



## Vegetation Responses to Fixed Stocking Densities in Highly Variable Montane Pastures in the Chinese Altay<sup>☆</sup>

Chaoyan Lv<sup>a,1,2</sup>, Eva Schlecht<sup>b,\*,2</sup>, Sven Goenster-Jordan<sup>c</sup>, Andreas Buerkert<sup>c</sup>, Ximing Zhang<sup>a</sup>, Karsten Wesche<sup>d,e,f,2</sup>

<sup>a</sup> Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China

<sup>b</sup> Animal Husbandry in the Tropics and Subtropics, University of Kassel and University of Göttingen, 37213 Witzenhausen, Germany

<sup>c</sup> Organic Plant Production and Agroecosystems Research in the Tropics and Subtropics, University of Kassel, 37213 Witzenhausen, Germany

<sup>d</sup> Senckenberg Museum of Natural History Görlitz, 02806 Görlitz, Germany

<sup>e</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany

<sup>f</sup> International Institute Zittau, Technische Universität Dresden, 02763 Zittau, Germany

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### ABSTRACT

Variability in aboveground herbaceous biomass and its quality were studied in response to three different stocking densities during a 2-yr grazing experiment with sheep on a montane summer pasture in the Chinese Altay. We determined herbaceous cover and aboveground biomass in 16 paddocks of 0.25 ha each. Vegetation cover showed high spatial variation, prompting us to implement a randomized block design. Forage intake of one male sheep per paddock was quantified four times per grazing season by collection of total feces and estimation of diet digestibility. Sheep weight was recorded every 3 wk. Aboveground herbaceous dry mass (DM) was characterized by pronounced annual variation. Biomass quality declined with progressing season and increasing sheep density. Daily organic matter intake per sheep ranged from 0.7 to 1.4 kg, which was paralleled by a biomass removal of 710–1560 kg DM/ha at densities of 8–24 sheep/ha. At 8 sheep/ha, animals gained weight throughout each grazing period, whereas weight losses of 40–100 g/d occurred at higher densities. These results challenge the presently followed concept of a fixed stocking density for summer pastures in Altay Prefecture, Xinjiang, China. Such practice may result in low herbage allowances and thus deficient sheep nutrition in one year, as well as underutilization of forage resources in another. Flexible adjustment of stocking densities is also advisable for montane pastures where spatiotemporal variability, although less pronounced than in desert steppes of the Altay foothills, is nonetheless highly relevant.

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### Introduction

Livestock grazing is the most widespread form of land use (Herrero et al., 2013), and overgrazing is a key threat for extensive terrestrial ecosystems (Kwon et al., 2016). Overgrazing and the related term “grazing degradation” broadly imply that livestock impact surpasses sustainable levels, yet specific criteria and assessment methodologies are far from

agreed upon. Studies typically employ indicators based on biodiversity (plant species richness and cover), ecosystem productivity (many remote sensing studies), and soil condition (macronutrient contents and erosion), and some studies do not disclose the indicators at all (Veron et al., 2006; von Wehrden et al., 2012).

Even within a given indicator scheme, grazing effects are heterogeneous in both space and time. In dry rangelands, variable precipitation triggers landscape-scale differences (e.g., in aboveground biomass) (Vetter, 2005; Lehnert et al., 2016). Temporal variability has different facets, with many rangelands being exposed to strong intra-annual changes (seasons) and interannual variability (Schönbach et al., 2012). Moisture and nutrient availability are further modified by soil and microtopography, adding small-scale spatial variability (Li et al., 2015). Spatiotemporal variability and indicator uncertainty trigger extensive debates among rangeland ecologists and call for a more complex view explicitly addressing livestock foraging, animal population dynamics, and carrying capacities (Illius and Connor, 1999; Sullivan and Rohde, 2002; Hambler et al., 2007).

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\*Correspondence: Eva Schlecht, Section Animal Husbandry in the Tropics and Subtropics, University of Kassel and University of Göttingen, Steinstrasse 19, 37213 Witzenhausen, Germany. Tel.: +49 5542 981201; fax: +49 5542 981230

E-mail address: [schlecht@uni-kassel.de](mailto:schlecht@uni-kassel.de) (E. Schlecht).

<sup>1</sup> Current address: Chaoyan Lv, College of Biology and Agriculture, Zunyi Normal University, 6 Wujiang Ave, Zunyi, Guizhou, China.

<sup>2</sup> Chaoyan Lv, Eva Schlecht, and Karsten Wesche contributed equally to the manuscript.

Apparent spatiotemporal variability challenges management schemes that rely on fixed stocking rates. In more productive rangelands, high and largely constant forage availability allows herds to build up, exerting strong pressure on vegetation and becoming a driving factor of ecosystem change (Illius and Connor, 1999). Fixing stocking rates then is an option to prevent detrimental effects such as overgrazing. In less productive rangelands with more variable conditions, livestock numbers typically fluctuate in response to highly variable forage availability and thus climate, being a driven component in such ecosystems (Sullivan and Rohde, 2002). Few studies do, however, explicitly adopt a combined livestock-rangeland perspective (von Wehrden et al., 2015).

Some of the world's most intact dry grasslands are found in temperate Eurasia. At a total area of around 10 Mio km<sup>2</sup>, the Eurasian steppe biome represents the largest continuous rangeland region worldwide (Wesche et al., 2016). Half of it is located in Mongolia and China including Tibet, where mobile and highly flexible livestock grazing is still the main form of land use (Wesche et al., 2016). Increasing livestock numbers raise concerns about grazing degradation, yet in spite of a vast body of literature the extent of grazing degradation remains under discussion (Wang et al., 2008; Harris, 2010; Addison et al., 2012). Several studies analyzing grazing effects on vegetation are available from Inner Mongolia (Wang et al., 2009a; Bösing et al., 2014; Dickhoefer et al., 2016) and parts of Tibet (Long et al., 2008; Ding et al., 2014; Hoffmann et al., 2016). Many of the respective sites have a moderate level of interannual climate variability (coefficient of variation [CV] of interannual precipitation variability < 25%), while desert steppes and dry alpine pastures experience much more irregular rains (CV precipitation > 30%). Effects of grazing change along the variability gradient (Wang and Wesche, 2016), yet detailed data are missing from the vast and variable rangelands of northwestern China and southeastern Mongolia.

In view of the apparent lack of comprehensive, multi-indicator approaches to measure grazing impact, applied rangeland management and governmental policies are often more elementary and rely on at least partly questionable assumptions (Harris, 2010; Addison et al., 2012). Political decision makers often suppose that traditional highly flexible mobile pastoralism without land tenure results in strong degradation of its resource base (Addison et al., 2012; Gongbuzeren et al., 2015), calling for land ownership or individual long-term use rights, paddock-based management, and typically fixed stocking rates to achieve sustainable rangeland use (Schönbach et al., 2012; Müller et al., 2014). Such management schemes are in stark contrast to the highly flexible nomadic pastoralism in the region and have massive consequences for local livelihoods (Sjögersten et al., 2013; Shang et al., 2014): Inflexible management schemes may be detrimental in environments with high spatiotemporal variability and thus have unwanted consequences for rangeland health (Wang et al., 2015; Hoffmann et al., 2016).

