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## Tradeoffs between forage quality and soil fertility: Lessons from Himalayan rangelands

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### ABSTRACT

Pastoralists on Eurasian rangeland often believe that traditional management practices involving moderate rotational grazing ensure sustainable yield, increase plant digestibility and promote biodiversity. To assess the generality of these suppositions we compared biomass production, community leaf C, N and P stoichiometry, leaf trait diversity and carbon and nutrient pools in root and soil for moderately grazed vs. ungrazed plots in Tibetan alpine meadows. We used five leaf traits (leaf C, leaf N and leaf P concentrations; SLA: specific leaf area, and LDMC: leaf dry matter content) as indicators of plant digestibility and rangeland quality. We measured these foliar traits and the ramet numbers for component species in moderately grazed plots as well as in enclosures (3–11 years) at five sites across the Qinghai-Tibetan plateau. Community weighted mean (CWM) trait values and functional dispersion (FDIs) were used to quantify the mean and the variance in the distribution of trait values, respectively. Both the leaf  $P_{CWM}$  and leaf  $P_{FDIs}$  generally increased under grazing and the  $LDMC_{CWM}$  decreased, leading to improved plant digestibility and rangeland quality (e.g. high, community-wide leaf nutrients). The leaf  $C_{CWM}$ , leaf  $N_{CWM}$  and  $SLA_{CWM}$  increased under grazing but the FDIs of these traits tended to decrease. Grazing generally increased species diversity but decreased aboveground biomass, organic carbon, and nutrient concentrations in soil and root, especially decreasing root nitrogen and soil available phosphorus. Both root biomass and the leaf  $C:N_{CWM}$  decreased in grazed plots at wet sites, but increased at dry sites. The community-wide increase and greater interspecific diversity in leaf nutrient concentrations coupled with decreasing  $LDMC_{CWM}$  show that grazing induced an increase in plant digestibility, nutrient concentrations, and nutrient diversity in these alpine meadows. However, this increase in forage quality comes at the cost of losses in both carbon stock and nutrient availability that depress biomass production. Our findings and a review of related literature suggest that traditional grazing practices involve a trade-off between short-term yield and sustainability, a management challenge that must be addressed on rangelands with low soil fertility.

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### 1. Introduction

From the beginning of agriculture during the Mesolithic–Neolithic transition, Eurasian grasslands have been subject to grazing by livestock (Hejman et al., 2013; Miede et al., 2014). Traditional management practices in these rangelands often try to ensure sustainable yield via a regime involving rotational grazing (Briske et al., 2011; Fernández-Giménez and Estaque, 2012; Reid

et al., 2014). For instance, in Tibetan and European alpine regions, pastoralists live at low-altitude pasture during winter but move their livestock and even their homes to high-altitude pasture in summer (Hernández-Morcillo et al., 2014; Miede et al., 2014; Molnár, 2014). Similarly, in Mongolian and Kazakhstan steppe a nomadic rangeland management regime characterized by moving livestock to track the shifting availability of water and forage prevails (Cerny, 2010; Liao et al., 2014). Additionally, excessive livestock often are slaughtered in autumn to ensure moderate grazing intensity during the winter when rangeland productivity is low (Galvin, 2009). These traditional management regimes are intended not only to ensure sustainable yield but also to keep forage digestibility high and promote diversity in the rangeland

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plant community (Glindemann et al., 2009; Teague et al., 2013; Török et al., 2016).

In principle, moderate grazing should increase community species diversity by reducing competitive exclusion (Olff and Ritchie, 1998; Hille Ris Lambers et al., 2012; Niu et al., 2015b), creating spatial heterogeneity favouring establishment, and increasing seed dispersal and colonization (Parson and Dumont, 2003). Forage digestibility potentially can be ensured through regrowth of perennial herbs under continuous removal of aboveground biomass by grazing (Huber et al., 1995; Glindemann et al., 2009). Hence, it is possible that productivity can be sustained under traditional rotational grazing regimes if the loss of soil nutrients through removal of biomass can be compensated by increases in mineralization rate, compositional turnover and soil microbial activity (Bagchi and Ritchie, 2010a, 2011; Ziter and MacDougall, 2013). In fact, both pastoralists and researchers have found increasing evidence for declining productivity and biodiversity in Chinese grasslands during recent decades (Nan, 2005; Kang et al., 2007; Harris, 2010; Ho and Azadi, 2010) as well as reduction in soil nutrient stocks (Hong et al., 2014; Yang et al., 2014b). Studies on the cause of these declines often focus on the consequence of rapidly changing climate factors, but overlook land use change and shifts in grazing management (but see Addison et al., 2012; Eldridge et al., 2015). Hence there is a need to further examine the sustainability of the traditional rotational grazing regime in Tibetan rangelands.

