PhD thesis title:

Pastoral Resources in the Naryn Oblast, Kyrgyzstan, under Post-Soviet Transformation - Effects of Livestock Grazing on Vegetation and Soils

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Cumulative Dissertation

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Und wenn wir abends durch die Schlucht fuhren, dann schien es mir jedesmal, als wäre ich in eine andere Welt versetzt. Ich hörte Danijar mit geschlossenen Augen zu, und vor mir entstanden seltsam bekannte, mir aus frühester Kindheit vertraute Bilder: Mal glitten hoch oben über Nomadenzelten flockige graublaue Frühlingswolken dahin; mal sprengten stampfend und wiehernd Pferdeherden auf das sommerliche Weideland, Hengstfüllen darunter mit wehendem Stirnhaar und wildem schwarzen Feuer in den Augen, die ihre Mutterstuten ausgelassen umkreisten, mal zogen Schafen in ruhigem, breitem Strom über die Vorberge, mal stürzte ein Wasserfall von hohen Felsen herab, die Augen blendend mit seinem weißen, brausenden Gischt; mal sank die Sonne hinter dem Fluß sanft in das üppige Steppengras, und ein einsamer ferner Reiter am feurigen Horizont sprengt ihr nach – mit der Hand schien er an sie heranzureichen -, bis auch er im Gras und in der Dämmerung untertauchte.

(**Tschingis Aitmatov** Kyrgyz author - *Dshamilija*)

Outline

Zusammenfassung

Weideflächen, die in etwa 40% der globalen terrestrischen Oberflächen einnehmen, stellen gekoppelte sozial-ökologische Systeme dar. Sie repräsentieren das Erbe seit Jahrhunderten bestehender landwirtschaftlich geprägter Kulturen, und beinhalten eine große Artenvielfalt. Große Teile dieser Weideflächen sind von weitreichenden Veränderungen wie z.B. Degradierungsprozessen betroffen. Um nachhaltige Managementstrategien entwickeln zu können, ist ein besseres Verständnis von komplexen Weideökosystemen und deren Nutzungsregimen unabdingbar. Die hier präsentierte kumulative Dissertation soll durch die Analyse von ökologischen Aspekten der Weidenutzung in Kirgistan weiterführende Erkenntnisse liefern. Ein besonderer Fokus liegt hierbei auf der Untersuchung von Boden- und Vegetationsparametern entlang eines Nutzungsgradienten.

Im Zuge des post-sowjetischen Transformationsprozesses wurde die Bevölkerung Kirgistans vor neue Herausforderungen in Bezug auf die Sicherung ihrer Lebensgrundlage gestellt. Gegenwärtig ist die Viehhaltung für viele Haushalte die wirtschaftliche Grundlage. Allerdings können traditionelle Weidepraktiken, wie die saisonale Weidemigration, aufgrund hoher Kosten und fehlender Infrastruktur nicht mehr aufrechterhalten werden. Als Konsequenz daraus überschreiten große Teile der Weideflächen, hauptsächlich die Winterweiden in der Nähe von Siedlungen, ihre Tragfähigkeit und sind von Degradierungsprozessen betroffen. Daher stellt die ökologische Bewertung als auch die Abschätzung zukünftig verfügbarer Weideressourcen auf kirgisischen Hochweiden im Naryn-Oblast das Ziel der vorliegenden Dissertation dar.

Anhand von erstmals erfassten Daten im Kara-Kujur Tal des stark landwirtschaftlich geprägten Naryn-Oblast konnte der Beweidungseinfluss auf verschiedene Einflussgrößen wie Bodenparameter, Vegetationsstruktur, Anteil an Biomasse, funktionelle Pflanzenmerkmale und Artenvielfalt dargestellt werden. Es hat sich gezeigt, dass die intensive Nutzung der Winterweiden edaphisch durch höhere pH-Werte und geringere Anteile an organischer Substanz widergespiegelt wird. Die Sommerweiden konnten als grundsätzlich nährstoffreicher beschrieben werden. Unterschiede in der floristischen Zusammensetzung konnten in erster Linie auf die geringere Nutzungsintensität der Sommerweiden zurückgeführt werden. Winterweiden werden durch die ranglose *Bupleurum thianschanicum-Androsace dasyphylla*-Gesellschaft charakterisiert,

wohingegen auf den Sommerweiden die ranglose *Trisetum spicatum-Ptilagrostis mongholica*-Gesellschaft vorherrscht. Des Weiteren zeigen signifikante Unterschiede in der Biomasse den gravierenden Einfluss von dauerhafter Beweidung, wobei die Winterweiden im Vergleich zu Sommerweiden nicht einmal die Hälfte des Biomasseanteils aufweisen. Auch anhand funktioneller Pflanzenmerkmale, wie z.B. Wuchshöhe, Blühbeginn oder Blatteigenschaften (spezifische Blattfläche und Blattgewicht pro Fläche), konnten Unterschiede zwischen den Sommer- und Winterweiden festgestellt werden. Arten der Winterweiden sind primär durch eine Abwehr-Strategie gekennzeichnet mit entsprechend geringerer Wuchshöhe, einer früheren Blühphase oder auch einem generell höheren Blattgewicht pro Fläche, was typisch für langsam wachsende Pflanzen ist, deren Blattbildung auf längere Lebensdauer ausgerichtet ist. Die Analyse von Artenvielfalt und Diversitätsindizes hat ergeben, dass eine dauerhafte Beweidung mit dem Verlust von Arten einhergeht, so dass Sommerweiden signifikant artenreicher sind. Allerdings ist der Anteil von seltenen, endemischen Arten auf Winterweiden höher. Dies untermauert die Notwendigkeit der Erhaltung von Biodiversität durch nachhaltige Weidenutzung.

In einem einführenden Abschnitt dieser Dissertation werden der historische Hintergrund und die politischen Umwälzungen erläutert, die einen maßgeblichen Einfluss auf den Umgang mit den Weideressourcen in Kirgistan gehabt haben. Des Weiteren wird auf den noch sehr lückenhaften Forschungsstand in der Region eingegangen. In dem darauffolgenden Kapitel werden die methodischen Ansätze der Datenerfassung dargelegt und die angewandten statistischen Methoden beschrieben. Daran schließt ein Überblick der vier publizierten Artikel, die den Hauptteil dieser Dissertation bilden, an, gefolgt von einer Übersicht weiterer Publikationen und Vorträge. In einem letzten Abschnitt werden die zentralen Erkenntnisse zusammenfassend diskutiert und eine Synthese aus ökologischen und sozio-ökonomischen Daten inklusive einiger Vorschläge für eine nachhaltige Weidenutzung gegeben.

Abstract

Rangelands, which occupy around 40% of the global land area, can be perceived as socio-ecological systems, representing the heritage of centuries-old pastoral cultures, and containing a great variety of species. Large parts of those rangelands are increasingly affected by far-reaching degradation processes. In order to develop sustainable management strategies, a better understanding of complex pastoral ecosystems and its utilization regimes is indispensable. The cumulative dissertation thesis presented here seeks to improve knowledge and understanding through the analysis of ecological aspects in the context of grazing intensity in Kyrgyzstan. The main focus lies on the investigation of soil and vegetation parameters along a grazing gradient.
During the post-Soviet era, the Kyrgyz Republic was subjected to far-reaching political and economic transformations with various social and commercial restrictions, especially for communities on the local level. Today, most households maintain animal husbandry to sustain their livelihoods. Traditional pasture practices, however, such as annual migratory livestock movements are no longer followed due to high costs and a lack of infrastructure. As a consequence, large parts of the rangelands, in particular winter pastures close to settlements, exceed their carrying capacity and undergo degradation processes. In the light of the above, this PhD thesis aims at providing an ecological assessment as well as an evaluation of the future availability of pastoral resources of Kyrgyz high-mountain pastures in the Naryn Oblast.

Based on the first-time recorded data within the Kara-Kujur valley as part of the Naryn Oblast, the largest and most important Kyrgyz Oblast concerning agriculture, the impact of grazing intensity on different aspects such as soil parameters, vegetation structure, amount of biomass, functional plant traits and biodiversity has been analyzed. Based on our investigations we were able to demonstrate that the intensive use of winter pastures is reflected edaphically by higher pH values and lower contents of organic matter. By contrast, the soils of summer pastures are richer in nutrients. Differences in the floristic composition between winter and summer pastures have to be attributed mainly to a higher grazing intensity on winter pastures. The latter are characterized by rankless *Bupleurum thianschanicum-Androsace dasyphylla* communities, whereas on summer pastures rankless *Trisetum spicatum-Ptilagrostis mongholica* communities are dominant. In addition, significant differences regarding the amount of biomass show the severe impact of permanent grazing, with winter pastures producing less than half of the biomass compared to summer pastures. We found significant differences between summer and winter pastures in terms of functional plant traits, e.g. plant height, flowering start or leaf traits (specific leaf area and leaf mass per area). Species of winter pastures are primarily characterized by a resistance strategy with correspondingly lower plant height, earlier flowering or a generally higher leaf mass per area, which is typical for slow-growing species whose leaves are built to persist. The analysis of species richness and diversity indices has also shown that intense grazing is associated with the loss of species, demonstrated by summer pastures which are significantly richer in species. However, winter pastures showed a more frequent occurrence of rare endemic species. This underlines the need for preserving biodiversity through the implementation of sustainable grazing management.

The introductory section of this thesis discusses the historical background and political changes which are directly linked to the management of pasture resources in Kyrgyzstan. The state of the art regarding pastoral ecological research in Kyrgyzstan is also presented. The subsequent chapter describes the methodical approach of data collection as well as the applied statistical methods. This is followed by an overview of the four articles representing the main part of this dissertation as well as by references to further publications and oral presentations. In a final section, the central findings are summarized and discussed, followed by a synthesis of ecological and socio-economic data, including suggestions for sustainable pasture use.

1. Introduction

Since millennia, humans have lived in and exploited rangelands, which cover over 40% of the earth´s land surface. They represent linked social-ecological systems where livestock grazing has always been an integral part and a distinctive way of life has evolved in which pastoralist seasonally moved with their livestock to better pastures. Due to recent human population growth and sedentarization of former nomadic societies, traditional herding practices are nowadays mostly abandoned with devastating effects on social and ecological conditions (Grice and Hodgkinson 2002; Vetter 2005; Rahimon 2012). Rangelands are progressively converted to areas for crop cultivation or degraded by overgrazing. As a result, desertification processes are increasing and affect about a third of the world´s dry lands, indicated by the loss of vegetation and soil cover followed by wind and rain erosion (e.g. Vetter 2005; Wrobel and Redford 2010; Taft et al. 2011). Socio-ecological dynamics and appropriate management of arid and semi-arid rangelands (i.e. parts of the African country, Australia, several countries of South America, the Great Plains of America or regions of Central Asia) have been debated since the 1980s, in view of the growing vulnerability of pastoralists and their livelihoods. Represented by the considerable multi-dimensional conservation value of these highly valuable ecosystems, the survival of species and the pastoral cultures conservation has become an imperative for global policies in the economic, social and environmental sphere. To solve environmental problems more effectively, a new culture for environmental stewardship is required, including the integration of social and natural sciences (Vetter 2005; Wrobel and Redford 2010; Archer 2010). In this context, the BMBF (Bundesministerium für Bildung und Forschung) launched the funding initiative “EU and Central Asia – a partnership for the future” in 2015. This PhD thesis is based on research embedded in the project TRANSPAST whose aim, as a part of the initiative, was to contribute to research on sustainable land use systems in Kyrgyzstan, using an interdisciplinary approach, and to encourage the cooperation in science and education with academic institutes in the Kyrgyz republic (capacity building). Because the stewardship for vegetation composition, cover and production is essential for sustainable rangeland management, the research focused on the investigation of changing pastoral use under post-Soviet transformation, and the resulting impact on the ecological state of high-mountain pastures in the Naryn Oblast.

The Kyrgyz Republic, located in Central Asia, is characterized by the Tian Shan mountain system, which covers the major part of the country (Fig. 1). Altitudes range from 840 m in the capital Bishkek to over 7.000 m in both the Tian Shan and Pamir-Alai ranges. The steppes and meadows of these mountain ranges were used during centuries by pastoral nomads (Farrington 2005; Eisenman et al. 2013). The climatic conditions in Kyrgyzstan vary from dry continental in the plains to cold and harsh at higher elevations. Due to the topography, the climate is characterized by sharp small-scale differences (Gottschling 2006). The land area of 198.500 km² is inhabited by approximately 5.3 million people and counts seven provinces (Oblast). The Naryn Oblast represents the largest one with the highest percentage of Kyrgyz pastures, approximately 30%. Thus, wide areas of the Naryn Oblast are used as grazing lands (Crewett 2012; Eisenman et al. 2013). To cope with arid and semi-arid ecological conditions, rangeland ecosystems and mobile livestock keeping by pastoral nomads have co-adapted and co-evolved during centuries. Most pastoralists moved their flocks between seasonal pastures. The herds mainly consist of sheep and horses but there are also flocks of goats, cows and yaks. In summer, they grazed on montane and alpine pastures at higher altitude (*dzailoo*) and in winter on pastures at lower elevation (*kyshtoo*). Animal husbandry is still the most important livelihood strategy for a large proportion of the rural population in Kyrgyzstan, where nomadism was the predominant land use system prior to the colonization by the Soviet Union in 1936 (Baibagushev 2011; Schmidt 2013). The livestock sector represented one of the strongest components of the regional economy during Soviet and post-Soviet times. The basis for this economic sector is supplied by the vast rangelands, which occupy almost 45% of the Kyrgyz land area, representing more than 9 million hectares (Baibagushev 2011; Taft et al. 2011; Sakbaeva et al. 2012).

Beginning with the occupancy by the Soviet Union and challenged again by the independence in 1991, Kyrgyzstan was subjected to fundamental political, economic and agricultural changes (e.g. Dörre 2012; Shigaeva et al. 2007; Robinson 2016). Under the Soviet regime formerly autonomously acting pastoralists were superseded by state owned farms (*sovkhozes*) and collective farms (*kolkhozes*). Sedentarization and collectivization campaigns were pushed forward. The livestock industry has been massively expanded and the flock size exceeded the carrying capacity of the pastures up to two or three times (Schoch et al. 2010). However, vertical transhumance between high-mountain rangelands and lower pasture areas has been mostly maintained during occupancy (Robinson 2016).

The first years after independence saw a drastic reduction in livestock numbers, and a temporarily decreasing grazing pressure. During this period the return to a subsistence lifestyle was for most of the Kyrgyz people the only possibility to sustain their livelihood (Borchardt et al. 2011; Dörre 2012; Zhumanova et al. 2016). As a result of this new organization, livestock numbers increased again in the further course of post-Soviet transformation and recently rebounded toward Soviet era levels with 15 million animals in 2014 (Levine et al. 2017). But the dissolution of the institutionalized organizations was accompanied by the loss of the annual migratory herd movements (Crewett 2012; Kreutzmann 2013). The herders are nowadays rarely able to organize the migration of livestock themselves because of long distances and a weak state of infrastructure, which resulted in severe changes of traditional pasture practices. In consequence, summer pastures at higher altitude experience increasing abandonment, while winter pastures which are close to settlements and exposed to intense grazing pressure, are subject to vegetation and soil degradation (Hoppe et al. 2016a, 2016b; Shigaeva et al. 2016). According to recent estimates, degradation processes affect 45 to 75% of Kyrgyz pasture areas (Robinson 2016; Levine et al. 2017).

Due to the political changes during the last decades, these linked socio-ecological rangeland systems were confronted with new challenges. Frequent abandonment of traditional pasture practices, i.e. seasonal livestock migration, provoked various modifications in ecosystem structure and functioning. It is largely known that unsustainable livestock keeping, particularly in semi-arid and arid ecosystems, can lead to land degradation including the loss of biodiversity (e.g. Magurran 2013; Gamoun et al. 2015). The impact of grazing on soil properties and vegetation structure in the northeast of the Naryn Oblast is unknown to date. The Kara-Kujur valley, our study area, is a remote area where animal husbandry is the primary source of livelihood for the majority of people (Asykulov and Esenaman uulu; unpublished data). Thus, increasing rangeland degradation processes might threat the livelihood of large parts of the resident population. Some studies have been done to investigate this issue in other parts of Kyrgyzstan (e.g. Epple 2001; Borchardt et al. 2011; Taft et al. 2011), but due to different site and climate conditions their results are not transferable to our research area. To fill this gap, this PhD thesis intends to assess the impact of disturbances on the ecological state of high-mountain pastures in the Naryn Oblast, by analyzing to what extent changing grazing regimes affect soil and vegetation properties. We selected several soil and vegetation indicators because of their relevance in the context of varying grazing pressure (e.g. Bagella and Caria 2011; Borchardt et al. 2011; Taft et al. 2011). This includes not only different soil parameters such as the pH value or the content of soil organic matter but also the determination of highly diagnostic species of the different pasture types as well as the assessment of species diversity patterns. By analyzing a common set of plant functional traits as well as the occurrence of rare endemic species, it was possible to get more detailed insights into vegetation response to grazing. We collected respective data for the first time in the Kara-Kujur valley and used various statistical approaches for analyses with the objective to present reliable results concerning rangeland conditions in the Naryn Oblast, as a basis for implementing sustainable management strategies.

The following sections deal with the transformation of pasture practices in Kyrgyzstan, the impact of a differentiated grazing intensity, the data collection as well as the used statistical methods, and provide a synthesis of ecological and socio-economic parameters including an outlook of the future availability of pastoral resources. The cumulative PhD thesis is composed of four articles, which will be shortly presented in chapter 4. The complete articles are attached at the end of this document.

2. State of the art

Mobile livestock keeping was a prevalent form of animal husbandry in regions of Central Asia. Nomadic pastoralism has always been characterized by herders, which graze their livestock on a variety of pasture areas following an irregular pattern of movements (e.g. Rahimon 2012; Fujita and Ariunbold 2014). In Kyrgyzstan this long existing form of land use was fundamentally transformed within the twentieth century, when the Republic was faced by structural and reformist intervention, which resulted in a two phase modernization. The Soviet era was marked by collectivization movements and the post-Soviet period was characterized by privatization and deregulation processes. The life of the Kyrgyz people, which has always been linked to agriculture and especially livestock keeping, changed dramatically during this heteronomy (e.g Farrington 2005; Schmidt and Sagynbekova 2008; Shigaeva et al. 2016). Particularly, the idea to settle nomads and to adapt their lifestyle to modern expectations and perceptions provoked severe changes concerning traditional pasture practices. Because of these interventions, the question whether the evolving pasture practices could or should still be termed nomadic was increasingly raised by researchers. To date there is an ongoing discussion about the notion of ‘nomadism’ or ‘former nomads’ in the context of Central Asian countries, because many former herders gave up the practice of transhumance (Farrington 2005; Dörre and Borchardt 2012; Kreutzmann 2012).

The interest in those traditional pasture practices rises on the one hand due to the general discussion about sustainable land use strategies and increasing degradation effects, and is on the other hand forced by the demand of self-governance of local communities as well as the problem of land distribution (Jacquesson 2010; Steinmann 2010; Liechti 2012, Kreutzmann 2013; Levine et al. 2017). With regard to the first years after independence, the post-Soviet period in Kyrgyzstan is an example of poorly implemented reforms to change from socialist economy towards modern market capitalism, represented by the neoliberal Washington Consensus. Since then, state administration and political institutions struggle to establish legislative reforms (for example the new pasture law of 2009), which are acceptable and applicable by the Kyrgyz population (Steinmann 2010; Kreutzmann 2013). This discrepancy between socio-political objectives and the implementation of sustainable land use strategies will be further discussed in chapter 5.

The issue of degrading rangelands in the Kyrgyz Republic has been already addressed (e.g. Epple 2001; Wagner 2009; Borchardt et al. 2011; Dörre and Borchardt 2012), but the study areas were mostly located in the South-West of Kyrgyzstan with its different climate and site conditions. Other related studies focused more on political aspects (Ludi 2003; Shigaeva et al. 2007; Crewett 2012, 2015; Liechti 2012; Schmidt 2013). Only few studies (Farrington 2005; Taft et al. 2011; Isakov and Thorsson 2015; Imanberdieva 2015; Levine et al. 2017) provided some information relevant to our topic and our research area. Farrington (2005) reported on a wide variety of post-Soviet livestock management (i.e. herding cooperatives, herding as a single family unit, herding partnership, diversifying income-generating activities beyond herding as well as the complete ending of all nomadic herding practices) and the abandonment of pasturelands (mostly concerning the remote summer pastures) in Eastern Kyrgyzstan. He concluded that Kyrgyz transhumant practices have been significantly modified but that nomadic pastoralism still remains at the core of the Kyrgyz identity. In the study of Taft el al. (2011), patterns of plant species composition and diversity were analyzed along major environmental gradients throughout the Kyrgyz Republic, however not including our research area. Nonetheless, they detected some dominant species within montane grasslands (average altitude 2.456 m), which we also found in our study area such as: *Festuca valesiaca* (characterized by a wide environmental profile and being a predictor of the initial stages of human degradation, also detected by: Isakov and Thorsson 2015; Imanberdieva 2015), *Galium turkestanicum* or *Geranium saxatile*. Isakov and Thorsson (2015) implemented a State and Transition Model (STM) to assess the land condition in the heart of the Naryn Oblast. The study area was divided into lowlands (steppe types and semi-desert types from approximately 2.000 m to 2.600 m) and upland pastures (meadow types and meadow-steppe types from approximately 2.600 m to 3.100 m). They found that long term exploitation locked the pastures in a degradation cycle, but they also pointed out that this cycle can be broken by optimal management strategies. The survey of Imanberdieva (2015) concerning plant formations in At-Bashy valleys, located in the south of the Naryn Oblast, revealed several similarities with regard to dominant species (e.g. *Kobresia humilis*, *Koeleria cristata*, *Stipa caucasica*, *Ranunculus alberti*, *Carex stenocarpa* or *Phlomoides oreophila*). Nevertheless, the listed communities are only related to climatic conditions and not embedded in a broader context, i.e. anthropogenic disturbances. The social-ecological research project of Levine et al. (2017) aimed at detecting degraded pasture areas in the eastern part of the Naryn Oblast by a series of interviews among herders. Their cognitive approach showed divergent narratives often due to varying herding experiences. In sum, it was not possible to find either specific publications focusing on the same study site, or to compare our findings in detail with existing studies because of different site conditions or differing scientific concepts. Thus, due to the surveys and analyses which were done for the first time within our study area, this PhD thesis has a pioneer character. Until now, there was no detailed information concerning soil quality and vegetation structure under different grazing regimes in the Kara-Kujur valley, as part of the vast pasture areas within the Naryn Oblast.

To fill this gap a first overview about the floristic composition in summer season (first article) was given, followed by a general overview about the difference in principal physical and chemical soil properties and plant communities on summer and winter pastures, subjected to contrasting grazing pressure (second article). This general overview was necessary because it is difficult to transfer overall conclusions or derived degradation trends from other regions to our research area. Soil conditions are considered to be the most reliable indicator for degradation of grazing lands because degraded soils do not recover rapidly (von Wehrden et al. 2012). Several authors (e.g. Wu et al. 2008; Xiong et al. 2014; Su et al. 2015) have already pointed out that parameters such as soil organic carbon, total nitrogen and cation exchange capacity show significantly lower values when a pasture is degraded, which was confirmed by our results. The distinctly higher grazing pressure winter pastures are subjected to, seems to be responsible for the soil deterioration. The matter of fact that livestock grazing strongly affects the structure, richness and composition of vegetation has been largely discussed (e.g. Peper et al. 2011; Gamoun et al. 2015; Wang et al. 2017), and the impact of grazing on species composition in Kyrgyzstan has already been assessed by Epple (2001), Borchardt et al. (2011, 2013) and Taft et al. (2011). Nevertheless, their results cannot be directly compared with our determined rankless communities since they show notable differences. By comparing plots at the same altitude but under different grazing regimes, it was furthermore possible to demonstrate that vegetation patterns are more influenced by grazing intensity than by elevation.

The third paper considered plant functional traits as indicators for diverging grazing regimes on the two pasture types. Within the last decades it has been demonstrated that similar plant traits were associated with a specific response to grazing, and that these relationships can help in the understanding of plant responses to environmental factors.

Important insights into grazing-induced changes in structure and dynamics of vegetation can be generated, because grazing is both depending on and affecting plant functional traits, called feedback loop (e.g. Louault et al. 2005; Díaz et al. 2007; Evju et al. 2009). By inspecting the trait composition of a plant community it is possible to draw conclusions about the capability of the composing species to attain resources, disperse, reproduce and respond to particular ecological processes (Díaz et al. 2002; Gutiérrez-Girón and Gavilán 2013). We selected traits such as plant height, growth form, flowering start as well as LMA (Leaf Mass per Area) and SLA (Specific Leaf Area), because they are considered as being good predictors of grassland response to disturbances (e.g. Díaz et al. 2007; Zheng et al. 2010). To date, there are hardly any studies in Kyrgyzstan using a plant functional trait approach. Only Borchardt et al. (2013) analyzed plant traits in relation to grazing disturbance in SW Kyrgyzstan, highlighting the modification of plant functional traits along grazing gradients. The results of our third article showed that an intensification of grazing can be associated with two main strategies of species response. The majority of plants on winter pastures pursue a resistance strategy (i.e. low stature, SLA and growth form, increasing LMA and early flowering), while species on summer pastures are characterized by a tolerance strategy (higher stature, SLA and growth form, lower LMA as well as late flowering).

The fourth paper focused on diversity analyses, including inventory and differentiation diversity as well as related indices (similarity indices) such as the Jaccard and the Sørensen index. Diversity patterns of ecological communities have been strongly influenced by land use. Particularly in semi-arid and arid ecosystems, unsustainable livestock farming is considered the biggest driver of land degradation, including the loss of biodiversity. In recent years a large number of studies focused on species diversity and diversity indices, but the multitude of different measures of diversity made a fair comparison difficult (e.g. Magurran 2013; Hanke et al. 2014; Moreno et al. 2017). To quantify and compare species diversity Chao et al. (2014) generated a reliable method (non-asymptotic approach), which allows detailed inferences about the sampled assemblages. By using this framework it is possible to derive both theoretical formulas and analytic estimators to measure and assess species diversity. To what extent changing grazing regimes affect plant species diversity of mountain pastures in the Naryn Oblast remains largely unknown. Studies done by Borchardt et al. (2011) or Taft et al. (2011) cannot be considered for a general comparison because of different climate and site conditions, or because of the neglect of spatial and temporal aspects of grazing intensity. We additionally inspected rare endemic species because, according to several authors, especially rare and endemic species are threatened by impacts such as overgrazing and habitat loss and their decline might affect ecosystem functioning (e.g. Mouillot et al. 2013; Soliveres et al. 2016). Studies focusing on effects of grazing on rare endemic plant richness of Kyrgyz high-mountain pastures have not been published so far.

3. Assessment of grazing impact – a methodological overview

It is largely known that grazing can have severe effects on vegetation and soil conditions (Han et al. 2008; Gamoun et al. 2015; Wang et al. 2017). However, the relation between post-Soviet transformation processes and ecological changes of mountain pastures in the Naryn Oblast has rarely been evaluated so far. Based on former ecological studies (Wagner 2009; Borchardt et al. 2011), parameters such as soil properties and vegetation structure, in a broader context, were selected as relevant factors to assess the grazing impact on pasture resources. Because plants are the main contributors of soil organic carbon (SOC), quality and quantity of litter and roots is determined by vegetation which underlines the important relationship between soil and plants. Moreover, soil-vegetation feedback processes designate complex responses and interactions with regard to other biotic and abiotic factors (e.g. Ostle et al. 2009; Wang et al. 2017). The analysis of plant functional traits and their variation along grazing gradients allows better understanding of changing ecosystem functions and may further explain degradation processes. Because of its direct link to the functional trait composition of an ecosystem, the inspection of species diversity, representing number and kinds of species, can generate more detailed insights (Chapin III et al. 2000). For example plant height, closely related to the amount of biomass, is a reliable indicator for disturbances even under diverse land use history and climate combinations (e.g. Díaz et al. 2001; Jauffret and Lavorel 2003). The research area as well as the data collection and analysis will be shortly described in this section.

3.1 Study area and data collection

In the summer months of 2014 and 2015, we collected data in the main study area the Kara-Kujur valley, Naryn Oblast (41° N, 76° E), accompanied by our Kyrgyz colleagues. Additional data were collected in the Naryn State Reserve and its buffer zone further south, where plots were implemented to serve as reference data for less grazed and ungrazed areas (see Fig. 1). Over 70% of the Naryn Oblast, including the Kara-Kujur valley, is covered by mountains with a minimum altitude of 2.000 m a.s.l. It is the largest Oblast but has the lowest resident population (population density of 5.7 per km²), with mainly rural population (about 85%) which is mostly dependent on agriculture and animal husbandry. Large parts of the remote pastures are not accessible due to poor road networks (UCA 2014). We have experienced the missing infrastructure ourselves. Reaching the summer pastures was only possible by horse.

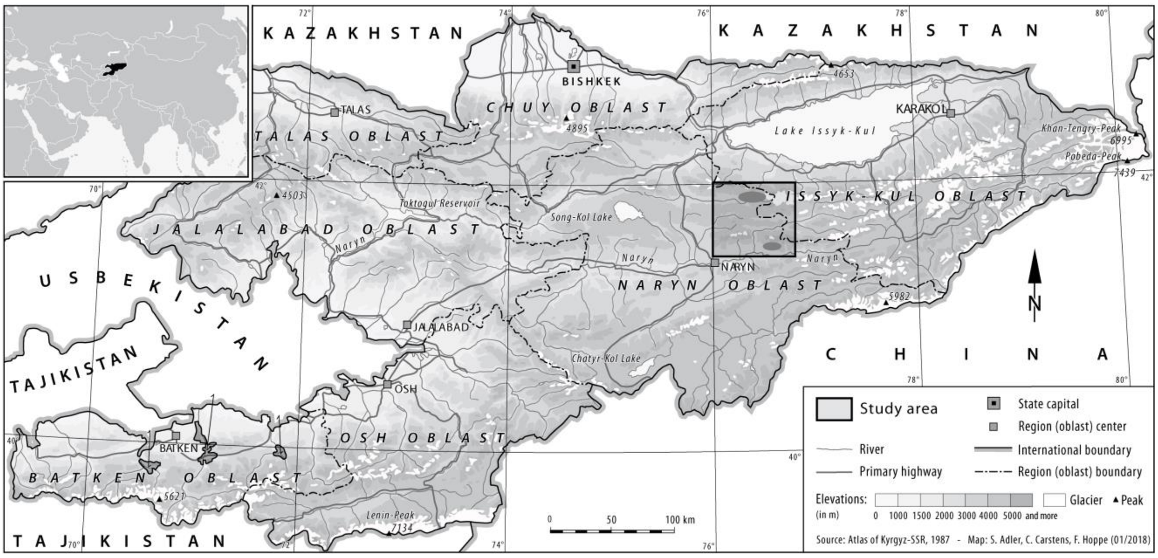

Figure 1: Location of the study area in NE Naryn Oblast. The main research area (Kara-Kujur valley) is marked by the northern oval, while the smaller southern oval represents the Naryn State Reserve and its buffer zone.

A total of 86 sample plots were placed randomly along an altitudinal gradient (between 2.800 m and 3.400 m a.s.l., including winter and summer pastures as well as 6 plots in the Naryn State Reserve), respecting different slope inclinations and expositions as strata. Soil samples were taken from the upper mineral horizon (0-15 cm depth) within each plot with a standard relevé size of 5m x 5m. One sample consisted of three subsamples of 100 cm^3 per relevé, using soil sampling rings. Within each plot, biomass from the surface of one square meter was collected and air-dried. The collected samples were air dried on-site and then transported to Germany for further analysis in the laboratory of the Institute of Geography, University of Hamburg (soil samples), and in the laboratory of the Department Animal Ecology and Conservation, University of Hamburg (biomass samples). For each plot all vascular plants were listed and their cover-abundance according to the traditional Braun-Blanquet scale assessed (Braun-Blanquet 1964). The listed plants were determined by Georgy Lazkov in the herbarium of the National Academy of Science in Bishkek, Kyrgyzstan. The complete data set of soil samples, biomass samples and vegetation surveys represents a comprehensive basis for further analyses. Only one problem concerning biomass samples occurred during the field trip to the State Reserve by horse: Because of long riding distances in direct sunlight some biomass samples were unfortunately rotten.

Our Kyrgyz colleagues were responsible for the acquisition of socio-economic data. The Naryn Oblast consists of five districts, where the Kara-Kujur valley is part of the district Kochkor (UCA 2014). By interviewing the responsible authorities at regional level and the village administration, they collected information about livestock numbers and pasture use rights of the local herders.

3.2 Applied statistical analysis

During the whole dissertation process different statistical approaches were applied. The analyses were done in R, complemented by the JUICE software. Even if the statistical techniques were already presented within the original publications, a short review is necessary to provide a complete overview.