Departing from the previously mentioned, scarcely investigated spatiotemporal variability pattern of alpine pastures, the present study tests the concept of officially prescribed fixed stocking densities in high-altitude summer pastures in Altay Prefecture, Xinjiang, China. Adopting a combined livestock-rangeland perspective, we tested three alternative levels of livestock densities and investigated 1) temporal variation in aboveground biomass and its quality; 2) forage intake of sheep as affected by stocking density and biomass quality; and 3) sheep live weight changes resulting from (2).

## Methods

### Study Area: Environment and Vegetation

The study was conducted in Qinghe County (also spelled Qinggil), Altay Prefecture, Xinjiang Uyghur Autonomous Region of China, from June until September in 2012, 2013, 2014, and 2015. The experimental site was established in the mountains north of Qinghe Centre, situated

at Akbulak (47°12'23.62" N, 90°14'58.20" E, 2 400 m a.s.l.). The higher altitudes of the Chinese Altay mountain range receive reliable rainfall in summer, and snowfall can be expected between September and April; the Altay foothill zone emerges from the dry Dzungarian Gobi. Long-term mean annual precipitation in Qinghe Centre (46°40'28" N, 90°22'59" E, 1 253 m a.s.l.) is 174 mm (1958–2007), with considerable interannual variation (coefficient of variation 30%). Rainfall increases with altitude and annual amounts at the study site were comparatively high, averaging 214 mm across the 4 yr of measurement. Interannual variability was pronounced with 314, 188, 133, and 221 mm total annual precipitation in 2012, 2013, 2014, and 2015 (own measurements).

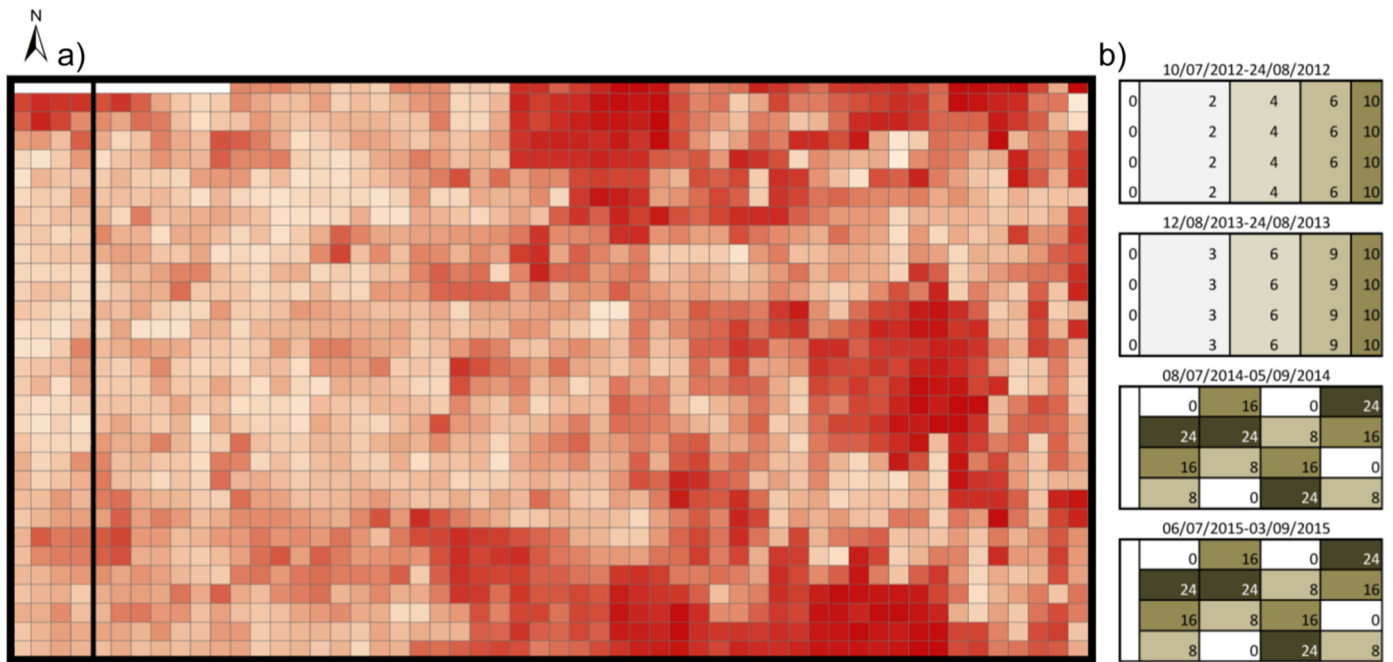
The high-altitude rangelands are used as summer pasture between June and August depending on the actual weather. According to local herders, grazing has been in place at least for decades and probably much longer (Jordan et al., 2016). The study site was located near the timberline with some groves of *Picea obovata* Ledeb. in the surroundings. The site had a northern exposure and sloped from north to south, with the upper third of the plot being flat and the lower two thirds showing an inclination of 5–10%. The rangeland is an upper montane to subalpine meadow steppe with a heterogeneous cover of grasses and forbs. In September 2012, vegetation cover was visually estimated for 1 664 quadrats of 10 x 10 m<sup>2</sup> located with differential Global Positioning System (Juno SB handheld, Trimble Inc., Sunnyvale, CA). Estimates were carried out by the same person throughout yet adjusted by initial joint estimating with a further two experienced vegetation ecologists. Total vegetation cover showed pronounced small-scale spatial variability ranging from 8% to 93% (Fig. 1a), with a general increase from the western to eastern boundaries of the plot. This was mainly driven by an increase in cover of perennial grasses (Fig. A1; available online at <https://doi.org/10.1016/j.rama.2019.05.007>). Shrubs tended to be more common in the western part of the plot, yet even there they remained well below 10% of surface cover.

Plant species richness is relatively high at typically 20–27 vascular plant species/100 m<sup>2</sup>. The most important species include *Helictotrichon pubescens* (Huds.) Schult. & Schult.f., *Festuca valesiaca* Schleich. ex Gaudin, *Alchemilla pinguis* Juz., *Cerastium cerastoides* (L.) Britton, *Dracocephalum nutans* L., and *Galium verum* L. (C. Oyundari, unpublished data). All plant species relevant in terms of biomass are perennial and can tolerate the usual summer grazing in the region.