In contrast to the abandonment of many pastures in European grasslands in recent decades, Tibetan rangelands have been subjected to a changing pattern of differential grazing pressures associated with development of settlements around which grazing is concentrated (Yan et al., 2005; Li and Huntsinger, 2011; Fan et al., 2015). Combined with increased demand for livestock production, this has led to overgrazing and accelerated rangeland degradation near these new towns and villages (Li et al., 2007; Harris, 2010; Fan et al., 2015). Increased livestock production has reduced the return of soil available phosphorus (e.g. losses with output of meat, bone and milk) but increased the demand for soil available phosphorus due to enhanced plant growth in response to removal of aboveground biomass by grazing. Nitrogen deposition and climate warming may be further increasing plant growth (Du et al., 2004; Shen et al., 2015). Consequent deficiencies in soil available phosphorus can significantly impact rangeland sustainability via: i) promoting rangeland degradation and depressing productivity through limits on plant growth and regrowth; ii) changing forage quality by shifting community functional structure and C:N:P stoichiometry in plants (Sterner and Elser, 2002; Stiefs et al., 2010); and iii) increasing community biodiversity by favoring infrequent species (Wassen et al., 2005). Despite these possibilities, to our knowledge, few studies have examined the relationships among soil fertility, forage quality, community C:N:P stoichiometry and biodiversity in response to shifts in the traditional grazing regime.

We assess these relationships in Tibetan alpine meadows, which provide an especially useful natural laboratory for this purpose. First, traditional rotational grazing has persisted in Tibetan rangeland despite rapid changes in land use and a marked increase in livestock production in recent decades (Miehe et al., 2009; Harris, 2010). Second, recent general studies in Chinese rangelands document an enrichment of soil nitrogen and increasing productivity (Peng et al., 2011; Shen et al., 2015) and an associated decline in soil available phosphorus (Hong et al., 2014; Yang et al., 2014b). Third, grazing has been shown to depress productivity and favor infrequent species through niche differentiation (Niu et al., 2015a, 2015b). Fourth, the Chinese rangelands have high root biomass and plant phosphorus content in common species (He et al., 2008), increasingly so in recent decades (Mi et al.,

2015). Last but not least, addition of P fertilizer significantly increases productivity (Yang et al., 2014a; Zhou et al., 2015). Hence we hypothesize that the traditional rotational grazing in the Qinghai-Tibetan Plateau induces depletion of soil available phosphorus and depresses productivity, but ensures forage quality and promotes species diversity.

