the applicability of these statistical analyses for our approach.

However, in comparison to the original spectral bands, the simulated bands differ in spatial resolution, sensor geometry, as well as signal to noise ratio (Feilhauer et al. 2013). The signal of simulated bands correspond directly to the target of the hyperspectral reflectance measurements and is thus more suitable for comparison than real data sets that often feature uncertainties due to positioning errors and are seldom available for the same acquisition date. Simulation of the sensor reflectance from hyperspectral field spectrometric data does, however, not include the varying pixel sizes. For the simulation of sensors bands, we thus specifically chose space borne sensors with a high spatial resolution and the pixel size varying between 1.8 m – 6.5 m.

The simulated band data were in our case only used to assess which sensor enables the highest spectral separability between the tested species. Earlier studies used band simulations of different sensors and found that the bandwidths as well as the spectral response functions have a significant influence on the spectral separability of tested species (Teillet et al. 1997, Herold et al. 2003, Steven et al 2003). Moreover, prior studies found that the simulated band data were comparable with the actual signal measured by Landsat ETM.

4.4.2 Spectral separability of the target species

The NMDS and ISA revealed that the target species, besides their dominant forms, very often occurred with lower coverage in the other vegetation types. Consequently, our vegetation data exhibited a high co-occurrence of the target species. *B. litwinowii* in particular invaded sites in which *R. caucasicum* and *H. rhamnoides* formed dominant stands. These results are consistent with other studies conducted in the Kazbegi region that found *R. caucasicum* to facilitate the growth of *B. litwinowii* seedlings by enhancing the microclimate and nutrient availability of the habitat (Akhalkatsi et al. 2006). A similar process can be assumed for the *H. rhamnoides* stands. *H. rhamnoides* benefits from a symbiotic relationship with nitrogen fixing Actinomyceta (Bolibok et al. 2009). In the vegetation relevés *V. lobelianum* always occurred in the presence of *B. litwinowii* (see Fig. 4). This can be explained by the fact that the data were selected from a database that did not include vegetation relevés from pastures with dominant *V. lobelianum* stands. However, some studies report that *B. litwinowii* and tall herb communities with *V. lobelianum* grow in close proximity (Walter 1974, Nakhutsrishvili et al. 2006, Togonidze & Akhalkatsi 2015). The separability of the reflectance signal extracted from the vegetation relevés was, thus, considerably lower than the separability achieved with the simulated data. Moreover, the simulated bands detected significant differences in the NIR, whereas no significant differences were found in the data derived from the real Rapid Eye imagery. This can be explained by the fact that the spatial resolution of 5 m was rather coarse. As a result, the *R. caucasicum* cluster included a high coverage of *B. litwinowii*, as can be seen in Fig. 4. This influence leads to a less pronounced reflectance pattern. Thus, our results indicate a good overall separability only for floristically homogeneous stands, depending on the sensor chosen, as well as the date of image data acquisition.

The best spectral separability was achieved with RapidEye and WorldView-2 data. Both sensors offer more than four bands and include the red edge. Generally, adding more bands, i.e. information, to the distance metric increases the distance. The importance of the red edge and its sensitivity towards plant specific biophysical properties was assessed in many studies (e.g. Curran 1983, Filella & Penuelas 1994, Weichelt et al. 2011). It can thus be concluded that the increase of the JMD with the extra red edge band is mainly related to the biophysical properties such as chlorophyll content and leaf inclination of the shrubs, especially when, *R. caucasicum* (evergreen shrub) and *V. lobelianum* (tall herb) are compared.

When comparing the two image acquisition dates, a better separability was achieved with the September image. The red edge band is sensitive to plant senescence, marked by the decrease of chlorophyll concentration, and coupled with an increasing amount of cellulose (Curran 1983, Filella & Penuelas 1994). This characteristic influence of phenology may explain the relevance of

the red edge for the differentiation of the tall herb *V. lobelianum* from the *H. rhamnoides* shrubs. Many individuals of *V. lobelianum* already showed brown foliage as a result of senescence and damage due to the incoming irradiation in the ultra violet range. However, *V. lobelianum* and *B. litwinowii,* as well as *V. lobelianum* and *R. caucasicum*, exhibited an overall moderate separability. This indicates that the reflectance signals of tall herbs and shrubs can easily be confused due to their similar growth forms. Further research and analyses of other tall herbs will be needed to tackle this issue.