Soil variables respond more slowly to variations in grazing intensity (Milchunas and Lauenroth, 1993), and thus we did not expect major changes over time. We took mixed topsoil samples at the end of the experiment in 2015 only and subjected them to standard nutrient analysis (see chemical analysis later). Soils tended to be rich in soil organic carbon (C), with a relatively high nitrogen (N) concentration and thus narrow C/N ratio (Table A3; available online at <https://doi.org/10.1016/j.rama.2019.05.007>). Ratios of about 10 are typical for mineral soils in dry rangelands of Mongolia and northern China (Wesche and Ronnenberg, 2010; Giese et al., 2013), while soils of mountain rangelands in eastern Tibet have a higher share of organic matter (Hafner et al., 2011). Spatial heterogeneity was considerable even in ungrazed paddocks, where average soil N concentration varied between 0.30% and 0.57% and values of soil C between 3.13% and 5.88%.

Government regulations determine the day of departure to and return from the summer pasture area, as well as the number of animals to be grazed there, and government representatives closely monitor livestock keepers' compliance with the regulations. Whereas official stocking densities were not disclosed, a daily herbage allowance of about 26 kg dry matter (DM) per sheep unit has been determined for our study region (Jordan et al., 2016<sup>3</sup>). As we did not expect short-term experimental manipulation to trigger changes in plant species composition, this variable was not recorded.

<sup>3</sup> Calculated from data presented in Jordan et al. (2016): Table 1, stocking rate small ruminants, China, summer pasture and Table 2, duration of stay and herbage offer, China, summer pasture.



**Figure 1.** Overview of plot location and experimental design. **a**, High-resolution survey of vegetation cover in the experimental site as of the yr 2012 (cover estimated visually, location recorded with differential GPS, small numbers refer to plot order). Cover values range from 8% (very light color) to 93% (dark red color), with a general increase from west to east (1 664 plots, grid size 10 × 10 m). **b**, Experimentally established grazing paddocks in the pre-experiment (2012, 2013) and experiment. Numbers refer to livestock densities (sheep/ha). Paddocks remained the same in 2014/2015. Subplots for biomass sampling changed within paddocks.

### Experimental Design and Sampling

Given that base-line data were missing, we conducted a pre-experimental phase (2012 and 2013) to estimate reasonable stocking densities for the main experiment in 2014 and 2015. A large enclosure (300 × 150 m<sup>2</sup>, further referred to as “plot”) was fenced against livestock (small mammals had access) in 2012 (Fig. 1a). Animal densities in the pre-experiment were manipulated by adjusting paddock size in 2012 and 2013 (Fig. 1b). In 2014 and 2015, the plot was split into four blocks including four paddocks of 2 500 m<sup>2</sup> each that represented the treatments. The experiment (2014 and 2015) was laid out in a randomized block design with  $n = 4$  paddocks per treatment (including control) arranged as shown in Fig. 1b. On the basis of aboveground biomass measured in 2012 and 2013 (Fig. A2; available online at <https://doi.org/10.1016/j.rama.2019.05.007>), we set animal densities to 0–24 sheep/ha (Table A1). The sheep were grazed inside the paddocks for a 56-d grazing period in summers of both 2014 and 2015. New adult male and female sheep were bought from nearby herder families in the spring of each year. The animals were of the Altay breed found in western Xinjiang. This fat-rumped sheep is renowned for producing carpet wool but is primarily reared for meat production. The average live weight of an adult Altay ram is 82 kg and of a ewe 69 kg (Cheng, 1984), yet our animals weighed between 25 and 45 kg across the 2 yr. The animals stayed within their paddocks for the full 56 d and always had ad libitum access to drinking water and mineral licks.

We monitored the development of aboveground biomass and sheep live weight (overview of all measurements in Table A1). Recording intervals typically spanned about 20 d starting in early July (depending on seasonal vegetation development) and ending at the end of August/beginning of September. In 2012 and 2013, aboveground biomass was clipped at 1-cm height in 12 quadrats of 0.25 m<sup>2</sup> within each of the five subplots, and in 2014 and 2015, four 0.25-m<sup>2</sup> quadrats were sampled in each of the 16 paddocks. We did not use extra enclosure cages within paddocks and our measurements thus directly reflect the animal impact in the grazed paddocks; they were compared with the biomass data of the four ungrazed control plots. Sampled biomass was

pooled per paddock, air-dried in well-aerated cotton bags in the field, and transported to the laboratory (see later).

At the start and end of the 2014 and 2015 grazing period, the animals' live weight (LW, kg) was determined in the early morning by weighing them in a hammock with a tripod-based, battery-powered suspension balance (range 0–300 kg, accuracy 0.1 kg); animals were additionally weighed around d 20 and d 40 after the start of the grazing period.

To determine feed intake of the sheep, the total amount of excreted fecal DM was quantified at four periods spread equally across the grazing periods of 2014 and 2015, whereby their first day always coincided with the weighing date of the animals. One male sheep from each flock grazing the different paddocks was fitted with a fecal collection bag attached to a harness. The bag was left on the animal for 5 d consecutively and thoroughly emptied every 8–12 h. At each emptying, the total amount of fresh feces was determined by weighing on a portable electronic scale (range 0–5 kg, accuracy 1 g). The fresh material was air-dried in cotton bags kept in the shade. When completely dry, the fecal matter was weighed again. At the end of each 5-d period, the dry feces were pooled into one composite sample per animal; after complete homogenization a sample of 250 g air-dry material was kept for analysis.

### Chemical Analyses of Samples

The biomass samples were redried in the laboratory (60°C) and ground to pass a 1-mm screen (FOSS sample mill, Cyclotec 1093, Foss GmbH, Haan, Germany). Fecal samples were also redried and milled to 1-mm particle size. Biomass and fecal samples were analyzed in duplicate for concentrations of DM, crude ash (ash), organic matter (OM; calculated as 100 [DM] minus ash), N, phosphorus (P; biomass only), C, neutral detergent fiber (NDF), and acid detergent fiber (ADF) following the handbook of VDLUFA (2012, method numbers given in brackets later). For DM determination, about 1.5 g of sample material were dried at 105°C for 24 h (method 3.1) and subsequently incinerated at 550°C overnight (method 8.1) to determine the ash and OM concentration,

respectively. Concentrations of NDF and ADF (in DM) were determined sequentially in a semiautomated Ankom220 Fiber Analyzer (ANKOM Technology, Macedon, NY) without using decalin and sodium sulphite (methods 6.5.1 and 6.5.2). The concentration of P was determined in an ash solution (method 10.6.1.) by spectrophotometry (Hitachi U-2000, Hitachi Ltd., Tokyo, Japan). The N and C concentrations of the samples were determined with a Vario MAX CHN analyzer (Elementar Analysensysteme GmbH, Hanau, Germany; method 4.1.2). The concentration of crude protein (CP) was calculated on the basis of the samples' N concentration ( $CP = N \times 6.25$ , Allen et al., 2011). From the CP concentration in fecal OM ( $CP_f$ ), the organic matter digestibility (OMD) of the diet ingested by a sheep during each 5-d sampling period was estimated according to Wang et al. (2009b) by the following equation:

$$OMD (\%) = 0.899 - 0.644 \times \exp\left(\frac{-0.5774 \times CP_f (\text{g/kg OM})}{100}\right) \quad (1)$$

Subsequently, the animals' organic matter intake (OMI) was calculated by dividing the fecal mass (g OM/d) by the indigestible fraction ( $1 - OMD/100$ ) of the diet (Cordova et al., 1978). Daily OMI was expressed per animal and per kilogram of metabolic weight ( $MW = \text{kg}^{0.75} \text{ LW}$ ).