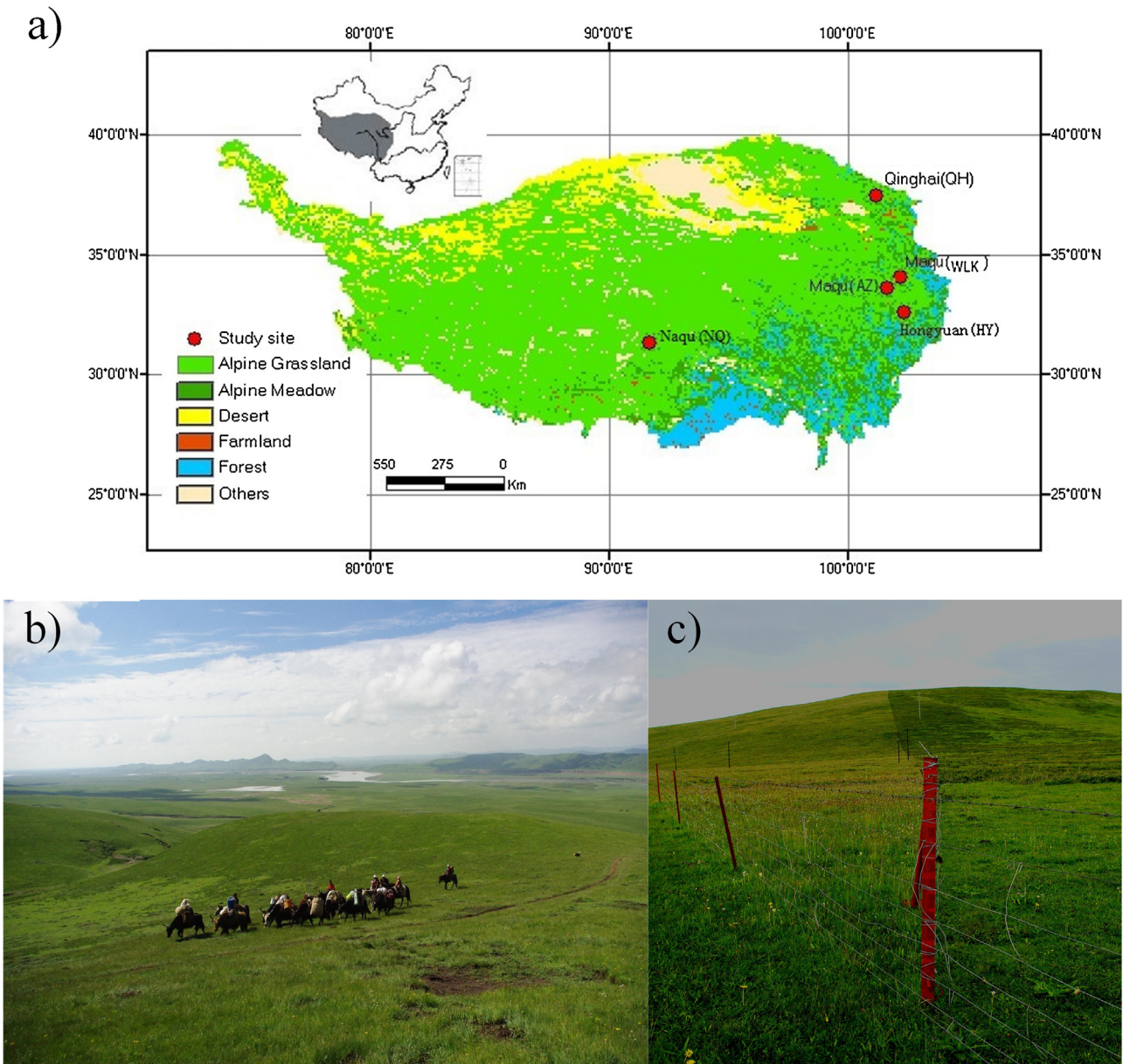
To test these expectations, we adopted a trait-based approach to assessing the effect of grazing on rangeland quality and soil nutrient availability gauged through changes in plant community functional structure (Diaz et al., 2007a; Garnier and Navas, 2012; Wood et al., 2015), which was quantified by the mean (*i.e.* community weighted mean, CWM) and variance (*i.e.* functional diversity, FDis) of trait distributions (Pakeman et al., 2011; Ricotta and Moretti, 2011). The CWM is calculated for a trait as the mean of trait values of each species weighted by the respective relative abundance of the species in the community, thus linking to delivery of ecosystem services through a mass effect (Garnier et al., 2004; Diaz et al., 2007a). The FDis assesses trait diversity weighted by species relative abundances in the community, and is related to ecosystem function via a diversity effect that can strengthen resilience (Diaz et al., 2007a; Lavorel et al., 2011). Using these metrics, we quantified community functional response to grazing by tracking changes for several key traits involved in community assembly and delivery of ecosystem services, e.g. aspects of forage quality (see below). To test our expectations that grazing mediated tradeoffs in rangeland digestibility and soil fertility, we examine the effect of grazing on these measures of community functional structure, linking them with soil nutrient availability.