4.5. Conclusions

Shrub encroachment plays a key role in many alpine and arctic environments. To assess the influence of encroachment on the ecosystem, spatial information about the encroaching species may be beneficial. The different growth forms of the encroaching shrub communities in the Greater Caucasus provided an excellent opportunity to investigate spectral distinctness. Accordingly, the targeted shrub species exhibited a good overall spectral separability.

Our results indicate that multispectral remote sensing, with high spatial resolution sensors, is capable of providing the necessary information to differentiate, classify and in return monitor the encroachment in alpine environments.

The encroachment patterns of the target species, however, exhibited a high co-occurrence, which is also expected to occur in other arctic and alpine environments. This results in a moderate separability on vegetation type level considering actual RapidEye imagery and highlights the importance of considering the small scale heterogeneity of the vegetation types.

References

Akhalkatsi, M., Abdaladze, O., Nakhutsrishvili, G. & Smith, W. K . 2006. Facilitation of seedling microsites by Rhododendron caucasicum extends the Betula litwinowii Alpine treeline, Caucasus Mountains, Republic of Georgia. *Arctic Antarctic and Alpine Research* 38: 481–488.

Bolibok, L., Kowalczyk, M. & Drozdowski, S. 2009. Assessment of vegetative and generative expansion of sea buckthorn (*Hippophae rhamnoides* L.) on outer dumping ground of Belchatow lignite mine in terms of its application in directed succession reclamation process. *Sylwan* 153: 203–216.

Braun-Blanquet, J. 1964. Pflanzensoziologie: Grundzüge der Vegetationskunde. Springer-Verlag, Vienna, AT.

Bray, J. R. & Curtis, J. T. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* 27: 325-349.

Camarero, J. J. & Gutiérrez, E. 2004. Pace and Pattern of Recent Treeline Dynamics: Response of Ecotones to Climatic Variability in the Spanish Pyrenees. *Climatic Change* 63: 181–200.

Curran, P. J. 1983. Multispectral Remote-Sensing for the estimation of Green Leaf-Area Index. *Philosophical Transactions of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences* 309: 257–270.

Davis, S. M., Landgrebe, D. A., Phillips, T. L., Swain, P. H., Hoffer, R. M., Lindenlaub, J. C. & Silva L. F. 1978. *Remote sensing: The quantitative approach*, p. 405. Mc Graw-Hill International Book Co., NY, US.

DeMarco, J., Mack, M. C. & Bret-Harte, M. S. 2011. The Effects of Snow, Soil Microenvironment, and Soil Organic Matter Quality on N Availability in Three Alaskan Arctic Plant Communities. *Ecosystems* 14: 804–817.

Dengler, J., Jansen, F., Glöckler, F., Peet, R. K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., Mucina, L., Rodwell, J.S., Schaminée, J. H. J., & Spencer, N. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22: 582–597.

Dial, G., Bowen, H., Gerlach, F., Grodecki, J. & Oleszczuk R. 2003. IKONOS satellite, imagery, and products. *Remote Sensing of Environment* 88: 23–36.

Dufrene, M. & Legendre P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Feilhauer, H., Thonfeld, F., Faude, U., He, K. S., Rocchini, D. & Schmidtlein, S. 2013. Assessing floristic composition with multispectral sensors—A comparison based on monotemporal

and multiseasonal field spectra. *International Journal of Applied Earth Observation and Geoinformation* 21: 218–229.

Filella, I. & Penuelas, J., 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass and hydric status. *International Journal of Remote Sensing* 15: 1459–1470.

Gagnidze, R. 2005. Vascular Plants of Georgia – A Nomenclatural Checklist. 248 pp. Georgian Academy of Sciences, N. Ketskhoveli, Institute of Botany, I. Javakhishvili Tbilisi State University, Department of Botany, Tbilisi.

Gigauri, K., Akhalkatsi, M., Nakhutsrishvili, G. & Abdaladze, O. 2013. Monitoring of vascular plant diversity in a changing climate in the alpine zone of the Central Greater Caucasus. *Turkish Journal of Botany* 37: 1104–1114.