### Data Analysis

Data were summarized by arithmetic mean and standard error unless stated otherwise. Linear mixed models were used to analyze data on biomass and feces quantity and quality for yr 2014 and 2015. We used sheep density (sheep/ha), date, and year as main factors, suppressing most interaction terms except for density  $\bullet$  yr and density  $\bullet$  date. Block and paddock nested below block were used as random factors. Residuals of models were graphically checked for normality and consistency, and data were log-transformed if needed. We estimated P values using the REML method and also compared delta Akaike information criteria on the basis of stepwise model simplification. All analyses were conducted in R (R Core Team, 2015) with packages lmer and lmerTest (Bates and Maechler, 2009; Kuznetsova et al., 2016). Plots were compiled with the help of sciplot (Morales, 2015).

## Results

### Biomass Production

In each year aboveground herbaceous biomass yield was  $> 1000$  kg DM/ha in early July before grazing treatments started (Fig. 2). If

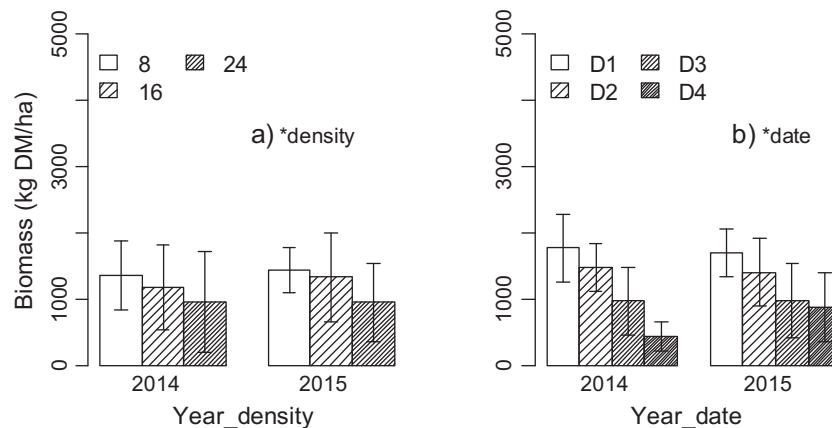
ungrazed, biomass increased further toward its peak at the end of July/early August (i.e., our second round of sampling) and started to decline rapidly toward the end of the growing season (end of August/early September). Biomass on control plots showed modest variability over years, with mean values ( $\pm$  standard deviation) in July 2014 and 2015 of  $2310 \pm 740$  and  $2080 \pm 680$  kg DM/ha. Foraging by sheep induced differences between peak biomass in the control paddocks and herbaceous biomass available in the grazed paddocks of 1390, 1250, and 950 kg DM/ha (averaged across seasons and years). Spatial heterogeneity was large, with mean values for the blocks (pooled across paddocks) at the start of the grazing season ranging from 1300 to 2145 kg DM/ha in 2014 and from 1440 to 2145 kg DM/ha in 2015.

### Forage Quality

The quality of herbaceous biomass (all values expressed on DM basis) changed with the advancement of the summer season, while study years introduced differences in carbon and nitrogen values only (Table 1). Ash contents were between 7% and 10%; they declined in the course of the grazing season, especially in 2014 and, to a lesser extent, with increasing sheep densities. C was in the expected range of 45–50% and increased from the beginning of July to late August/early September, without any strong response to sheep density. Nitrogen concentrations were moderately high at 1.5–1.8%, corresponding to 90–110 g CP/kg DM. Intensified grazing at higher sheep densities reduced biomass N concentration, yet seasonal patterns were more pronounced, with highest N concentrations determined in early July. Phosphorus concentration (g/kg DM) in herbaceous biomass was only analyzed in the ungrazed paddocks at the onset of the grazing season (early July) and averaged  $1.36 (\pm 0.52)$  and  $1.54 (\pm 0.53)$  in 2014 and 2015, respectively. The concentrations of NDF and ADF were increasing as the summer season progressed, showing thus a reciprocal pattern to the concentrations of ash and nitrogen. NDF and ADF concentrations were significantly higher at higher sheep densities (see Table 1).

### Herbage Allowance, Feed Intake, and Live Weight Changes of Sheep

The 88-mm difference in annual rainfall amount between 2014 (133 mm) and 2015 (221 mm) had only modest effects on peak standing biomass in the control paddocks (see earlier), as well as on aboveground biomass across all grazed paddocks at the onset of the grazing season (2014: 1772 kg DM/ha, 2015: 1691 kg DM/ha). On the basis of the definition of a sheep unit (SU) as an animal of 40 kg LW (Hu and Zhang, 2006), herbage allowance (Table 2) at the onset of grazing amounted to 211, 104, and 76 kg DM/SU at a density of 8, 16, and 24 sheep/ha in



**Figure 2.** Development of standing aboveground forage biomass (kg DM/ha) for the experiment (mean and standard deviation). Data were split by yr (2014–2015) and **a**, sheep density (8, 16, 24), as well as **b**, sampling date (D1: early July; D2: end of July; D3: late August; D4: end of August/early September). The plots show the main effects (data log-transformed,  $p_{\text{year}} = 0.060$ ,  $p_{\text{date}} < 0.001$ ,  $p_{\text{density}} = 0.017$ ), plus the tested interactions for **a**, yr  $\bullet$  density ( $p_{\text{year} \times \text{density}} > 0.2$ ), and **b**, yr  $\bullet$  date ( $p_{\text{year} \times \text{date}} < 0.001$ ). For full data see Figure A2; <https://doi.org/10.1016/j.rama.2019.05.007>

**Table 1**  
Composition of herbaceous biomass as influenced by yr, sheep density (sheep/ha), and sampling date (4/growing season). Data depict number of sheep units (SU<sup>1</sup>) per hectare and arithmetic mean of crude ash (ash), nitrogen (N), carbon (C), neutral detergent fiber (NDF), and acid detergent fiber (ADF) concentrations (% in dry matter). Results of linear mixed-model analyses are given below; interactions other than those reported were not estimated.<sup>1, 2</sup>