Before assessing the grazing intensity and its impact on vegetation and soil properties, we first implemented a multivariate cluster analysis to determine different vegetation types (e.g. Gronau and Moran 2007; Aggarwal and Reddy 2013). Based on a hierarchical-agglomerative method (UPGMA) and complemented by expert knowledge, the different plots were assigned to the corresponding pasture type (winter pastures, summer pastures or state reserve). The following physical and chemical soil parameters of the pastures types were determined: soil pH, water and organic matter content, electric conductivity (EC), C/N ratio, effective cation exchange capacity (CEC_{eff}), bulk density and grain size distribution. An indirect gradient analysis (NMDS) was performed to evaluate the influence of different environmental factors, designated by Legendre and Legendre (2012) as an appropriate method, and the goodness-of-fit was tested. The human impact was assessed by estimating the grazing pressure by direct observation of different parameters such as plant height, vegetation cover, browsing damage and the amount of dung, which were transferred into a grazing scale. To assure that the different pasture types are not predetermined by spatial structure, a mantel statistic was calculated, indicating no significant correlation between the species assemblages and their geographical distribution (this was part of the second article).

The final diagnostic species of the proposed phytosociological units (i.e. pasture types) were determined by calculating the phi-coefficient (ϕ), using the JUICE software (Chytrý et al. 2002; Tichý 2002). By applying a threshold value of 0.3 diagnostic species were differentiated into diagnostic ($\phi > 0.3$) and highly diagnostic ($\phi > 0.5$) species (Michl et al. 2010). Based on this classification plant functional trait analyses were performed and visualized by barplots and mosaic plots. The significance of the results was tested by either a Kruskal-Wallis test or a t-test and for the mosaic plots by the Pearson residuals from independence. Traits such as plant height, growth form, flowering start as well as LMA (Leaf Mass per Area) and SLA (Specific Leaf Area) were selected and examined because they are considered as being good predictors of grassland response to disturbances (e.g. Díaz et al. 2007; Zheng et al. 2010). Since we did not collect information on LMA and SLA of our diagnostic species, the global database of plant traits, called TRY, provided the required information (Kattge et al. 2011). Furthermore, the amount of biomass as indicator for grazing intensity was analyzed (this was part of the third article).

In the context of ecosystem functioning and the effects of anthropogenic disturbances diversity terms and indices were inspected. With regard to diversity terms, we focussed on inventory (alpha) and differentiation (beta) diversity (Whittaker 1960; Legendre 2008; Tuomisto 2010). To characterize the species diversity of an assemblage, we used the non-asymptotic approach proposed by Chao et al. 2014, generating integrated rarefaction and extrapolation curves based on the first three Hill numbers ($q = 0$: species richness, $q = 1$: Shannon diversity, $q = 2$: Simpson diversity). This concept integrated the two basic types of measures for inventory diversity: estimated species richness and the species-abundance distribution expressed by Shannon and Simpson indices (Jurasinski et al. 2009). To describe changes in species composition along environmental gradients differentiation diversity was analyzed by calculating the Jaccard and the Sørensen indices (Anderson et al 2011; Legendre and De Cáceres 2013). This was complemented by the performance of an analysis of similarity (ANOSIM) to test statistically whether there is a significant difference between species composition of winter and summer pastures (Clarke 1993). To visualize the results of the ANOSIM, a PCoA was subsequently performed based on the same distance matrices (Legendre and De Cáceres 2013). In addition, the occurrence of rare endemic species (according to Czerepanov 1995) was studied in order to include qualitative aspects of the pasture's plant species diversity (this was part of the fourth paper).

4. Overview of original publications

In the context of degradation and management of grazing resources, and aiming at analyzing the main factors which are affecting pasture capacity and condition, this PhD thesis was conducted. To get closer insights into the effects of disturbances by livestock grazing in the Naryn Oblast, various factors such as soil parameters, species composition, plant functional traits, the amount of biomass and diversity indices on different pastures types were analyzed. The results were presented in the following papers, published in peer-reviewed journals except for the first one. The short presentation of each publication (the complete articles are attached at the end of this document) is complemented by an overview of the personal contribution.

4.1 Article I

ZHUSUI KZYZ T, **HOPPE F**, LAZKOV G A, SCHICKHOFF U, USUPBAEV A (2014): Survey of summer vegetation on high mountain pastures in the Kara-Kujur valley, Kyrgyzstan. ISSN: 1694-6731. УДК: 574: 581.9 (575.2) (04). (In Russian)

Аннотация: Проведено исследование летнего аспекта растительности. Получены новые сведения о флористическом составе степей и лугов пастбищ высокогорий долины Кара-Куджур.

Abstract: The occurrence of plant species in summer season has been studied. New information has been obtained on the floristic composition of the steppes and meadows of pastures in the highlands of the Kara-Kujur valley.

Personal contribution: I assisted my Kyrgyz colleagues by conducting the vegetation surveys in the Kara-Kujur valley in summer 2014.

4.2 Article II

HOPPE F, ZHUSUI KYZY T, USUPBAEV A, SCHICKHOFF U (2016) Rangeland degradation assessment in Kyrgyzstan: vegetation and soils as indicators of grazing pressure in Naryn Oblast. Journal of Mountain Science 13: 1567–1583. doi: 10.1007/s11629-016-3915-5

Abstract: Rangelands occupy more than 80% of the agricultural land in Kyrgyzstan. At least 30% of Kyrgyz pasture areas are considered to be subject to vegetation and soil degradation. Since animal husbandry is the economic basis to sustain people's livelihoods, rangeland degradation presents a threat for the majority of the population. We present for the first time an ecological assessment of different pasture types in a remote area of the Naryn Oblast, using vegetation and soils as indicators of rangeland conditions. We analyzed the current degree of utilization (grazing pressure), the amount of biomass, soil samples, and vegetation data, using cluster analysis as well as ordination techniques. Winter pastures (*kyshtoo*) are characterized by higher pH values (average of 7.27) and lower organic matter contents (average of 12.83%) compared to summer pastures (*dzailoo*) with average pH values of 6.03 and average organic matter contents of 21.05%. Additionally, summer pastures show higher above-ground biomass, and higher species richness and diversity. Our results support the hypothesis that winter pastures, which are located near settlements, suffer from over-utilisation, while the more distant summer pastures are subjected to much lower grazing pressure.

Personal contribution: The conception and implementation of the study was the main part of the personal contribution. This includes the data collection on-site, the analysis of the samples as well as the statistical evaluation of the ecological factors such as soil properties and vegetation structure. The assessment of contrasting grazing pressure on winter and summer pastures was also part of the work, supplemented by the creation of the figures and writing the major part of the text. The coauthors Taalaigul Zhusui Kyzy and Adilet Usupbaev provided assistance for the data collection on-site and helped with local expert knowledge. Udo Schickhoff supported the conception of the study and made a substantial contribution to the editorial work.

4.3 Article III

HOPPE F, ZHUSUI KYZY T, USUPBAEV A, SCHICKHOFF U (2016) Contrasting grazing impact on seasonal pastures reflected by plant functional traits: Search for patterns in Kyrgyz rangelands. Geo-Öko 2016: 165–200. [ISSN: 16161-0983]

Abstract: At least 30% of Kyrgyz grazing lands are considered to be subject to vegetation and soil degradation. Since animal husbandry is the economic basis to sustain

people's livelihoods, rangeland degradation presents a threat for the majority of the population. Recently, the usage of plant functional traits as a powerful tool for the characterization of vegetation dynamics in response to anthropogenic and natural disturbances has been put forward. Grazing, one of the most severe disturbances to vegetation is both depending on and affecting plant functional traits. We hypothesized that the contrasting grazing intensity of summer and winter pastures in the Naryn region (central Kyrgyz highlands) is reflected by selected plant functional traits. We used traits such as plant height, flowering start, plant growth form as well as SLA (Specific Leaf Area) and LMA (Leaf Mass per Area). Additionally, we analyzed the amount of biomass as indicator for grazing intensity. Based on a phytosociological classification of the main pasture types (summer and winter pastures), community structure and the traits of dominant plant species have been analyzed. Our results show that high grazing pressure has resulted in decreased plant height and SLA and favored plants with an earlier flowering start as well as rosette and prostrate plants (hemicryptophytes). Respective changes are representative for winter pastures, whereas sets of plant attributes on summer pastures are consistently associated with lower grazing pressure. Our results support the growing recognition that plant functional trait analysis is a promising way to generate insights into the mechanisms of plant response to grazing in high-altitude rangelands.

Personal contribution: The finalization of the entire data set, including the second part of data collection and its statistical evaluation as well as the compilation of the requisite plant functional trait data formed part of this publication. The diagnostic species of the different pasture types were conclusively determined and analyzed with regard to the selected traits. The amount of biomass as indicator for grazing intensity was additionally evaluated and all results were integrated in the final manuscript. The coauthors Taalaigul Zhusui Kyzy and Adilet Usupbaev were equally involved in data acquisition and Adilet Usupbaev provided further information, from Russian sources, concerning selected plant species traits. The text revision was done by Udo Schickhoff who gave helpful advices during the whole writing process.

4.4 Article IV

HOPPE F, SCHICKHOFF U, OLDELAND J (2017) Plant species diversity of pastures in the Naryn Oblast (Kyrgyzstan). DIE ERDE. (accepted)

Abstract: Throughout the Soviet colonial period and in particular after independence in 1991, traditional pastoral practices in Kyrgyzstan have been less performed and sometimes even neglected. Kyrgyz winter pastures close to settlements suffer from degradation, while remote summer pastures are less frequented, causing dissimilarities in the species composition of communities. It is largely unknown to what extent novel grazing regimes modified during the post-Soviet transformation process in Kyrgyzstan have affected plant species diversity of mountain pastures. This paper aims to analyze inventory (α) and differentiation (β) diversity of pastures in the Naryn Oblast, where winter pastures are subjected to increased grazing pressure. We used a non-asymptotic approach in order to infer Hill numbers, i.e. the *effective number of species* at different levels of q (where q = 0: species richness, q = 1: Shannon diversity, q = 2: Simpson diversity) to make fair comparisons among assemblages of winter and summer pastures. We established sample-size-based rarefaction (interpolation) and prediction (extrapolation) curves, and assessed beta diversity by implementing an ANOSIM and by calculating Jaccard and Sørensen indices. We also inspected the occurrence of rare endemic plants, which might play a key role in local ecosystem processes and are important for biodiversity conservation. Grazing pressure on winter pastures in Kyrgyzstan has increased during the post-Soviet transformation process, resulting inter alia from abandoned seasonal livestock migration and unbalanced grazing intensity between seasonal pastures. Our results show that inventory diversity is higher on summer pastures and that species composition between summer and winter pastures differs significantly. Winter pastures are less species rich but have a higher percentage of rare endemic species.

Personal contribution: The conceptual design and the data preparation were components of the personal achievement. Furthermore, inventory and differentiation diversity as well as the diversity indices were calculated and visualized. Rare endemic plants were detected and compared with regard to their occurrence on winter and summer pastures. Textual work was done and has been afterwards revised by the coauthors Udo Schickhoff and Jens Oldeland, who additionally gave statistical advice.

5. Conclusions and outlook

In this conclusion, the obtained insights will be reviewed first, before the effects of the socio-political changes in the post-Soviet Kyrgyz Republic will be discussed and a synthesis of the ecological and socio-economical aspects will be provided. With regard to the findings several suggestions will be presented to implement sustainable management strategies with the aim to maintain and protect these valuable high-mountain pastures.

5.1 The effects of overgrazing on soil and vegetation properties

The analyses conducted during this PhD project clearly showed that the diverging grazing pressure on winter and summer pastures provokes severe changes concerning parameters such as soil properties, plant communities and species traits, the amount of biomass as well as species diversity. The central findings of this work are:

A. First-time determination of plant communities (diagnostic and highly diagnostic species) of different pasture types in the Kara-Kujur valley, Naryn Oblast

B. Identification of the grazing intensity as decisive factor concerning:

    B.1 Soil properties
    B.2 Amount of biomass
    B.3 Functional composition of the vegetation
    B.4 Plant species diversity

C. Highlighting the particular status of winter pastures as significant habitats for rare endemic species

On item A: The pasture vegetation types can be differentiated into two rankless communities. Winter pastures are occupied by *Bupleurum thianschanicum-Androsace dasyphylla* communities, while summer pastures are covered by *Trisetum spicatum-Ptilagrostis mongholica* communities. Even if comparable studies were already done, mostly in SW-Kyrgyzstan, it was not possible to transfer general conclusions to our research area. The determination of plant communities, including diagnostic and highly diagnostic species, has shown that there are remarkable differences. All highly diagnostic species on winter pastures such as *Bupleurum thianschanicum*, *Androsace dasyphilla*, *Plantago arachnoidea* and *Potentilla moorcroftii* have not been found in one of the other related studies (i.e. Epple 2001; Wagner 2009; Borchardt et al. 2011; Taft et al. 2011; Imanberdieva 2015). These new findings emphasize the apparently unique characteristics of winter pastures. The highly diagnostic species of summer pastures were also rarely found in other studies, apart from Imanberdieva (2015), who detected four species within the At-Bashy valleys including: *Trisetum spicatum*, *Ptilagrostis mongholica*, *Ranunculus alberti* and *Carex stenocarpa*.

On item B.1: Our results indicate properties of *Kastanozem* soils, which are widespread in Kyrgyzstan. These are potentially rich soils but the periodic lack of soil moisture presents a major obstacle to high yields (IUSS Working Group WRB 2014). Soil properties of summer pastures are characterized by lower pH values and lower bulk density than winter pastures and on the other hand by higher carbon (C), nitrogen (N), water and organic matter content as well as higher CEC (cation exchange capacity). We were able to show that plots of winter and summer pastures, which are located at same altitudes and which show similar exposition, differed significantly in soil properties such as pH value and organic matter content. It is likely that these differences result from higher stocking rates on winter pastures, implying a higher amount of dung and stronger trampling impact (see also Cui et al. 2005; Sakbaeva 2012). The continuous growth of the total number of livestock reported by our Kyrgyz colleagues reinforced this assumption. Since 2008 an increase of 44% (from 11.293 to 16.256 in 2014) was recorded (Asykulov and Esenaman uulu; unpublished data).

On item B.2: With regard to aboveground biomass, the negative influence of higher grazing pressure (e.g. Zheng et al. 2010; Sun et al. 2011), exemplified by winter pastures, was clearly reflected. Winter pastures have an average biomass dry weight of 50.4 g m^2, which is half as much as the amount on summer pastures (average dry weight of 124.7 g m^2). By comparing this with the amount of biomass collected on the alpine meadows of the State Reserve (average value of 286.4 g m^2) the negative influence of grazing intensity is clearly demonstrated.

On item B.3: The analysis of a common set of plant functional traits allowed us to assess vegetation responses to grazing impact. For example, reduced plant height as a result of a higher grazing impact has been reported by several authors too (e.g. Jauffret and Lavorel

2003; Díaz et al. 2007; Zheng et al 2015). Concerning leaf traits our analyses showed that species on winter pastures with resource conservation strategies are negatively correlated with SLA, while LMA is higher, which is associated with slow-growing species whose leafs are built to persist (Poorter et al. 2009; Zheng et al 2015). In addition, the low data amount concerning traits such as SLA and LMA emphasize that most of our diagnostic species are poorly studied, especially on winter pastures (e.g. *Bupleurum thianschanicum* although occurring with a frequency of 94%).

On item B.4: The importance of biodiversity for ecosystem functioning and particularly for ecosystem resilience has already been reported by several authors, who also pointed out that a comparison of species richness among multiple assemblages facilitates a better understanding of causes and patterns of biodiversity and the assessment of effects of anthropogenic disturbances (Dornelas et al. 2011; Chao and Chiu 2016). Our results corroborate this statement by showing significant differences in species diversity (i.e. species richness, Shannon diversity and Simpson diversity) between summer and winter pastures. Evidence had been provided (e.g. Rahbek 2005; Grytnes and McCain 2013) that, in arid to semi-arid mountains environments, species richness increases from humidity-limited lower altitudes towards higher elevation before it decreases again (hump-shaped pattern). But by comparing plots at same elevation but subjected to contrasting grazing pressure, we were able to demonstrate that decreasing grazing intensity on summer pasture results in higher species richness. Therefore, the influence of intense livestock grazing tends to be the driving factor in the Kara-Kujur valley, while the altitudinal gradient is of subordinate importance. It has been shown that ecosystem performance is promoted by high functional diversity and that resilience is promoted by high response diversity. According to Török et al. (2016), the effects of grazing should be evaluated by including classical diversity measures and by plant trait based approaches, which we have done in article 3 and 4.

On item C: Winter pastures are characterized by a high percentage of rare endemic species. According to Lazkov and Umralina (2015), endemic species in particular continue to be discovered in Central Asia and are still new to science. Higher endemism on winter pastures is highlighted by three of the four highly diagnostic species being Middle Asian endemics: *Bupleurum thianschanicum*, *Plantago arachnoidea* and *Potentilla moorcroftii*. Even if species diversity is lower on winter pastures, following the intermediate disturbance hypothesis according to Connell (1978), stating that diversity is decreasing when an intermediate intensity threshold is exceeded, the proportion of rare endemic species is apparently not, or just marginally, affected. To assess more explicitly the influence of these rare endemic species on ecosystem functioning, further analyses are required. In general, it has been shown that rare species deliver more unusual functions and have a higher potential to enhance the resilience of ecosystem functioning. Thus, minor and apparently unimportant species in rangelands might confer resilience to droughts and heavy grazing, for instance by acting as keystone species in soil resource dynamics (Chapin III et al 2000; Walker 2000; Mouillot et al. 2013; Soliveres et al. 2016). This emphasizes again the unique characteristic of these pastures.

5.2 Regulatory framework for pasture management

The example of winter pastures in the Kara-Kujur valley made evident that the survival of species in the vast rangelands of the Naryn Oblast is nowadays threatened by degradation processes, often due to an unsustainable management of natural resources. Various studies worked on this issue with examples from Kazakhstan (e.g. Hayashi et al. 2006; Rachkovskaya and Bragina 2012), Tajikistan (e.g. Akhmadov et al. 2006; Vanselow 2011) and Kyrgyzstan (e.g. Shigaeva et al. 2007; Baibagushev 2011; Isakov and Thorsson 2015; Zhumanova et al. 2016) or through a comparative approach (e.g. Ludi 2003; Shigaeva et al. 2013; Robinson 2016), to mention just a few among many others.

In Kyrgyzstan socio-political changes after the independence in 1991 resulted in a steep economic decline, followed by deindustrialization and social disintegration. Many people lost their employments and a large number of households, especially in rural areas, were forced to return to self-subsistence, meaning agricultural production. To provide immediate support the republic´s herding collectives were disbanded and animals, equipment and machinery were distributed among collective members. Anyhow, most of the households unexpectedly found themselves to be individual livestock owners without herding experience and state support (Farrington 2005, Shigaeva et al. 2007; Dörre and Borchardt 2012). Nonetheless, the state kept being the owner of the vast pasturelands and until 2009 the strategy was to lease pastures to both individual herders and economic entities. Depending on the type and location of these pastures, local, regional or national authorities were responsible for their management, provoking several discrepancies and conflicts. As a result, this period was marked by informal and unequal resource allocations and therefore a new law on pastures was established in 2009 (Crewett 2012; Dörre and Borchardt 2012). Previously, land use remained mostly uncontrolled, so that the idea of the locally elected pasture committees was to guide the newly decentralized pasture management system, with the aim to avoid unsustainable pasture use and to reduce degradation processes. But these committees are often faced with various confrontations because of intergroup inconsistencies and hence following challenges in implementation and adaption to the existing context. Furthermore, local herders and pasture users do not see the pasture committees as an institution that represents their interests, rather as a way for the government to exercise control and raise taxes. Thus, the planned objective to involve local communities in resource use and pasture management has not been achieved until now and pasture users are asserting their own practices while official decisions are ignored (e.g. Kasymov and Thiel 2014; Crewett 2015b; Dörre 2015; Shigaeva et al. 2016; Levine et al. 2017).

5.3 Preservation of pastorals resources vs. livelihood security

The socio-political history of Kyrgyzstan clearly illustrates the discrepancy between the preservation of traditional practices and pastoral resources in the context of subsistence agriculture. For most of the households (with or without herding experiences) livestock keeping is today the main source of income. Therefore, a high number of livestock and the fattening of animals is the primary interest and pasture condition as well as traditional practices, such as seasonal migration, do not seem to be a factor that is object of people's concern. A wide range of farmers do not realize the problem within current land management practices and that there is a limited carrying capacity of pastures resources. As a consequence they rarely respect the introductions given by the pasture committee, which is reducing the efficiency of the management system (e.g. Schoch et al. 2010; Liechti 2012; Zhumanova et al. 2016). This is a crucial aspect with regard to pastoral resources conservation, because several authors found that the lack of management is a particularly important factor concerning pasture degradation (e.g. Dörre and Borchardt 2012; Levine et al. 2017). But in order to implement sustainable management strategies, it is necessary that herders and pasture users participate in establishing an equilibrium between livestock grazing and the carrying capacity of pastures. Unfortunately, as reported by our Kyrgyz colleagues, reliable numbers on livestock quantity are difficult to obtain. This is mainly due to two reasons. First, local herders often indicate false information concerning livestock numbers to avoid the fees associated with pasture tickets, of which the price is calculated based on animal numbers. This has also been described by Schoch et al. (2010), Crewett (2015b) or Shigeva et al. (2016). Second, the remote location of our study area, 140 km from the district center (UCA 2014) results in a relatively low influence and a small number of regulatory policies of the public authorities.

Nevertheless, pasture degradation in large regions of Kyrgyzstan is most likely a result of complex interactions of manifold factors, including land use and climate changes. Our valuable data set is, however, based on a rather short sample period of two years. Long-term monitoring might reveal further information and insights on soil properties, plant communities including functional diversity and their response to grazing. Additional investigations on changes in precipitation, snowmelt and evapotranspiration may reveal further details on pastures quality and fodder availability as well (e.g. Reyers et al. 2013; Gan et al. 2015). And even though our example is a special case from the Naryn Oblast, the general problem of inconsistencies with regard to pastoral resources conservation and the need of local households to sustain their livelihoods by animal husbandry affects not only Kyrgyzstan but most of the states of the former Soviet Union (e.g. Kreutzmann 2012; Robinson 2016).

5.4 Sustainable pasture management strategies for the Naryn Oblast

It is obviously not possible that high-mountain pastures endure as non-used and isolated areas. It is therefore even more important that traditional practices (i.e. nomadic pastoralism) will be maintained because this lifestyle currently seems to incorporate the best balance between ecosystem functioning and human interactions. Thus, the future availability of pastoral resources depends firstly on a well organized management of pasture use and secondly on a new awareness of local herders with regard to a limited carrying capacity of pastures resources, concerning mainly pastures close to settlements. Shigaeva et al. (2016) showed in their study conducted in the Naryn Oblast that, with regard to a successful implementation of pasture management strategies, it is indispensable to take communities´ and individuals´ perspectives into account. The externally imposed rules do not correspond to local needs and conditions, i.e. missing infrastructure and variations in pasture conditions, making it impossible for local user to accept and adopt these official decisions. In addition, the loss of pastoral cultures and their valuable knowledge are amplified by increasing migration processes affecting mainly the rural population. Due to several economic crises of the transformation period, labor migration is a main livelihood strategy for many households since the 1990s (Sagynbekova 2016). Thus, a reinforcement of the local economy is strongly needed to maintain population in rural areas and the related agricultural expertise.

In the long-term, a better understanding of rangelands and their residents is an essential element. This demands the development of approaches that ensure the resilience of these linked socio-ecological systems in the face of economic, social, environmental and climate changes (e.g. Wrobel and Redford 2010; Rahimon 2012). To maintain resilience and adaptability of social-ecological systems, a heterogeneous collection of individuals, their functions and their interactions is an essential factor. To sustain an ecosystem the existence of various functional groups and the variability in species´ responses to environmental changes is more important than the number of species per se (Folke 2006). The example of the poorly studied species on winter pastures and their potential positive effects on ecosystem resilience clearly sets out that further investigations are strongly needed. Detailed analysis of the effects of endemic species with regard to ecosystem functioning might reveal further insights as well.

This PhD thesis provides data for a better understanding of the impact of disturbances on the ecological state of mountain pastures in the Kara-Kujur valley. Based on our analyses and the results obtained we were able to draw a number of conclusions, for example about the importance of a specific rotation grazing system or the involvement of local communities to implement sustainable pasture management strategies. These findings can be largely transferred to other regions where livestock farming plays a major role and which are affected by post-Soviet transformation processes.

6. List of publications

Original manuscripts in the framework of the PhD thesis

ZHUSUI KZYZ T, **HOPPE F**, LAZKOV G A, SCHICKHOFF U, USUPBAEV A (2014): Survey of summer vegetation on high mountain pastures in the Kara-Kujur valley, Kyrgyzstan. ISSN: 1694-6731. УДК: 574: 581.9 (575.2) (04). (In Russian)

HOPPE F, ZHUSUI KYZY T, USUPBAEV A, SCHICKHOFF U (2016a) Rangeland degradation assessment in Kyrgyzstan: vegetation and soils as indicators of grazing pressure in Naryn Oblast. Journal of Mountain Science 13: 1567–1583. doi: 10.1007/s11629-016-3915-5

HOPPE F, ZHUSUI KYZY T, USUPBAEV A, SCHICKHOFF U (2016b) Contrasting grazing impact on seasonal pastures reflected by plant functional traits: Search for patterns in Kyrgyz rangelands. Geo-Öko 2016: 165–200. [ISSN: 16161-0983]

HOPPE F, SCHICKHOFF U, OLDELAND J (2017) Plant species diversity of winter pastures in the Naryn Oblast (Kyrgyzstan) is threatened by overgrazing. DIE ERDE. (accepted)

Additional publications

HOPPE F, SCHICKHOFF U (2014): Degradation of pastoral resources in the Kyrgyz Republic under post-Soviet transformation. In: Gavin D, Beierkuhnlein C, Holzheu S, Thies B, Faller K, Gillespie R, Hortal J (eds.): Conference program and abstracts. International Biogeography Society 7th Biennial Meeting. 8–12 January 2015, Bayreuth. Frontiers of Biogeography Vol. 6, suppl. 1: 108.

HOPPE F, SCHICKHOFF U, ZHUSUI KZYZ T, USUPBAEV A (2016): Rangeland degradation assessment in Kyrgyzstan: Vegetation and soils as indicators of grazing pressure in Naryn Oblast. In: Röder J, Brandl R (eds.): 150 years of Ecology – lessons for the future. 46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. 5-9 September 2016. Marburg, Germany: 59. ISSN 0171-1113

7. Oral presentations

HOPPE F, SCHICKHOFF U (2015): Degradation of pastoral resources in the Kyrgyz Republic under post-Soviet transformation. Poster presentation. International Biogeography Society 7th Biennial Meeting 2015, Bayreuth.

HOPPE F, SCHICKHOFF U (2015): Boden- und Vegetationsdegradierung von montanen Weidegebieten im postsowjetischen Kirgistan. Presentation. Jahrestagung des AK Hochgebirge „Interdisziplinarität in der Hochgebirgsforschung“. Hamburg.

HOPPE F, SCHICKHOFF U (2016): Analyzing montane pasture use and degradation in the Kyrgyz Republic under post-Soviet transformation. Poster presentation. Central Asian Workshop "Persistence and Change of Institutions in Natural Resources Management in Central Asian context". Berlin.

HOPPE F, (2016): Degradation of pastoral resources in the Kyrgyz Republic under post-Soviet transformation – Presentation of the Main Results. Presentation: final symposium TRANSPAST. Bishkek, Kirgizstan.

HOPPE F, SCHICKHOFF U, ZHUSUI KZYZ T, USUPBAEV A (2016): Rangeland degradation assessment in Kyrgyzstan: Vegetation and soils as indicators of grazing pressure in Naryn Oblast. Poster presentation. 46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland. Marburg.

HOPPE F, SCHICKHOFF U, ZHUSUI KZYZ T, USUPBAEV A (2017): Abandoned seasonal livestock migration reflected by plant functional traits: A case study in Kyrgyz rangelands. Poster presentation. European Geosciences Union - General Assembly 2017. Wien, Austria.

HOPPE F, SCHICKHOFF U (2017): Assessing similarity of species composition with incidence data: A case study from Kyrgyz high-mountain rangelands. Poster presentation. AK Biogeographie. Erlangen.

HOPPE F, SCHICKHOFF U (2018): Soil properties, plant communities and diversity indices as indicators for varying grazing intensity on winter and summer pastures in Kyrgyzstan. Presentation. Jahrestagung des AK Hochgebirge „Gebirgsräume im Wandel“. Innsbruck.

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Attachment: Original publications

Article I

Zhusui Kzyz T, **Hoppe F**, Lazkov G A, Schickhoff U, Usupbaev A (2014): Survey of summer vegetation on high mountain pastures in the Kara-Kujur valley, Kyrgyzstan. ISSN: 1694-6731. УДК: 574: 581.9 (575.2) (04). (In Russian)

УДК: 574: 581.9 (575.2) (04)

Жусуй кызы Т.[1], Хоппе Ф.[2], Лазьков Г.А.[1], Шиккхофф У.[2], Усупбаев А.К.[1].

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Летний аспект растительности пастбищ высокогорий долины Кара-Куджур

Аннотация

Проведено исследование летнего аспекта растительности. Получены новые сведения о флористическом составе степей и лугов пастбищ высокогорий долины Кара-Куджур.

Материалы и методы исследований

Объектом исследований послужил растительный покров пастбищ высокогорий долины Кара-Куджур в позднелетний период 2014 г. Были выделены 52 пробные площадки (5x5 м каждая) по методу Жозиас Бра́ун-Бланке́ (1964). Это метод классификации растительного покрова, предполагающий выделение типичных растительных комплексов по большому набору совместно произрастающих видов растений. Описание таких растительных сообществ предполагает их дальнейший анализ в связи с различными абиотическими и биотическими условиями произрастания. Пробные площадки были установлены случайным отбором. Для каждой пробной площадки фиксировались: координаты; погодные условия; экспозиция, высота над ур. м.; флористический состав, проективное покрытие, биомасса, высота травостоя; отбирались пробы почв на определение химического состава; выявлялось наличие экскрементов.

При определении видового состава растений и их названий, были использованы следующие литературные источники: «Флора СССР», тт. I–XXX (1934–1964); «Флора Киргизской ССР», тт. I–XI (1950–1965); «Определитель растений Средней Азии» тт. I–X (1968–1993); Лазьков Г. А., Султанова Б. А. «Кадастр флоры Кыргызстана» (2011).

Административно высокогорная часть Кара-Куджурской долины находится в Нарынском районе Нарынской области Кыргызской Республики.

Согласно ботанико-географическому районированию Центрального Тянь-Шаня (Головкова, 1962) Долина Кара-Куджур относится к Северо-Западному пустынно-степному округу Султан-сазы-Кара-Куджурскому геоботаническому району. Долина Кара-Куджур вытянута с востока на запад, и длина его составляет 60 км, а наиболее широкая часть 5–6 км. Западная часть ее почти на протяжении 20 км узкая, со скалистыми бортами; с продвижением к востоку она расширяется, и склоны, окаймляющие её, принимают пологие очертания. Наиболее высокогорной частью является северная, где отбельные вершины Терскей Ала-Тоо достигают 4000 м над уровнем моря. Хребет Кара-Джурга, отделяющий долины Кара-Куджур от Султа-сазы имеет меньшие гипсометрические отметки.

Основной водной артерией долины является р. Кара-Куджур, образующая большой водосборный бассейн и впадает в реку Джвуван-арык, являющийся притоком реки Чу.

Климатические условия Султан-сазы-Кара-Куджурского геоботанического района резко континентальные, с большими колебаниями суточных температур. Зимы продолжительные (до 6 месяцев), малоснежные, лето жаркое. Годовое количество осадков до 380 мм, а в отдельные сухие годы всего лишь 160 мм в год. Большая часть осадков выпадает летом. Наблюдается постоянно дующие ветры, которые усиливают сухость климата. (Головкова, 1962).

Результаты исследований

Наиболее распространенными типами растительности в исследуемой части долины Кара-Куджур являются степи. Луга имеют широкое распространение на субальпийских и альпийских высотах, но они менее развиты, чем степи. Леса отсутствуют. Нет здесь и типичных горных тундр и криофильных подушечников. Болота имеют весьма ограниченное пространство.

Летний аспект флоры пастбищ высокогорий долины Кара-Куджур богат и оригинален. Здесь выявлено свыше 190 видов цветковых растений, относящихся к 120 родам и 36 семействам. Из них один вид *Taraxacum syrtorum* Dshanaeva является эндемиком Кыргызстана (Лазьков, Султанова, 2011).

Деревья на исследуемой территории отсутствуют. Произрастают 2 вида кустарников: *Caragana jubata* (Pall.) Poir., *Salix caesia* Vill. Травянистые растения наиболее многочисленны и представлены 191 видом.

Наиболее значимые семейства флоры пастбищ высокогорий долины Кара-Куджур по числу видов: Poaceae (30), Compositae (28), Ranunculaceae (13), Rosaceae (10), Fabaceae (9), Caryophyllaceae (9), Gentianaceae (8), Brassicaceae (6), Labiatae (9), Scrophulariaceae (8), Umbelliferae (7), Boraginaceae (6), Cruciferae (6), Cyperaceae (6), Liliaceae (6), Primulaceae (6). Остальные семейства представлены менее чем 5 видами.