Gould, W.A., Edlund, S., Zoltai, S., Raynolds, M., Walker, D. A., & Maier, H. 2002. Canadian Arctic vegetation mapping. *International Journal of Remote Sensing* 23 (21): 4597-4609.

Herold, M., Roberts, D. A., Gardner, M. E., Dennison, P. E., 2004. Spectrometry for urban area remote sensing-Development and analysis of a spectral library from 350 to 2400 nm. *Remote Sensing of Environment* 91: 304-319.

Holtmeier, F.-K. & Broll, G. 2007. Treeline advance–driving processes and adverse factors. *Landscape Online* 1: 1–33.

Jia, G. J., Epstein, H. E., & Walker, D. A. 2003. Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters* 30 (20).

Keggenhoff, I., Elizbarashvili, M., Amiri-Farahani, A. &, King L. 2014. Trends in daily temperature and precipitation extremes over Georgia, 1971–2010. *Weather and Climate Extremes* 4: 75–85.

Ketskhoveli, N., Kharadze, A. L., Ivanishvili, M. A., & Gagnidze, R. I. 1975. Botanical description of the Georgian military road (Tbillisi-Kazbegi-Ordjonikidze). 95 p. *XII. International Botanical Congress*.

Kikvidze, Z., Khetsuriani, L. & Kikodze, D. 2005. Small-scale guild proportions and niche complementarity in a Caucasian subalpine hay meadow. *Journal of Vegetation Science* 16: 565–570.

Knapp, A. K., Briggs, J. M., Collins, S. L, Archer, S. R., Bret-Harte, M. S., Ewers, B. E., Peters, D. P., Young, D. R., Shaver, G. R., Pendall, E. & Cleary, M. B. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14: 615–623.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445–459.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29 (1): 1-27.

Lichtenegger, E., Bedoschwili, D., Hübl, E. & Scharf, E. 2006. Höhenstufengliederung der Grünlandvegetation im Zentralkaukasus. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* 143: 43–81.

Manevski, K., Manakos, I., Petropoulos, G. P. & Kalaitzidis, C. 2012. Spectral discrimination of Mediterranean Maquis and Phrygana vegetation: Results from a case study in Greece. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 5: 604–616.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M, Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C. B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H. E. & Hik, D. S. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6: pp. 15.

Nakhutsrishvili, G. 1999. The vegetation of Georgia (Caucasus). *Braun-Blanquetia* 15: 5–74.

Nakhutsrishvili, G. 2012. The Vegetation of Georgia (South Caucasus). pp. 235 Springer-Verlag, Vienna, AT.

Nakhutsrishvili, G., Abdaladze, O. & Akhalkatsi, M. 2006. Biotope types of the treeline of the Central Greater Caucasus. In: Gafta, D. & Akeroyd, J. (eds.) *Nature conservation: Concepts and practice*, pp. 211-225. Springer – Verlag, Vienna, AT.

Nakhutsrishvili, G. & Gagnidze, R. 1999. Die subnivale und nivale Hochgebirgsvegetation des Kaukasus. *Phytocoenosis - Supplementum Cartographiae Geobotanicae* 11:173–183.

Nakhutsrishvili, G. 1976. Ecological Investigations at Kazbeg High Mountain Station. *Soviet Journal of Ecology* 7: 256–260.

Nakhutsrishvili, G. 1990. Ecological analysis of the effect of human activity on high-mountain meadows of the Caucasus. *Soviet Journal of Ecology* 21: 103–106.

Nilson, T. & Peterson, U. 1994. Age dependence of forest reflectance: Analysis of main driving factors. *Remote Sensing of Environment* 48: 319–331.

Oksanen J. 2011. Multivariate Analysis of Ecological Communities in R: vegan tutorial.

Pottier, J., Malenovský, Z., Psomas, A., Homolová, L., Schaepman, M. E., Choler, P., Thuiller, W., Guisan, A. & Zimmermann, N. E. 2014. Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy. Biology Letters 10 (7).

Pyšek, P. & Šrutek, M. 1989. Numerical Phytosociology of the subalpine belt of the Kazbegi region, Caucasus, USSR. *Vegetatio* 81: 199–208.

Richards, J.A. 1993. *Remote sensing digital image analysis: an introduction*. Springer-Verlag, Vienna, AT.