		SU/ha <sup>2</sup>	Ash	N	C	NDF	ADF
Density ●	date						
0	1	0	8.7	1.6	47.2	52.4	29.7
0	2	0	9.1	1.5	47.2	53.3	30.9
0	3	0	7.6	1.1	47.4	60.5	35.3
0	4	0	7.4	0.9	47.4	62.8	36.4
8	1	5.9	8.2	1.6	47.6	53.4	29.3
8	2	5.9	8.7	1.4	47.1	57.2	31.5
8	3	5.9	7.7	1.1	47.5	61.1	34.3
8	4	5.9	6.9	1.0	47.8	62.1	33.0
16	1	11.9	8.6	1.6	47.1	52.7	28.9
16	2	11.9	8.1	1.2	46.9	60.4	33.7
16	3	11.9	7.9	1.0	47.5	63.4	37.1
16	4	11.9	5.9	0.8	48.0	67.9	40.6
24	1	18.1	8.5	1.6	44.0	51.5	28.6
24	2	18.1	7.8	1.1	47.3	60.5	35.6
24	3	18.1	6.4	0.8	48.1	69.2	41.7
24	4	18.1	6.1	0.7	48.6	69.6	45.8
Density ●	yr						
0	2014	0	8.4	1.3	48.4	55.9	33.1
0	2015	0	7.9	1.2	46.2	58.6	33.0
8	2014	6.9	7.8	1.3	48.6	57.8	32.2
8	2015	4.8	7.9	1.2	46.4	59.1	31.8
16	2014	13.7	7.5	1.2	48.5	61.2	35.5
16	2015	10.0	7.7	1.1	46.2	61.0	34.7
24	2014	20.4	7.2	1.1	49.0	62.6	38.4
24	2015	18.6	7.2	1.0	45.0	62.8	37.5
<i>Independent variable</i>		<i>Results of linear mixed-model analyses</i>					
Density		0.031	0.039	0.881	< 0.001	< 0.001	< 0.001
Yr		0.540	0.020	< 0.001	0.116	0.403	
Date		< 0.001	< 0.001	0.051	< 0.001	< 0.001	
Density ● yr		0.770	0.979	0.355	0.360	0.944	
Density ● date		0.048	0.034	0.411	< 0.001	< 0.001	

Dates: the start dates of each measurement period were in 2014: 11.07. (= 1); 30.07. (= 2); 20.08. (= 3) and 05.09 (= 4); in 2015: 07.07. (= 1); 29.07. (= 2); 22.08. (= 3); 31.08. (= 4).

<sup>1</sup> SU: sheep unit, an animal of 40 kg live weight (Hu and Zhang, 2006).

<sup>2</sup> SUs averaged across yr for density ● date interaction comparison.

2014, while the respective values for 2015 were 273, 154, and 88 kg DM/SU. There were significant differences between years ( $P < 0.001$ ) and sheep densities ( $P < 0.001$ ), as well as a year ● density interaction ( $P < 0.01$ ). Averaged across years and sheep densities, herbage allowance declined as the summer season and thus grazing progressed, to 115, 75, and 53 kg DM/SU (see Table 2) at the second, third, and fourth measuring date ( $P < 0.001$ ). Feed intake (g OM/kg MW ● d), as calculated from total fecal mass and ingesta digestibility, only slightly differed ( $P = 0.118$ ) between 2014 and 2015 (see Table 2). Effects of sheep density on feed intake per kg MW were overall modest yet increased toward the end of a year's grazing season (density ● date interaction, see Table 2).

After converting DM herbage allowance to organic matter values by accounting for the average dry biomass crude ash content of 7.7%, we compared these values with the animals' OM intake per measurement period. This comparison indicated that increasing sheep density dramatically reduced the animals' selection possibilities: Whereas herbage allowance was on average 8.8 times higher than feed intake at a density of 8 sheep/ha in both years (see Table 2), it was only 4.3 and 2.3 times higher than feed intake at 16 and at 24 sheep/ha, respectively ( $P < 0.001$ ). The reduced selection possibilities also explain the observed changes in the digestibility of the ingested diet as derived from the fecal CP concentration (see Table 2), which across years and measurement periods averaged 66% at 8 sheep/ha and 65% at 16 and 24 sheep/ha. Although the main effect of density was nonsignificant, density affected digestibility in the 2015 summer (density ● yr interaction). Temporal changes were pronounced, and digestibility declined with seasonal development of the vegetation and continued foraging, regardless of density.

Sheep showed a net gain in live weight across the 2014 and 2015 grazing seasons (Fig. A3b; available online at <https://doi.org/10.1016/j.rama.2019.05.007>), but overall weight gain was relatively low in 2014 at densities above 8 sheep/ha, resulting in a trend toward density ● yr interaction. In July 2014 and July 2015, animals gained live weight irrespective of sheep density (Fig. 3). In the second phase of 2014 (early August), weight changes were less pronounced but still positive at 8 sheep/ha and practically zero at 16 sheep/ha. At a density of 24 sheep/ha the animals lost weight at a rate of  $-92$  g LW/d per sheep. In late August 2014, sheep weight remained essentially unchanged at a density of 8 sheep/ha and profoundly decreased at higher densities ( $-93$  g LW/sheep ● d and  $-104$  g LW/sheep ● d at 16 and 24 sheep/ha). In 2015, all animals gained weight until early August irrespective of sheep density, and only in the last part of the summer densities of 16 and 24 sheep/ha also resulted in losses of  $-40$  g LW/sheep ● d. Male and female sheep showed no consistent differences with respect to weight change (Fig. A3) and were thus not distinguished for analysis.

Fecal mass (g OM/kg MW ● d) was affected by sheep density and year but not measurement date, whereas feces quality did not differ between treatments but between measurement dates (except for ash) and years (Tables 3 and A4; <https://doi.org/10.1016/j.rama.2019.05.007>). At concentrations of 19–20%, feces of sheep contained about twice as much ash than the ingested herbaceous biomass, whereby any contact of the feces with soil can be ruled out. Fecal ash concentrations increased slightly with progressing season but were invariant to sheep density, as were all other proximate components in feces (see Tables 3 and A4). Fecal concentrations of NDF and ADF increased toward the end of the season, while concentrations of C and N declined, being, however, significantly higher in 2014 than in 2015.