Видовой состав, зафиксированный на пробных площадках:

Achillea millefolium, Aconitum nemorum, Aconitum rotundifolium, Adenophora himalayana, Agropyron batalinii, Agropyron propinquum, Alchemilla retropilosa, Alchemilla sibirica, Alfredia acantholepis, Allium platyspathum, Allium atrosanguineum, Allium schoenoprasoides, Allium semenovii, Allium tianschanicum Alopecurus pratensis, Androsace dasyphylla, Androsace septentrionalis, Androsace sericea, Anemone protracta, Angelica brevicaulis, Arenaria meyeri, Arnebia tibetana, Artemisia aschurbajewii, Artemisia dracunculus, Artemisia rhodantha, Aster canescens, Aster serpentimontanus, Astragalus alpinus, Astragalus tibetanus, Bromus inermis, Bromus paulsenii, Bupleurum thianschanicum,Campanula glomerata,Caragana jubata, Carduus nutans,Carex aterrima,Carex melanantha,Carex stenocarpa, Carex turkestanica, Carum carvi, Cerastium cerastoides,Cerastium pusillum, Chorispora sibirica,Cirsium esculentum,Codonopsis clematidea,Cortusa brotheri, Corydalis gortschakovii, Crepis multicaulis, Dactylisglomerata, Delphinium oreophilum, Dianthus superbus, Doronicum turkestanicum, Draba altaica, Dracocephalum bipinnatum, Dracocephalum imberbe, Dracocephalum integrifolium, Dracocephalum nodulosum, Dracocephalum stamineum, Elymus flexilis, Ephedra fedtschenkoae, Erigeron aurantiacus, Erigeron lachnocephalus, Eritrichium villosum,Euphorbia alatavica, Euphrasia pectinata,Festuca alatavica, Festuca rubra,Festuca valesiaca,Galium turkestanicum, Galium verum, Gastrolychnis apetala, Gentiana kaufmanniana,Gentiana algida,Gentiana barbata, Gentiana falcata, Gentiana karelinii, Gentiana kirilowii, Gentianella turkestanorum,Geranium saxatile, Glaux maritima, Goniolimon ortocladum, Hedysarum kirgisorum, Hedysarum neglectum, Hedysarum sp., Helictotrichon desertorum, Helictotrichon schellianum, Hierochloe odorata, Hippuris vulgaris, Hordeum brevisubulatum, Hordeum sp., *Inula rhizocephala, Isatis costata, Ixiolirion tataricum, Kobresia capilliformis, Kobresia humilis, Koeleria cristata,* *Lagotis integrifolia, Lappula microcarpa, Lappula rupestris, Leontopodium ochroleucum, Ligularia alpigena, Ligularia thomsonii,Lindelofia stylosa, Lomatogonium carinthiacum, Lonicera alberti, Minuartia verna, Myosotis alpestris, Orostachys thyrsiflora,Oxytropis globiflora, Oxytropis lapponica, Oxytropis penduliflora, Papaver croceum, Parnassia laxmannii, Pedicularis oederi, Pedicularis dolichorhiza, Pedicularis ludwigii, Pedicularis macrochila, Phleum alpinum, Phleum pratense, Phlomoides oreophila, Picris nuristanica, Plantago arachnoidea, Plantago depressa, Plantago lanceolata, Poa alpina, Poa pamirica, Poa relaxa, Poa supina, Polygala hybrida, Polygonum nitens, Polygonum songaricum, Polygonum viviparum, Potentilla anserina, Potentilla asiae-mediae, Potentilla asiatica, Potentilla hololeuca, Potentilla moorcroftii, Potentilla nivea, Potentilla pamiroalaica, Potentilla sericea, Primula algida, Ptilagrostis mongolica, Puccinellia hackeliana, Pulsatilla campanella, Pyrethrum karelinii, Pyrethrum pyrethroides, Ranunculus alberti, Ranunculus popovii, Ranunculus pulchellus, Ranunculus songaricus, Rhodiola gelida, Rhodiola linearifolia, Rumex acetosa, Salix caesia, Saussurea caespitans, Saussurea leucophylla, Saussurea sordida, Scabiosa alpestris, Schmalhausenia nidulans, Schulzia albiflora, Scrophularia kiriloviana, Scutellaria oligodonta, Semenovia transiliensis, Serratula marginata, Seseli mucronatum, Silene graminifolia, Stachyopsis oblongata, Stellaria brachypetala, Stellaria soongorica, Stipa caucasica, Stipa krylovii, Stipa purpurea, Stipa regeliana,Taphrospermum altaicum,Taraxacum pseudoalpinum, Taraxacum syrtorum, Thalictrum alpinum,Thalictrum minus, Thesium alatavicum, Thlaspi ferganense, Torularia korolkowii, Tragopogon turkestanicus, Triglochin maritima, Trisetum spicatum, Trollius dschungaricus, Trollius lilacinus, Tulipa heterophylla,Valeriana ficariifolia,Veronica ciliata,Viola dissecta, Viola tianschanica, Ziziphora clinopodioides.*

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Article II

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Rangeland degradation assessment in Kyrgyzstan: vegetation and soils as indicators of grazing pressure in Naryn Oblast

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Abstract: Rangelands occupy more than 80% of the agricultural land in Kyrgyzstan. At least 30% of Kyrgyz pasture areas are considered to be subject to vegetation and soil degradation. Since animal husbandry is the economic basis to sustain people's livelihoods, rangeland degradation presents a threat for the majority of the population. We present for the first time an ecological assessment of different pasture types in a remote area of the Naryn Oblast, using vegetation and soils as indicators of rangeland conditions. We analysed the current degree of utilization (grazing pressure), the amount of biomass, soil samples, and vegetation data, using cluster analysis as well as ordination techniques. Winter pastures (*kyshtoo*) are characterized by higher pH values (average of 7.27) and lower organic matter contents (average of 12.83%) compared to summer pastures (*dzailoo*) with average pH values of 6.03 and average organic matter contents of 21.05%. Additionally, summer pastures show higher above-ground biomass, and higher species richness and diversity. Our results support the hypothesis that winter pastures, which are located near settlements, suffer from over-utilisation, while the more distant summer pastures are subjected to much lower grazing pressure.

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Introduction

Animal husbandry has always played a major role in the life of Kyrgyz people, and the livestock sector has been one of the strongest components of the regional economy during Soviet and post-Soviet times (Ludi 2003; Baibagushev 2011; Dörre 2012; Schmidt 2013). Montane and alpine rangelands, which occupy an area of more than 9 million hectares (45% of the Kyrgyz land area), represent the significant basis for this economic sector (Baibagushev 2011; Taft et al. 2011; Dörre

2012; Sakbaeva et al. 2012). Prior to the colonization by the Soviet Union, nomadism was predominant in Kyrgyzstan. The pastoral nomadic land use system was adapted to local arid and semi-arid ecological conditions. Most pastoralists practised mobile livestock keeping and their flocks moved between seasonal pastures. The herds were driven up to montane and alpine pastures (*dzailoo*) in summer, and they grazed on pastures at lower elevations (*kyshtoo*) in winter (Shigaeva et al. 2007; World Bank 2007; Jacquesson 2010). The core of Kyrgyz nomadic lifestyle was represented by sheep and horses. For the most part herds still consist of sheep and horses but there are also flocks of goats, cows and yaks (Steimann 2010).

Under the Soviet regime, the transhumant grazing system was largely maintained. At the same time, the livestock industry had been massively expanded. According to Schoch et al. (2010), the flock size was two or three times higher than the carrying capacity of the pastures. Sedentarization and collectivization campaigns were forced and the formerly autonomously acting pastoralists were replaced by *sovkhozes* (state owned farms) and *kolkhozes* (collective farms) according to the Soviet model of agriculture management. The Kyrgyz Socialist Soviet Republic (KSSR) was destined to develop a wool, milk, and meat production industry (Farrington 2005; Dörre and Borchardt 2012; Kreutzmann 2013). Like Schoch et al. (2010) pointed out: “All in all, the Soviet livestock sector can be described as a high-output but unsustainable system”. The first years after independence saw a drastic reduction in livestock numbers, and a temporarily decreasing grazing pressure. In the period from 1989 to 1996 the number of sheep decreased from 10.3 million to 3.7 million (Schoch et al. 2010; Schmidt 2013). In the further course of post-Soviet transformation, livestock numbers have increased again considerably. At least 30% of pasture areas are currently subject to vegetation and soil degradation (e.g. Baibagushev 2011; World Bank 2014; Kulikov et al. 2016).

After the Soviet era and the end of the state-dominated system, land and livestock were privatised. This period was marked by far-reaching political and economic transformations with various social and commercial restrictions, especially for communities on the local level (Blank 2007; Borchardt et al. 2010; Dörre and Borchardt 2012). For most of the Kyrgyz people, the return to a subsistence lifestyle was the only possibility to sustain their livelihood (Laruelle and Peyrouse 2010; Borchardt et al. 2011). The dissolution of the institutionalized organisation embodied by the *kolkhozes* and *sovkhozes* presented an unexpected challenge for the farmers under the post-soviet regime. They were not prepared for a self-dependent, non-governmental management (Borchardt et al. 2011; Schmidt 2013). The period of post-Soviet transformation is defined by low efficiency and instability of the pasture economy (Esengulova et al. 2008; Schoch et al. 2010).

The adoption of a sedentary lifestyle provoked severe changes of traditional pasture practices. During the occupation, the *kolkhozes* organised annual migratory herd movements (Ludi; 2003; Crewett 2012; Kreutzmann 2013), providing a more homogeneous distribution of grazing pressure. Nowadays the herders themselves are responsible for the migration of livestock, but remote summer pastures are particularly difficult to reach. High individual migration costs and long distances as well as a weak state of infrastructure are responsible for the under-utilization of remote pastures (Crewett 2012; Dörre 2012). Summer pastures at higher elevations experience increasing abandonment (Esengulova et al. 2008; Schmidt 2013; Shigaeva et al. 2013), while the utilization of winter pastures, which are located close to settlements, is intensified with an increasing risk of vegetation and soil degradation. The investigation of the ecological consequences of this discrepancy, in particular with regard to the local context, represents a current gap in research. The Naryn Oblast provides the main pasture lands in Kyrgyzstan, and will play a major role in ensuring the long term sustainability of livestock farming - the source of Kyrgyz livelihood (Imanberdieva 2015). However, the ecological state of Naryn rangelands and pasture resources has not been assessed to date.

The issue of degrading rangelands in the Kyrgyz Republic has been already addressed (e.g., Wagner 2009; Borchardt et al. 2011; Dörre and Borchardt 2012), but the study areas were mostly located in the South-West of Kyrgyzstan with its different climate and site conditions. Other related studies focused more on political aspects (Ludi

2003; Shigaeva et al. 2007; Crewett 2012; Schmidt 2013). Only very few studies (Farrington 2005; Taft et al. 2011; Imanberdieva 2015) provide some information relevant to our research area. To fill this research gap the focus is on analysing and comparing the ecological status of pastures under different grazing regimes. Since our study area (the *Kara-Kujur* valley in the Naryn Oblast) is considered as scientifically unexplored (Borchardt et al. 2011; Taft et al. 2011; Eisenman et al. 2013), the primary objective is to (1) determine principal soil physical and chemical properties; (2) to analyse floristic differentiation of (sub-) alpine pasture types and to classify characteristic plant communities; (3) and to assess the grazing impact. We hypothesize that the increasing utilization level of winter pastures results in a deterioration of soil properties, and that the contrasting grazing intensity of summer and winter pastures is reflected in vegetation traits such as floristic composition, species richness and species diversity. We further expect that a differentiation of the pasture types will be possible based on the indications of soil properties and vegetation characteristics.

1 Study Area

The Kyrgyz Republic is characterized by the Tian Shan mountain system, which covers the major portion of the country. About 94% of the land surface is mountainous (Farrington 2005; Eisenman et al. 2013; World Bank 2014). One quarter of the territory (474.708 km²) is classified as steppe. Steppe formations correspond to the general climatic conditions (aridity and strong winds), but have been enlarged due to human impact such as logging and grazing, which leads to an ongoing degradation of pasture land (Imanberdieva 2015). In this study we will use the term '*degradation*' in accordance with Johnson and Lewis (2007), who restrict the usage of the term 'land degradation' to cases where a considerable decrease regarding the productivity of a land system is assessed and where this decrease is the result of human-induced processes rather than natural events. Here, the decrease in productivity will be measured by indicators such as amount of biomass, maximum plant height and organic matter content and the impact of human activities will be assessed by indicators like grazing impact and bulk density (as a result of livestock trampling).

This study was conducted in the Middle Tian Shan, in the north-east of the Naryn Oblast (41° N, 76° E), which is characterized by (sub-) alpine steppes and meadows (Figure 1). Naryn is not only the largest Oblast in Kyrgyzstan (45.200 km²), but also the one with the highest percentage of Kyrgyz

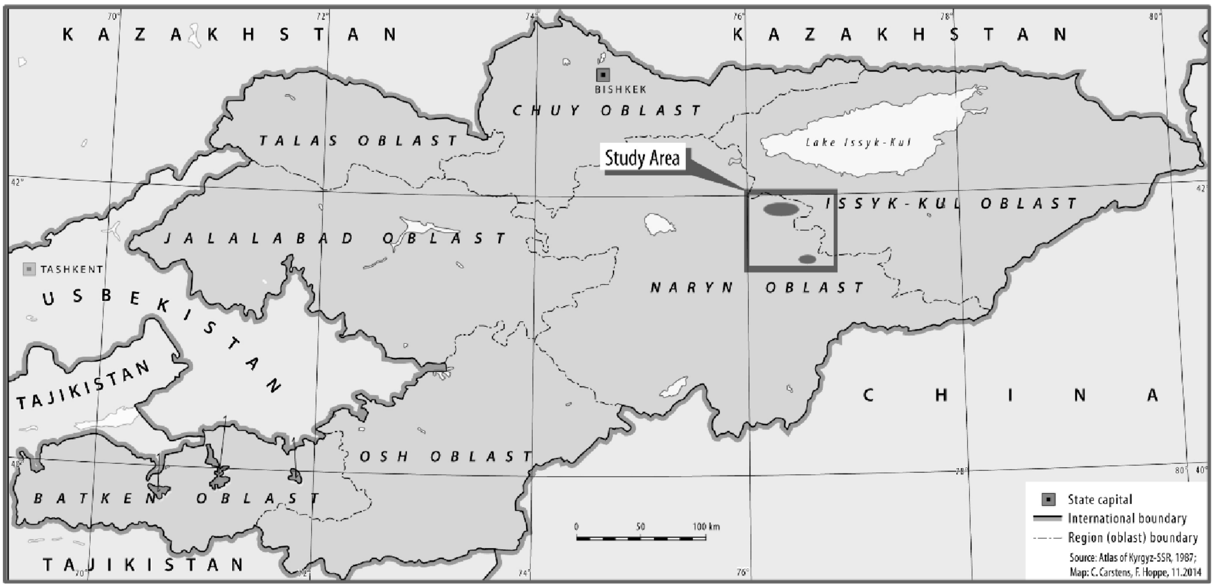

Figure 1 Location of study area. The Kara-Kujur valley is marked by the northern oval, while the smaller southern oval represents the State Reserve and its buffer zone.

pastures, approximately 30% (Crewett 2012). A large part of the Naryn Oblast is used as grazing land which sustains increasing livestock numbers (Blank 2007; UCA 2014). The climate in Kyrgyzstan varies from dry continental in the plains to cold and harsh at higher elevations. Due to the topography, the climate is characterized by sharp local differences. The *Kara-Kujur* valley is part of an inner basin landscape and is significantly drier than the northern and southern mountain range of Kyrgyzstan (Gottschling 2006). The average annual precipitation amounts to 200 to 300 mm only. Winters are cold and long with average temperatures of -15° in January. Accordingly, the vegetation period, i.e the agricultural season is comparatively short (Gottschling 2006; Eisenman et al. 2013; UCA 2014).

Kyrgyzstan has a rich flora which contains more than 4.100 species of vascular plants (approximately 450 species for fodder), characterized by a notable percentage of Middle Asian endemics (Taft et al. 2011; Eisenman et al. 2013, Ch. 1). The vegetation structure is extremely complex, with a huge variety of different vegetation types. The classification of plant communities is still a subject of discussion (Umralina and Lazkov 2008). The term 'Middle Asia' refers to the former Soviet Central Asian Republics Kazakhstan, Turkmenistan, Uzbekistan, Tajikistan and Kyrgyzstan (cf. Cowan 2007).

2 Materials and Methods

2.1 Data collection

Vegetation, biomass and soil samples were collected in the valley of *Kara-Kujur* in summer 2014. We completed 52 vegetation relevés according to the Braun-Blanquet approach (Dierschke 1994). We used a standard relevé size of 5 m × 5 m. We conducted stratified random sampling, with different slope inclinations and expositions as strata. Sample plots were placed randomly along an altitudinal gradient (between 2.800 m and 3.400 m, including winter and summer pastures). In addition, we sampled three plots in the Naryn State Reserve and its buffer zone (at elevations between 2.800 m and 3.150 m). These three plots serve as reference data for less grazed and ungrazed areas.

For the total of 52 plots we listed all vascular plants and assessed their cover-abundance according to the traditional Braun-Blanquet scale with 7 classes (Braun-Blanquet 1964; Kent 2012). The listed plants were determined in the herbarium of the National Academy of Sciences in Bishkek. The Nomenclature of vascular plant species follows Czerepanov (1995). Soil samples were taken (three subsamples of 100 cm^3 per relevé, using soil sampling rings) from the upper mineral horizon (0-15 cm depth). Further, biomass from the surface of one square meter within each plot was collected and air-dried. We complemented field sampling by an assessment of human impact. Grazing impact was estimated by direct observation of different parameters, such as plant height, vegetation cover, browsing damage and the amount of dung. We transferred those information into a grazing scale with 5 classes (1 = no grazing, 5 = heavy grazing).

2.2 Data analysis

2.2.1 Cluster analysis

We implemented a multivariate cluster analysis to determine different vegetation types. The original cover-abundance values were transformed according to van der Maarel (1979). The transformed scale is completely numeric and was used to apply the *hclust* function of the R-Package *vegan* (van der Maarel 2007). In this study we used a hierarchical-agglomerative method, which follows a bottom-up approach. The clustering is based on the average-linkage algorithm also known as *Unweighted Pair Group Method with Arithmetic mean* (UPGMA) (Gronau and Moran 2007; Loewenstein et al. 2008; Aggarwal and Reddy 2013). The algorithm presents a perfect adjustment between the minimum and maximum algorithm, which is more sensitive to outliers (Leyer and Wesche 2007; Vanselow 2011). The goodness-of-fit was tested by calculating the cophenetic correlation coefficient (*c*), given and discussed by Saraçli et al. (2013). This is a widely used measure, which allows the comparison of the deviance of a cluster from the original dissimilarity matrix (Sokal and Rohlf 1962). As stated in the study of McGarigal et al. (2000), a value of $c \geq 0.75$ signifies a good result for the cluster analysis. The calculation of the cophenetic correlation coefficient for our cluster analysis revealed a value of 0.79, which confirms a good representation of the original distance matrix used for cluster analysis (Oldeland et al. 2010).

2.2.2 Classification, indicator species and diversity analysis

To complement the cluster analysis and to differentiate plant communities of different pasture types, we applied the traditional classification method of the Braun-Blanquet approach (Dierschke 1994). The differentiation of vegetation units is based on diagnostic species. Determinations of diagnostic species followed the criteria of constancy differences proposed in Dierschke (1994). Species have to fulfill the criterion of a constancy difference of two classes to be classified as diagnostic species. In many cases manual and numerical classifications yield different results, that is one reason why the unification of traditional and numerical approaches is often recommended (Wildi 1989; De Cáceres et al. 2009). Thus, Indicator Species Analysis (ISA) was performed. By implementing ISA, an indicator value index is defined to measure the association between a site group representing habitat or community types and a species. The most characteristic species of each group (referring to our rankless communities) are identified that way as indicator species, indicating the strength of the association to the respective group and simultaneously the species' ecological preference (Dufrêne and Legendre 1997). The analysis reveals additional information about two components (A and B). In this case A is defined as specificity or positive predictive value, meaning the probability that inspected sites belong to the target site group due to the occurrence of this species. Component B represents sensitivity or fidelity, which stands for the probability that the species occurs on sites belonging to the target site group (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009). Additionally, we calculated the Shannon-Weaver diversity index to define alpha-diversity (Shannon and Weaver 1963; Magurran 2004).

2.2.3 Soil investigation

We determined the following physical and chemical parameters in the laboratory of the Institute of Geography, University of Hamburg: soil pH, water and organic matter content, electric conductivity (EC), C/N ratio, effective cation exchange capacity (CEC_{eff}), bulk density and grain size distribution. Soil pH was measured in a 1:2.5 soil: 0.01 M calcium chloride solution. Kissel et al. (2009) recommended the measurement of pH using a 0.01 M $CaCl_2$ instead of a measurement in H_2O to minimize errors. The water content was determined after drying the samples at 105°C and the organic matter after drying them at 430°C. The electric conductivity (EC) was determined in a 1:2.5 soil: demineralized water solution. Before determining the C/N ratio, the pre-treated samples were grounded with a ball mill (Retsch Inc.). The C/N ratio was calculated after measuring the carbon and nitrogen content with a TruMac determinator (leco Inc.). For the effective cation exchange capacity (CEC_{eff}), and the analysis of element concentrations respectively, all samples underwent a percolation process with ammonium chloride (NH_4Cl). The element concentrations Al, Ca, Fe, K, Mg, Mn, and Na were determined with ICP-OES (Optima 2100, Perkin Elmer Inc.). Bulk density was calculated for each sample with the equation: bulk density = dry bulk density + 0.009 * *c* (mass of clay in %). For the grain size analysis all soil samples were pretreated with hydrogen peroxide (H_2O_2) to eliminate organic matter and partly with hydrochloride acid (HCL) to eliminate carbonates. Prior to the measurement, a dispersion medium of $Na_4P_2O_7$ was added. Sand fractions were determined through forming fabrics and a set of ASTM sieves. The separation of the smaller granulometric fractions was made using the fractionated sedimentation technique with subsequent drying and weighing. All these techniques are described in Carter and Gregorich (2008).

2.2.4 Ordination and measurement of spatial autocorrelation

We used NMDS (Non-metric Multidimensional Scaling) as ordination technique, because the priority lies on the representation of the objects in a small number of dimensions (usually two or three). For this purpose NMDS is an appropriate method (Legendre and Legendre 2012). To measure the goodness-of-fit of the monotone regression, we plotted the original distances (based on a Bray-Curtis triangle matrix) against the new distances in the ordination space (= R^2). Deviations from this condition of monotonicity are indicated by stress. The non-metric fit R^2 is defined as $R^2 = 1\text{-}S \times S$ where S indicates the stress value (Venables and Ripley 2002, Oksanen 2013). The higher the stress value is, the lower the R^2 will be and the condition of monotonicity will be restricted (Legendre and Gallhert 2001; Legendre and Legendre 2012). In our implemented analysis a stress value of 0.181463 was calculated, hence the R^2 with a value of 0.967 is still close to 1 (the optimum).

Spatial autocorrelation was tested by calculating a mantel statistic. The results, visualized in a mantel correlogram (Figure 2), indicate that there is no significant correlation between the species assemblages and their geographical distribution (Oden and Sokal 1986; Borcard et al. 2011; Diniz-Filho et al. 2013). It is important to assure that the different pasture types are not predetermined by the spatial structure. Additionally, a correlation matrix (Appendix 1) was implemented to evaluate the connection of the explanatory variables. The matrix is computed based on Pearson´s correlation coefficient. To test the significance of relationships, we used the chi-square statistic, which confirmed that the data are normally distributed (Legendre and Legendre 2012). For statistical evaluation, the collected data were analyzed in R© (R version 3.1.2; 2014-10-31) using the Packages *MASS*, *indicspecies*, *vegan* and *EcoGenetics* (Venables and Ripley 2002; De Cáceres and Legendre 2009; Oksanen et al. 2016; Roser et al. 2015).

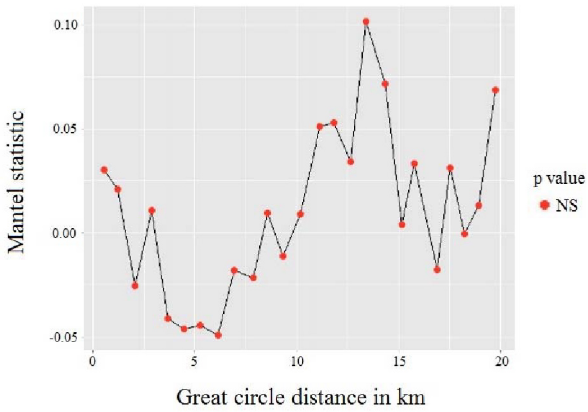

Figure 2 Mantel correlogram of the Hellinger-transformed and detrended species data after Holm correction. There is no significant (NS) correlation between both matrices.

3 Results

3.1 Classification of different pasture types

The classification using the average linkage cluster algorithm has been visualized by a cluster dendrogram (Figure 3). The upper end of the scale shows maximum dissimilarities, whereas the bottom end of the scale (ordinate axis) indicates relevés which are more similar to each other (Sokal and Rohlf 1962; Leyer and Wesche 2007). The dendrogram clearly shows two different pasture types: 18 plots were detected to be part of the winter pastures (on the left side of the dendrogram) and 28 plots to be part of the summer pastures (on the right side of the dendrogram). The cluster analysis additionally identified three plots of the State Reserve and its buffer zone (plots 3, 4, 5) as well as three outliers (plots 34, 50, 52). The same arrangement is presented by the ordination using NMDS (Appendix 2). For further investigations the outliers will be excluded. Based

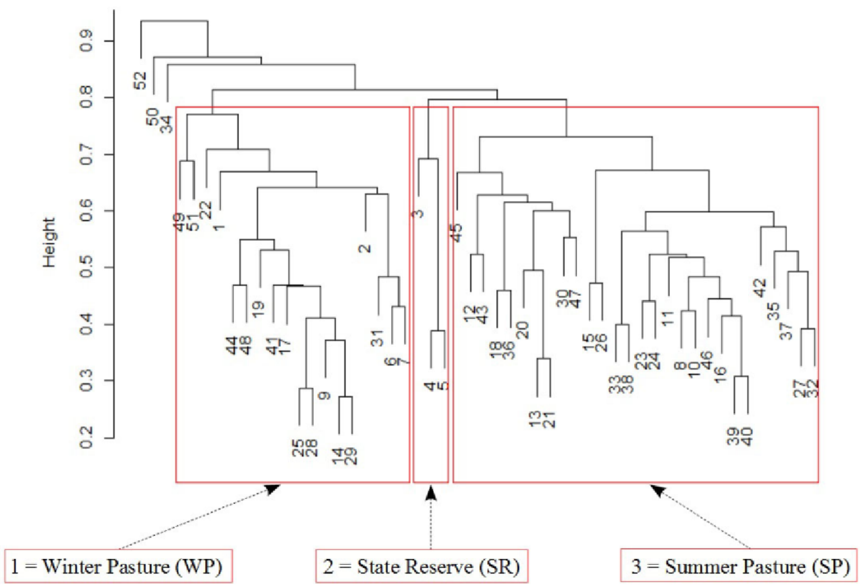

Figure 3 Results of the cluster analysis (based on the average-linkage algorithm) presented as dendrogram of different pasture types.

on the results of the Mantel test and the correlation matrix, we showed that the differentiation of pasture types is mainly driven by grazing impact, which is positively correlated with pH value and negatively correlated with soil organic matter content and maximum plant height. A weak negative correlation exists between grazing impact and altitude. However, by comparing plots of summer and winter pastures which are located at same elevations and which show similar exposition, we demonstrated that grazing pressure is the main driver for the differentiation of pastures types (Table 1).

3.2 Vegetation analysis

A total of 166 vascular plants were identified within the 52 plots. On average, 23 (standard deviation ± 7) species occurred per plot (minimum: 8, maximum: 35). The most species-rich genera were *Potentilla* (8 spp.), *Allium*, *Carex* (5 spp. each) and *Pedicularis* and *Stipa* (4 spp. each). *Gentiana karelinii, Trisetum spicatum*, *Gentianella turkestanicum* and *Cerastium pusillum* were identified as diagnostic species of summer pastures, while diagnostic species of winter pastures include *Bupleurum thianschanicum*, *Stipa purpurea*, *Plantago arachnoidea* and *Potentilla moorcroftii*. Additionally we identified four main companion species: *Festuca valesiaca*, *Taraxacum maracandium*, *Leontopodium ochroleucum and Kobresia humilis*. The complete list of species is presented in Appendix 3.

Complementarily, we performed an indicator species analysis (ISA). The results of the ISA (Table 2) revealed similar results with regard to the phytosociological identification of diagnostic species. The table only exposes species with a *p*.value = 0.001 (significant) and an indicator value index (*stat*) > 0.65. Species identified as diagnostic species of winter and summer pastures (as a result of the traditional classification) turned out to be at the same time significant indicator species, i.e. highly indicative of ecological conditions of respective relevé groups. Concerning the summer pastures, ISA indicates three additional species: *Carex stenocarpa*, *Trollius dschungaricus* and *Phlomoides oreophila*. These species show less constancy compared to diagnostic species, but occur with high cover-abundance, which explains high indicator value indices. Supported by this analysis we can differentiate the pasture vegetation types into two rankless communities: Winter pastures are covered by *Bupleurum thianschanicum-Stipa purpurea* communities, while summer pastures are occupied by *Trisetum spicatum-Gentiana karelinii* communities.

Species richness analysis showed highest values in the State Reserve and its buffer zone, with an average of 33 species per site (standard

Table 1 Vegetation patterns are more influenced by grazing pressure than by elevation. Altitude, exposition, species richness, and soil properties (pH = pH value, organ_mat = organic matter content, height_max = plant height) are listed for the winter and summer pasture sites at same elevations.

Winter pasture	Summer pasture
Plot 9 (3040 m)	Plot 35 (3035 m)
Exposition: 320°, 15 species	Exposition: 350°, 35 species
pH = 7.2, organ_mat = 12.95%, height_max=15 cm	pH = 6.5, organ_mat = 22.51%, height_max = 45 cm
Plot 17 (3110 m)	Plot 23 (3107 m)
Exposition: 180°, 12 Species	Exposition: 120°, 28 species
pH = 7.0, organ_mat = 11.67%, height_max=15 cm	pH = 5.8, organ_mat = 14.12%, height_max = 35 cm
Plot 41 (3221 m)	Plot 16 (3251 m)
Exposition: 200°, 20 species	Exposition: 220°, 34 species
pH = 7.4, organ_mat = 8.78%, height_max = 40 cm	pH = 5.5, organ_mat = 16.48%, height_max = 50 cm

Table 2 Indicator species analysis of winter and summer pastures

Group 1 (Winter pastures) #sps. 6				
Species	A	B	stat	p. value
Bupleurum thianschanicum	0.9216	0.8889	0.905	0.001***
Stipa purpurea	1.0000	0.5000	0.707	0.001***
Plantago arachnoidea	0.9167	0.5000	0.677	0.001***
Potentilla moorcroftii	0.9000	0.5000	0.671	0.001***
Group 3 (Summer pasture) #sps. 25				
Species	A	B	stat	p.value
Trisetum spicatum	0.9636	0.8214	0.890	0.001***
Gentiana karelinii	0.8772	0.8571	0.867	0.001***
Cerastium pusillum	0.9750	0.7143	0.835	0.001***
Gentianella turkestanorum	0.8600	0.6786	0.764	0.001***
Carex stenocarpa	0.9383	0.5357	0.709	0.001***
Trollius dschungaricus	1.0000	0.5000	0.707	0.001***
Phlomoides oreophila	0.8136	0.5357	0.660	0.001***

deviation ± 1.5). Summer pastures average out at a richness of 27 species per site (standard deviation ± 4). Winter pastures exhibit lowest species richness with 17 species per site on average (standard deviation ± 3). This pattern is confirmed by the Shannon´s diversity index. Summer pastures are generally characterized by a higher diversity index (between 2.8 and 3.4), while winter pastures show diversity indices between 2.2 and 3.0.

3.3 Biomass and assessment of grazing pressure

Aboveground dry weight biomass was measured as a comparative proxy for grazing pressure. Average values for winter pastures (45.5 g m^{-2}) were found to be much lower compared to summer pastures (126.3 g m^{-2}). The significant differences concerning the amount of biomass between summer and winter pastures were confirmed by implementing a t-test ($p \leq 0.05$). Dry weight biomass of the two plots in the buffer zone was more than twice as high as the weight calculated for summer pastures (Figure 4). Samples from the State Reserve were unfortunately rotten due to logistic inconveniences.