Steven, M. D., Malthus, T. J., Baret, F., Xu, H., Chopping, M. J., 2003. Intercalibration of vegetation indices from different sensor systems. *Remote Sensing of Environment* 88: 412-422.

Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin, F. S., Racine, C. H. 2001. Snow–Shrub Interactions in Arctic Tundra: A Hypothesis with Climatic Implications. *Journal of Climate* 14: 336–344.

Tape, K., Sturm, M. & Racine, C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12: 686–702.

Tappeiner, U. & Cernusca, A. 1989. Canopy structure and light climate of different alpine plant communities: Analysis by means of a model. *Theoretical and Applied Climatology* 40: 81–92.

Teillet, P. M., Guindon, B. & Goodenough, D. G. 1982. On the Slope-Aspect Correction of Multispectral Scanner Data. *Canadian Journal of Remote Sensing* 8: 84–106.

Teillet, P. M., Staenz, K., William, D. J., 1997. Effects of spectral, spatial, and radiometric characteristics on remote sensing vegetation indices of forested regions. *Remote Sensing of Environment* 61: 139-149.

Tephnadze, N., Abdaladze, O., Nakhutsrishvili, G., Simmering, D., Waldhardt, R. & Otte A. 2014. The impacts of management and site conditions on the phytodiversity of the upper montane and subalpine belts in the Central Greater Caucasus. *Phytocoenologia* 44: 255–291.

Togonidze, N. & Akhalkatsi, M. 2015. Variability of plant species diversity during the natural restoration of the subalpine birch forest in the Central Great Caucasus. *Turkish Journal of Botany* 39: 1-6.

Ustin, S. L & Gamon, J. A. 2010. Remote sensing of plant functional types. *New Phytologist* 186: 795–816.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97–114.

Waldhardt, R., Abdaladze, O., Otte, A. & Simmering, D. 2011. Landschaftswandel im Kaukasus Georgiens. Interdisziplinäre Forschung für eine nachhaltigere Zukunft. *Spiegel der Forschung* 28: 4–15.

Walter, H. 1974. Die Vegetation Osteuropas, Nord- und Zentralasiens. Stuttgart: Gustav Fischer Verlag.

Ward, J. H. 1963. Hierarchical Grouping to Optimize an Objective Function. *Journal of the American Statistical Association* 58: 236–244.

Weichelt, H., Rosso, P., Marx, A., Reigber, S., Douglass, K. & Heynen, M. 2011. White Paper - The RapidEye Red Edge Band. *RapidEye White Papers* 1–6.

Wilson, S. D. & Nilsson, C. 2009. Arctic alpine vegetation change over 20 years. *Global Change Biology* 15: 1676–1684.

Summary

High mountain ecosystems and their services are of global importance. They take 20 percent of the terrestrial surface, offer habitat to humans, a diverse fauna and flora, and play a key role for fresh water supply. But for all that, they are prone to global change. Remote, high mountain regions, especially from former Soviet Union States experience a strong change in the agricultural sector, mainly the abandonment of agricultural land use, which impacts socio economy, ecosystem functioning and biodiversity in the end.

The unique species composition of high mountain grassland and the related ecosystem services, such as biomass or erosion mitigation are most likely to change with the ongoing abandonment in high mountain regions, mapping and monitoring of high mountain grassland properties and key ecosystem processes is therefore highly needed. Thus, this study focuses on modelling the vegetation composition, biomass and plant functional groups (content of graminoid, herbaceous and legume plants) of the subalpine grassland, as well as the recognition of shrub encroachment, by means of remote sensing. Shrub encroachment has already been observed in the study region and plays a key role in many arctic and alpine environments. The identification of species identity is of great importance to assess potential consequences.

The species-rich, extensive grassland in the isolated Kazbegi region, Greater Caucasus, Georgia is the main winter fodder source and thus of importance for the local subsistence agriculture, based on pastured cattle for dairy production.

The results of the vegetation analysis show that the subalpine grassland vegetation is closely related to the physical site conditions (elevation a.s.l. and exposition to the east), characterized by broad transitions between grassland types with distinct attributes, such as aboveground biomass, vegetation cover, species richness and plant functional groups. The shrub stands of *Betula litwinowii*, *Rhododendron caucasicum* and *Hippophae rhamnoides* are of distinct growth forms and species composition. However, *Betula litwinowii*, *Rhododendron caucasicum* and the tall herb *Verartrum lobelianum* co-occur in the tree line ecotone, challenging a clear delineation.