We measured above- and below-ground biomass as well as C:N:P stoichiometry for all the species in grazed as well as ungrazed communities at each of five sites distributed from east to north and west on the Qinghai-Tibetan Plateau (Fig. 1). We also measured five key leaf traits (leaf C, leaf N and leaf P concentration, SLA: specific leaf area, LDMC: leaf dry matter content) to assess digestibility and rangeland quality. Plant digestibility is generally positively correlated with leaf N and SLA, but negatively correlated with LDMC and leaf C (Al Haj Khaled et al., 2006; Pontes et al., 2007; Duru et al., 2008; Gardarin et al., 2014) due to the high digestible biomass fraction in plant tissues associated with low structural carbohydrate content in cell walls together with a low degree of lignification (Choong et al., 1992; Bruinenberg et al., 2002). Additionally, forage quality depends not only on digestibility but also N and P concentration in aboveground biomass (Van Soest, 1994; Owensby et al., 1996; Grant et al., 2000; Danger et al., 2013) as well as forage C:N:P stoichiometry and nutritional diversity (Sterner and Elser, 2002). For ruminants, high forage quality often tends to be related to high digestibility and nutrient concentration in biomass and high plant biochemical diversity (Whitehead, 2000; Provenza et al., 2003; Reynolds and Kristensen, 2008). In short, in the present study we examine the effect of grazing in Tibetan alpine meadows on biomass production, the CWM and FDis of key functional traits, the C:N:P stoichiometry of plants and soil, and species diversity in the plant community. We use these data to test whether traditional grazing regimes promote forage quality and species diversity at a cost in depletion of soil available phosphorus and reduced productivity.

## 2. Material and methods

### 2.1. Study sites

We conducted a field experiment in alpine meadows distributed from east to north and west on the Qinghai-Tibetan Plateau (Fig. 1a): AZ and WLK sites in Maqu county of Gansu province (WLK: *cf.* Niu et al., 2014; AZ: *cf.* Zhang et al., 2014), HY site in Hongyuan County of Sichuan province (*cf.* Zhao et al., 2013), QH



**Fig. 1.** The location of five Sites on Tibetan Plateau (a), landscape of WLK site showing pastoralists moving their stock to high-altitude range (b) and comparison of vegetation (c) between ungrazed (left on the fence) and grazed meadow (right on the fence). Photos by Kechang Niu in June 2010.

site in Mengyuan County of Qinghai province (cf. Wang et al., 2012) and NQ site in Naqu County of the Tibet Autonomous Region, China. The five sites are distributed along a gradient in the diversity of Tibetan rangeland (Supplemental Table S1): AZ is a wet alpine meadow with relatively high daytime temperatures and growing season precipitation, and deep soil and high productivity; HY and WLK are more typical alpine meadows with intermediate productivity, but relatively high species diversity, and WLK also is relatively dry; QH is an alpine meadow with a relatively cold and short growing season; and NQ is a dry and cold high alpine meadow with shallow soil and low productivity (cf. Niu et al., 2015a).

The management regime in all these alpine grasslands involves switching livestock between low- and high-altitude pasture in summer and winter. Although there is a long history of grazing by wild and domesticated species in the Tibetan plateau, grazing by yak and Tibetan sheep has increased markedly at all sites in the last three decades (Miehe et al., 2009). Under the “Rangeland

Household Contract System” and the “Herder Settlement” policy, many villages and towns have been built at lower elevations to accommodate previously nomadic pastoralists (Li, and Huntsinger, 2011). Nearby rangeland was fenced and a parcel allocated to each family, resulting in increased grazing intensity around town sites from later September to May, although villagers still move their livestock to unfenced high elevation pasture from May to September (Fig. 1b)

## 2.2. Experimental design

At each study site we built exclosures (1–13 ha, within the designated rangeland of a village family) that were designed to exclude grazing by both small and large mammals. At the time of the study the alpine meadows within the exclosure had been protected from grazing for 11 years at WLK and for 3–6 years at the other sites. Grazing was excluded throughout the year at HY and QH but occasionally allowed within the exclosures during the



non-productive winter months at AZ, WLK and NQ sites. Outside of the enclosure, the meadows were moderately grazed by domesticated yaks and sheep during all months except for 40–60 days between June and mid-August when herds were moved to high-altitude pasture (Niu et al., 2010; Niu et al., 2012).