**Table 2**

Sheep units<sup>1</sup> (SU) per hectare and arithmetic mean of mean live weight (LW, kg), organic matter (OM) digestibility (%) of the ingested diet, and daily organic matter (OM) intake per sheep unit (g OM/SU • d) and per kilogram of metabolic weight (MW; g OM/kg<sup>0.75</sup> LW • d), herbage allowance (HA, kg DM/SU), and ratio of HA (kg OM/SU • d) to OM intake (kg OM/SU • d) as influenced by yr, sheep density (density; sheep/ha), and date. Results of linear mixed-model analyses are given below; HA was log-transformed for testing. Interactions other than those reported were not estimated.<sup>1, 2</sup>

		SU/ha <sup>2</sup>	Live weight (kg/sheep)	OM digestibility	OM intake per SU	OM intake per kg MW	HA	HA: OM intake
Density • date								
8	1	5.9	29.5	70.5	1 315	83	242	10.3
8	2	5.9	35.9	67.4	1 280	81	210	8.5
8	3	5.9	38.7	64.6	1 200	76	144	7.6
8	4	5.9	39.1	61.8	1 010	64	101	
16	1	11.9	30.9	71.1	1 333	84	129	5.4
16	2	11.9	36.5	66.3	1 146	72	90	4.0
16	3	11.9	38.8	61.7	992	62	59	3.6
16	4	11.9	39.2	60.4	924	58	45	
24	1	18.1	32.1	71.8	1 441	91	82	3.3
24	2	18.1	37.8	66.1	1 060	67	47	2.2
24	3	18.1	36.7	61.8	955	60	23	1.6
24	4	18.1	36.9	59.8	816	52	14	
Density • yr								
8	2014	6.9	40.4	65.6	1101	69	145	8.3
8	2015	4.8	31.1	66.5	1301	82	203	9.2
16	2014	13.7	40.6	64.4	1015	64	65	4.0
16	2015	10.0	32.0	65.3	1182	74	96	4.6
24	2014	20.4	41.8	63.8	980	62	36	2.2
24	2015	18.6	29.9	65.9	1156	73	46	2.4
<i>Independent variable</i>		<i>Results of linear mixed-model analyses</i>						
Density		0.817		0.636	0.038	0.079	< 0.001	< 0.001
Yr		< 0.001		0.002	0.118	< 0.001	< 0.001	0.051
Date		< 0.001		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Density • yr		0.071		0.018	0.386	0.553	0.003	0.334
Density • date		0.016		0.589	0.001	0.030	0.265	0.438

Date: the start dates of each measurement period were in 2014: 11.07. (= 1); 30.07. (= 2); 20.08. (= 3) and 05.09. (= 4); in 2015: 07.07. (= 1); 29.07. (= 2); 22.08. (= 3); 31.08. (= 4).

<sup>1</sup> SU: sheep unit, an animal of 40 kg live weight (Hu and Zhang, 2006).

<sup>2</sup> SUs averaged across years for density • date interaction comparison.

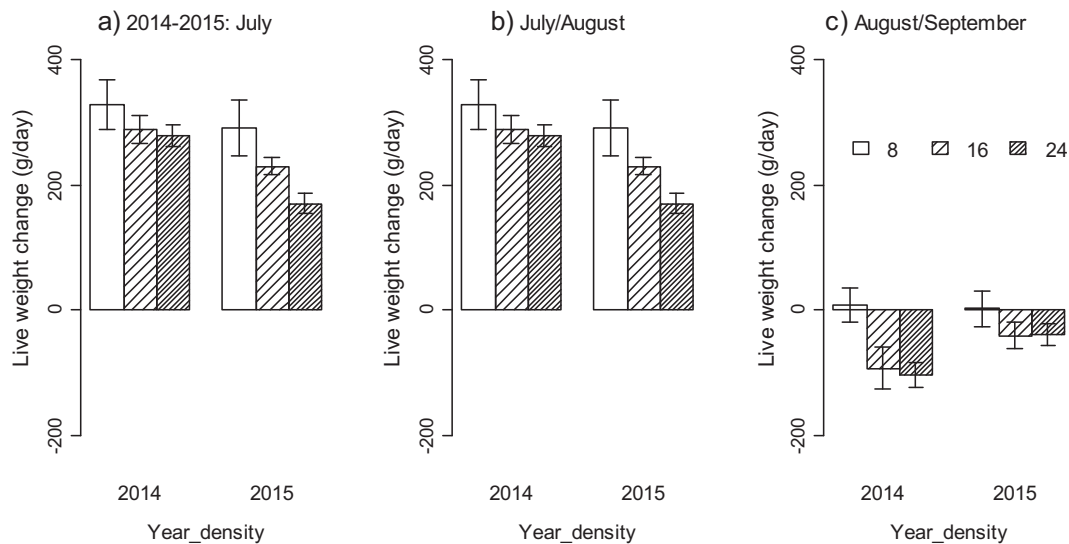
**Discussion**

Although the experiment covered a limited area of slightly over 4 ha and a short time span of 2 yr, results on vegetation cover, biomass quantity and quality, as well as livestock-based variables, point to a pronounced variability in both time (years, season) and space (blocks). They also show that there are immediate feedback effects among

livestock density, aboveground herbaceous biomass, and quality, which question the suitability of fixing stocking rates in these environments.

*Variability in Vegetation Patterns and Biomass Quality*

Our initial surveys (Fig. A1) pointed to the high importance of perennial grasses, which is typical for Eurasian steppes (Wesche et al., 2016).



**Figure 3.** Daily live weight change (mean and standard error) of sheep per treatment for period a, early to mid-July, b, late July to mid-August, and c, late August to early September. Data were split by yr (2014–2015) and sheep density (8, 16, 24). Results of linear mixed models for main factors: density  $P < 0.001$ , yr  $P < 0.001$ , date  $P < 0.001$ , density • yr  $P = 0.092$ , density • date  $P < 0.001$ .

**Table 3**  
Quantitative fecal organic matter excretion (FOM<sub>ex</sub>) of sheep (per kilogram of metabolic weight, g OM/kg<sup>0.75</sup> LW • d) and proximate composition of feces as influenced by yr and date. Quality data (arithmetic mean and standard error of the mean) depict crude ash (ash), nitrogen (N), neutral detergent fiber (NDF), and carbon (C) concentrations (in % of dry matter) in feces. Results of linear mixed-model analyses are given below; ash was log-transformed to meet model assumptions. Interactions other than those reported were not estimated. Data on sheep density (density; sheep/ha) are not shown, as this variable had no statistical influence on feces quality.

Date	FOM <sub>ex</sub>	Ash	N	NDF	C
2014					
1	24.3	17.5	2.81	53.6	46.8
2	24.1	18.4	2.15	55.7	46.4
3	21.1	22.1	1.83	56.3	44.0
4	20.7	19.4	1.74	59.5	45.4
SEM	0.57	0.59	0.071	0.54	0.35
2015					
1	25.2	16.1	2.88	51.3	45.6
2	24.6	21.0	2.38	53.3	43.1
3	27.8	20.9	1.93	54.3	43.2
4	25.0	20.1	1.78	58.9	44.2
SEM	0.50	0.45	0.066	0.61	0.25
<i>Independent variable</i>					
<i>Results of linear mixed-model analyses</i>					
Density	0.017	0.474	0.763	0.827	0.377
Yr	< 0.001	0.995	0.001	< 0.001	< 0.001
Date	0.137	< 0.001	< 0.001	< 0.001	0.001
Density • yr	0.546	0.992	0.502	0.998	0.630
Density • date	0.125	0.726	0.436	0.073	0.922

Date: start dates of each measurement period were in 2014: 11.07. (=1); 30.07. (=2); 20.08. (=3) and 05.09. (=4); in 2015: 07.07. (=1); 29.07. (=2); 22.08. (=3); 31.08. (=4).