The assessment of grazing pressure revealed substantial differences between winter and summer pastures. All plots belonging to winter pastures were associated with a grazing pressure between class 3 (moderate) and 5 (heavy), whereas summer pastures never exceeded class 3. To date, the over-utilisation of winter pastures is an ongoing process. The number of livestock in the Naryn Oblast as well as in the *Kara-Kujur* valley increased continuously since 2008. The total number of grazing animals in the *Kara-Kujur* valley (including all kinds of domestic livestock: cow, horse, yak, sheep and goat) increased by 44%, from 11.293 in 2008 to 16.256 in 2014 (Asykulov and Esenaman uulu; unpublished data).

3.4 Soil properties

Soil properties of summer pastures are characterized by lower pH values and lower bulk density than winter pastures on the one hand, and higher carbon (C), nitrogen (N), water and organic matter content as well as higher CEC (cation exchange capacity) and higher amount of clay on the other hand (Table 3). Winter pastures have generally higher pH values (Figure 5a) and lower soil organic matter contents (Figure 5b), pointing to considerable differences between summer and winter pastures with regard to nutrient availability and other plant and soil interactions.

By implementing an ANOVA the differences were tested and the results showed that pH values [$F(1,44) = 56.21$; *** $p \leq 0.001$] and organic matter content [$F(1,44) = 47.99$; *** $p \leq 0.001$] are

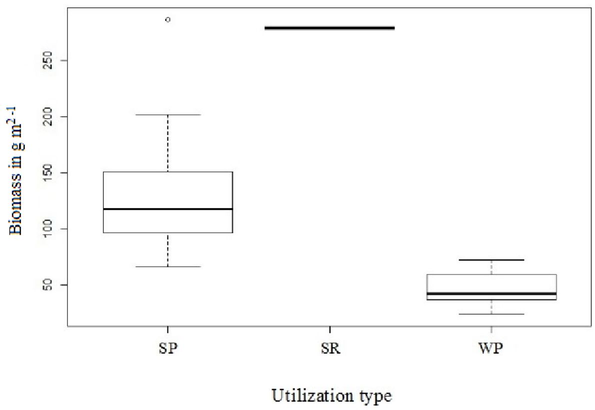

Figure 4 Dry weight biomass of the differentiated site groups.

Table 3 Soil properties (average values) of different pasture types. Standard deviations in brackets. S = sand, U= silt, T = clay.

Pasture type	pH ($CaCl_2$)	water content [%]	organic matter [%]	C [g/kg]	N [g/kg]	CEC_{eff} [μmolc/g]	bulk density [g/cm³]	grain size distribution [%]
State reserve (SR)	5.61 (± 0.35)	3.79 (± 0.93)	21.15 (± 5.23)	87.99 (± 25.79)	7.92 (± 1.79)	395.27 (± 53.74)	1.13 (± 0.06)	S: 1.50 U: 62,27 T: 36.23
Summer pasture (SP)	6.03 (±0.52)	4.24 (± 1.93)	21.05 (± 5.07)	91.41 (± 27.86)	7.58 (± 1.71)	449.60 (± 118.60)	1.15 (± 0.16)	S: 4.18 U: 55.71 T: 40.12
Winter pasture (WP)	7.27 (± 0.39)	3.12 (± 0.07)	12.83 (± 2.02)	52.72 (± 6.72)	4.69 (± 0.81)	423.89 (± 40.98)	1.29 (± 0.14)	S: 6.22 U: 57.87 T: 35.90

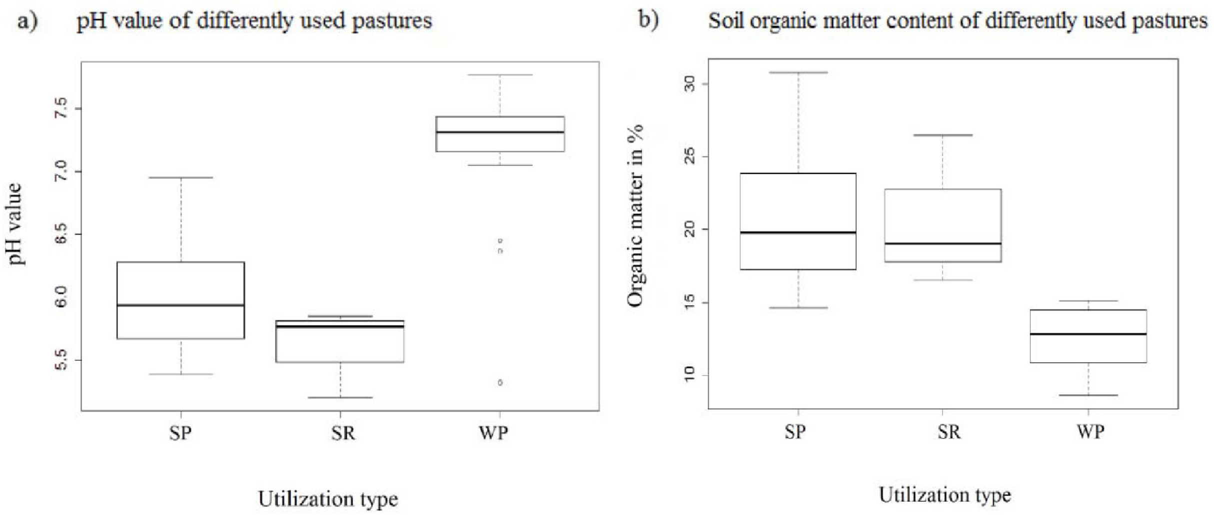

Figure 5 Boxplots of soil pH value (a) and soil organic matter content (b) of differentiated site groups. SP = summer pastures, SR = state reserve, WP = winter pastures.

significantly different between summer and winter pastures.

Soil analyses indicate a high base saturation around 99% for each plot, which is often related to elevated pH values as well as elevated clay contents. These soil characteristics suggest a potential high fertility. Our results indicate properties of *Kastanozem* soils, which are widespread in Kyrgyzstan and often show a drought-limited land use potential.

3.5 Indirect gradient analysis

Results of the gradient analysis clearly show that pH values are strongly correlated with grazing impact (Figure 6a). Both environmental factors are of significance for the differentiation of winter pastures. In contrast, altitude and soil organic matter content are the major environmental factors for the internal differentiation of summer pastures. Soil water content does not seem to be a driving factor concerning the differentiation of the pasture types. The influence of single nutrients is generally lower, compared to those of the pH value for example (length of the arrow). Nevertheless, the amount of primary nutrients tends to be higher on summer pastures (Figure 6b), so that they consequently can be described as nutrient-richer environments than winter pastures. Lower species richness on winter pastures is associated with a lower vegetation cover (Figure 6c). Summer pastures are correlated with a denser vegetation cover. Plant height (here the maximum plant height of each plot is measured) is strongly correlated with summer pastures (Figure 6d). This attribution is influenced by the near-natural plots of the State Reserve as well as the buffer zone, which is indicated by the drift of the arrow to the upper corner.

4 Discussion

Grazing regimes potentially affect rangeland ecology to a large extent. Since livestock farming is the most dominant land use in those ecosystems (e.g. Kreutzmann 2012; Alkemade et al. 2013), elaborated analyses as well as long-term monitoring of grazing impacts are needed as a basis to develop sustainable grazing management strategies. The number of studies on the ecological state (soil conditions and vegetation structure) of the Kyrgyz rangelands has grown in recent years, but up to date no detailed information on pastures in the Naryn region is available. It is difficult to transfer general conclusions or derived degradation trends from other regions to the Naryn Oblast. The present study focused on specific soil and vegetation indicators for habitat degradation (as defined in the study area section) which are discussed in the light of available knowledge from other mountain grazing lands in Kyrgyzstan and

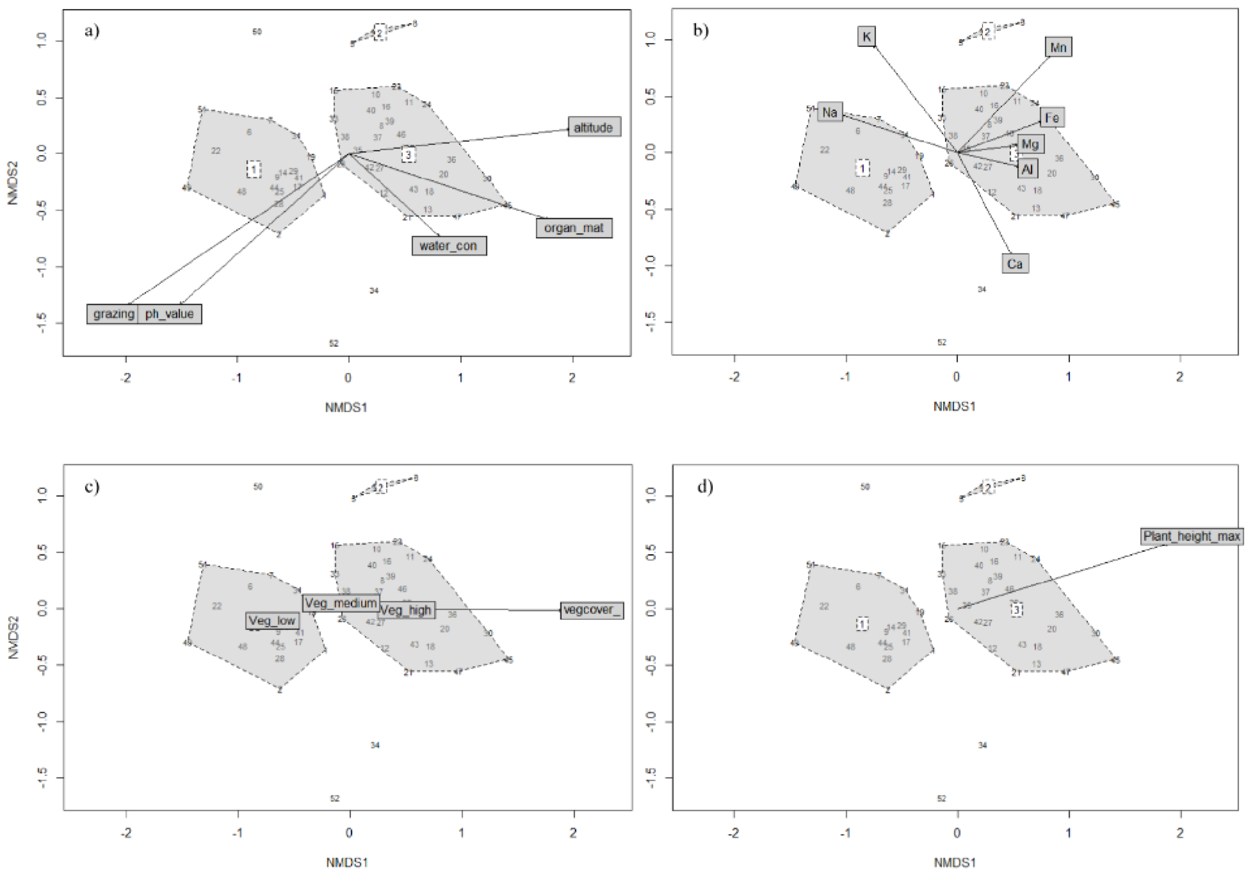

Figure 6 Indirect gradient analysis using different environmental factors. a) environmental factors: grazing impact, pH value, water content (water_con), organic matter content (organ_mat) and altitude; b) nutrients: sodium (Na), calcium (Ca), aluminium (Al), magnesium (Mg), iron (Fe), manganese (Mn), potassium (K); c) vegetation cover; d) plant height; winter pastures = 1, state reserve = 2, summer pastures = 3.

beyond.

4.1 Soil indicators

As presented in the results section, soil parameters of the heavily used winter pastures significantly differ from those of the summer pastures and indicate more unfavourable site conditions. Von Wehrden et al. (2012) considered soil condition to be the most reliable indicator for degradation of grazing lands because degraded soils do not recover rapidly. Several authors have already pointed out that parameters such as soil organic carbon, total nitrogen and cation exchange capacity show significantly lower values when a pasture is degraded (e.g. Wu et al. 2008; Xiong et al. 2014; Su et al. 2015). Our results corroborate this statement. Soil properties such as organic matter content, total nitrogen content as well as cation exchange capacity are lower on winter pastures compared to summer pastures (Table 3). Soil pH is known to be a crucial factor concerning soil organic matter accumulation and decomposition. Generally higher pH values on winter pastures, compared to lower pH values in the State Reserve and on summer pastures, suggest a relationship between grazing intensity and soil pH. Increasing pH values have most likely to be attributed to a higher amount of animal excreta arising from over-utilisation of pastures (Britton et al. 2005; Cui et al. 2005; Sakbaeva et al. 2012). Deteriorating soil conditions of winter pastures become obvious by comparing winter and summer pastures at same elevations (Table 1). Cui et al. (2005) analysed pastures with contrasting grazing intensity in Inner Mongolia and showed that over-grazing is related to trampling and the increase of soil hardening and bulk density, limiting water and soil organic matter transportation between soil horizons (see also Stavi et al. 2008; Tang et al.

2015). Decreasing soil organic matter and nitrogen content leads to reductions in soil fertility and quality (Yan et al. 2013), which may result in less dense vegetation cover. A dense grass cover, on the other hand, reduces surface runoff and provides essential protection against soil erosion in sloping terrain (Kulikov et al. 2016). The correlation between excessive pasture use and lower soil organic matter and nitrogen content has also been confirmed in other studies (Glaser 2000; Han 2008; Sakbaeva et al. 2012). Comparing the soil properties of winter pastures, summer pastures, and the State Reserve it becomes obvious that winter pastures show a much lower soil quality. Our results suggest that soil deterioration has to be attributed to the distinctly higher grazing pressure winter pastures are subjected to. This statement is supported by the fact that our data do not show significant spatial autocorrelation (Fig. 2), and by the assumption that the State Reserve and remote summer pastures represent near-natural conditions. Thus, recently increasing livestock numbers pose a challenge concerning the implementation of sustainable grazing management.

4.2 Vegetation patterns

Our differentiated rankless communities do not correspond to any other differentiated plant community on grazing lands in Kyrgyzstan to date, underlining the pioneer character of the present study. Similarities exist in terms of species assemblages and community structures influenced by grazing impact. Borchardt et al. (2011) detected two communities in alpine grazing lands of the Fergana Range (SW-Kyrgyzstan): one at high elevation under low grazing impact (*Phlomoides-Geranium*) and one at lower elevation with higher grazing impact (*Plantago-Polygonum*). The former, however, does not correspond to our *Trisetum spicatum-Gentiana karelinii* community of summer pastures since only one common species (*Phlomoides oreophila*) occurs in both communities. The *Bupleurum thianschanicum-Stipa purpurea* community of winter pastures indicates little similarities with the *Plantago-Polygonum* community of Borchardt et al. (2011). Both communities are subjected to high grazing impact and characterized by species of the genus *Plantago* (Borchardt et al. 2011). However, there are notable differences. The presumable diagnostic species of the differentiated communities in this study do not occur on mountain grazing lands in other parts of Kyrgyzstan (cf. Epple 2001; Wagner 2009; Borchardt et al. 2011; Taft et al. 2011; Imanberdieva 2015), pointing to a heterogeneous vegetation mosaic in comparable, but isolated habitats. Nonetheless, all diagnostic species are native to Middle Asia and listed in Czerepanov (1995). Interestingly, the diagnostic species of winter pastures (*Bupleurum thianschanicum*, *Stipa purpurea*, *Plantago arachnoidea* and *Potentilla moorcroftii*) are Middle Asian endemics, i.e. they do not occur in other regions like Caucasus or Siberia (Czerepanov 1995).

Stipa purpurea, in this study a major element of the *Bupleurum thianschanicum-Stipa purpurea* community, is known to be tolerant against cold and drought and dominant on alpine steppes of the Tibetan Plateau (Sheehy et al. 2006; Yang et al. 2015). The dominance of *Stipa purpurea* seems to be independent of the level of degradation (Tang et al. 2015), which is in line with its presence on heavily used winter pastures assessed in our study. *Plantago arachnoidea* is described as less palatable and mainly consumed by sheeps and goats (Rahim and Maselli 2011; Undeland 2012), which could explain the relatively strong presence on winter pastures. *Trisetum spicatum*, one of the diagnostic species of summer pastures (*Trisetum spicatum-Gentiana karelinii* community), is characterized by strong disturbance tolerance. Mark and Whigham (2011) showed that *Trisetum spicatum* can persist environmental changes such as nutrient enrichment and mechanical disturbance. Our most common companion species, *Festuca valesiaca*, shows a wide distribution on alpine and meadow steppes in Kyrgyzstan (Wagner 2009; Rahim and Maselli 2011; Taft et al. 2011, Imanberdieva 2015). Taft et al. (2011) found montane grasslands of the central Tien Shan to be dominated by F*estuca valesiaca*. This species is consumed by all traditional kinds of grazing animals but nevertheless classified as strongly grazing- (and drought-) tolerant (Rahim and Maselli 2011; Ma et al. 2014; Imanberdieva 2015). Taft et al. (2011) and Imanberdieva (2015) pointed out that F*estuca valesiaca* is positively selected by grazing impacts and may be used as an indicator of steppe degradation. All of the winter pasture plots, with one exception, are inhabited by this species.

4.3 Species richness, grazing impact and biomass

Our results showed that plant species richness increases from winter to summer pastures. At the same time, this increase occurs to some extent along an elevational gradient. Thus, the vertical pattern of increasing species richness could be attributed either to grazing impacts or to a natural altitudinal zonation. Several studies on elevational species richness and diversity gradients in arid to semi-arid mountain environments provided evidence that species richness increases from humidity-limited lower altitudes towards higher elevations before it decreases again when environmental conditions become too unfavourable (e.g. Richter 2000; Körner 2003; Rahbek 2005; Van de Ven et al. 2007). Peak species richness in arid and semi-arid mountains is found at altitudes where the interplay of temperature and precipitation provides optimum hygrothermal conditions. This is often the case in subalpine to lower alpine altitudinal zones (Körner 1995; von Wehrden and Wesche 2007). In the context of the non-equilibrium concept (Ellis and Swift 1988), von Wehrden et al. (2012) showed that rainfall variability is considered to be a critical driver in rangeland dynamics. In areas with lower rainfall variability the potential of degradation under grazing pressure is higher than in rangelands where rainfall variability is more pronounced. According to their 'global annual mean precipitation map' our study area is characterized by a lower rainfall variability (CV < 33%), which increases the potential of degradation given a sufficient size of herbivore populations (see also Vetter 2005; Wesche and Treiber 2012). It has to be taken into account though that much of the precipitation in Central Asia is of convective nature, resulting in high spatial and temporal heterogeneity of neighbouring sites (Ruppert et al. 2012; Wesche and Treiber 2012; Zhou et al. 2016). Thus, it is very likely that equilibrium and non-equilibrium dynamics co-occur in one ecosystem at a variety of spatial and temporal scales (cf. Fernandez-Gimenez and Allen-Diaz 1999; Silcock and Fensham 2013).

The increase in species richness towards higher elevations could be an effect of climatological vertical gradients. However, the comparison of different plots from same elevations subjected to contrasting grazing pressure (Table 1) suggests that decreasing grazing intensity towards summer pastures results in higher species richness and diversity as well as in a higher amount of biomass. Thus, the natural elevational gradient of species richness is obviously accentuated by grazing impacts in that way that winter pastures at lower elevations decrease in species richness, and summer pastures at higher elevations increase in species richness. This finding is supported by results of Gao et al. (2009), who examined the influence of grazing and drought on species richness in semi-arid steppes in Inner Mongolia, and found that heavy grazing significantly reduces species richness and diversity. Moreover, the effects of drought stress have greater impact on heavily grazed sites indicating an interaction of these parameters. Especially in arid and semi-arid grazing lands, species richness provides a positive effect on ecosystem services. In particular, ecosystem services linked to C and N cycling are maintained by species richness, which in turn sustain soil fertility and C sequestration (Maestre et al. 2012).

Borchardt et al. (2013) focused on the connection between plant functional traits and grazing impact in SW-Kyrgyzstan and found that vegetation types at same elevations vary in their species composition depending on grazing pressure. The factor grazing correlated significantly with traits such as 'low plant height', 'annual life cycle', 'basal growth form' and 'long flowering time'. Similarly, Epple (2001) showed that communities in SW-Kyrgyzstan subjected to high grazing pressure are characterized by particular features such as low coverage values of the herbaceous layer, stunted growth in most herbaceous species, and increased occurrence of shrub seedlings. In contrast, many authors have shown that moderate grazing may lead to an increase in species richness and diversity (e.g. Hart 2001; Borchardt et al. 2011; Taft et al. 2011), in line with the intermediate disturbance hypothesis, stating that diversity increases when disturbances are intermediate

(Connell 1978). High species richness in the buffer zone of the State Reserve and on most summer pastures subjected to low or moderate grazing pressure confirms this hypothesis. The assessment of grazing pressure using a grazing scale with five classes showed that exceeding an intermediate level of disturbance (class 3) results in decreasing species richness and deteriorating soil conditions – as exemplified by winter pastures of this study.

Many previous studies found evidence that effects of intense livestock grazing result in declining plant cover and biomass, trampling damages, destruction of root systems, and ultimately in habitat degradation and biodiversity loss (e.g. Alkemade et al. 2013; Yan et al. 2013; Gamoun et al. 2015; Tang et al. 2015). Nevertheless, the consequences of grazing on plant species richness or the amount of biomass depend on the grazing intensity as well as the particular environment as stated above (see also Olff und Ritchie 1998). A case study from arid and semi-arid areas in China clearly revealed a negative effect of grazing on total biomass (Yan et al. 2013). Biomass and plant cover are considered key indicators to evaluate the degree of grassland degradation (Xiong et al. 2014; Alkemade et al. 2013). The lower amount of biomass on winter pastures found in the present study corroborates this indicator function.

4.4 Requirement of sustainable management strategies

Mobile animal husbandry has nowadays gained increased attention as a useful adaptation to the effects of climate change such as drought and desertification (Reid et al. 2008; Steimann 2010). For sustainable pasture use in the Naryn Oblast, an improved coordination of seasonal migration is indispensable, not only to protect over-utilized winter pastures from degradation but also to prevent that abandoned summer pastures will be affected by an invasion of weeds and unpalatable secondary plant species, which will affect pasture´s economic value (Vallentine 2001; Esengulova et al. 2008). The recently introduced 'pasture committees' as the main actors in the management and control of pastures are responsible for the establishment of seasonal rotation and concepts of pasture use, but they appear to have low efficiency (Ibraimova 2009; Jacquesson 2010). A power asymmetry between wealthy herders with large herds of livestock and marginalized non-wealthy herders has been found to be one of the principle reasons. Wealthy livestock owners are often represented in new governance structures (pasture committees) and are able to protect their own interests (Dörre 2012; Kasymov and Thiel 2014). According to Esengulova et al. (2008), local users should be more strongly encouraged to participate and feel responsible in order to consolidate the pasture management on community level. But to date, the over-utilization of pastures is not always considered to be a fundamental issue. Unused remote pastures, for instance, are perceived by local people as never ending pasture resources (Liechti 2010). Grazing-induced degradation of rangelands is not only a problem in Kyrgyzstan, but has global dimensions (Reid et al. 2008). New approaches are needed to sustainably manage and better protect grazing lands, which provide several ecosystem services such as carbon storage. An increasing number of studies (e.g. Cui et al. 2005; Han et al. 2008; Sommer and Pauw 2011; Sanaullah et al. 2014) indicate, in the context of climate change, the high capacity of rangeland ecosystems to sequestrate C in soil. The soil C stock in grassland ecosystems could substantially change by intensive grazing, causing a modification of global cycles and potentially influence climate change (Cui et al. 2005; Han et al. 2008; Sommer and Pauw 2011). Thus, the relevance of sustainable grazing management and restoration of degraded pastures should not be underestimated.

5 Conclusions

The presented results indicate that rangeland conditions in the Naryn Oblast strongly depend on grazing intensity. Assessed effects of grazing impacts constitute a solid basis for the differentiation of pasture types. The hypothesis that winter pastures which are close to settlements and exposed to intense grazing pressure suffer from degradation could be verified, reflected by higher pH values, lower organic matter contents and biomass amount as well as lower species richness and diversity indices. Summer pastures at higher elevations are much less affected by grazing impacts, as evident from higher soil quality, higher stand density and biomass amount as well as higher species richness and diversity. Based on vegetation and soil indicators, efforts of management and biodiversity conservation of intensely used pastures should be reinforced. In order to implement a sustainable grazing management, we suggest considering the introduction of a specific rotation grazing system with a scheduled transfer of grazing and resting time between grazing units. Rotation grazing should be incorporated into management plans which generally specify a reduced time period of grazing within the overall grazing season in order to optimize the quantity and quality of forage produced and its utilization by grazing animals. Currently, it seems that the complex interdependence between new formal institutions and traditional pasture rules is one of the major barriers for implementing sustainable grazing management. In any case, long-term monitoring is needed to derive adapted management options in order to prevent continued degradation of winter pastures and to minimize the risk of reductions in livestock performance.

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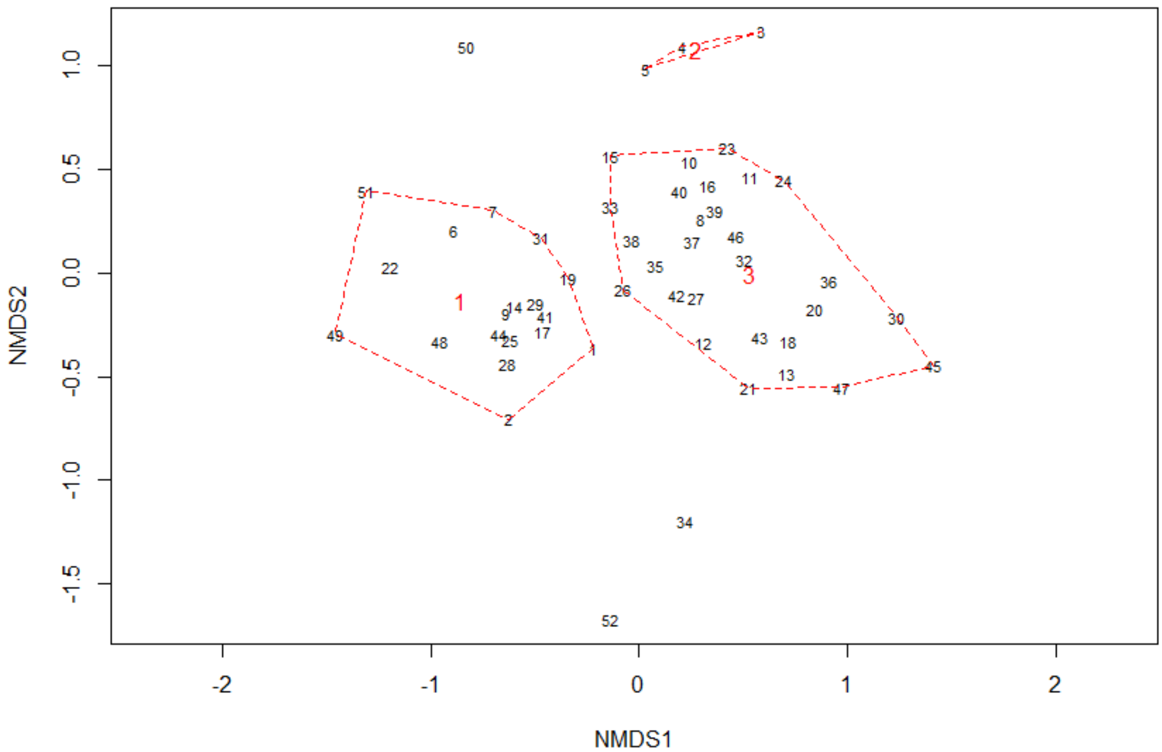
The following appendix (Appendixes 1, 2) is the Electronic Supplementary Material of the article entitled "Rangeland degradation assessment in Kyrgyzstan: vegetation and soils as indicators of grazing pressure in Naryn Oblast " at http://dx.doi.org/10.1007/s11629-016-3915-5.

Appendix 1 Correlation matrix of the explanatory variables, with correlation coefficients (above) and asymptotic p-values (below). Variables with significant p-value (< 0.01) are in bold.

	pH value	organic matter	water content	plant height	grazing	altitude
pH value	1	-0.37	-0.05	-0.057	0.56	-0.55
organic matter	-0.37	1	0.68	0.57	-0.51	0.32
water content	-0.05	0.68	1	0.23	-0.29	0.25
plant height	-0.57	0.57	0.23	1	-0.68	0.5
grazing	**0.56**	**-0.51**	-0.29	**-0.68**	1	**-0.37**
altitude	-0.55	0.32	0.25	0.5	-0.37	1
	pH value	organic matter	water content	plant height	grazing	altitude
pH value		0.0068	0.7481	0.0000	0.0000	0.0000
organic matter	0.0068		0.0000	0.0000	0.0000	0.0223
water content	0.7481	0.0000		0.0982	0.0368	0.0772
plant height	0.0000	0.0000	0.0982		0.0000	0.0001
grazing	**0.0000**	**0.0000**	0.0368	**0.0000**		**0.0062**
altitude	0.0000	0.0223	0.0772	0.0001	0.0062	



Appendix 2 NMDS-ordination space shows three relevé groups: 1 = winter pasture (WP), 2 = state reserve (SR) and 3 = summer pasture (SP). Location of group 2 (SR) underlines higher affinity to the summer pastures as low grazing areas.

Article III

Hoppe F, Zhusui Kyzy T, Usupbaev A, Schickhoff U (2016) Contrasting grazing impact on seasonal pastures reflected by plant functional traits: Search for patterns in Kyrgyz rangelands. Geo-Öko 2016: 165–200.

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CONTRASTING GRAZING IMPACT ON SEASONAL PASTURES REFLECTED BY PLANT FUNCTIONAL TRAITS: SEARCH FOR PATTERNS IN KYRGYZ RANGELANDS

AUSWIRKUNGEN UNTERSCHIEDLICHER BEWEIDUNGSINTENSITÄT AUF FUNKTIONALE PFLANZENMERKMALE VON SOMMER- UND WINTERWEIDEN IM KIRGISISCHEN HOCHLAND

FRANZISKA HOPPE, TAALAIGUL ZHUSUI KYZY, ADILET USUPBAEV & UDO SCHICKHOFF

SUMMARY

At least 30 % of Kyrgyz grazing lands are considered to be subject to vegetation and soil degradation. Since animal husbandry is the economic basis to sustain people's livelihoods, rangeland degradation presents a threat for the majority of the population. Recently, the usage of plant functional traits as a powerful tool for the characterization of vegetation dynamics in response to anthropogenic and natural disturbances has been put forward. Grazing, one of the most severe disturbances to vegetation is both depending on and affecting plant functional traits.

We hypothesized that the contrasting grazing intensity of summer and winter pastures in the Naryn region (central Kyrgyz highlands) is reflected by selected plant functional traits. We used traits such as plant height, flowering start, plant growth form as well as SLA (Specific Leaf Area) and LMA (Leaf Mass per Area). Additionally, we analyzed the amount of biomass as indicator for grazing intensity. Based on a phytosociological classification of the main pasture types (summer and winter pastures), community structure and the traits of dominant plant species have been analyzed.

Our results show that high grazing pressure has resulted in decreased plant height and SLA and favored plants with an earlier flowering start as well as rosette and prostrate plants (hemicryptophytes). Respective changes are representative for winter pastures, whereas sets of plant attributes on summer pastures are consistently associated with lower grazing pressure. Our results support the growing recognition that plant functional trait analysis is a promising way to generate insights into the mechanisms of plant response to grazing in high-altitude rangelands.

Keywords: Alpine grazing lands, biomass, grazing impact, LMA, plant height, SLA

ZUSAMMENFASSUNG

Mindestens 30 % der kirgisischen Weideflächen sind von Vegetations- und Bodendegradation betroffen. Da für viele Haushalte Viehhaltung die wirtschaftliche Grundlage darstellt, ist die Degradation von Weideflächen mit hohen Risiken für die ländliche Existenzsicherung verbunden.

Die Verwendung von funktionalen Pflanzenmerkmalen zur Analyse von Vegetationsdynamik, insbesondere mit Hinblick auf die Reaktion durch weidebedingte Störungen, hat sich in den letzten Jahren zunehmend bewährt. Weidequalität und -kapazität hängen in hohem Maße von funktionalen Pflanzenmerkmalen ab, welche wiederum mit zunehmender Beweidungsintensität sehr stark verändert werden können.

Diese Studie geht von der Hypothese aus, dass die ungleiche Weidenutzung von Winter- und Sommerweiden in der Naryn-Region im zentralen kirgisischen Hochland durch ausgewählte Pflanzenmerkmale (Wuchshöhe der Pflanze, Blühbeginn, Wuchsform, Blattgewicht pro Fläche (LMA), spezifische Blattfläche (SLA) widergespiegelt wird. Als weiterer Indikator für den Beweidungsdruck wurde der Anteil der Biomasse analysiert. Basierend auf einer pflanzensoziologischen Klassifizierung der Hauptweidetypen (Winter- und Sommerweiden) wurden strukturelle Eigenschaften der Pflanzengesellschaften sowie die funktionalen Merkmale der dominanten Arten untersucht. Unsere Ergebnisse zeigen, dass hoher Beweidungsdruck zu einer Verringerung der Wuchshöhe der Pflanzen und der spezifischen Blattfläche geführt hat und Arten mit einem frühen Blühbeginn und einer bodennahen Wuchsform begünstigt werden. Entsprechende Veränderungen sind charakteristisch für die Winterweiden, während die funktionalen Merkmale auf den Sommerweiden weitaus geringeren Beweidungsdruck indizieren.

