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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

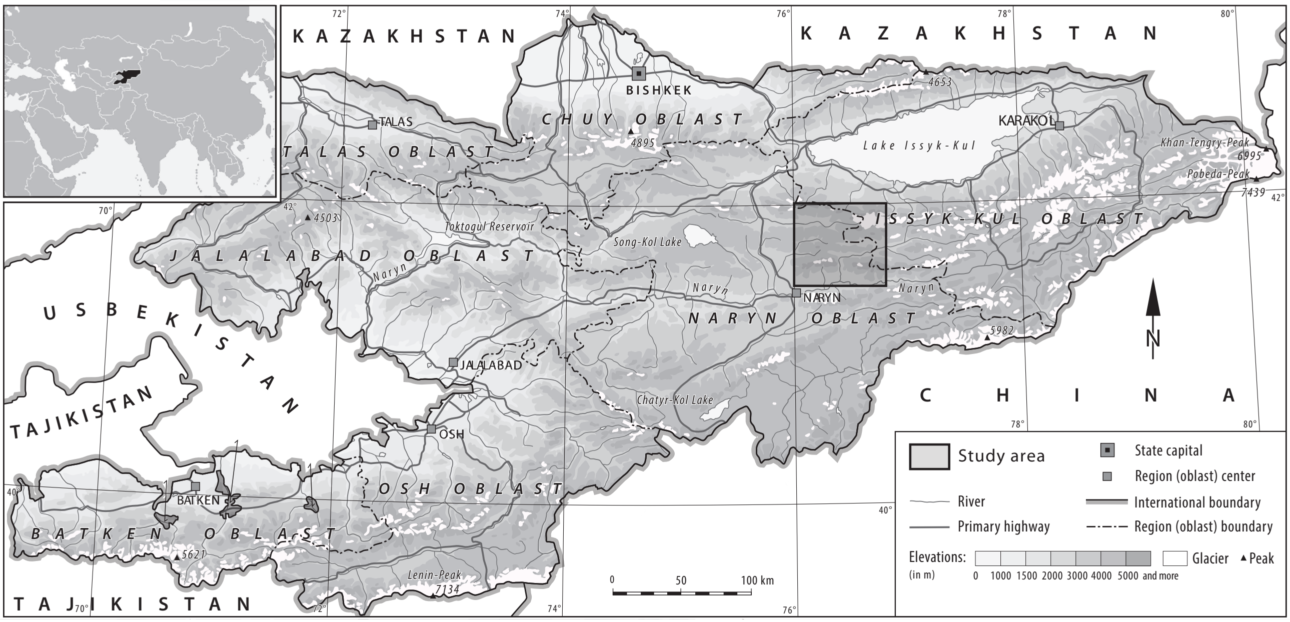

Fig. 1 Location of research area in the north-east of the Naryn Oblast. Source: own elaboration by S. Adler, C. Carstens and F. Hoppe 1/2018 based on Academy of the Kyrgyz SSR, 1987

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

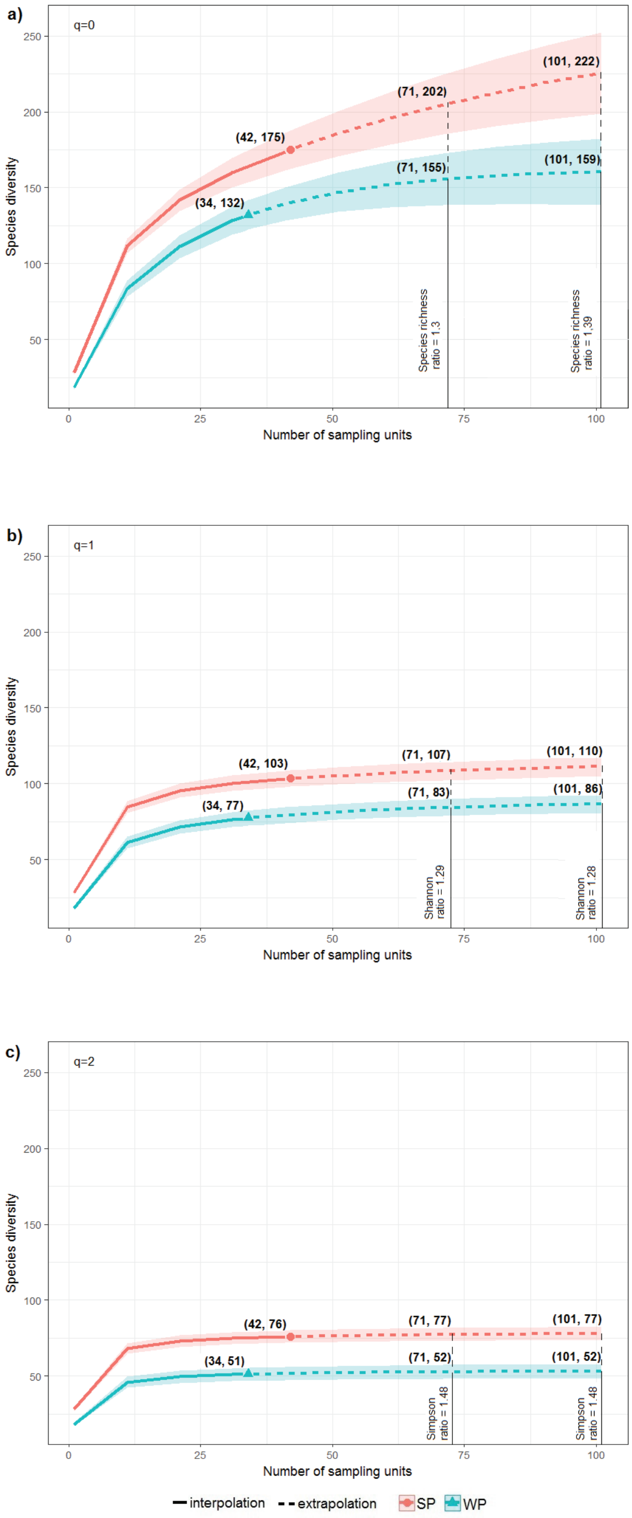

Fig. 2 *Sample-size-based rarefaction (solid line) and extrapolation (dashed line) of the first three Hill numbers (a = species richness, b = Shannon diversity and c = Simpson diversity). Observed samples on summer pastures (SP) are marked by a dot and on winter pastures (WP) by a triangle. Species richness, 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.

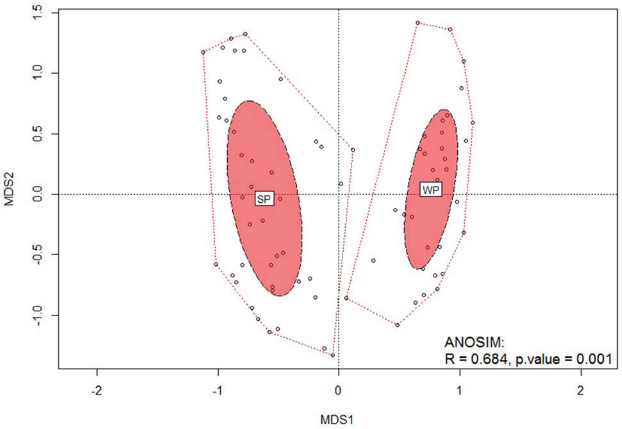

Fig. 3 *Differentiation of species composition between summer and winter pastures (SP and WP). The PCoA is based on the ANOSIM. Source: own elaboration*

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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