The local history of grazing resulted in extant rangeland species being grazing tolerant, and we thus did not expect major changes in vegetation composition and biodiversity in the course of the study. The spatial variability in vegetation cover was tremendous as determined in 2012 and ranged from < 10% to > 90%. A similarly wide range in cover exists between the desert steppes of the Altay's foothills to its best mountain pastures (von Wehrden et al., 2009; C. Oyundari, unpublished data). This demonstrates that differences in microtopography and soil conditions trigger small-scale spatial heterogeneity in vegetation cover analogous to large-scale gradients in climate and topography.

Biomass quantity and quality varied clearly over time, and although the sampling intervals covered only a few weeks each summer, sampling date was the single most influential variable for aboveground herbaceous biomass. Seasonal vegetation development in the short summers of Central Asia is generally pronounced, as has been shown by studies in different environments from mountain pastures to steppes and semidesert rangelands (Long et al., 1999; Schönbach et al., 2012; Ge et al., 2015). Biomass quality was always high at the onset of the grazing season, reflecting that greening is late in the Altay so that freshly flushed forage is available as late as the end of June.

The second year of the experiment differed in sums of precipitation as the potentially most influential variable (Hoffmann et al., 2016), and hence biomass quantities differed between years but were less than in desert steppes or deserts of the Mongolian plateau (Wang et al., 2014).

At mean values of peak standing biomass between 1 500 and 4 000 kg DM/ha across grazed and ungrazed paddocks, the quantities of herbaceous mass were relatively high and closely matched the values reported by Jordan et al. (2016) for unfenced summer pastures in the Chinese Altay. The biomass yield was similar to tall-grass steppes of Inner Mongolia (Giese et al., 2013; Hoffmann et al., 2016) and to parts of the Tibetan plateau (Hong et al., 2015; Li et al., 2017). Pastures of the drier Mongolian Altay (Khishigbayar et al., 2015) and some high-altitude pastures (> 4 000 m) of Tibet show lower values (Ma et al., 2010; Miao et al., 2015). Biomass development in the ungrazed paddocks indicated that herbage continued to grow until the end of July or even until mid-August, followed by senescence and seed shedding. In the grazed paddocks, the same pattern was observed for a density of 8 sheep/ha, although at a lower overall amount of standing biomass due to grazing. With 16 and 24 sheep/ha, which initially corresponded to 14 and 20 SU/ha in 2014 and to 10 and 16 SU/ha in 2015 (Table 3), herbage regrowth did, however, not compensate biomass removal and values of standing crop thus declined from the beginning of the

grazing season onwards. High biomass removal may thus override the potential for compensatory herbage growth as shown for Mongolian steppe grasses (van Staalduinen and Anten, 2005).

Plant N concentrations of 1.5–1.8% (equivalent to a crude protein content of 9–11%) were lower than in dry deserts or high-altitude regions of Tibet where harsh environmental conditions constrain growth and thus prevent nutrient dilution within the plants (Long et al., 1999; Wesche and Ronnenberg, 2010). The N concentrations at our Altay site were also below the range of 1.4–2.5% N reported by Schönbach et al. (2009) and Dickhoefer et al. (2014) for a long-term grazing experiment at 1 200-m altitude on the Mongolian plateau in China, with stocking densities of 0–9 sheep/ha. Our values are, however, in close agreement with the CP concentrations reported for Altay summer pastures across China and Mongolia (Jordan et al., 2016) and in the range typical for more mesic pastures in Central Asian mountains (Ma et al., 2010; Miao et al., 2015).

Along with the concentrations of C, NDF, and ADF (see later), the N concentration in the herbaceous vegetation differed between 2014 and 2015. This is in line with the review by Hoffmann et al. (2016) indicating that interannual variation in precipitation has the most decisive effect on biomass quality, followed by seasonal quality changes due to the plants' physiological stages (i.e., germination, tillering, shooting, flowering, and maturity) and, least, forage selection and grazing by herbivores (Schönbach et al., 2009; Dickhoefer et al., 2014).

Phosphorus concentrations in herbaceous biomass were determined for the control paddocks only, at the onset of the 2014 and 2015 grazing season. The nitrogen-to-phosphorus ratio varied between approximately 13 (2014) and 10 (2015) and was thus rather narrow compared with Tibetan pastures, indicating that P constitutes no major limitation for plant growth in the Chinese Altay (Güsewell, 2004; Hong et al., 2014, 2015).

Even though less important than precipitation and sampling date, sheep density did affect the concentrations of ash, N, C, NDF, and ADF in the herbaceous biomass. Concentrations of the latter two fiber fractions were close to values reported by Jordan et al. (2016) for Altay summer pastures in China and Mongolia. Their range was also similar to Tibetan pastures, where Long et al. (1999) determined NDF concentrations of 40–75% and Miao et al. (2015) found ADF contents of 30–40%. Grazing induces regrowth of shoots, and freshly flushed tissues have a lower fiber content than older, ungrazed plants and plant parts (Miao et al., 2015). However, the partly still high amount of aboveground biomass at measuring date 3 in 2015 points to substantial regrowth even in

grazed paddocks, but this was not paralleled by an improved or at least stable nutritional quality of the sampled biomass. Rather, biomass N concentrations decreased and NDF and ADF concentrations increased by mid-August 2015 as compared with early and late July. This may be ascribed to selective feeding of sheep (Hao et al., 2013), whereby ungrazed plants in an advanced maturity stage may mask the presence of highly nutritious young plants in pooled vegetation samples (Weir and Torell, 1959).

In paddocks where selective grazing of sheep was limited by high animal density, the lower plant N concentration indicated that the plants on this Altay pasture could not compensate for the N harvest by sheep through further uptake of soil N. This is opposed to findings in Inner Mongolia where plant N concentration increased significantly with increasing grazing pressure (Schönbach et al., 2012; Hoffmann et al., 2016). In our study area, N depletion of the vegetation started to emerge at the lowest density of 8 sheep/ha, which, at the start of grazing in 2014 and 2015, respectively, was equivalent to 7 and 5 SU/ha only (Table 3) and became pronounced at higher stocking densities. In the long run, even relatively moderate stocking densities are thus likely to decrease forage crude protein content and the associated soil N pool (Niu et al., 2016; Wang and Wesche, 2016) in this environment. Given that steppes and mountain grasslands are typically nitrogen limited (Wesche and Ronnenberg, 2010; Tang et al., 2017), overall rangeland productivity—primary and secondary—is likely to deteriorate in consequence.