Die Ergebnisse stützen die Erkenntnisse ähnlicher Studien, dass die Analyse funktionaler Pflanzenmerkmale einen adäquaten Ansatz für die Erfassung weidebedingter Vegetationsdynamik darstellt.

Schlüsselworte: Beweidungsdruck, Biomasse, Blattgewicht, Hochweiden, Spezifische Blattfläche, Wuchshöhe der Pflanzen

1 INTRODUCTION

Prior to the colonization by the Soviet Union in 1936, nomadism was the predominant land use system in Kyrgyzstan. Rangeland ecosystems and mobile livestock keeping by pastoral nomads have co-adapted and co-evolved to cope with arid and semi-arid ecological conditions, and to increase land use efficiency (Shigaeva et al. 2007; Baibagushev 2011; Schmidt 2013). The flocks moved between seasonal pastures, mainly between montane and alpine summer pastures (*dzailoo*) and winter pastures located at lower altitudes (*kyshtoo*). Montane rangelands represent 45 % of Kyrgyz land area, thus they are the essential basis for the livestock sector (Taft et al. 2011; Dörre 2012; Sakbaeva et al. 2012). Under the Soviet regime, formerly autonomously acting pastoralists were superseded by state owned farms (*sovkhozes*) and collective farms (*kolkhozes*) and sedentarization and collectivization campaigns were pushed forward. The livestock industry has been massively expanded and the flock size exceeded the carrying capacity of the pastures up to two or three times (Schoch et al. 2010). After the Soviet era, livestock numbers saw a drastic reduction and a temporally decreasing grazing pressure. Because of the end of the state-dominated system, which resulted in a privatization of land and livestock, a return to a subsistence lifestyle was for most of the Kyrgyz people the only possibility to sustain their livelihood (Borchardt et al. 2011; Schmidt 2013). As a result of this new way of life, livestock numbers increased again in the further course of post-Soviet transformation. The dissolution of the institutionalized organizations was accompanied by the loss of the annual migratory herd movements (Crewett 2012; Kreutzmann 2013). The herders are nowadays rarely able to organize the migration of livestock themselves because of long distances and a weak state of infrastructure, which resulted in severe changes of traditional pasture practices. In consequence, summer pastures at higher altitude experience increasing abandonment, while winter pastures which are close to settlements and exposed to intense grazing pressure are subject to vegetation and soil degradation. According to recent estimates approximately 30 % of Kyrgyz rangeland areas are affected by degradation processes (Esengulova et al. 2008; Baibagushev 2011; Shigaeva et al. 2013; Hoppe et al. 2016).

Grazing is one of the most serious disturbances to vegetation and soil properties, affecting grazing land quantity and quality. Because grazing is both depending on and affecting plant functional traits (feedback loop), important insights into grazing-induced changes in structure and dynamics of vegetation can be generated based on this codependency (Díaz et al. 2007, Evju et al. 2009). In recent decades, the usage of plant functional traits has been put forward as a powerful tool for the characterization of vegetation dynamics in response to anthropogenic and natural disturbances, (Westoby 1998; McIntyre et al. 1999; Jauffret & Lavorel 2003; Westoby & Wright 2006; Díaz et al. 2007; Sharafatmandrad et al. 2014). It has been documented that, for example, reduced plant height is a reliable indicator for these disturbances even under diverse land use history and climate combinations (Díaz et al. 2001; Jauffret & Lavorel 2003). Based on specific morphological, physiological or life-history traits, sets of species, responding in a similar way to perturbations, can be classified – called plant functional groups (Gitay & Noble 1997; Díaz et al. 2002; Duckworth et al. 2000). By inspecting the trait composition of a plant community it is possible to draw conclusions about the capability of the composing species to attain resources, disperse, reproduce and respond to particular ecological processes (Díaz et al. 2002; Gutiérrez-Girón & Gavilán 2013).

To date, there are hardly any studies in Kyrgyzstan using a plant functional trait approach. Borchardt et al. (2013) analyzed plant traits in relation to grazing disturbance in SW Kyrgyzstan, and highlighted the modification of plant functional traits along grazing gradients. Apart from a study regarding phenotypic and genetic characterization of Kyrgyz *Festuca valesiaca* (Ma et al. 2014), no other studies on plant functional traits and their response to grazing pressure on Kyrgyz rangelands were published. Research deficits in using plant functional traits as predictors of grassland response to disturbances are particularly prevalent in the Naryn region in the central Kyrgyz highlands where even the species composition of plant communities is still largely unexplored. Hoppe et al. (2016) established a first phytosociological classification of winter and summer pastures in the Naryn region, and analyzed vegetation-environment relationships focusing on soil properties. We use this data as a basis for a detailed plant functional trait analysis of different pasture types with respect to plant height, growth form, flowering start as well as LMA (Leaf Mass per Area) and SLA (Specific Leaf Area). We selected these traits because they are considered as being good predictors of grassland response to disturbances (e.g. Díaz et al. 2007; Zheng et al. 2010). Maximum plant height is associated with growth form and both of them are correlated with ecophysiological adaptation in many ways, such as competitive ability, potential lifespan, resistance to severe climatic conditions and the ability to establish and attain reproductive size between two disturbance events (Duckworth et al. 2000; Jauffret & Lavorel 2003; Grime 2001; Pérez-Harguindeguy et al. 2013). In the context of analyzing the influence of herbivores on floral traits, flowering start is a commonly used attribute (Sletvold et al. 2015; Tóth et al. 2016). Specific leaf area (SLA) has been proposed as a diagnostic plant functional traits as well as LMA, an inverse of SLA (Díaz et al. 2001; Garnier & Navas 2012; De la Riva et al. 2016). Data concerning these both traits were acquired from the TRY database (Kattge et al. 2011). Additionally, we analyzed the amount of biomass as indicator for grazing intensity. We did not include life history, however, because 99 % of our diagnostic species are perennial. We hypothesize that higher grazing pressure on winter pastures is reflected by specific modifications of plant functional traits, in particular by decreasing plant height and decreasing SLA. We further hypothesize that plants with an earlier flowering start as well as prostrate plants instead of erect plants are positively selected by higher grazing pressure.

2 MATERIAL AND METHODS

2.1 STUDY AREA

Our study was conducted in the Middle Tian Shan (41° N, 76° E), in the north-east of the Naryn Oblast (Fig.1). This area is characterized by (sub-)alpine steppes and meadows, which correspond to the general climatic conditions (aridity and strong winds). Our study area, the *Kara-Kujur* valley, is part of an inner basin landscape and is significantly drier as the bordering mountain range. Because of cold and long winters, the growing season is comparatively short (Gottschling 2006, UCA 2014). The vegetation mosaic is extremely heterogeneous, reflected by a rich flora of more than 4.100 species of vascular plants (Taft et al. 2011, Eisenman et al. 2013). The classification of plant communities is still rather preliminary given the huge variety of different vegetation types in an underresearched area (Umralina & Lazkov 2008). For a detailed description of our study area see Hoppe et al. (2016).

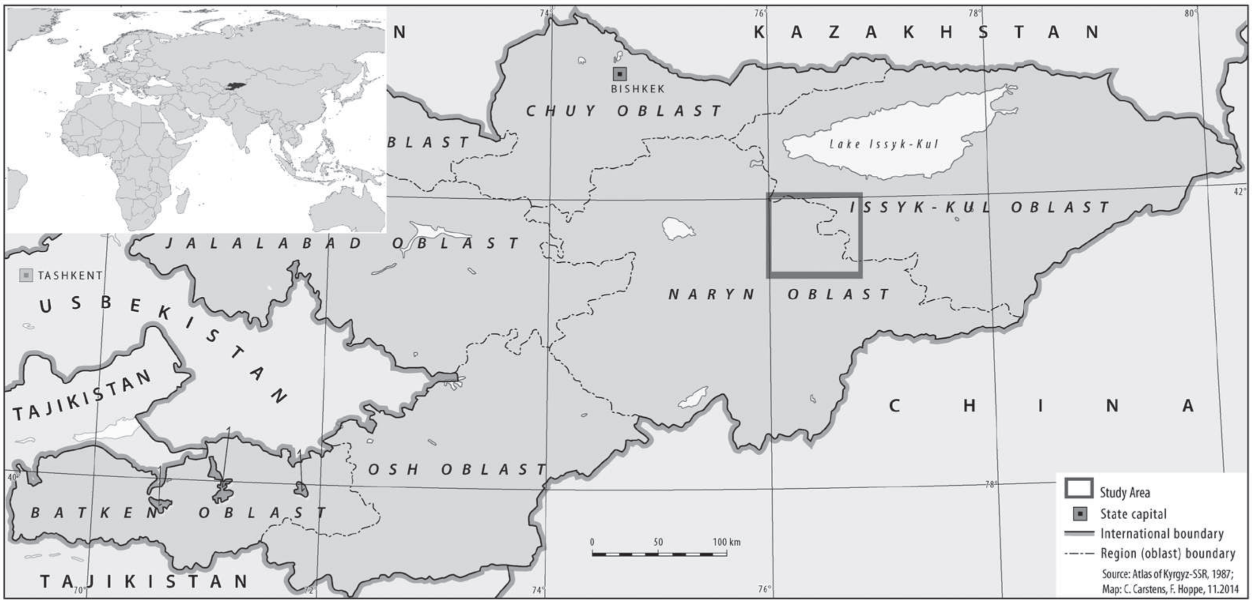

Fig.1: *Location of the study area in NE Naryn Oblast.*

Abb. 1: *Das Untersuchungsgebiet im Nordosten des Naryn-Oblast.*

2.2 DATA COLLECTION

Sampling was conducted in 2014 and 2015 in the *Kara-Kujur* valley, Naryn Oblast. We collected biomass from the surface of one square meter and soil samples and completed vegetation relevés according to the Braun-Blanquet approach (detailed description of sampling in Hoppe et al. 2016). During the fieldwork campaigns a total of 86 plots were sampled, consisting of 80 plots taken in the Kara-Kujur valley and 6 plots in the Naryn State Reserve and its buffer zone, used as reference data for less grazed and ungrazed areas. In each plot, maximum and average plant height was recorded and all vascular plants were listed and their cover-abundance assessed (Braun-Blanquet 1964; Kent 2012). The collected species were determined in the herbarium of the National Academy of Sciences in Bishkek. Floristic nomenclature of all vascular plants follows Czerepanov (1995).

We did not collect information on leaf mass per area (LMA) and specific leaf area (SLA) of our diagnostic species independently, instead we used the information provided by TRY (a global database of plant traits). Within this database, which has started the collection of plant trait data in 2007, c. 5.6 million records for about 100.000 plant species are compiled (Kattge et al. 2011, 2015). The TRY database is a reliable platform and has been widely used (491 citations in ISI Web of Knowledge, status 15.02.2017). Concerning the flowering start and the growth form of diagnostic species, information was elaborated by using the flora of the USSR Vol. I-XXX (Botanicheskii institute 1968-) as well as the Flora of the Kyrgyz SSR Vol. I-XI (Kyrgyz SSR ilimder akademii͡asy 1650-1965).

2.3 DATA ANALYSES

For the classification of different vegetation types we implemented a hierarchical-agglomerative method (UPGMA), which was already used in a previous analysis (for details see Hoppe et al. 2016). For this purpose, the original cover-abundance values of data gathered in 2014 and 2015 were transformed according to van der Maarel (1979). Based on the cluster dendrogram and complemented by expert knowledge, the plots were assigned to the corresponding pasture type (Fig.1 in Appendix). These three groups (winter pastures, summer pastures and the State Reserve) were transferred to JUICE software (Tichý 2002). Diagnostic species of the proposed phytosociological units (i.e. pasture types) were determined by calculating the phi-coefficient (ϕ) among all groups (Sokal & Rohlf 1995; Chytrý et al. 2002). A threshold value of 0.3 was defined for the selection of diagnostic species which were differentiated into diagnostic (ϕ > 0.30) and highly diagnostic (ϕ > 0.50) (Michl et al. 2010). Simultaneously, a Fisher's exact test with a significance concentration at 0.05 was calculated (Tichý 2002). For the trait analysis we primarily concentrated on winter and summer pastures because of the poor data volume concerning the state reserve.

A Kruskal-Wallis test was used to check the significance of maximum and average plant height as well as biomass. To compare flowering start and growth form of the species of different pasture types, the first twelve diagnostic species with a phi coefficient above 0.30 (representing diagnostic species) were selected and analyzed. We generated mosaic plots, which display relationships between categorical variables. In(dependence) analysis is based on the underlying contingency table. Information is given by the surface of the rectangle, which is proportional to the number of observations, as well as by the Pearson residuals from independence (significance testing), represented by the colour (HCL shading) of each rectangle (Zeileis et al. 2007). Mosaic plots for growth form and flowering start show whether there are particular combinations dominating in the data set.

Information concerning SLA, as a ratio of leaf area to dry leaf mass, and its inverse LMA

(1/SLA) were acquired from the TRY database. Because most of our diagnostic species are poorly studied, such as *Bupleurum thianschanicum, Androsace dasyphylla*, and *Ptilagrostis mongholica* (see Hoppe et al. 2016), we were not able to gather information for all of our species. We included the following diagnostic species in this analysis: *Plantago arachnoidea, Potentilla moorcroftii, Koeleria cristata* and *Stipa purpurea* for winter pastures, and *Trisetum spicatum, Carex stenocarpa, Gentiana karelinii, Bistorta vivipara* and *Parnassia laxmannii* for summer pastures (species listed in descending order of phi-coefficient). If there was more than one reference we chose those with a higher affinity to our sampled altitude (2800 to 3400 m). The significance of these results was tested by implementing a t-test. All statistical analysis were done in R© (R version 3.2.3; 2015-12-10) using the Packages *ggplot2, pgirmess, vcd* and *vegan*.

3 RESULTS

Diagnostic and highly diagnostic species for the proposed phytosociological units are presented in a synoptic table (Tab. 1), which includes winter and summer pastures, the State Reserve as well as companion species (the complete synoptic table with all species are listed in Tab.1 in Annex). We determined 13 diagnostic and highly diagnostic species for winter pastures, 28 diagnostic and highly diagnostic species for summer pastures and 12 companion species. Because of the poor data volume, the proposed diagnostic species for the State Reserve have to be considered as preliminary results. Former phytosociological classification (see Hoppe et al. 2016) has been verified and slightly modified. For winter pastures the highly diagnostic species are (listed in descending order of phi-coefficient): *Bupleurum thianschanicum*, *Androsace dasyphylla*, *Plantago arachnoidea*, *Potentilla moorcroftii* and *Koeleria cristata*. Summer pastures are characterized by the following highly diagnostic species: *Trisetum spicatum*, *Ptilagrostis mongholica*, *Gastrolychnis apetala*, *Trollius dschungaricus*, *Cerastium pusillum*, *Ranunculus alberti*, *Festuca alatavica* and *Carex stenocarpa*. Thus, we can differentiate the pastures vegetation types into two rankless communities: Winter pastures are occupied by *Bupleurum thianschanicum-Androsace dasyphylla* communities, while summer pastures are covered by *Trisetum spicatum-Ptilagrostis mongholica* communities.

Table 1: *Synoptic table of the proposed rankless communities with modified fidelity phi coefficient and percentage frequency (superscript). By applying a threshold of phi ≥ 0.3 and a significant concentration at α = 0.05 according to Fisher's exact test, diagnostic species were selected. We distinguished highly diagnostic species (φ > 0.50) which are highlighted in dark grey and high diagnostic species (φ > 0.30) which are highlighted in light grey.*

Tab. 1: *Synoptische Tabelle der ranglosen Gesellschaften mit Angaben zum modifiziertem Treue-Phi-Koeffizienten und den prozentualen Häufigkeiten (hochgestellt). Durch die Festlegung eines Schwellenwertes von phi ≥ 0.3 und einer signifikanten Konzentration bei α = 0.05, gemäß des exakten Tests nach Fisher, konnten diagnostische Arten bestimmt werden. Hierbei werden hoch diagnostische Arten (φ > 0.50), mit dunkelgrau unterlegt, und diagnostische Arten (φ > 0.30), mit hellgrau unterlegt, differenziert.*

Group No.	1	2	3
No. of relevés	34	42	4
Number of diagnostic species	12	27	6
Companion species:			
Festuca valesiaca	--- 91	--- 86	--- 83
Taraxacum maracandicum	--- 44	--- 62	--- 50
Leontopodium ochroleucum	--- 82	--- 76	--- 33
Potentilla multifida	22.8 65	--- 40	--- 50
Euphorbia alatavica	--- 24	13.1 62	--- 67
Kobresia humilis	--- 50	--- 45	--- .
Potentilla nivea	--- 41	--- 38	--- 17
Erigeron lachnocephalus	--- 38	--- 31	--- 33
Aster serpentimontanus	--- 44	--- 31	--- .
Galium verum	--- 29	--- 14	--- 33
Helictotrichon schellianum	--- 24	--- 36	--- 17
Group 1 (Winter Pastures):			
Bupleurum thianschanicum	92.9 94	--- 5	--- .
Androsace dasyphylla	67.6 53	--- .	--- .
Plantago arachnoidea	58.5 44	--- 2	--- .
Potentilla moorcroftii	51.4 32	--- .	--- .
Koeleria cristata	41.6 68	--- 17	--- .
Stipa caucasica	40.3 21	--- .	--- .
Scutellaria oligodonta	37.2 18	--- .	--- .
Stipa purpurea	35.5 38	--- .	--- .
Oxytropis globiflora	34.9 35	--- 5	--- 17
Astragalus tibetanus	33.8 21	--- 5	--- .
Elytrigia batalinii	30.2 18	--- 5	--- .
Potentilla pamiroalaika	30.2 12	--- .	--- .
Viola dissecta	29.8 15	--- 2	--- .
Group 2 (Summer Pastures):			
Trisetum spicatum	--- 6	64.2 86	--- 17
Ptilagrostis mongholica	--- .	60.0 43	--- .
Gastrolychnis apetala	--- 9	55.6 48	--- .

Trollius dschungaricus	--- .	55.6 [55]	--- [17]
Cerastium pusillum	--- [9]	53.4 [64]	--- .
Ranunculus alberti	--- [6]	52.1 [40]	--- .
Festuca alatavica	--- [3]	51.7 [52]	--- [17]
Carex stenocarpa	--- [9]	50.0 [55]	--- [17]
Allium semenovii	--- .	48.0 [29]	--- .
Aconitum rotundifolium	--- [6]	46.6 [60]	--- [33]
Gentiana karelinii	--- [9]	45.3 [55]	--- .
Primula algida	--- .	43.6 [24]	--- .
Bistorta vivipara	--- .	42.0 [45]	--- .
Parnassia laxmannii	--- [3]	42.0 [26]	--- .
Draba altaica	--- [3]	39.6 [24]	--- .
Saussurea sordida	--- [9]	39.4 [57]	--- [17]
Lomatogonium carinthiacum	--- .	38.7 [19]	--- .
Gentiana algida	--- .	36.1 [17]	--- .
Rhodiola linearifolia	--- [3]	34.3 [19]	--- .
Seseli mucronatum	--- [3]	34.2 [33]	--- [17]
Gentiana kaufmanniana	--- [12]	33.3 [38]	--- [17]
Gentianopsis barbata	--- .	33.3 [14]	--- .
Oxytropis penduliflora	--- .	33.3 [14]	--- .
Gentianella turkestanorum	--- [9]	32.7 [45]	--- [33]
Hedysarum kirgisorum	--- .	31.2 [48]	--- [50]
Schmalhausenia nidulans	--- .	30.3 [12]	--- .
Tulipa heterophylla	--- .	30.3 [12]	--- .
Ligularia alpigena	--- [6]	29.5 [52]	--- [33]

Group 3 (State Reserve):

Galium turkestanicum	--- .	--- [7]	83.8 [83]
Dianthus superbus	--- .	--- [10]	70.0 [67]
Phleum alpinum	--- .	--- .	65.5 [50]
Ziziphora clinopodioides	--- .	--- .	65.5 [50]
Bistorta elliptica	--- .	--- [17]	65.2 [67]
Pedicularis macrochila	--- .	--- [2]	63.2 [50]
Silene graminifolia	--- [3]	--- [2]	60.5 [50]
Artemisia dracunculus	--- [12]	--- .	53.8 [67]
Codonopsis clematidea	--- .	--- .	52.2 [33]
Valeriana ficariifolia	--- .	--- .	52.2 [33]
Noccaea ferganensis	--- .	--- .	52.2 [33]

Scabiosa alpestris	--- .	--- .	52.2 33
Gypsophila cephalotes	--- .	--- .	52.2 33
Geranium saxatile	--- 21	17.8 55	51.5 83
Pedicularis ludwigii	--- 12	--- 5	51.7 50
Euphrasia pectinata	--- 3	--- 14	51.3 50
Tragopogon vvedenskyi	--- .	--- 2	49.4 33
Anemonastrum protractum	--- .	--- 2	49.4 33
Phlomoides oreophila	--- 6	16.7 57	47.2 83
Erigeron pseudoseravschanicus	--- 3	--- 2	46.3 33
Alopecurus pratensis	--- .	--- 7	44.4 33

Plant height, growth form and flowering start:

Analysis showed that there is a significant difference (Kruskal-Wallis test = p.value ≤ 0.001) between the maximum plant height of winter and summer pastures (Fig. 2). The average maximum plant height on winter pastures is around 29 cm only, whereas summer pastures as well as plots of the State Reserve show an increase of average maximum plant height by 20 cm.

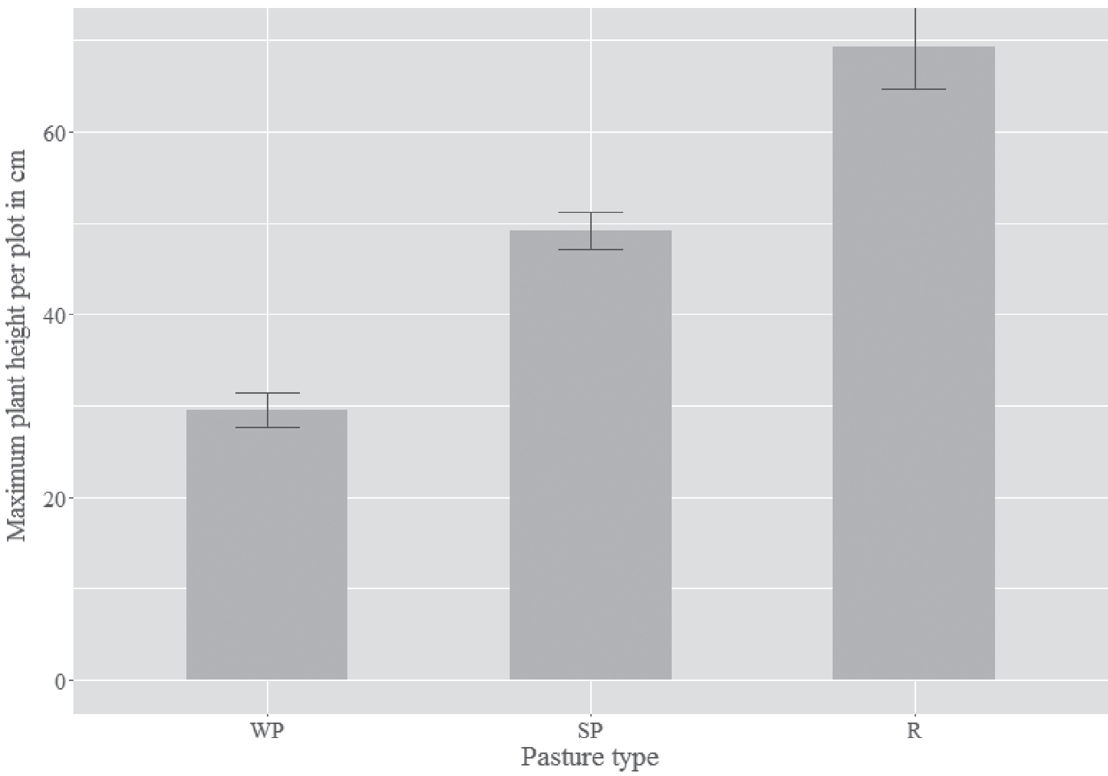

Fig. 2: *Average maximum plant height of winter pastures (WP), summer pastures (SP) and the State Reserve (R). Error bars represent the 95 % confidence interval.*

Abb. 2: *Durchschnittliche maximale Wuchshöhe der Pflanzen auf Winterweiden (WP), Sommerweiden (SP) und im Naturreservat (R). Der Fehlerbereich stellt das 95 %-Konfidenzintervall dar.*

Regarding growth form (Fig. 3), the mosaic plot displays that winter pastures are more dominated by prostrate or suberect plants (e.g. *Oxytropis globiflora*), whereas summer pastures are mainly characterized by erect plants (e.g. *Trollius dschungaricus*). Basal rosette plants on winter pastures are represented by the highly diagnostic species *Androsace dasyphylla*. The only rosette plant on summer pastures, *Primula algida*, is a diagnostic species with leaves forming a rosette and scapes up to 25 cm. Flowering starts earlier on winter pastures (e.g., *Stipa caucasia* in April and *Astragalus tibetanus* in May) than on summer pastures, characterized for instance by *Festuca alatavica* and *Gentiana karelinii* which start flowering as late as July (Fig. 4). Even if the result of the associated log-linear model (sum-of-square statistics) indicated no statistical significance concerning diverging growth form and flowering start on winter and summer pastures ($\alpha = 0.05$; p-value: growth form = 0.16, flowering start = 0.18), the

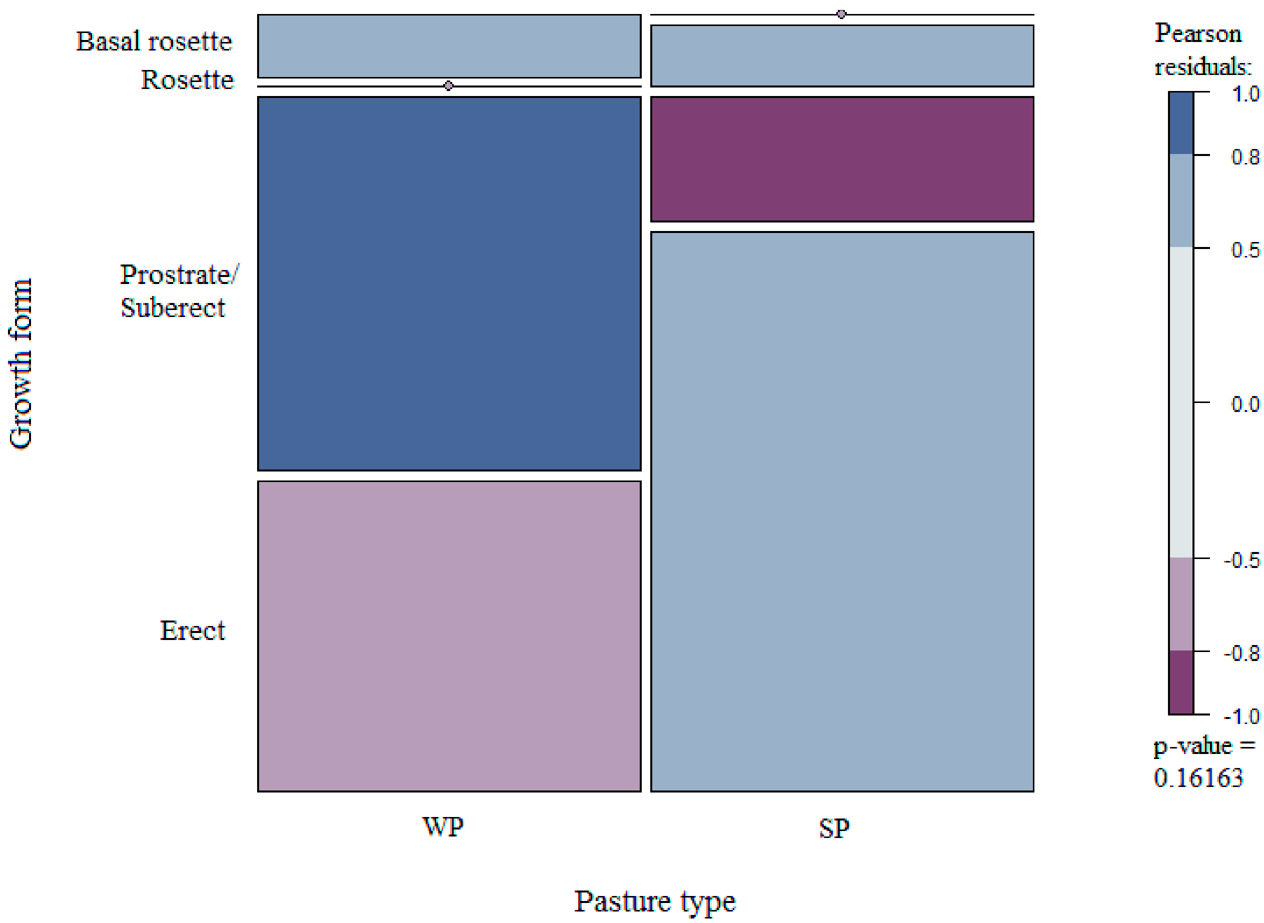

Fig. 3: *Comparison of main growth forms on winter and summer pastures. Erect plants are predominant on summer pastures, while prostrate/suberect plants characterize winter pastures (represented by the surface and shading of the rectangles). No observation within a pasture type is marked by solid lines.*

Abb. 3: *Vergleich der vorherrschenden Wuchsformen auf Winter- und Sommerweiden. Arten mit einem aufrechten Wuchs dominieren auf Sommerweiden, während niedriger/halb aufrechter Wuchs die Winterweiden charakterisiert (dargestellt durch Größe und Farbgebung der Rechtecke). Durchgehende Linien kennzeichnen das Nicht-Vorkommen entsprechender Wuchsformen.*

pattern of deviation from independence is visualized by choosing data-driven cutoffs within the range of residuals (0.5 and 0.8 for growth form, and 0.5 and 1.0 for flowering start). The cells, which are responsible for the dependence, are visualized by blue or red shading.

Leaf Mass per Area (LMA) and Specific Leaf Area (SLA):

Differences between winter and summer pastures were significant among the species we compared (t-test = p.value ≤ 0.05). Winter pastures are characterized by species with a lower SLA (Fig. 5) and a higher LMA (Fig. 6). The highly diagnostic species on winter pastures, *Potentilla moorcroftii*, represents a very low SLA with 78.49 cm^2/g, and an elevated LMA with a value of 127.4 g/m^2. An opposite pattern can be detected on summer pastures, where *Gentiana karelinii* shows, among all species, the highest SLA with a value of 235.85 cm^2/g and the lowest LMA with 42.4 g/m^2. Information (provided by TRY) concerning both species was gathered from the same altitude, allowing for a reliable comparison (cf. Wright et al. 2004).