The results of the gradual modelling approaches show that species composition, biomass and to a lesser degree plant functional groups can be modelled by multispectral imagery, vegetation indices and topographical parameters. Species composition is furthermore a good predictor for biomass, even though the saturation effect is present at high yields in both approaches. Moreover, hyperspectral and multispectral data result in similar model fits.

The separation of shrub reflectance indicated that *Betula litwinowii* and *Hipopphae rhamnoides* can be delineated in imagery, whereas *Betula litwinowii* and *Rhododendron caucasicum*, as well as *Betula litwinowii* and *Veratrum lobelianum* show a more similar reflectance pattern. However, overall separability was high, especially in simulated RapidEye and WorldView-2 reflectance. The satellite image taken in September further showed a better separability than the one acquired in July.

Identification of species-rich grassland types with a high conservational value, from the resulting multi scale maps helps to apply site specific and case sensitive grassland management. At the same time the yield map can be used to identify the few highly productive sites in the landscape. The distribution of plant functional groups provides important information about the usability, such as hay meadow, and the erodibility. The encroaching shrub species and their distinct growth forms offered an excellent opportunity to study distinctiveness and the applicability of different sensors.

A multi scale prognosis of grassland properties, as well as the delineation of shrub encroachment on species level, are important factors for sustainable land use planning in the high mountain landscape. They further allow an integrative analysis of the high mountain landscape for modified, site specific agricultural land use measures, with the help of normative scenarios.

Zusammenfassung

Gebirgsökosysteme und ihre Ökosystemleistungen sind global von großer ökonomischer und ökologischer Bedeutung. Sie nehmen 20 Prozent der Landfläche ein und bieten somit Lebensraum für Mensch, Pflanze und Tier. Allerdings sind Gebirgsökosysteme stark durch den globalen Wandel betroffen. Dies gilt insbesondere für die peripheren Hochgebirgsregionen der vormaligen Staaten der Sowjetunion, welche einem weitreichenden Wandel in der Agrarstruktur unterliegen, der sich vor allem in der Aufgabe der Landnutzung zeigt und daher sowohl sozioökonomische als auch ökologische Konsequenzen hat.

Die einzigartige Artenzusammensetzung des Hochgebirgsgrünlandes und die damit verbundenen Ökosystemleistungen, wie z. B. Biomasseertrag oder Erosionsminderung werden durch Landnutzungsaufgabe zumeist negativ beeinflusst, ihre Erfassung und Kartierung ist daher von großer Bedeutung. Aufgrund dessen stehen die Abbildbarkeit der graduellen Unterschiede von Grünlandeigenschaften wie z. B. der Artenzusammensetzung, der oberirdischen Biomasse und der funktionellen Artengruppen und auch die Erfassung von Verbuschungsprozessen, mithilfe von Fernerkundungsdaten im Fokus der Studie. Sukzession von Gebüschen spielt in einigen alpinen und arktischen Ökosystemen eine Schlüsselrolle, das Erkennen der Artidentität, um die möglichen Einflüsse auf das Ökosystem zu bewerten, ist hierbei von besonderer Bedeutung.

Das artenreiche, großflächige Grünland der Untersuchungsregion Kazbegi im Großen Kaukasus Georgiens ist, aufgrund der Abgeschiedenheit der Region, die einzige Winterfutterquelle und daher von besonderer Bedeutung für die lokale Subsistenzlandwirtschaft, vor allem der Weidetierhaltung zur Milchgewinnung.

Die Ergebnisse der Vegetationsanalysen zeigen, dass die primär durch die physischen Standortparameter (Höhe m NN, Ost-Ausrichtung) bedingte Grünlandvegetation in der subalpinen Höhenstufe in der Region Kazbegi durch breite Übergänge zwischen Wiesen- und Weidentypen gekennzeichnet ist und sich durch charakteristische Eigenschaften wie z.B. die Biomasse, Vegetationsdeckung, Artenreichtum, sowie funktionelle Gruppen (Anteil Grasartige, Krautige, Leguminosen) differenziert. Die Gebüsche von *Betula litwinowii*, *Rhododendron caucasicum* und *Hippophae rhamnoides*, zeigen deutlich unterschiedliche Wuchsformen und Artenspektren. *Betula litwinowii*, *Rhododendron caucasicum* und die Hochstaude *Verartrum lobelianum* treten allerdings in der Kampfzone gemeinsam auf, was eine Abgrenzung deutlich erschwert.