The grazing effects on biomass quality were, however, not directly reflected in feces quality. Neither C and N nor fiber concentrations of dung responded to increased grazing intensity. This can be partly explained by a trend toward lower OM digestibility of ingesta of sheep in the high-density paddocks (see later).

#### Forage Intake and Live Weight Changes of Sheep

In 2014, biomass removal at densities of 8, 16, and 24 sheep/ha (or respectively 7, 14, and 20 SU/ha) corresponded to  $\approx$ 30%, 40%, and 65% of the total amount of aboveground biomass, and the corresponding figures in 2015 were 45%, 50%, and 75% for densities of 5, 10, and 16 SU/ha, even though herbage allowance per SU had been slightly higher in 2015 than in 2014. The tested stocking densities were thus at the upper limit of reasonable grazing management, or even beyond, as indicated by the live weight changes discussed later. Intake values of  $\geq$  80 g OM/kg MW  $\bullet$  d (at 8 sheep/ha) certainly covered the animals' requirements for maintenance and growth (Dickhoefer et al., 2016). Whether at intake values below 70 g OM/kg MW  $\bullet$  d sheep can meet their requirements depends on the quality of the ingested herbage and on its spatial distribution, which determines the distances animals need to cover while foraging (Lin et al., 2011). In our study, a daily intake below 60 g OM/kg MW was insufficient to cover the animals' nutritional requirements despite a diet digestibility of around 60%, whereas sheep in Inner Mongolia still gained weight under such conditions (Dickhoefer et al., 2016). In our study the animals' nutritional requirements seemed to be elevated, although energy expenditure for walking in search of feed was probably moderate in our 0.25 ha—sized paddocks as compared with the 2-ha paddocks grazed in the long-term experiment in Inner Mongolia (Hoffmann et al., 2016). Yet the limited scope for forage selection at 16 and 24 sheep/ha (see earlier) might have forced the animals to ingest herbage of relatively poor quality. This inference is supported by the declining diet digestibility at higher sheep densities from mid-July onwards. Conversely, Glindemann et al. (2009) and Dickhoefer et al. (2016) did not find a significant influence of sheep density on diet digestibility as determined from fecal crude protein concentration. On the other hand, and similar to our findings, these authors also observed a significant influence of month or season on diet digestibility.

In both experimental years, forage nitrogen concentrations were below 1.2% from mid-August onwards. At this level, the diet ingested

by sheep supplied less nitrogen than required for optimal microbial fermentation and synthesis processes in the rumen (Coleman and Moore, 2003). Therefore, even in paddocks where the quantitative feed intake was still  $>$  60 g OM/kg MW  $\bullet$  d (8 sheep/ha), the declining nitrogen concentration in the forage might have limited weight gain of sheep from mid-August (measuring date 3) onwards. In the other two treatments (16 and 24 sheep/ha), the combination of insufficient forage supply and low diet quality led to weight losses from the end of July onwards in 2014 and from mid-August onwards in 2015.

#### Implications

Subalpine rangelands such as our study site account for close to 1 Mio km<sup>2</sup> in Central Asia; alpine meadows and similarly moist environments such as forest steppes cover another 0.8 and 1.5 Mio km<sup>2</sup>, respectively (Pfeiffer et al., 2018). The largest share of these grasslands is in China and thus subject to management approaches that often build on fixed stocking densities. Our results shed new light on current policies for these rangelands.

Small-scale spatial heterogeneity (in vegetation cover and composition, soil C and N) was pronounced, while season and, to a lesser extent, year affected almost all variables analyzed. This suggests that spatial and temporal variability play an important role for aboveground herbaceous biomass and its nutritional quality in the mountain steppes of the Chinese Altay. Biomass development exhibited a strongly seasonal pattern with nutritional quality being highest in early July, while quantities peaked in midsummer. Both factors were rapidly declining afterwards, explaining why the area can be used as summer pasture only.

Sheep density, whether expressed in head or animal units per unit area, had marked effects on biomass quality, with concentrations of C and N declining and fiber contents increasing with increasing stocking density. Seasonal development of biomass quality and quantity, as well as sheep density, interacted in their effects on the animals' live weight changes. While fresh pastures could sustain even high densities of 24 sheep or 20 SU per hectare in early July, densities of  $>$  16 sheep or 13 SU per hectare resulted in close to zero or even negative live weight changes from about mid-August onwards. However, according to Hoffmann et al. (2016), interannual variability precludes easy prediction of temporal patterns. In the present case this is reflected in the live weight changes recorded until mid-August: Due to lower starting weights (and thus lower values of SU/ha), these remained positive across all sheep densities in 2015, while in 2014 sheep at high densities hardly grew as the summer season progressed. A rigid fixing of animal numbers that does not account for their live weight may therefore result in unsustainably low herbage allowances in one year and in an under-utilization of forage resources in another. The current governmental policy of fixing a stocking rate for mountain summer pastures in Altay Prefecture might be modified by adjusting livestock densities to regular seasonal changes in vegetation parameters, notably biomass, nitrogen, and fiber content, by introducing a sequence of departure dates for subgroups of livestock from mid-summer onwards or prolonging sojourning time on the summer pasture in exceptionally favorable years. Obtaining the necessary data at appropriate spatial and temporal resolution may prove difficult. Herders have, however, always employed fairly simple but sound estimators like live weight development or overall body condition of their animals to decide when it was time to leave a given pasture. In that sense, a less technical but presumably equally effective management approach may simply rely on allowing herders to respond in a flexible manner.

In view of the general patterns observed, but certainly not in absolute terms, the present results are in line with studies from dry rangelands across Central Asia and beyond. Fixed stocking rates and rangeland management based on average values are not advisable in these regions because of the high temporal variability in precipitation (Fernandez-Gimenez and Allen-Diaz, 1999; Wang et al., 2014). Herders traditionally buffer temporal changes by herd movements, yet numbers



of mobile herders are declining in China and paddock-based management is increasing (Long et al., 2008; Li and Huntsinger, 2011). Given that not all pastures are equally intensively used in the area, more flexible movements may not only be reasonable for highly variable (semi) desert rangelands (coefficient of interannual variation in precipitation > 35%, von Wehrden et al., 2012) but also applicable for moister environments such as mountain pastures. Our study thus adds to a growing body of literature showing that static management schemes may not be helpful for many sites in Central Asia, where elements of traditional land use such as flexibility and mobility may be worth revisiting (Dong et al., 2011; Gongbuzeren et al., 2015).

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rama.2019.05.007>.

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