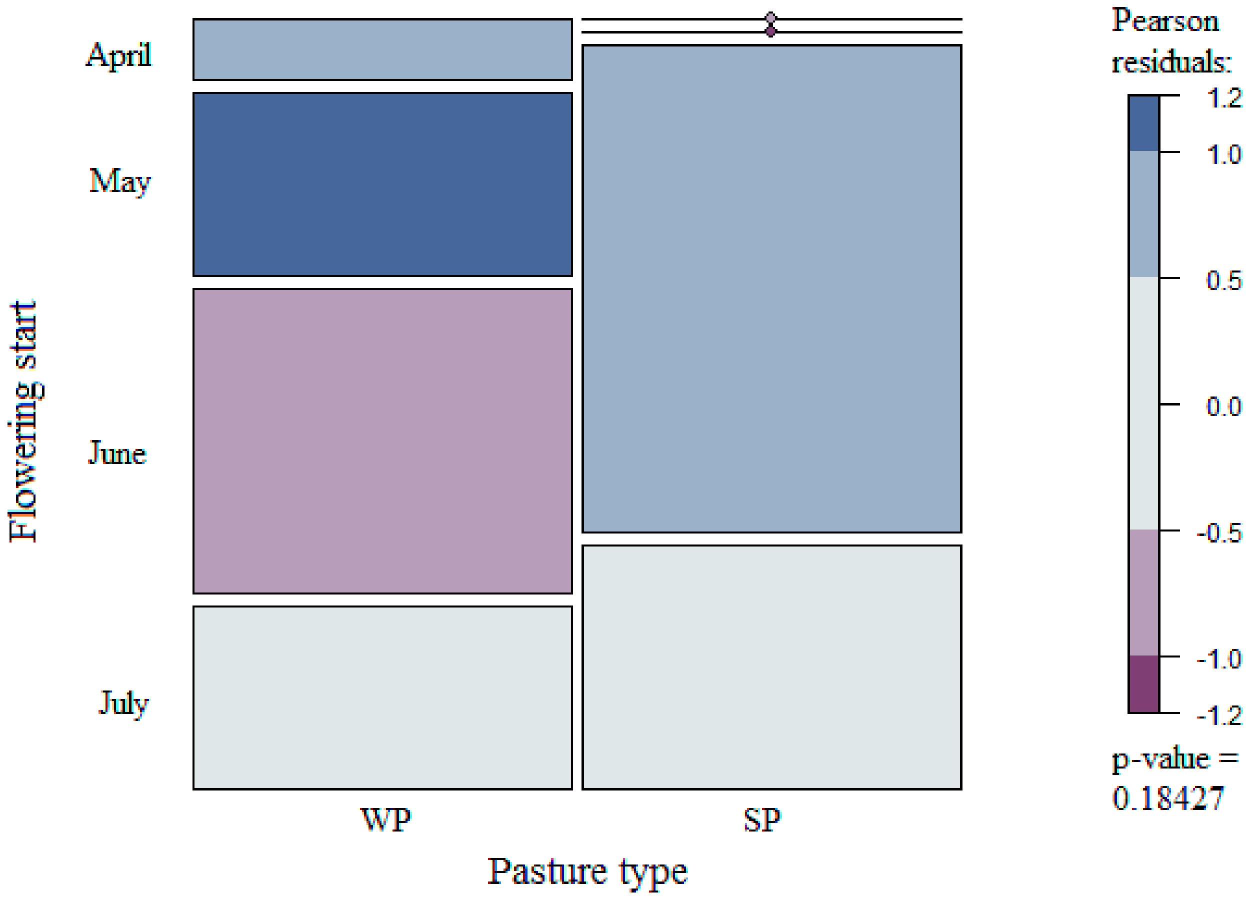

Fig. 4: *Comparison of flowering start between winter and summer pastures. On summer pastures, none of the species starts flowering before June (see the two solid lines).*

Abb. 4: *Vergleich des Blühbeginns der Arten auf Winter- und Sommerweiden. Auf den Sommerweiden beginnt keine der Arten vor Juni zu blühen (siehe die beiden durchgehenden Linien).*

Biomass:

Biomass analysis of a total of 86 plots yielded significant differences between the pasture types, visualized in Fig.7. Winter pastures have an average biomass dry weight of 50.4 g m^{2} $^{-1}$, summer pastures an average dry weight of 124.7 g $m^{2\ -1}$. Alpine meadows of the State Reserve even show an average value of 286.4 g $m^{2\ -1}$, thus as twice as high as the weight calculated for summer pastures. Significant differences between winter and summer pastures were confirmed by the Kruskal-Wallis test (p.value ≤ 0.001). As with other traits such as plant height, these differences reflect a gradient of decreasing grazing intensity from winter to summer pastures.

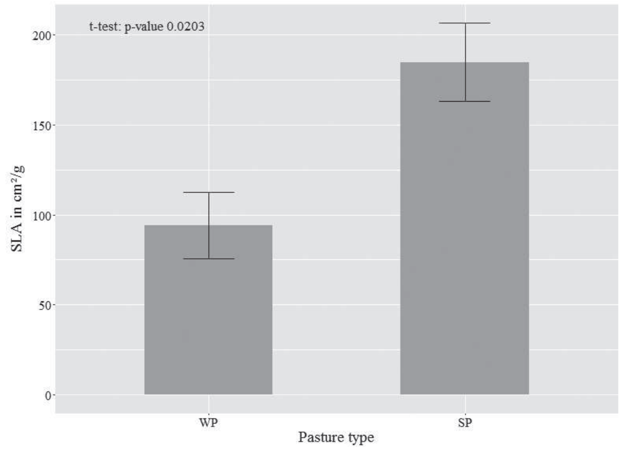

Fig. 5: *Average specific leaf area (SLA) of species dominant on winter and summer pastures (WP: n= 3, SP: n= 5). Outliers were removed; Error bars represent the 95 % confidence interval.*

Abb. 5: *Durchschnittliche spezifische Blattfläche von dominanten Arten auf Winter- und Sommerweiden (Winterweiden: n=3, Sommerweiden: n=5). Ausreißer sind von der Berechnung ausgeschlossen; der Fehlerbereich stellt das 95 %-Konfidenzintervall dar.*

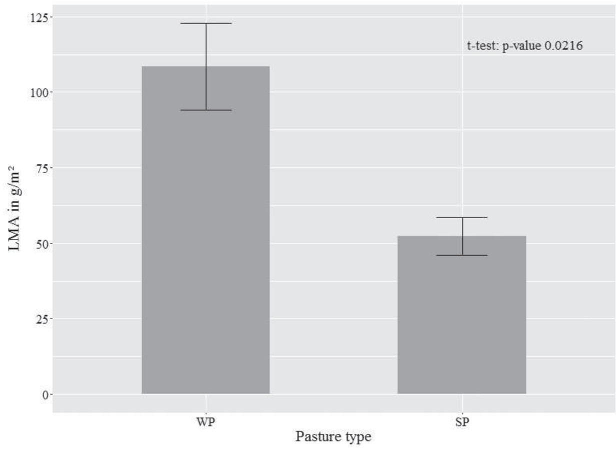

Fig. 6: *Average leaf mass per area (LMA) of species dominant on winter and summer pastures (WP/SP: n= 4). Outliers were removed; Error bars represent the 95 % confidence interval.*

Abb. 6: *Durchschnittliches Blattgewicht pro Fläche von dominanten Arten auf Winter- und Sommerweiden (Winterweiden/ Sommerweiden: n=4). Ausreißer sind von der Berechnung ausgeschlossen; der Fehlerbereich stellt das 95 %-Konfidenzintervall dar.*

4 DISCUSSION

In order to better predict vegetation responses to grazing impact, many studies assessed vegetation changes in terms of a common set of plant functional traits (McIntyre et al. 1999; Díaz et al 2007). The predictive value of these common plant functional traits needs to be tested in different vegetation types and under different climatic conditions since the same traits do not consistently indicate species' responses to grazing under different environmental conditions (Díaz et al. 2001; Pakeman 2004; Wesuls et al. 2012, Neyret et al. 2016). A recent meta-analysis across continents showed a set of traits to be typical for pasture plants, but also confirmed a certain inconsistency in the predictive power of plant functional traits (Díaz et al. 2007). Under semi-arid to sub-humid climatic conditions in Kyrgyzstan, a first study in high-altitude grazing lands using plant functional traits as predictors for the response to grazing was in line with the more general results of respective studies showing, for instance, that small, prostrate and rosette plants are favoured over high, erect and tussock plants under increased grazing intensity (Borchardt et al. 2013). Increased grazing pressure on winter pastures in Kyrgyzstan has to be attributed to changing grazing regimes in the post-Soviet transformation process, resulting inter alia in abandoned seasonal livestock migration and an unbalanced grazing intensity between seasonal pastures (e.g. Baibagushev 2011; Dörre & Borchardt 2012). Whether the predictive power of the plant functional traits selected in this study is appropriate under the specific environmental and grazing regime conditions in Kyrgyzstan will be discussed below.

Plant height, growth forms and flowering start:

The hypothesis that the maximum plant height in the State reserve as well as on summer pastures is higher than on winter pastures was confirmed (cf. Fig. 2). We found the same pattern for average plant height, indicating the grazing gradient between seasonal pastures (see Fig. 2 in Appendix). The interaction between grazing intensity and decreasing plant height has been reported by several authors (e.g. Jauffret & Lavorel 2003; Díaz et al 2007; Zheng et al. 2015). Most likely, decreasing plant stature is a kind of resistance strategy of species to reduce herbivore selectivity (Zheng et al. 2015). Plant height was designated by Díaz et al. (2001) as "the best single predictor of grazing response" and can thus be used as a reliable indicator of degradation processes (Jauffret & Lavorel 2003). Díaz et al (2007) also reported that, in grassland systems with a long history of grazing, which is the case in Kyrgyzstan, a general trend of positive response of shorter plants has been detected. This is supported by Borchardt et al. (2013) showing a significantly negative correlation between grazing and plant height. Nevertheless, the attribute 'plant height' is very dynamic and the importance of plant height in the context of grazing intensity needs to be considered in combination with a set of other traits (Klimesova et al. 2008; Garnier & Navas 2012; Wesuls et al. 2012).

Growth form is defined by the direction and extent of growth, which includes distribution of leaves, canopy structure as well as its height (Pérez-Harguindeguy et al. 2013). Thus, similar results concerning plant height and growth form have been achieved in many studies. High grazing pressure on winter pastures promotes species which optimize the height and position of the foliage to avoid or resist the impact of livestock (Kahmen & Poschlod 2004; Török et al. 2016). Correspondingly, more than half of the species predominant on winter pastures in our study are characterized by rosette and prostrate growth forms, in contrast to summer pastures where approximately two thirds of the species show erect growth forms (cf. Fig. 3). This result corroborates the significantly negative correlation between grazing and erect growth form found by Borchardt et al. (2013).

Livestock migration to summer pastures usually starts around May (Crewett 2012; Dörre und Borchardt 2012). Since the end of the Soviet era, less herders are able to organize the seasonal migration so that summer pastures are less affected by grazing. Our results have shown that in response to cessation of grazing, late-flowering species increase (cf. Fig.4). Several authors additionally found that these individuals also have higher pollination success (Evju et al. 2009; Sletvold et al. 2015). Moreover, late-flowering species are often characterized by a higher forage quality (Tóth et al. 2016), which underlines the importance of the seasonal migration to summer pasture to maintain livestock health and performance. In line with the assessed negative influence of increased grazing intensity on late-flowering

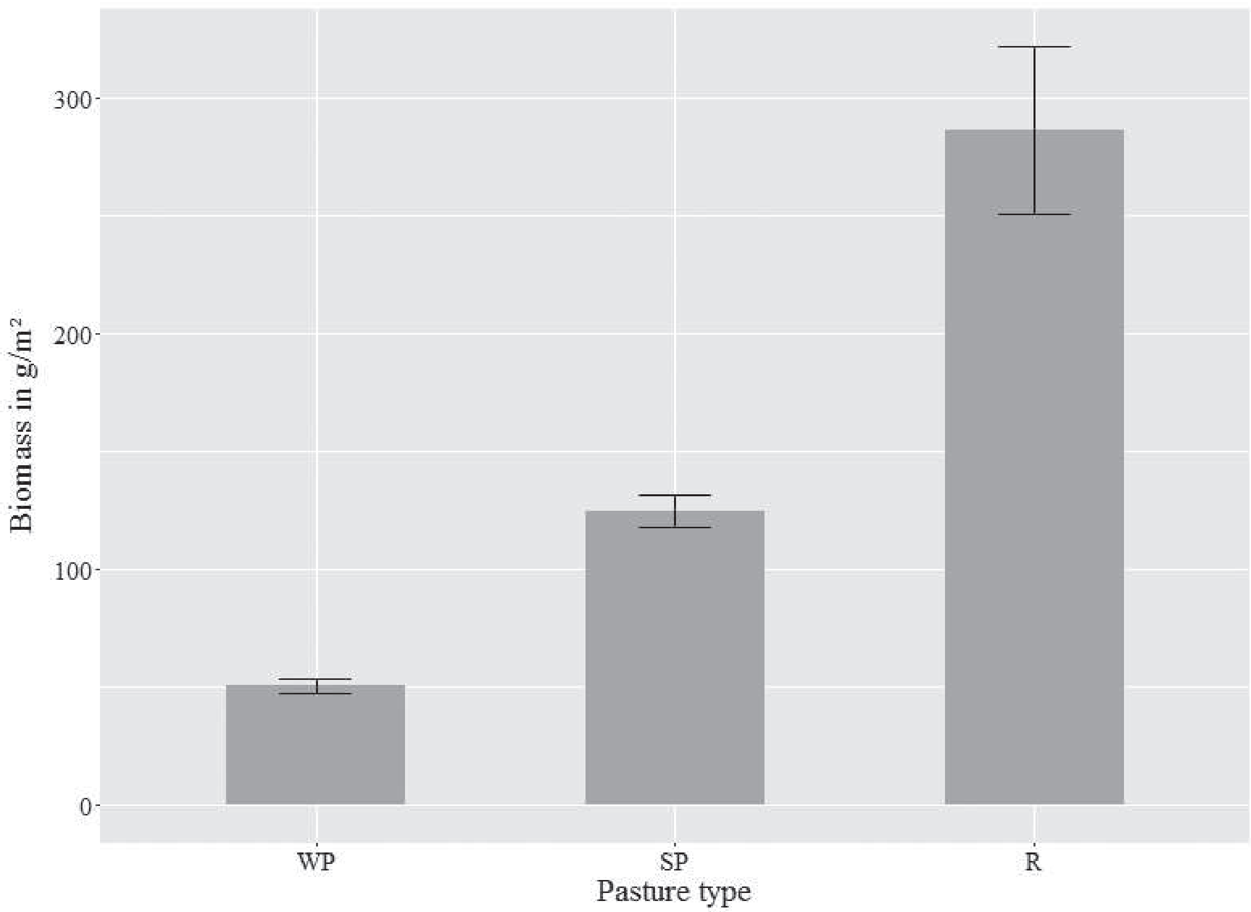

Fig. 7: *Average aboveground biomass of different pasture types (winter pastures (WP), summer pastures (SP) and the State Reserve (R). Error bars represent the 95 % confidence interval.*

Abb. 7: *Durchschnittliche oberirdische Biomasse der verschiedenen Weidetypen (Winterweiden (WP), Sommerweiden (SP) und das Naturreservat (R). Der Fehlerbereich stellt das 95 % Konfidenzintervall dar.*

species we found that flowering on winter pastures starts earlier and is particularly broader in its temporal range. This can be explained by the continuous grazing of livestock on winter pastures, even in summer time.

Leaf Mass per Area (LMA) and Specific Leaf Area (SLA):

Among the leaf traits, SLA and LMA have been proposed as central variables in the definition of plant functional traits, as they are indicators of ecophysiological characteristics such as disturbance tolerance and leaf longevity (Díaz et al. 2001; Scheepens et al. 2010; De la Riva et al. 2016). Our results showed that species of winter pastures are correlated with lower SLA and higher LMA (Figs. 5 and 6). Gross et al. (2008) reported that plants with resource conservative strategies, often characterized by a lower photosynthesis and transpiration rate, are negatively correlated with SLA. This is supported by other studies showing that decreasing SLA is an effective ecological strategy to avoid grazing and to increase resistance to grazing (e.g. Lavorel & Garnier 2002; Niu et al. 2010; Patty et al. 2010), exemplified by species on winter pastures. On the other hand, high SLA is associated with fast-growing species and low investment in leaf thickness and toughness, thus with plant tolerance to grazing since these species show higher regrowth capacity (e.g. Evju et al. 2009; Zheng et al. 2015). Interestingly some authors (Ma et al. 2010; Scheepens et al. 2010) found a decrease of SLA with increasing elevation, mostly caused by harsher climatic conditions, which could not be confirmed by our results (cf. Fig. 5). In a previous study, we found that grazing impact seems to have a stronger influence on species performance than the altitudinal gradient (see Hoppe et al. 2016). The results concerning SLA characteristics on winter pastures (lower altitude, lower SLA) and summer pastures (higher altitude, higher SLA) confirm this hypothesis.

Nutrient-richer environments (i.e. summer pastures) favour, in particular, species with fast-growing leaves and low LMA, because these species are better able to outcompete potential neighbours (Neyret et al. 2016). Higher LMA, as reported in this study for species on winter pastures, has been associated with slow-growing species whose leafs are built to persist (Poorter et al. 2009). This leads to the assumption that plants with higher LMA pursue the strategy of resistance and nutrient retention, accompanied by decreasing SLA.

Notwithstanding the above, some authors noted that leaf traits, such as SLA and LMA, are affected by inter- and intraspecific variation, mostly induced by changes in temperature or light reception (e.g. Kahmen & Poschlod 2004; Scheepens et al. 2010; Neyret et al. 2016). The analysis and interpretation of plant functional traits is extraordinarily complex, implying multiple constraints in separating and assessing the individual role of each trait.

Biomass:

The amount of biomass is often associated with plant height. Increasing grazing intensity generally results in decreasing plant height and plant biomass (Zheng et al. 2010; Sun et al. 2011). Our results are in line with this general relationship, given the substantially higher amount of biomass on summer pastures and in the State Reserve (cf. Fig. 7). Zheng et al. (2010) also reported a correlation between reduced aboveground biomass and decreasing SLA under high grazing pressure, pointing to the resistance strategy of species on winter pastures explained in the context of the SLA analysis.

Soil and plant functional traits:

Several authors have highlighted an interrelation between soil properties and plant functional traits (e.g. Kahmen & Poschold 2008; Orwin et al. 2010; Zheng et al. 2010; Garnier & Navas 2012). As already reported in Hoppe et al. (2016) the different pastures types and soil properties are related to each other, most probably as a result of grazing intensity. Winter pastures are characterized by higher pH values as well as higher bulk density, compared to summer pastures. Soil organic matter content, water content as well as C and N concentration, however, are lower on winter than on summer pastures (see Tab.2 in Appendix). The amount of primary nutrients tends to be higher on summer pastures, so that they can be described as nutrient-richer environments (Hoppe et al. 2016). Soil physical and chemical properties affect the specific manifestation of plant functional traits. For instance, SLA, which represents the relative growth rate of a species, is positively related to resource richness and vice versa. Water and nutrient availability promote equally plant height and leaf architecture (Lavorel & Garnier 2002; Kahmen & Poschold 2004; Zheng et al. 2010, 2015). While higher values of LMA contribute to nutrient retention and protection from desiccation (De la Riva et al. 2016). Similar results have been reported for soil organic matter content, which is negatively affected by increasing grazing intensity and may lead to reduced vegetation biomass as well as changes in plant species composition (Sun et al. 2011).

Our findings are in line with results from many other studies on grazing-induced modifications of plant trait characteristics. However, plant height is not always significantly correlated with lower grazing intensity (e.g. Wesuls et al. 2012). Also, different results concerning leaf traits and the response to grazing have been documented (e.g. Scheepens et al. 2010). Inconsistent trait response in different research areas can be a result of historical and present grazing regimes or of a stronger influence of environmental gradients, suggesting that different plant functional types can coexist (Louault et al. 2005; Wesuls et al. 2012). Basically, the interaction between herbivory and plant species involves feedback loops among disturbances and traits (e.g. Strauss & Agrawal 1999; Craig 2010). As already reported in Hoppe et al. (2016), moderate grazing, as an intermediate disturbance, can lead to a positive feedback cycle resulting in increasing plant performance (such as plant height and species richness) and more favourable soil properties (as shown for summer pastures). However, the ability of plant species to compensate disturbance events is limited. Hence, if grazing intensity exceeds recovery capabilities, to some extent exemplified by winter pastures, a negative feedback loop can be initiated (Craig 2010). The close linkage of positive and negative feedback loops produces complex temporal fluctuations between grazing intensity and plant quality.

5 CONCLUSIONS

Changes in grazing intensity are reflected by plant functional traits. Based on our results, two main strategies of species response can be associated with an intensification of grazing: resistance or tolerance (Evju et al. 2009; Zheng et al. 2015). The majority of plants on winter pastures pursue a resistance strategy with low stature (plant height), low SLA and growth form, increased LMA and early flowering. Summer pastures, on the other hand, are more characterized by species following a tolerance strategy, which implies higher stature, higher SLA and growth form, lower LMA as well as late flowering. Due to intra- and interspecific variations regarding plant functional traits, induced by changes in temperature, water availibility, light or soil properties, multiple studies under various environmental conditions are highly needed to fully understand the species trait response to grazing (cf. Pakeman 2004; Orwin et al. 2010).

The adverse effects on species communities and performance of winter pastures, resulting from a contrasting grazing impact on seasonal pastures, emphasize the demand of sustainable grazing management strategies. A specific rotation system with a scheduled transfer of grazing and resting time between grazing units, to optimize the quantity and quality of forage produced and its utilization by grazing animals, is therefore an indispensable prerequisite. Efforts of management and biodiversity conservation of intensely used pastures should be reinforced to prevent continued degradation of winter pastures and to minimize the risk of reductions in livestock performance.

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APPENDIX

Tab 1: *Complete synoptic table of the proposed rankless communities with modified fidelity phi coefficient and percentage frequency (superscript). The last column represents the outliers.*

Tab. 1: *Vollständige synoptische Tabelle der ranglosen Gesellschaften mit Angaben zum modifiziertem Treue-Phi-Koeffizienten und den prozentualen Häufigkeiten (hochgestellt). Die letzte Spalte stellt die Ausreißer dar.*

Group No	**1**	**2**	**3**	**4**
No. of relevés	**34**	**42**	**6**	**4**
Number of diagnostic species	**12**	**27**	**21**	**-**
<u>Companion specie:</u>				
Festuca valesiaca	--- ^{91}	--- ^{86}	--- ^{83}	---
Taraxacum maracandicum	--- ^{44}	--- ^{62}	--- ^{50}	--- ^{50}
Leontopodium ochroleucum	--- ^{82}	--- ^{76}	--- ^{33}	---
Potentilla multifida	22.8 ^{65}	--- ^{40}	--- ^{50}	--- ^{25}
Euphorbia alatavica	--- ^{24}	13.1 ^{62}	--- ^{67}	--- ^{50}
Kobresia humilis	--- ^{50}	--- ^{45}	---	---
Potentilla nivea	--- ^{41}	--- ^{38}	--- ^{17}	---
Erigeron lachnocephalus	--- ^{38}	--- ^{31}	--- ^{33}	--- ^{25}
Aster serpentimontanus	--- ^{44}	--- ^{31}	---	---
Galium verum	--- ^{29}	--- ^{14}	--- ^{33}	--- ^{25}
Helictotrichon schellianum	--- ^{24}	--- ^{36}	--- ^{17}	---
<u>Group 1 (Winter Pastures):</u>				
Bupleurum thianschanicum	92.9 ^{94}	--- ^{5}	---	---
Androsace dasyphylla	67.6 ^{53}	---	---	---
Plantago arachnoidea	58.5 ^{44}	--- ^{2}	---	---
Potentilla moorcroftii	51.4 ^{32}	---	---	---
Koeleria cristata	41.6 ^{68}	--- ^{17}	---	--- ^{50}
Stipa caucasica	40.3 ^{21}	---	---	---
Scutellaria oligodonta	37.2 ^{18}	---	---	---
Stipa purpurea	35.5 ^{38}	---	---	--- ^{25}
Oxytropis globiflora	34.9 ^{35}	--- ^{5}	--- ^{17}	---
Astragalus tibetanus	33.8 ^{21}	--- ^{5}	---	---
Elytrigia batalinii	30.2 ^{18}	--- ^{5}	---	---
Potentilla pamiroalaika	30.2 ^{12}	---	---	---
Viola dissecta	29.8 ^{15}	--- ^{2}	---	---

Group 2 (Summer Pastures):

Trisetum spicatum	--- [6]	64.2 [86]	--- [17]	--- [25]
Ptilagrostis mongholica	--- ·	60.0 [43]	--- ·	--- ·
Gastrolychnis apetala	--- [9]	55.6 [48]	--- ·	--- ·
Trollius dschungaricus	--- ·	55.6 [55]	--- [17]	--- ·
Cerastium pusillum	--- [9]	53.4 [64]	--- ·	--- [25]
Ranunculus alberti	--- [6]	52.1 [40]	--- ·	--- ·
Festuca alatavica	--- [3]	51.7 [52]	--- [17]	--- ·
Carex stenocarpa	--- [9]	50.0 [55]	--- [17]	--- ·
Allium semenovii	--- ·	48.0 [29]	--- ·	--- ·
Aconitum rotundifolium	--- [6]	46.6 [60]	--- [33]	--- ·
Gentiana karelinii	--- [9]	45.3 [55]	--- ·	--- [25]
Primula algida	--- ·	43.6 [24]	--- ·	--- ·
Bistorta vivipara	--- ·	42.0 [45]	--- ·	--- [25]
Parnassia laxmannii	--- [3]	42.0 [26]	--- ·	--- ·
Draba altaica	--- [3]	39.6 [24]	--- ·	--- ·
Saussurea sordida	--- [9]	39.4 [57]	--- [17]	--- [25]
Lomatogonium carinthiacum	--- ·	38.7 [19]	--- ·	--- ·
Gentiana algida	--- ·	36.1 [17]	--- ·	--- ·
Rhodiola linearifolia	--- [3]	34.3 [19]	--- ·	--- ·
Seseli mucronatum	--- [3]	34.2 [33]	--- [17]	--- ·
Gentiana kaufmanniana	--- [12]	33.3 [38]	--- [17]	--- ·
Gentianopsis barbata	--- ·	33.3 [14]	--- ·	--- ·
Oxytropis penduliflora	--- ·	33.3 [14]	--- ·	--- ·
Gentianella turkestanorum	--- [9]	32.7 [45]	--- [33]	--- ·
Hedysarum kirgisorum	--- ·	31.2 [48]	--- [50]	--- ·
Schmalhausenia nidulans	--- ·	30.3 [12]	--- ·	--- ·
Tulipa heterophylla	--- ·	30.3 [12]	--- ·	--- ·
Ligularia alpigena	--- [6]	29.5 [52]	--- [33]	--- [25]

Group 3 (State Reserve):

Galium turkestanicum	--- ·	--- [7]	83.8 [83]	--- ·
Dianthus superbus	--- ·	--- [10]	70.0 [67]	--- ·
Phleum alpinum	--- ·	--- ·	65.5 [50]	--- ·
Ziziphora clinopodioides	--- ·	--- ·	65.5 [50]	--- ·
Bistorta elliptica	--- ·	--- [17]	65.2 [67]	--- ·
Pedicularis macrochila	--- ·	--- [2]	63.2 [50]	--- ·
Silene graminifolia	--- [3]	--- [2]	60.5 [50]	--- ·
Artemisia dracunculus	--- [12]	--- ·	53.8 [67]	--- [25]

Codonopsis clematidea	--- ·	--- ·	52.2 ^{33}	--- ·
Valeriana ficariifolia	--- ·	--- ·	52.2 ^{33}	--- ·
Noccaea ferganensis	--- ·	--- ·	52.2 ^{33}	--- ·
Scabiosa alpestris	--- ·	--- ·	52.2 ^{33}	--- ·
Gypsophila cephalotes	--- ·	--- ·	52.2 ^{33}	--- ·
Geranium saxatile	--- ^{21}	17.8 ^{55}	51.5 ^{83}	--- ·
Pedicularis ludwigii	--- ^{12}	--- ^{5}	51.7 ^{50}	--- ·
Euphrasia pectinata	--- ^{3}	--- ^{14}	51.3 ^{50}	--- ·
Tragopogon vvedenskyi	--- ·	--- ^{2}	49.4 ^{33}	--- ·
Anemonastrum protractum	--- ·	--- ^{2}	49.4 ^{33}	--- ·
Phlomoides oreophila	--- ^{6}	16.7 ^{57}	47.2 ^{83}	--- ^{25}
Erigeron pseudoseravschanicus	--- ^{3}	--- ^{2}	46.3 ^{33}	--- ·
Alopecurus pratensis	--- ·	--- ^{7}	44.4 ^{33}	--- ·
----------	----------	----------	----------	----------
Elytrigia gmelinii	--- ^{29}	--- ^{17}	--- ·	--- ^{25}
Rumex acetosa	--- ·	20.9 ^{29}	--- ^{33}	--- ·
Stellaria brachypetala	--- ·	16.7 ^{29}	--- ^{17}	--- ^{25}
Myosotis alpestris	--- ·	14.8 ^{40}	--- ^{50}	--- ^{25}
Kobresia capilliformis	--- ·	20.9 ^{29}	--- ^{33}	--- ·
Alchemilla retropilosa	--- ^{6}	17.0 ^{24}	--- ·	--- ^{25}
Artemisia aschurbajewii	--- ^{18}	--- ^{31}	--- ^{50}	--- ^{25}
Bromopsis paulsenii	--- ·	--- ^{10}	--- ·	--- ·
Caragana jubata	--- ·	--- ^{10}	--- ·	--- ·
Ranunculus songaricus	--- ·	--- ^{10}	--- ·	--- ·
Oxytropis lapponica	--- ^{15}	--- ^{31}	--- ^{17}	--- ^{25}
Thalictrum alpinum	--- ^{12}	--- ^{29}	--- ^{50}	--- ·
Poaceae	--- ^{21}	--- ^{21}	--- ^{17}	--- ·
Euphrasia regelii	--- ^{15}	--- ^{17}	--- ·	--- ·
Astragalus alpinus	--- ^{6}	--- ^{24}	--- ^{33}	--- ^{25}
Pedicularis dolichorhiza	--- ^{21}	--- ^{17}	--- ·	--- ·
Potentilla orientalis	--- ^{12}	--- ^{2}	--- ·	--- ·
Saussurea caespitans	--- ^{12}	--- ^{2}	--- ·	--- ·
Hordeum brevisubulatum	18.5 ^{38}	--- ^{10}	--- ·	--- ^{50}
Bromopsis inermis	--- ^{9}	--- ·	--- ·	--- ·
Ephedra fedtschenkoae	--- ^{9}	--- ·	--- ·	--- ·
Iris loczyi	--- ^{9}	--- ·	--- ·	--- ·
Stipa regeliana	--- ^{12}	--- ^{12}	--- ·	--- ·
Pyrethrum karelinii	--- ^{3}	--- ^{10}	--- ·	--- ·
Carex turkestanica	--- ^{24}	--- ^{10}	--- ^{17}	--- ^{25}

Oxytropis sp.	--- [18]	--- [12]	--- ·	--- ·
Cirsium esculentum	--- [12]	--- [10]	--- [33]	52.5 [75]
Lichen.	--- [24]	--- [12]	--- ·	--- ·
Allium platyspathum	--- ·	23.4 [21]	--- [17]	--- ·
Poa supina	--- [12]	--- [10]	--- [33]	--- [25]
Alfredia acantholepsis	--- ·	10.2 [19]	--- [33]	--- ·
Carex sp.	--- [18]	--- [10]	--- ·	--- ·
Helictotrichon desertorum	--- [24]	--- [12]	--- ·	--- ·
Viola tianschanica	--- [6]	--- [12]	--- [17]	--- ·
Dichodon cerastoides	--- [3]	--- [17]	--- ·	--- [25]
Corydalis gortschakovii	--- [3]	--- [17]	--- [17]	--- ·
Aconogonon songaricum	--- ·	20.5 [19]	--- [17]	--- ·
Potentilla sp.	--- [18]	--- [7]	--- ·	--- ·
Allium atrosanguineum	--- ·	17.4 [17]	--- [17]	--- ·
Papaver croceum	--- ·	17.4 [17]	--- [17]	--- ·
Poa sp.	--- [12]	--- [10]	--- ·	--- ·
Potentilla asiatica	--- [3]	--- [12]	--- [33]	--- ·
Pedicularis oederi	--- ·	8.7 [14]	--- ·	--- [25]
Schulzia albiflora	--- ·	--- [12]	--- [33]	--- ·
Alchemilla sibirica	--- ·	--- [10]	--- [33]	--- ·
Allium schoenoprasoides	--- [12]	--- ·	--- [33]	--- ·
Aster sp.	29.8 [15]	--- [2]	--- ·	--- ·
Festuca rubra	--- [6]	--- [7]	--- [17]	--- ·
Gentiana sp.	--- [9]	--- [7]	--- ·	--- ·
Poa pratensis	--- [3]	--- [7]	--- [17]	--- [25]
Pedicularis sp.	--- [6]	--- [7]	--- ·	--- ·
Plantago depressa	--- [3]	--- [5]	--- ·	58.5 [50]
Poa alpina	--- ·	--- [7]	--- [17]	--- [25]
Potentilla hololeuca	--- [6]	--- [7]	--- ·	--- ·
Pulsatilla campanella	--- [6]	--- [5]	--- [17]	--- ·
Tragopogon turkestanicus	--- [6]	--- [2]	--- [17]	--- [25]
Veronica ciliata	--- [6]	--- [7]	--- ·	--- ·
Carex mela0ntha	--- ·	--- [7]	--- ·	--- [25]
Erigeron allochrous	--- [3]	--- [7]	--- ·	--- ·
Gentiana kirilowii	--- [9]	--- [2]	--- [17]	--- ·
Poa relaxa	--- [3]	--- [7]	--- ·	--- ·
Potentilla sericea	--- [6]	--- ·	--- [17]	--- [25]
Thalictrum minus	--- [6]	--- [2]	--- [17]	--- ·
Triglochin maritimum	--- [6]	--- [2]	--- ·	--- [25]
Achillea millefolium	--- ·	--- [7]	--- [17]	--- ·
Allium sp.	--- ·	--- [7]	--- ·	--- ·