Die Ergebnisse der fernerkundungsbasierten, graduellen Modellierungen zeigen, dass Artenzusammensetzung, Biomasse und mit Einschränkung die funktionellen Artengruppen der

Bestände anhand von multispektralen Satellitenbildern, Vegetationsindizes und Topographievariablen modellierbar sind. Die Artenzusammensetzung eignet sich desweiteren als Vorhersagevariable für Biomasse, kann den Saturationseffekt der Vegetationsindizes jedoch nicht umgehen. Hyperspektrale und multispektrale Daten erreichen zudem eine ähnliche Modellgüte in der Modellierung.

Die Analyse der Reflexionseigenschaften von Gebüschtypen zeigt, dass *Betula litwinowii* und *Hipopphae rhamnoides* sich deutlich voneinander abgrenzen lassen, wohingegen *Betula litwinowii* und *Rhododendron caucasicum* sowie *Betula litwinowii* und *Veratrum lobelianum* eine ähnliche Reflexion aufweisen. Die beste Unterscheidung wurde mit den simulierten Reflexionen der Sensoren RapidEye und WorldView-2 erreicht. In der Satellitenbildaufnahme vom September unterscheiden sich zudem die Arten besser als in der Aufnahme vom Juli.

Aus den erarbeiteten, multiskaligen Karten können die floristische Zusammensetzung des Grünlandes sowie artenreiche, schützenswerte Grünlandtypen identifiziert werden und somit in entsprechende Pflege- und Schutzmaßnahmen der Umweltplanung einfließen. Zugleich bietet die Biomassekarte die Möglichkeit, die wenigen ertragreichen Standorte in der weitläufigen Landschaft zu identifizieren. Die charakteristische Verteilung der Anteile von Grasartigen, Krautigen und Leguminosen in den Grünlandtypen liefert wichtige Informationen über die Nutzbarkeit z. B. als Heuwiese und auch über die Erosionsanfälligkeit. Die unterschiedlichen Wuchsformen der sich ausbreitenden Gebüsche boten eine günstige Möglichkeit, Reflexionseigenschaften zu untersuchen und die Anwendbarkeit verschiedener Sensoren zu testen.

Eine multiskalige Prognose von Grünlandeigenschaften sowie die Identifizierung von Verbuschungsstadien sind ein integraler Bestandteil für die Planung der landwirtschaftlichen Nutzung in peripheren Gebirgsregionen, sie erlauben auch die integrative Analyse der Hochgebirgslandschaft für modifizierte, standortgemäße landwirtschaftliche Nutzungsverfahren mithilfe normativer Szenarien.

Acknowledgements

This work would not have been possible without the great support of my supervisor Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte. She accepted me as doctoral student in her working group and gave me the opportunity to work in the high mountains of Georgia. Her trust, guidance and patience in all situations, encouraged me not to give up and helped me to complete this dissertation. I benefited from her broad knowledge, especially in phytosociology and species identification. It has always been a pleasure to work with her.

Special thanks go to Prof. Dr. Honermeier for his willingness to support my study by agreeing to be my second supervisor and evaluating my thesis.

Further, I would like to thank the Justus-Liebig University Giessen for the graduate scholarship, the Volkswagen Foundation and the DAAD for funding my dissertation and the RESA Science Archive for supplying the satellite imagery.

If not for the many colleagues and friends, who supported me throughout the dissertation project, this thesis would not have been possible. I would thus like to express my sincere gratitude to all who contributed to the study and especially to:

- Dr. Hannes Feilhauer for his great contributions to the remote sensing part, his help and advice, beginning from my masterthesis and continuing throughout the dissertation, and his gift to touch unerringly on sore points. Moreover, I would like to thank his working group at the Institute of Geography, Friedrich-Alexander University Erlangen-Nürnberg for their hospitality.

- Prof. Dr. Rainer Waldhardt for his valuable scientific advice and guidance, as well as for always giving a last-minute, helping hand when needed.

- Dr. Dietmar Simmering for teaching me vegetation analysis, his interest in my work, the manifold discussions about statistics and design, as well as the many cheerful coffee breaks.

- Josef Scholz-vom Hofe for inventing airplane-proof cutting frames, his skillful help in the laboratory with preparing the biomass and all technical concerns.

- My colleagues Dr. Martin Wiesmair, Dr. Sarah Harvolk, Dr. Kristin Ludewig for helpful comments on my manuscripts, fruitful discussions and the close cooperation.

- Dr. Matthias Höher for his administrative support as managing director of the ZEU and project coordinator.

Appendix

Table 1: Indicator Species Analysis (described in chapter four), species are considered as indicator species if the indicator value is >0.3 and p>0.05.

Species	Relative abundance			Indicator Value	p-Value
	HB	**GC**	**AC**		
***Hordeum brevisubulatum* meadow (HB)**					
Hordeum brevisubulatum	0.76	0.13	0.11	0.73	0.001
Carum caucasicum	0.84	0.14	0.02	0.69	0.001
Festuca pratensis	0.85	0.12	0.03	0.67	0.001
Rumex acetosa	0.74	0.22	0.04	0.65	0.001
Silene vulgaris	0.68	0.24	0.08	0.62	0.001
Phleum pratense	0.57	0.26	0.18	0.54	0.001
Poa trivialis	0.78	0.09	0.12	0.51	0.001
Vicia tenuifolia subsp. variabilis	0.78	0.14	0.08	0.47	0.001
Bunias orientalis	0.71	0.1	0.18	0.47	0.001
Poa pratensis	0.79	0.18	0.03	0.41	0.001
Vicia alpestris	0.53	0.28	0.18	0.4	0.001
Pastinaca armena	0.43	0.26	0.32	0.39	0.007
Taraxacum spec	0.47	0.3	0.22	0.33	0.004
Trifolium pratense	0.44	0.36	0.2	0.32	0.03
Geranium sylvaticum	0.67	0.23	0.1	0.32	0.001
Ranunculus ampelophyllus	0.8	0	0.2	0.31	0.002
Rumex obtusifolius	1	0	0	0.30	0.001
Ranunculus caucasicus	0.62	0.34	0.04	0.30	0.004
***Gentianella caucasea* grassland (GC)**					
Alchemilla sericata	0.1	0.63	0.27	0.63	0.001
Gentianella caucasea	0.17	0.77	0.06	0.56	0.001
Primula algida	0	0.81	0.19	0.54	0.001
Ranunculus oreophilus	0.19	0.62	0.19	0.50	0.001
Plantago atrata	0.15	0.45	0.4	0.41	0.001
Leontodon hispidus	0.22	0.46	0.33	0.39	0.002
Agrostis vinealis	0.4	0.52	0.07	0.36	0.008
Seseli alpinum	0	1	0	0.36	0.001
Cerastium arvense	0.4	0.39	0.21	0.36	0.023
Lotus corniculatus	0.14	0.52	0.34	0.33	0.004
Bupleurum polyphyllum	0.07	0.79	0.14	0.31	0.002
Anthoxanthum odoratum	0.09	0.85	0.06	0.31	0.001
***Astragalus captiosus* grassland (AC)**					
Astragalus captiosus	0	0.04	0.96	0.83	0.001
Silene linearifolia	0.04	0.11	0.84	0.60	0.001
Potentilla crantzii	0.1	0.21	0.69	0.49	0.001
Bromus variegatus	0.2	0.35	0.45	0.42	0.003
Poa alpina	0.09	0.31	0.61	0.41	0.001
Koeleria luerssenii	0.1	0.42	0.48	0.39	0.003
Campanula sibirica subsp. hohenackeri	0	0.18	0.82	0.34	0.001
Trifolium ambiguum	0.24	0.26	0.5	0.34	0.009
Galium verum	0.16	0.32	0.52	0.34	0.002
Minuartia oreina	0.03	0.43	0.54	0.31	0.017
Euphrasia hirtella	0.11	0.43	0.46	0.31	0.042
Medicago glomerata	0.17	0.11	0.72	0.30	0.002