Valeriana dubia	---	--- [2]	--- [17]	---
Stachyopsis oblongata	---	--- [2]	--- [17]	---
Aster vvedenskyi	--- [6]	---	--- [17]	---
Carex aterrima	---	--- [7]	---	---
Doronicum	---	--- [5]	--- [17]	---
Draba subamplexicaulis	---	--- [7]	---	---
Comastoma falcatum	---	--- [7]	---	---
Helictotrichon pubescens	---	--- [7]	--- [17]	---
Helictrotrichon sp.	--- [6]	--- [2]	---	---
Inula rhizocephala	---	--- [7]	---	---
Lindelofia stylosia	--- [3]	--- [5]	---	---
Minuartia verna	---	--- [5]	--- [17]	---
Arctopoa tibetica	---	--- [7]	---	---
Potentilla gelida	---	--- [7]	---	---
Potentilla tergemina	--- [6]	--- [2]	---	---
Saussurea leucophylla	---	--- [7]	---	---
Trollius lilacinius	---	--- [7]	---	---
Allium tianschanicum	--- [6]	---	---	---
Androsace septentrionalis	---	--- [2]	---	--- [25]
Androsace sericea	--- [6]	---	---	---
Eremogone meyeri	--- [3]	---	--- [17]	---
Artemisia rhodantha	--- [6]	---	---	---
Astragalus sp.	---	--- [2]	--- [17]	---
Blysmus compressus	--- [6]	---	---	---
Bryophyta	---	---	---	65.5 [50]
Cerastium bungeanum	---	--- [5]	---	---
Crepis multicaulis	---	--- [2]	--- [17]	---
Draba nemorosa	---	--- [2]	---	--- [25]
Dracocephalum integrifolium	--- [3]	---	--- [17]	---
Leymus flexisi	--- [6]	---	---	--- [25]
Erigeron heterochaeta	---	--- [5]	---	---
Erigeron sp.	--- [3]	--- [2]	---	---
Goniolimon ortocladum	--- [6]	---	---	---
Lappula microcarpa	--- [3]	--- [2]	---	---
Lappula rupestris	--- [3]	---	---	--- [25]
Linum pallescens	---	--- [5]	---	---
Poa litvinoviana	--- [3]	--- [2]	---	---
Poa tianschanica	---	--- [2]	---	--- [25]
Polygana comosa	---	--- [2]	--- [17]	---
Rhodiola gelida	---	--- [5]	---	---
Stellaria soongorica	---	--- [2]	--- [17]	---

Thalictrum simplex	---	--- [2]	---	---
Viola rupestris	---	--- [2]	--- [17]	---
Adenophora himalayana	--- [6]	---	---	---
Elymus tschimganicus	--- [15]	--- [7]	--- [17]	--- [25]
Allium hymenorhizum	--- [3]	---	---	---
Elytrigia repens	---	---	--- [17]	---
Anthoxanthum alpinum	---	---	--- [17]	---
Anthriscus sylvestris	---	---	--- [17]	---
Artemisia pamirica	--- [3]	---	---	---
Artemisia vulgaris	--- [3]	---	---	---
Asteraceae	--- [3]	---	---	---
Asterosea sp.	--- [3]	---	---	---
Astragalus nivalis	--- [3]	---	---	---
Botrychium lunaria	---	--- [2]	---	---
Calamagrostis compacta	---	--- [2]	---	---
Calamagrostis pseudophragmites	---	---	--- [17]	---
Campanula glomerata	---	---	--- [17]	---
Carex sp.	---	--- [2]	---	---
Carex sp.1	---	--- [2]	---	---
Carex sp.2	---	--- [2]	---	---
Cortusa brotheri	---	---	---	44.7 [25]
Delphinium oreophilum	---	---	--- [17]	---
Doronicum turkestanicum	---	---	--- [17]	---
Dracocephalum sp.	--- [3]	---	---	---
Psathyrostachys kronenburgii	--- [3]	---	---	---
Ephedra regeliana	--- [3]	---	---	---
Erigeron aurantiacus	---	--- [2]	---	---
Eritrichium villosum	---	--- [2]	---	---
Erysimum sisymbrioides	---	---	--- [17]	---
Galatella chromopappus	---	---	--- [17]	---
Geranium rectum	---	---	---	44.7 [25]
Geranium sp.	---	---	--- [17]	---
Glaux maritima	---	---	---	44.7 [25]
Hedysarum neglectum	---	--- [2]	---	---
Hieracium virosum	---	---	--- [17]	---
Hierochloe odorata	---	---	---	44.7 [25]
Hordeum sp. (new for science)	--- [3]	---	---	---
Iris ?	---	--- [2]	---	---
Ixiolirion tataricum	---	---	--- [17]	---
Kobresia	--- [3]	---	---	---
Lagotis integrifolia	---	--- [2]	---	---

Festuca olgae	--- [3]	--- ·	--- ·	--- ·
Ligularia narynensis	--- [6]	--- ·	--- ·	--- ·
Ligularia sp.	--- [3]	--- ·	--- ·	--- ·
Ligularia thomsonii	--- ·	--- ·	--- [17]	--- ·
Myosotis sp.	--- ·	--- [2]	--- ·	--- ·
Achoriphragma lancifolium	--- ·	--- [2]	--- ·	--- ·
Oxytropis nutans	--- ·	--- [2]	--- ·	--- ·
Oxytropis platysema	--- ·	--- [2]	--- ·	--- ·
Phleum phleoides	--- ·	--- ·	--- [17]	--- ·
Picris nuristanica	--- ·	--- ·	--- [17]	--- ·
Plantago lanceolata	--- [3]	--- ·	--- ·	--- ·
Polygonum cognatum	--- ·	--- ·	--- ·	44.7 [25]
Potentilla anserina	--- ·	--- ·	--- ·	44.7 [25]
Puccinellia hackelina	--- ·	--- ·	--- ·	44.7 [25]
Pulsatilla	--- ·	--- [2]	--- ·	--- ·
Pyrethrum alatavicum	--- ·	--- ·	--- [17]	--- ·
Pyrethrum pyrethroides	--- ·	--- ·	--- [17]	--- ·
Ranunculus popovii	--- ·	--- [2]	--- ·	--- ·
Ranunculus sp.	--- [3]	--- ·	--- ·	--- ·
Rosa alberti	--- ·	--- [2]	--- [17]	--- ·
Salix coesia	--- ·	--- ·	--- ·	44.7 [25]
Saussurea laespitans	--- [3]	--- ·	--- ·	--- ·
Semenovia transiliensis	--- ·	--- ·	--- [17]	--- ·
Serratula marginata	--- ·	--- [2]	--- ·	--- ·
Stipa capillata	--- [3]	--- ·	--- ·	--- ·
Stipa krylovii	--- [3]	--- ·	--- ·	--- ·
Taphrospermum altaicum	--- ·	--- ·	--- ·	44.7 [25]
Taraxacum glabrum	--- ·	--- [2]	--- ·	--- ·
Thymus seravschanicus	--- ·	--- ·	--- [17]	--- ·
Neotorularia humilis	--- [3]	--- ·	--- ·	--- ·
Trollius altaicus	--- ·	--- [2]	--- ·	--- ·
Veronica	--- [3]	--- ·	--- ·	--- ·
Veronica porphyriana	--- ·	--- ·	--- [17]	--- ·
Viola sp	--- ·	--- [2]	--- ·	--- ·

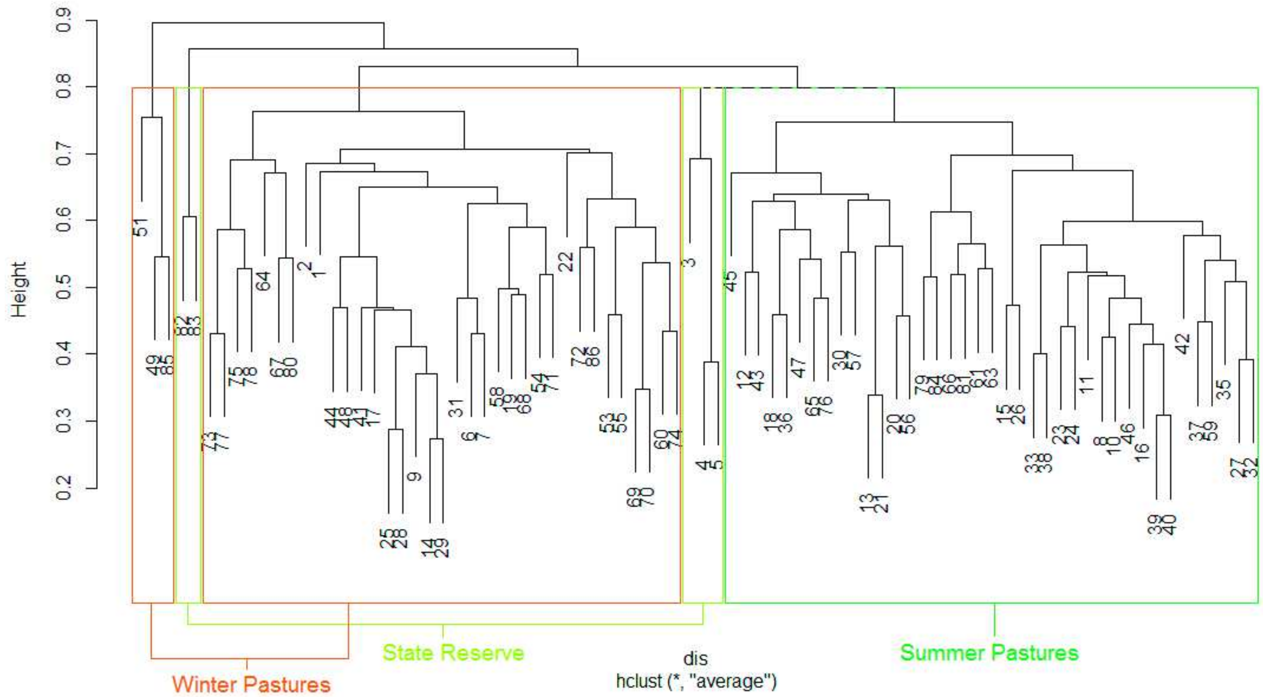

Fig.1: *Dendrogram of the cluster analysis (based on the average-linkage algorithm). Plots belonging to the different pasture types are marked by colours.*

Abb. 1: *Dendrogramm der Clusteranalyse (basierend auf dem Average-Linkage-Algorithmus). Die Plots der verschiedenen Weidetypen sind farblich markiert.*

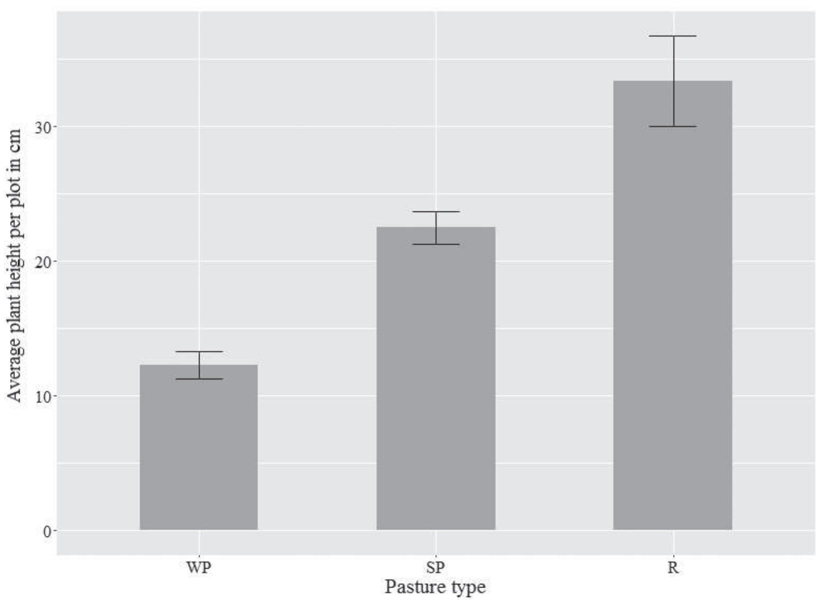

Fig.2: *Mean of average plant height of winter pastures (WP), summer pastures (SP) and the State Reserve (R). Error bars represent the 95 % confidence interval.*

Abb. 2: *Mittelwerte der durchschnittlichen Wuchshöhe der Pflanzen auf Winterweiden (WP), Sommerweiden (SP) und im Naturreservat (R). Der Fehlerbereich stellt das 95 %-Konfidenzintervall dar.*

Tab 2: *Soil properties (average values) of plots sampled in 2014 and 2015. Standard deviations in brackets. S = sand, U = silt, T = clay.*

Tab. 2: *Physikalische und chemische Bodeneigenschaften (Durchschnittswerte) der in 2014 und 2015 beprobten Flächen. Die Standardabweichung ist in Klammern angegeben. S = Sand, U = Schluff, T = Ton.*

Pasture type	pH ($CaCl_2$)	water content [%]	organic matter [%]	C [g/kg]	N [g/kg]	CEC_{eff} [µmolc/g]	bulk density [g/cm³]	grain size distribution [%]
State Reserve (SR)	5.77 (± 0.41)	3.24 (± 0.68)	21.40 (± 3.96)	92.52 (± 24.45)	7.34 (± 1.65)	383.62 (± 1.32)	1.05 (±0.11)	S: 2.51 U: 60.97 T: 36.52
Summer Pasture (SP)	6.01 (± 0.53)	3.99 (± 1.73)	20.75 (± 4.82)	88.96 (± 27.98)	7.12 (± 1.74)	434.06 (± 115.91)	1.14 (± 0.15)	S: 4.27 U: 55.13 T: 40.60
Winter Pasture (WP)	7.22 (± 0.50)	2.53 (± 1.02)	12.56 (± 2.45)	54.58 (± 9.85)	4.50 (± 0.85)	383.94 (± 54.09)	1.26 (± 0.12)	S: 6.57 U: 57.89 T: 35.54

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Article IV

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Plant species diversity of pastures in the Naryn Oblast (Kyrgyzstan)

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Abstract

Traditional pastoral practices in Kyrgyzstan have been transformed into more intensive forms of pastoral land use during the Soviet colonial period, and once again modified after independence in 1991. Kyrgyz winter pastures close to settlements are subject to degradation processes, while remote summer pastures are less affected. It is largely unknown to what extent current grazing regimes, repeatedly modified during the post-Soviet transformation process, have influenced plant species diversity of mountain pastures. This paper aims to analyze inventory (α) and differentiation (β) diversity of pastures in the Naryn Oblast, where winter pastures are subject to increased grazing pressure. We used a non-asymptotic approach in order to infer Hill numbers, i.e. the effective number of species at different levels of q (where q = 0: species richness, q = 1: Shannon diversity, q = 2: Simpson diversity) to make fair comparisons among assemblages of winter and summer pastures. We established sample-size-based rarefaction (interpolation) and prediction (extrapolation) curves, and assessed beta diversity by implementing an ANOSIM and by calculating Jaccard and Sørensen indices. We also inspected the occurrence of rare endemic plants, which might play a key role in local ecosystem processes and are important for biodiversity conservation. Increased grazing pressure on winter pastures mainly results from abandoned seasonal livestock migration and unbalanced grazing intensity between seasonal pastures. Our results show that inventory diversity is higher on summer pastures and that species composition between summer and winter pastures differs significantly. Winter pastures are less species-rich but have a higher percentage of rare endemic species.

Zusammenfassung

Traditionelle Formen der Weidewirtschaft wurden in Kirgistan im Zuge der Kolonialisierung durch die Sowjetunion in intensive Formen der Weidenutzung überführt, die nach der Unabhängigkeit erneut modifiziert wurden. Winterweiden, die sich meist in der Nähe von Siedlungen befinden, sind von Degradierungserscheinungen betroffen, während die Sommerweiden in höheren Lagen seltener frequentiert werden. Inwieweit der sich ändernde Weidedruck während des post-sowjetischen Transformationsprozesses die Diversität der Pflanzenarten auf den Hochweiden beeinflusst, ist weitgehend unbekannt. Dieser Artikel zielt darauf ab, die Bestands- (α) und die

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Differenzierungs- (β) Diversität der Weiden im Naryn Oblast zu analysieren, wo Winterweiden von zunehmender Nutzungsintensität betroffen sind. Wir haben hierfür einen nicht-asymptotischen Ansatz gewählt, um die ‚Hill numbers' (effektive Anzahl an Arten) auf unterschiedlichen Ebenen von q (q = 0: Artenreichtum, q = 1: Shannon-Diversität, q = 2: Simpson-Diversität) zu ermitteln und einen angemessenen Vergleich zwischen der Artenzusammensetzung von Winter- und Sommerweiden durchführen zu können. Basierend auf unseren Stichproben haben wir Interpolations- und Extrapolationskurven erstellt sowie die Beta-Diversität erfasst, indem wir eine ANOSIM implementiert und auch den Jaccard- und den Sørensen-Index berechnet haben. Zur Abschätzung der qualitativen Diversität wurde das Vorkommen von seltenen, endemischen Pflanzenarten untersucht, die eine Schlüsselrolle in lokalen Ökosystemprozessen und zur Erhaltung von Biodiversität spielen können. Aufgrund von fehlender saisonaler Weidemigration und einer unausgeglichenen Beweidungsintensität hat der Nutzungsdruck auf den Winterweiden im Zuge des post-sowjetischen Transformationsprozesses zugenommen. Unsere Ergebnisse zeigen, dass die Bestandsdiversität auf den Sommerweiden höher ist und sich die Artenzusammensetzung auf den Sommer- und Winterweiden signifikant unterscheidet. Winterweiden sind weniger artenreich, weisen allerdings einen größeren Anteil an seltenen, endemischen Arten auf.

Keywords alpha diversity, beta diversity, extrapolation, hill numbers, interpolation

Electronic supplementary material supplementary material (*Table S.1, Figures S.1* and *S.2*) available at: http://dx.doi.org./10.12854/erde-2018-384

1. Introduction

In many environmental research fields, such as biological diversity, conservation biology or historical biogeography, species richness and species diversity are key components (e.g. *Bock* et al. 2007; *Delang* and *Li* 2013; *Chao* and *Chiu* 2016). The importance of biodiversity for ecosystem functioning and particularly for ecosystem resilience demands thorough analysis for the management of natural resources and conservation efforts. A comparison of species richness among multiple assemblages facilitates a better understanding of causes and patterns of biodiversity and the assessment of effects of anthropogenic disturbances (*Dornelas* et al. 2011; *Chao* and *Chiu* 2016). Livestock grazing can have severe consequences on species diversity, including plant functional traits and functional diversity, respectively. Because grazing depends on and affects plant functional traits (feedback loop), important insights into grazing-induced changes in structure and dynamics of vegetation can be generated based on this codependency (*Díaz* et al. 2007; *Evju* et al. 2009; *Borchardt* et al. 2013; *Hoppe* et al. 2016a). Reduced plant height is, for example, a reliable indicator for anthropogenic and natural disturbances even under diverse land use history and climate combinations (*Díaz* et al. 2001; *Jauffret* and *Lavorel* 2003). Several authors stressed that intense grazing mostly leads to reduction in species richness, soil fertility and biomass production, and that the degree of decrease depends on spatial and temporal aspects of grazing pressure and the original type of vegetation (e.g. *Dornelas* et al. 2011; *Alkemade* et al. 2013; *Fujita* and *Ariunbold* 2014).

Increasing grazing pressure on Kyrgyz pastures is a current object of concern (*Hoppe* et al. 2016a, b; *Levine* et al. 2017). Kyrgyzstan was subjected to fundamental political, economic and agricultural changes in the last century, in particular after the occupancy by the Soviet Union and after independence in 1991 (e.g. *Dörre* 2012; *Shigaeva* et al. 2007; *Robinson* 2016). In previous centuries, nomadism has been the predominant land use system. Mobile livestock keeping by pastoral nomads has adapted to rangeland ecosystems with arid and semi-arid ecological conditions in order to increase land use efficiency (*Shigaeva* et al. 2007; *Baibagushev* 2011; *Schmidt* 2013). Flocks moved between seasonal pastures, mainly between montane and alpine summer pastures (*dzailoo*) and winter pastures (*kyshtoo*) located at lower altitudes. Under the Soviet regime, formerly autonomously acting pastoralists were superseded by state owned farms (*sovkhozes*) and collective farms (*kolkhozes*) and sedentarization and collectivization campaigns were pushed forward. Livestock numbers increased enormously during this period; however, vertical transhumance between high-mountain rangelands and lower pasture areas has been mostly maintained during occupancy (*Robinson* 2016). After the Soviet era, livestock numbers saw a drastic reduction and a temporally decreasing grazing pressure. During this period, the return to a subsistence lifestyle was, for most of the Kyrgyz people, the only possibility to sustain their livelihood (*Borchardt* et al. 2011; *Dörre* 2012; *Zhumanova* et al. 2016). As a result of this new way of life, livestock numbers increased again in the further course of post-Soviet transformation and recently rebounded toward Soviet era levels with 15 million animals in 2014 (*Levine* et al. 2017). But the dissolution of the institutionalized organizations was accompanied by the loss of the annual migratory herd movements. The herders are nowadays rarely able to organize the migration of livestock themselves because of long distances and a weak state of infrastructure which resulted in severe changes of traditional pasture practices (*Crewett* 2012; *Kreutzmann* 2013). In consequence, summer pastures at higher altitude experience increasing abandonment, while winter pastures which are close to settlements and exposed to intense grazing pressure, are subject to vegetation and soil degradation (*Hoppe* et al. 2016a, b; *Shigaeva* et al. 2016; *Levine* et al. 2017). According to recent estimates, degradation processes affect between 45 and 75% of Kyrgyz pasture areas (*Robinson* 2016; *Levine* et al. 2017).

Diversity indices and terms related to biodiversity were first introduced in the 1940s by *Fisher* et al. (1943). Since the 1960s, there is an ongoing discussion on their theoretical justification and statistical considerations (*Heip* et al. 1998; *Maurer* and *McGill* 2011; *Magurran* 2013; *Moreno* et al. 2017). In order to avoid conceptual ambiguities, we use the terms alpha, beta and gamma diversity according to the concepts introduced by *Whittaker* (1960). Alpha diversity, the richness in species of a particular stand or community, has long been used as basic parameter for describing biotic diversity and is titled here as 'inventory diversity'. Beta diversity, the extent of change of community composition, is designated as 'differentiation diversity' (e.g. *Legendre* 2008; *Tuomisto* 2010). We concentrate on alpha (inventory) and beta (differentiation) diversity because gamma diversity differs from alpha diversity just by the scale at which it is applied (*Juransinski* et al. 2009; *Tuomisto* 2010). Biodiversity estimation has, for a long time, struggled with problems, such as the sample size issue or the comparison of species diversity of different assemblages (e.g. *Colwell* et al. 2012; *Chao* et al. 2014). *Chao* et al. (2014) generated a reliable method (non-asymptotic approach) to characterize the species diversity of an assemblage. They proposed to use integrated rarefaction and extrapolation curves based on the first three Hill numbers (q = 0: species richness, q = 1: Shannon diversity, q = 2: Simpson diversity), which represent a unified sampling framework (see also *Colwell* et al. 2012 and *Chao* and *Jost* 2012). By using this framework, it is possible to derive both theoretical formulas and analytic estimators to measure and assess species diversity.

To what extent changing grazing regimes during the post-Soviet transformation process in Kyrgyzstan have affected plant species diversity of mountain pastures in the Naryn Oblast is largely unknown. *Borchardt* et al. (2011) reported from SW-Kyrgyzstan that increasing grazing pressure mostly decreases species richness, but we already have shown (see *Hoppe* et al. 2016b) that a general comparison with their results might be difficult because of different climate and site conditions. *Taft* et al. (2011) analyzed diversity patterns and endemism of Kyrgyz grasslands based on samples taken randomly all over the country (without considering spatial and temporal aspects of grazing intensity as an environmental factor influencing species composition and diversity). They found that particularly meadow steppes at intermediate elevations are characterized by high species diversity and that Kyrgyz grasslands are inhabited by a considerable number of Middle Asian endemics. According to several authors, especially rare and endemic species are threatened by impacts such as overgrazing and habitat loss and their decline might affect ecosystem functioning (e.g. *Mouillot* et al. 2013; *Soliveres* et al. 2016). Studies focusing on effects of grazing on species richness of rare endemic plants of Kyrgyz high-mountain pastures have not been published so far.

In sum, large knowledge gaps and research deficits can be identified with regard to changing plant species diversity of Kyrgyz summer and winter pastures. In order to generate detailed insights into the effects of increasing grazing pressure, this paper addresses two major research questions: 1) Are diverging grazing intensities of Kyrgyz summer and winter pastures reflected by inventory and differentiation diversity? 2) To what extent does the occurrence of rare endemic plants differ on summer and winter pastures?

2. Materials and methods

2.1 Study area and data collection

We collected vegetation data in the Kara-Kujur valley, Naryn Oblast (41° N, 76° E) during two field trips in 2014 and 2015 (*Fig. 1*). We completed vegetation relevés according to the Braun-Blanquet approach (*Braun-Blanquet* 1964) with a standard relevé size of 5 m x 5 m. Sample plots were placed randomly along an elevational gradient (between 2,800 m and 3,400 m), including winter and summer pasture (for a detailed description of the study area see *Hoppe* et al. 2016a, b). Kyrgyzstan is divided into seven provinces (Oblast). The Naryn Oblast presents the largest one with the highest percentage of Kyrgyz pastures, approximately 30%. Thus, wide areas of the Naryn Oblast are used as grazing land (*Crewett* 2012; *Eisenman* et al. 2013). Herds consist of all kinds of domestic grazers, mainly sheep and horses but also flocks of goats, cows and yaks. Since 2008, the total number of livestock is continuously increasing in the Kara-Kujur valley from 11,293 heads in 2008 to 16,256 in 2014, a rise of 44% (*Asykulov* and *Esenaman uulu*; unpublished data). Our raw data consist of 76 relevés containing 216 species records. The nomenclature of vascular plant species follows *Czerepanov* (1995). For the diversity analysis we transformed the raw data into incidence data (*Table S.1* in the Supplement), where the sampling units (plots) are randomly and independently sampled and only the incidence (presence-absence) of species in each sampling unit is recorded (*Chao* et al. 2014).

2.2 Inventory diversity

To compute and to plot sample-size and/or coverage-based rarefaction and extrapolation (R/E) curves we transformed our raw data into a species-by-sampling-unit incidence matrix (*Table S.1* in the Supplement). This matrix consists of *S* rows and *T* columns, where *T* = number of sampling units; the (*i,j*) elements is 1 if species *i* is detected in sampling unit *j*, and 0 when it is not detected (*Chao* et al. 2014; *Hsieh* et al 2016). *Chao* et al. (2014) listed the theoretical formulas (see Table 2 therein) to obtain each order *q* of the Hill numbers, also known as *effective number of species*. The order *q* of the Hill number determines the diversity measure's sensitivity to common or rare species. Species richness ($q = 0$) weighs all species equally, whereas the Simpson diversity ($q = 2$) gives more weight to the abundance of common species and is, thus, less influenced by the (non-)occurrence of rare species (*Heip* et al. 1998; *Jost* 2006; *Leinster* and *Cobbold* 2012; *Chao* et al. 2014). By calculating multiple orders of *q*, we built an integrated rarefaction/extrapolation sampling curve with confidence intervals. The rarefaction and the extrapolation part smoothly join at the point of the references sampling. The size in the R/E

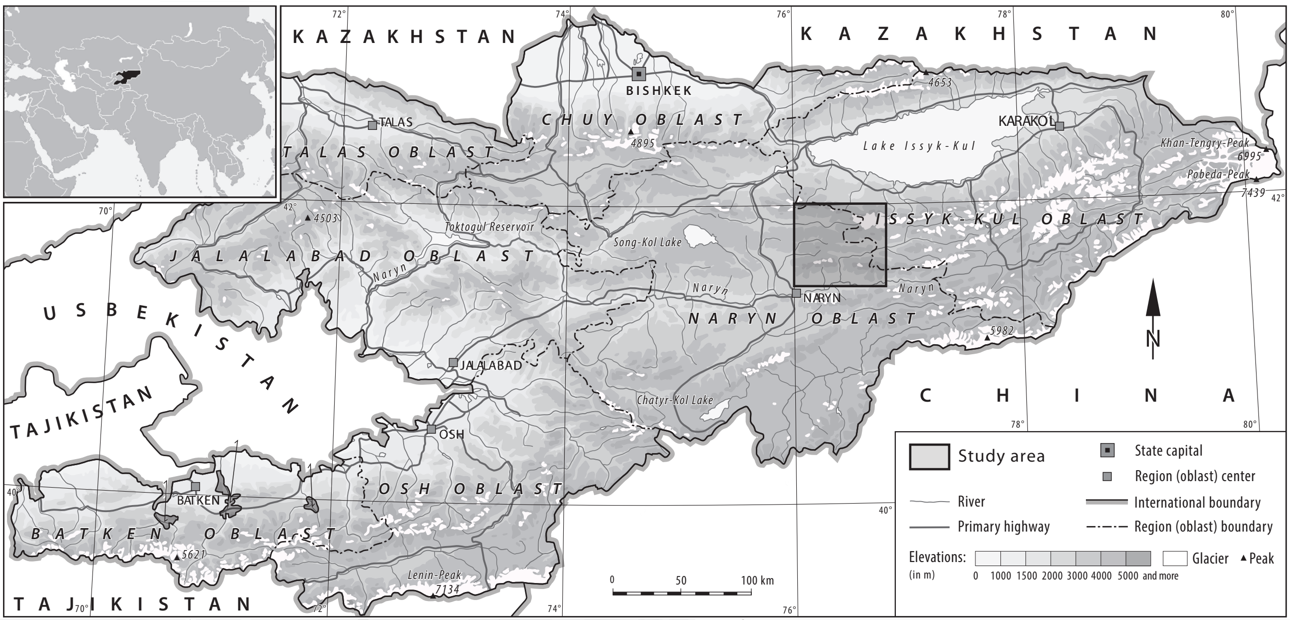

Fig. 1 Location of research area in the north-east of the Naryn Oblast. Source: own elaboration by S. Adler, C. Carstens and F. Hoppe 1/2018 based on Academy of the Kyrgyz SSR, 1987

curve should not be extrapolated to more than double or triple of the minimum observed sample size (see *Fig. 2*) when plotting species richness ($q = 0$), because the estimates may be subject to some prediction bias. This limitation does not concern Shannon and Simpson diversity ($q > 0$), if the data are not too poor (*Chao* et al. 2014; *Hsieh* et al. 2016). A similar trend has been reported regarding the sensitivity of the sample size. The under-sampling bias for Hill numbers of higher orders of q is progressively less severe (*Gotelli* and *Chao* 2013; *Chao* et al. 2014).

By extrapolating the data, two objectives can be differentiated. First, it is possible to estimate the richness of a smaller or larger sample and second, it is also possible to estimate the complete richness of the assemblage, represented by the asymptote of the R/E curve. When this asymptote is reached, additional sampling will not result in a higher number of species (*Gotelli* and *Colwell* 2011). The R/E curve is enlarged by a 95% confidence interval (based on a bootstrap method with 200 replications), which allows a rigorous statistical comparison. Significant differences at a level of 5% among the expected species richness are ensured, if the confidence intervals do not overlap (*Chao* and *Jost* 2012). *Chao* et al. (2015) suggested that coverage-based R/E curves are more robust and efficient than sample-size-based curves, but they also mentioned that, if R/E curves never cross, they will give the same qualitative ordering of species richness (see results).

2.3 Differentiation diversity

Beta diversity or differentiation diversity is a useful measure of the similarity in species composition between sites. It allows evaluating the effects of disturbances and serves to describe changes in species composition along environmental gradients (*Baselga* 2010; *Tuomisto* 2010; *Jost* et al. 2011). To assess differentiation diversity we calculated the Jaccard and Sørensen similarity matrices based on pairwise resemblances among sample units (*Jurasinski* et al. 2009; *Anderson* et al. 2011; *Legendre* and *De Cáceres* 2013). These two indices were chosen because they handle presence/absence data and are commonly used. Additionally, we performed an analysis of similarity ANOSIM (*Clarke* 1993) to test statistically whether there is a significant difference between species composition of winter and summer pastures. The analysis of similarity yields a test statistic (R), which compares observed dissimilarities between and within winter and summer pastures (using the Jaccard distance). Depending on the differentiation between those pasture types, R lies between 0 (completely different) and 1 (completely equal). To evaluate the significance of the test statistic (p value), 999 permutations of the species table were generated (*Clarke* 1993; *Anderson* et al. 2013). To visualize the results of the ANOSIM, we subsequently performed a PCoA based on the same distance matrices (*Legendre* and *De Cáceres* 2013).

The Sørensen and the Jaccard index are the most widely used classical indices (e.g. *Jost* et al. 2011; *Beck* et al. 2013; *Chao* et al. 2015). To estimate the percentage of shared species, we calculated the richness-based indices (*Table 1*), where the Sørensen index (C_{02}) is = $2S_{12}$ / ($S_1 + S_2$) and the Jaccard index (U_{02}) is: S_{12} / ($S_1 + S_2 - S_{12}$); representing S_1 as the number of species in assemblage 1, S_2 as the number of species in assemblage 2 and S_{12} as the number of shared species (*Gotelli* and *Chao* 2013; *Chao* et al. 2015). An empirical index (observed similarity measure) is calculated for comparison purpose only, because these empirical measures are often subject to large negative bias due to undetected shared species and unseen species in samples. Therefore, an estimated similarity measure is also calculated and recommended for practical use (*Table 1*). The magnitude of the differences represents the undersampling bias associated with the empirical index (*Chao* et al. 2015). The measure of similarity ranges from 0 (assemblages share no species) to 1 (compositionally identical assemblages). Both indices are designed to compare two assemblages, but they differ little in their perspective. The Sørensen index compares the number of shared species to the mean number of species in a single assemblage, while the Jaccard index compares the number of shared species in regard to the total number of species in the combined assemblages. Thus, the Sørensen index takes more a local view, while the Jaccard index takes a global view (*Chao* et al. 2005; *Jost* et al. 2011; *Gotelli* and *Chao* 2013). Nevertheless, one has to keep in mind that the classical incidence-based similarity indices we calculated are treating rare and abundant species equally, simplifying the relationships between assemblages, and potentially causing an inference problem (*Jost* et al. 2011; *Beck* et al. 2013; *Gotelli* and *Chao* 2013). *Jost* et al. (2011) underlined in general that estimation of differentiation and similarity, especially for measures based on species richness, is statistically challenging.

All statistical analyses were implemented in *R* (version 3.2.3) by using the packages *ggplot2*, *iNEXT*, *SpadeR* and *vegan* (*Wickham* 2009; *Hsieh* et al 2016; *Chao* et al. 2015; *Oksanen* et al. 2016).

2.4 Rare endemic species

The vegetation of Kyrgyzstan is extremely diverse and the Kyrgyz flora is considered to be one of the richest in Middle Asia (*Eisenman* et al. 2013; *Lazkov* and *Umralina* 2015). Species new to science continue to be discovered including many endemic species, which are of particular value to science, notably to conservation biology and biogeography (*Lazkov* and *Umralina* 2015). Rare species were classified as species with a total abundance of 1 (singletons) or 2 (doubletons) that occur in one or exactly two sampling units in replicated incidence data (*Chao* et al. 2005). We only counted the species which have been determined on species level, so that 24 rare species for winter pastures and 32 rare species for summer pastures were included in the analysis (see *Table S.1* in the Supplement). We checked these rare species for endemism based on *Czerepanov* (1995) in order to include qualitative aspects of the pasture's plant species diversity.

3. Results

3.1 Inventory diversity

The R/E curves show that for each order *q* the 95% confidence intervals (shaded areas) do not overlap, which indicates that species diversity between summer and winter pastures differ significantly (see *Fig. 2*). More precisely, plant species richness (q = 0) of summer pastures is significantly greater for any sample size than species richness of winter pastures (*Fig. 2a*). The curve for species richness rises steeply with sampling size, whereas the curves for Shannon and Simpson diversity level off at the point of the reference size (*Fig. 2b/c*). This illustrates that, regarding the sensitivity to sample size, Hill numbers of higher order are more influenced by the frequencies of the common species, and thus are less sensitive to sampling techniques. Here, the R/E curve is extended to a maximum size of 100 (respecting the potential prediction biases for species richness, q = 0, beyond the double or triple references sample size). We additionally produced a sample-size-based R/E sampling curve, which is extended to a size of 300, to visualize

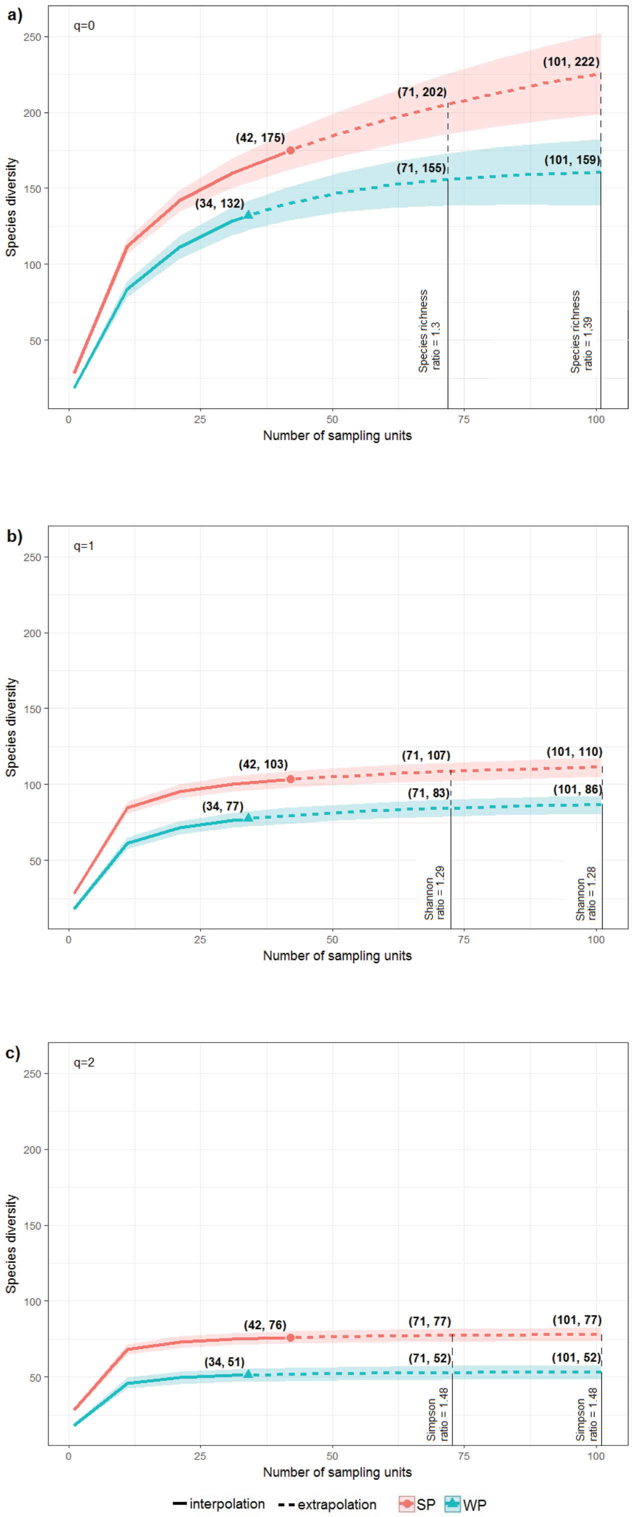

Fig. 2 *Sample-size-based rarefaction (solid line) and extrapolation (dashed line) of the first three Hill numbers (a = species richness, b = Shannon diversity and c = Simpson diversity). Observed samples on summer pastures (SP) are marked by a dot and on winter pastures (WP) by a triangle. Species richness, Shannon and Simpson ratios were calculated for sample size m = 71 and m = 101. Source: own elaboration*

the estimated asymptote (see *Fig. S.1* in the Supplement). This curve indicates that the asymptotic diversity estimate for species richness of summer pastures lies around 265, whereas the asymptote of order $q = 0$ of winter pastures is estimated at around 160. Finally, we checked whether the coverage-based R/E curve, which has been described as more robust, indicates a diverging result. *Figure S.2* in the Supplement clearly shows that the estimates are exactly the same and do not yield new information (at a complete coverage of 1, the asymptotic diversity estimate is around 265 as well), indicating that the sample-size-based R/E curve presents reliable and efficient results and gives the same qualitative ordering of species richness.

As *Figure 2* illustrates, the species richness ratio for winter and summer pastures lies between 1.31 (m = 71) and 1.39 (m = 101). The ratio of Shannon and Simpson diversity is more or less equal at both sample size with 1.29 and 1.28 (Shannon) and 1.48 (Simpson). The difference between the Shannon and Simpson ratio is, due to the stronger weight of common species, at order $q = 2$ (Simpson). In sum, the average diversity ratio is 1.37, which indicates a higher species number on summer pastures in the order of 37% (ignoring the weight of common or rare species).

3.2 Differentiation diversity

The ANOSIM revealed that the average of the within-group distances is smaller than the average of the between-group distances, i.e., there is a statistically significant difference (p = 0.001) in the species composition between summer and winter pastures (R = 0.684). Based on the R-value one would expect little overlap between the two groups. To visualize the ANOSIM, we carried out a principal coordinate analysis (PCoA) of the Jaccard distances (*Fig. 3*). In this two-dimensional space, the two pasture types are clearly separated and the two areas do not overlap. The intermediate R-value indicates that this pattern might be different on higher axes.

By using *SpadeR,* we additionally calculated similarity indices, which are presented in *Table 1*. Empirical and estimated similarity indices are almost equal, which indicates small to even no undersampling bias. The empirical indices are calculated based on the formula we presented in the *Materials and methods* part. This means for the empirical Sørensen index C_{02}: 2x88 / (131 + 173) = 0.579 and for the empirical Jaccard index U_{02}: 88 / (131 + 173 - 88) = 0.407. Thus, the estimates demonstrate that around 40-60% of the species are shared, depending on the local or global view of the indices. In turn, the measure 1-C_{02} or U_{02} quantifies the effective average proportion of non-shared species.

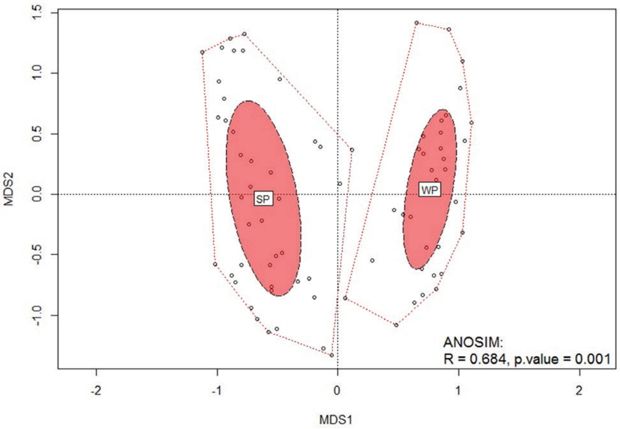

Fig. 3 *Differentiation of species composition between summer and winter pastures (SP and WP). The PCoA is based on the ANOSIM. Source: own elaboration*

Table 1 *Calculated similarity indices and standard error (SE). C_{02} represents the Sørensen index and U_{02} the Jaccard index, at order q = 0 for two communities. Source: own elaboration*

Empirical similarity indices				
	estimate	SE	95% lower	95% upper
C_{02} (q = 0, Sørensen)	0.579	0.023	0.535	0.623
U_{02} (q = 0, Jaccard)	0.407	0.020	0.367	0.447
Estimated similarity indices				
	estimate	SE	95% lower	95% upper
C_{02} (q = 0, Sørensen)	0.566	0.065	0.439	0.699
U_{02} (q = 0, Jaccard)	0.395	0.063	0.272	0.518

3.3 Rare endemic species

On winter pastures, represented by 34 sampling units (plots), 131 species were observed and 614 incidences were counted. On summer pastures, 173 species in 42 sampling units were observed and a total of 1,174 incidences have been counted (see *Table 2*). The number of observed shared species within the two communities is 88. Interestingly, the amount of rare species is, with approximately 18%, nearly equal on winter and summer pastures, even though species diversity is significantly higher on summer pastures (see *Fig. 2*). However, the percentage of rare endemic species (approx. 60%) on winter pastures is remarkable. Summer pastures show a lower amount of rare endemics (37%), which is still a substantial percentage.

Table 2 Number of observed species, total incidences and shared species. Proportion of rare species and rare endemic species of both pastures types were calculated. Source: own elaboration

	Winter pastures	Summer pastures
No. of observed species	131	173
No. of total incidences	614	1174
No. of shared species	88	
Rare species (singleton and doubleton)	24	32
Rare species in %	**18.32**	**18.49**
Middle Asian endemics of rare species	14	12
Middle Asian endemics of rare species in %	**58.33**	**37.5**

4. Discussion

Species diversity indices are nowadays used to obtain a quantitative estimate of biological variability, allowing us to compare biological entities in space and time (*Heip* et al. 1998; *Jost* 2006). Diversity estimates are affected by sample intensity. In particular, species richness is well known to be strongly biased by sampling size, while the Simpson index is the least biased diversity index (*Jost* 2006; *Colwell* et al. 2012). Based on the true diversities (Hill numbers), it was further possible to construct meaningful index-independent general formulas, which overcome many of these deficiencies (*Jost* 2006; *Chao* et al. 2014). The concept proposed by *Chao* et al. (2014) integrated the two basic types of measures for inventory diversity: estimated species richness and the species-abundance distribution expressed by Shannon and Simpson indices (*Jurasinski* et al. 2009). This unified framework now offers an approach to quantify and compare species diversity and allows detailed inferences about the sampled assemblages. Supplemented by the similarity analysis we performed, this method presents a reliable basis to estimate species diversity of Kyrgyz rangelands.

The degradation of vegetation cover in Kyrgyzstan, resulting from high stocking rates and overgrazing, has already been a problem during soviet times. In 1985, GIPROZEM, the State Institute for Land Management, considered around 24% of all pastures as degraded (*Robinson* 2016). Even if livestock numbers had decreased after independence, and some pastures have recovered due to less grazing pressure, the livestock sector has gained again in importance after the first decade of transformation. A major cause of pasture degradation today is that households tend to graze their livestock close to settlements reflecting the current trend towards reduced mobility of local herders (*Hoppe* et al. 2016b; *Lui* and *Watanabe* 2016; *Zhumanova* et al. 2016; *Wang* et al. 2017). Our results corroborate these findings, indicating lower species diversity on winter pastures which are located near settlements. *Fujita* and *Ariunbold* (2014) described similar patterns with regard to Mongolian pastures, where plant species richness decreased near herder's tents. In southern Morocco, *Akasbi* et al. (2012) reported negative effects on vegetation and biomass as well due to intense grazing near settlements. In arid to semi-arid mountain environments, evidence had been provided that species richness increases from humidity-limited lower altitudes towards higher elevation before it decreases again when environmental conditions become too unfavorable, described as hump-shaped pattern with a peak at intermediate elevation (e.g. *Richter* 2000; *Körner* 2003; *Rahbek* 2005; *Van de Ven* et al. 2007; *Grytnes* and *McCain* 2013). Thus, the increase in species richness towards higher elevation could be an effect of climatological vertical gradients. However, by comparing winter and summer pasture plots located at the same elevation but subjected to contrasting grazing pressure, we were able to show that decreasing grazing intensity on summer pasture results in higher species richness (*Hoppe* et al. 2016b). Therefore, the influence of intense livestock grazing tends to be the driving factor, while the elevational gradient is of subordinate importance. In the Kara-Kujur Valley, this gradient apparently plays a minor role concerning species diversity and composition. Lower species diversity on winter pastures as well as dissimilarities with regard to species composition on winter and summer pastures confirm this finding (see *Fig. 2*, *Table 1*). Calculation of the similarity indices Jaccard and Sørensen showed that summer and winter pastures are sharing only between 40-60% of the species, suggesting that disturbances such as intense grazing can affect the species composition. Differentiation diversity has been described as one key component for understanding the functioning of ecosystems and for ecosystem management (*Jurasinski* et al. 2009; *Baselga* 2010; *Jost* et al. 2011). Interestingly, both estimated indices were lower than the empirical one. By contrast, *Chao* et al. (2015: 39) reported that "any estimated similarity index is higher than its corresponding empirical value". This suggests that there is no or only a small undersampling bias concerning the empirical similarity measures.

Lower grazing intensity on summer pastures results in higher species diversity, as shown by the three R/E curves, in line with the intermediate disturbance hypothesis (*Connell* 1978). By assessing grazing pressure using a grazing scale, we previously showed (see *Hoppe* et al. 2016b) that exceeding an intermediate level of disturbance results in decreasing species richness and plant height, as exemplified by winter pastures in this study. Concordant results concerning species height and richness under intermediate grazing pressure have been pointed out by other authors (e.g. *Borchardt* et al. 2011; *Fujita* and *Ariunbold* 2014). *Wang* et al. (2017) reported from the Tibetan Plateau that some species such as *Kobresia* and *Carex* spp. benefit from moderate grazing and are thus dominant on meadows or steppes. In our case study, *Carex stenocarpa* (highly diagnostic species on summer pastures), *Carex aterrima* and *Kobresia capilliformis* (exclusively occurring on summer pastures, see *Table S.1* in the Supplement) could serve as examples corroborating this finding. In recent years, consensus is growing for the argument that high species diversity enhances ecosystem functioning (*Loreau* et al. 2002; *Beierkuhnlein* and *Jentsch* 2005; *Schulze* and *Mooney* 2012 and contributions therein). Several authors found that especially rare species, which are particularly vulnerable to climate or anthropogenic disturbances, often contribute to ecosystem functioning and resilience (e.g. *Cao* et al. 2001; *Lyons* et al 2005; *Mouillot* et al. 2013; *Soliveres* et al. 2016). For instance, *Soliveres* et al. (2016) showed that rare species in grasslands have a significantly more positive relationship with multifunctionality than common species, and suggested that a high diversity of rare species might be more beneficial to local ecosystem processes. Apparently, rare species tend to be less redundant than common species in the functional traits they possess (*Soliveres* et al. 2016). *Mouillot* et al. (2013) supported these findings and showed that rare species deliver more unusual functions (i.e. high functional distinctiveness) and have a higher potential to enhance the resilience of ecosystem functioning. This may gain importance with regard to future environmental uncertainty. Summer pastures with higher species diversity and a proportion of approximately 20% of rare species (see *Fig. 2*, *Table 2*) seem to represent the more resilient ecosystem compared to winter pastures. However, the same proportion of rare species on winter pastures could indicate that, even with lower species diversity, local ecosystem processes are not persistently disturbed. It has been shown that particular plants can have strong effects on ecosystem processes by providing specific functional traits or by interactions of species, which could determine essential ecosystem characteristics more than just the simple presence or absence of species (e.g. *Chapin III* et al. 2000; *Soliveres* et al. 2016). To verify whether the rare species on winter pastures are characterized by specific traits or similar properties, further analysis would be needed. Currently, such information is hardly available, because most of the species occurring in our research area are poorly studied (see *Hoppe* et al. 2016a, b).

Winter pastures represent areas of high endemism (see *Table 2*), while species diversity is lower than on summer pastures. Rare endemic plants on winter pastures are species such as *Goniolimon ortocladum*, *Allium thianschanicum* or *Lappula rupestris* (see *Table S.1* in the Supplement). *Taft* et al. (2011) analyzed endemism of Kyrgyz grasslands as well and found that 46% of the identified species were Middle Asian endemics. However, they did not correlate this percentage to an existing grazing gradient or the amount of rare species, so that a direct comparison is not possible. Our results have shown that summer pastures contain around 20% of rare species, with moderate grazing intensity confined to the summer months. Grazing rotation is currently missing on winter pastures, where livestock keeping is largely maintained all year round. A reduction of the high grazing pressure on winter pastures, which are severely affected by degradation processes (see *Hoppe* et al. 2016b), is warranted in order to protect the higher percentage of endemic species, to enhance species diversity and to positively impact ecosystem processes such as productivity. Several authors have demonstrated that herbivore density and overgrazing are key factors for the decline of rare endemic species (e.g. *Hobohm* and *Bruchmann* 2014; *Speed* and *Austrheim* 2017). Consequently, a specific rotation system should be introduced with a scheduled transfer of grazing and resting time between pasture units to relieve winter pastures from uncontrolled grazing pressure.

The abandoned seasonal livestock migration is seen by several authors (e.g. *Shigaeva* et al. 2016; *Zhumanova* et al. 2016; *Levine* et al. 2017) as a consequence of the still existing mismatch between local needs, resource conditions and regulation mechanisms. In many cases unsustainable pasture use reveals the weakness of the institutional and regulatory framework conditions considering dynamic challenges and risks local households are subjected to (*Shigaeva* et al. 2016; *Zhumanova* et al. 2016). With regard to Kyrgyzstan's newly decentralized pasture management system, this weakness is aggravated by interpersonal and intergroup inconsistencies within elected pasture committees (*Levine* et al. 2017). Notwithstanding the unsustainable livestock-keeping practices, *Zhumanova* et al. (2016) emphasized that, according to local farmers, environmental changes over time such as climate variability also have led to strong changes in pasture quality. Pasture degradation in large regions of Kyrgyzstan is most likely a result of complex interactions of manifold factors, including land use and climate change. In particular, reduced precipitation, earlier snowmelt and higher evapotranspiration may have serious consequences for pastures quality and fodder availability (e.g. *Reyers* et al. 2013; *Gan* et al. 2015). The reintroduction of traditional pasture practices with a rotation grazing system, which had existed for centuries, would improve the condition of grazing resources and increase plant species diversity on Kyrgyz mountain pastures.

5. Conclusions

In contrast to winter pastures, the relatively high species diversity on summer pastures does currently not indicate any signs of overgrazing. Winter pastures show a higher percentage of rare endemic species, indicating significance for nature conservation. A disproportionately higher grazing pressure on winter pastures adversely affects species richness, forage quality, and ultimately the livelihoods of the local people. Local households and herders as well as political institutions are strongly encouraged to implement sustainable livestock keeping practices in order to preserve the mountain pastures. The seasonal migration of the herds of animals plays a key role, whereas the reduction of discrepancies within the pasture committees is equally important to maintain the use potential of these natural resources.

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Supplementary information for

Plant species diversity of pastures in the Naryn Oblast (Kyrgyzstan)

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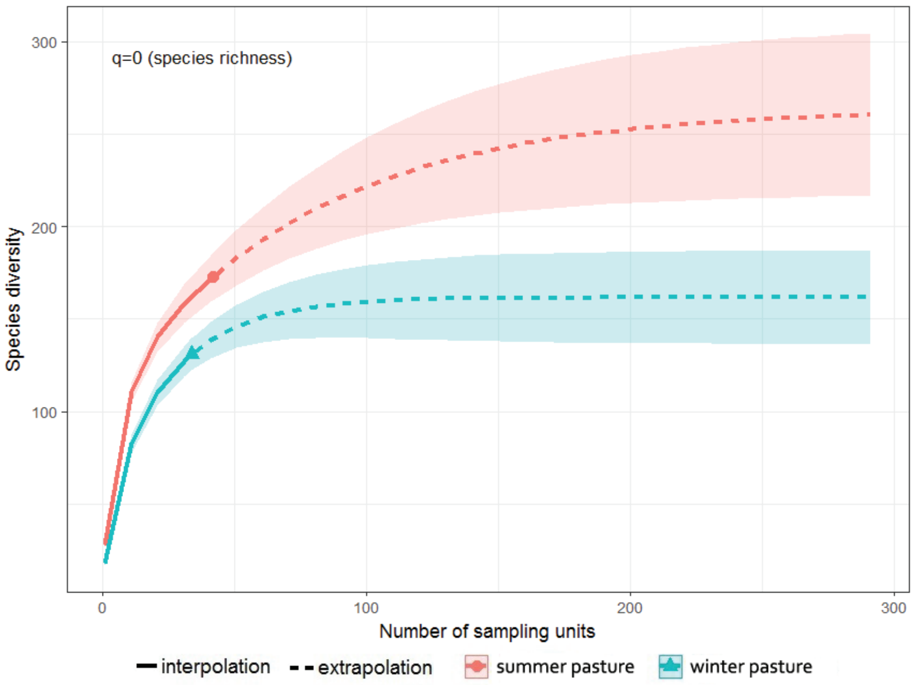

Fig. S.1 Sample-size-based R/E curve, extrapolated up to 300 to illustrate the asymptotic diversity estimates. Source: own elaboration

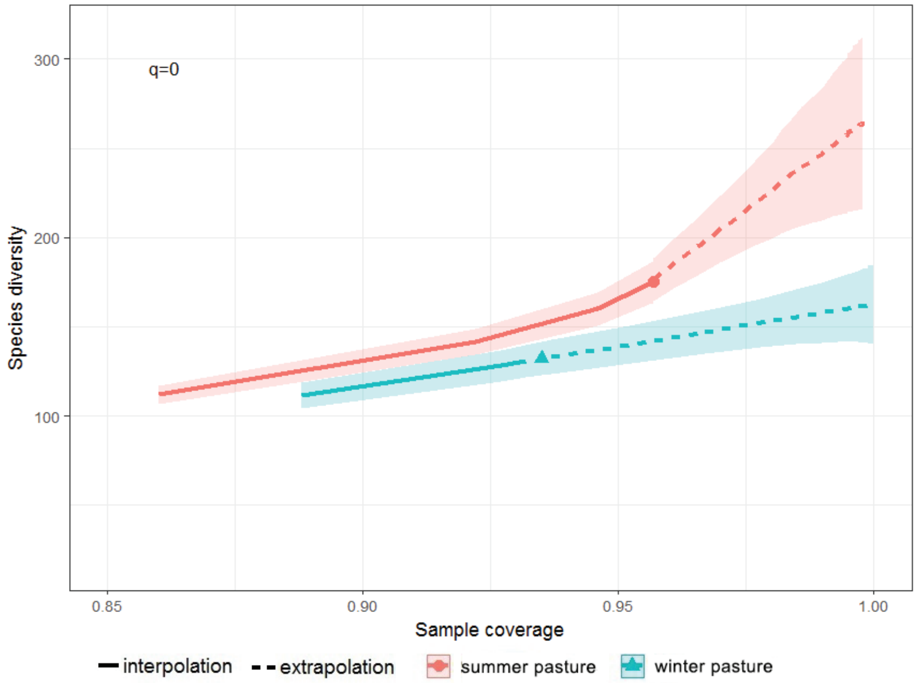

Fig. S.2 The coverage-based R/E curve shows similar results as the sample-size-based curve in terms of the asymptotic diversity estimates. Source: own elaboration

Table S.1 see next page

Table S.1 The species-by-sampling-unit incidence matrix has been extended by species names and the pasture type. The first block includes the companion species, the second diagnostic species of winter pastures and the third diagnostic species of summer pastures. Species that only occurred one or two times, i.e. singletons and doubletons, are bordered at the end of the matrix and the endemic species (according to Czerepanov) are written in bold. Source: own elaboration

	summer pastures (42 plots)	**winter pastures (34 plots)**
Companion species		
Festuca valesiaca	36	31
Taraxacum maracandicum	26	15
Leontopodium ochroleucum	32	28
Potentilla multifida	17	22
Euphorbia alatavica	26	8
Kobresia humilis	19	17
Potentilla nivea	16	14
Erigeron lachnocephalus	13	13
Aster serpentimontanus	13	15
Galium verum	6	10
Helictotrichon schellianum	15	8
Winter pastures		
Bupleurum thianschanicum	2	32
Androsace dasyphylla	0	18
Plantago arachnoidea	1	15
Koeleria cristata	7	23
Stipa purpurea	0	13
Potentilla moorcroftii	0	11
Stipa caucasica	0	7
Oxytropis globiflora	2	12
Helictotrichon desertorum	5	8
Hordeum brevisubulatum	4	13
Scutellaria oligodonta	0	6
Astragalus tibetanus	2	7
Elytrigia batalinii	2	6
Potentilla pamiroalaika	0	4
Viola dessecta	1	5
Potentilla orientalis	1	4
Saussurea caespitans	1	4
Bromopsis inermis	0	3
Ephedra fedtschenkoae	0	3
Iris loczyi	0	3
Summer pastures		
Trisetum spicatum	36	2
Cerastium pusillum	27	3
Ptilagrostis mongholica	18	0
Trollius dschungaricus	23	0
Bistorta vivipara	19	0
Festuca alatavica	22	1
Hedysarum kirgisorum	20	0
Carex stenocarpa	23	3
Gastrolychnis apetala	20	3
Saussurea sordida	24	3
Aconitum rotundifolium	25	2
Gentiana karelinii	23	3
Phlomoides oreophila	24	2
Ligularia alpigena	22	2
Gentianella turkestanorum	19	3
Geranium saxatile	23	7
Allium semenovii	12	0
Seseli mucronatum	14	1
Ranunculus alberti	17	2
Gentiana kaufmanniana	16	4
Parnassia laxmannii	11	1
Lomatogonium carinthiacum	8	0
Draba altaica	10	1
Primula algida	10	0
Rhodiola linearifolia	8	1
Gentiana algida	7	0
Gentianopsis barbata	6	0
Oxytropis penduliflora	6	0
Schmalhausenia nidulans	5	0
Tulipa heterophylla	5	0
Bromopsis paulsenii	4	0
Caragana jubata	4	0
Ranunculus songaricus	4	0
Elytrigia gmelinii	7	10
Kobresia capilliformis	12	0
Rumex acetosa	12	0
Stellaria brachypetala	12	0
Myosotis alpestris	17	0
Alchemilla retropilosa	10	2
Artemisia aschurbajewii	13	5
Oxytropis lapponica	13	4
Allium platyspathum	9	0
Thalictrum alpinum	12	4
Poaceae	9	6
Euphrasia regelii	7	5
Astragalus alpinus	10	2
Pedicularis dolichorhiza	7	7
Stipa regeliana	5	4
Carex turkestanica	4	7
Oxytropis sp.	5	6
Cirsium esculentum	4	4
Bistorta elliptica	7	0
Poa supina	4	3
Alfredia acantholepsis	8	0
Carex sp.	4	6
Euphrasia pectinata	6	1
Viola tianschanica	5	2
Artemisia dracunculus	0	4
Dichodon cerastoides	7	1
Corydalis gortschakovii	7	1
Pedicularis ludwigii	2	4
Aconogonon songaricum	8	0
Potentilla sp.	3	6
Galium turkestanicum	3	0
Allium atrosanguineum	7	0
Papaver croceum	7	0
Dianthus superbus	4	0
Poa sp.	4	4
Potentilla asiatica	5	1
Pedicularis oederi	6	0
Schulzia albiflora	5	0
Alchemilla sibirica	4	0
Allium schoenoprasoides	0	4

Aster sp.	1	5
Festuca rubra	3	2
Gentiana sp.	3	3
Poa pratensis	3	1
Alopecurus pratensis	3	0
Pedicularis sp.	3	2
Plantago depressa	2	1
Poa alpina	3	0
Potentilla hololeuca	3	2
Pulsatilla campanella	2	2
Pyrethrum karelinii	4	1
Silene graminifolia	1	1
Tragopogon turkestanicus	1	2
Veronica ciliata	3	2
Carex melanantha	3	0
Erigeron allochrous	3	1
Erigeron pseudoseravschanicus	1	1
Poa relaxa	3	1
Thalictrum minus	1	2
Triglochin maritimum	1	2
Achillea millefolium	3	0
Allium sp.	3	0
Carex aterrima	3	0
Draba subamplexicaulis	3	0
Comastoma falcatum	3	0
Helictotrichon pubescens	3	0
Helictrotrichon sp.	1	2
Elymus tschimganicus	3	5
Inula rhizocephala	3	0
Lindelofia stylosia	2	1
Gentiana kirilowii	1	3
Arctopoa tibetica	3	0
Trollius lilacinius	3	0
Potentilla gelida	3	0
Potentilla tergemina	1	2
Saussurea leucophylla	3	0
Erigeron sp.	1	1
Poa litvinoviana	1	1
Lappula microcarpa	1	1
Minuartia verna	2	0
Cerastium bungeanum	2	0
Rhodiola gelida	2	0
Linum pallescens	2	0
Erigeron heterochaeta	2	0
Doronicum sp.	2	0
Tragopogon vvedenskyi	1	0
Anemonastrum protractum	1	0
Androsace septentrionalis	1	0
Astragalus sp.	1	0
Crepis multicaulis	1	0
Draba nemorosa	1	0
Poa tianschanica	1	0
Polygana comosa	1	0
Pedicularis macrochila	1	0
Stachyopsis oblongata	1	0
Stellaria soongorica	1	0
Thalictrum simplex	1	0
Valeriana dubia	1	0
Viola rupestris	1	0
Botrychium lunaria	1	0
Calamagrostis compacta	1	0
Carex sp.	1	0
Carex sp.1	1	0
Carex sp.2	1	0
Erigeron aurantiacus	1	0
Eritrichium villosum	1	0
Hedysarum neglectum	1	0
Iris sp.	1	0
Lagotis integrifolia	1	0
Myosotis sp	1	0
Achoriphragma lancifolium	1	0
Oxytropis nutans	1	0
Oxytropis platysema Schrenk	1	0
Pulsatilla sp.	1	0
Ranunculus popovii	1	0
Rosa alberti	1	0
Serratula marginata	1	0
Taraxacum glabrum	1	0
Trollius altaicus	1	0
Viola sp.	1	0
Allium tianschanicum	0	2
Androsace sericea	0	2
Artemisia rhodantha	0	2
Aster vvedenskyi	0	2
Blysmus compressus	0	2
Leymus flexisi	0	2
Goniolimon ortocladum	0	2
Potentilla sericea	0	2
Adenophora himalayana	0	2
Ligularia narynensis	0	2
Eremogone meyeri	0	1
Dracocephalum integrifolium	0	1
Lappula rupestris	0	1
Allium hymenorhizum	0	1
Artemisia pamirica	0	1
Artemisia vulgaris	0	1
Kobresia sp.	0	1
Asteraceae	0	1
Asterosea sp.	0	1
Astragalus nivalis	0	1
Dracocephalum sp.	0	1
Psathyrostachys kronenburgii	0	1
Ephedra regeliana	0	1
Hordeum sp.	0	1
Festuca olgae	0	1
Ligularia sp.	0	1
Plantago lanceolata	0	1
Ranunculus sp.	0	1
Stipa capillata	0	1
Stipa krylovii	0	1
Neotorularia humilis	0	1
Veronica sp.	0	1

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertation selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, im Februar ______________________________