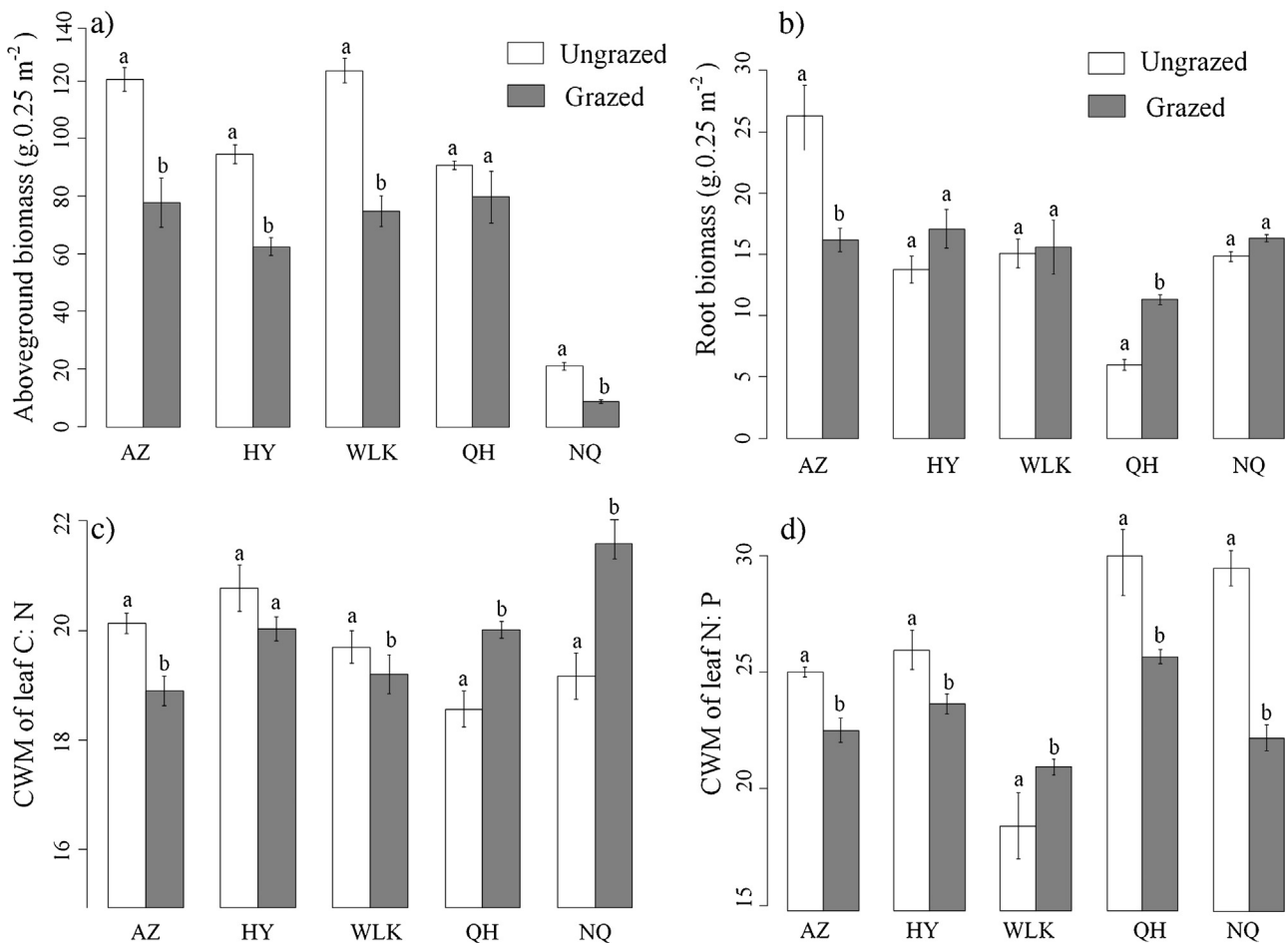
In June 2009–2010, at each site we randomly established eight  $5 \times 8$  m plots within the enclosures as well as another eight outside the enclosures. The grazed plots outside the enclosures were separated by 5–15 m, while ungrazed plots within the enclosures were separated by 2–8 m. We left 20–500 m between grazed and ungrazed plots to eliminate any effects of activities of small animals or the fence used for the grazing enclosure on plant growth. This degree of spatial separation between grazed and ungrazed plots should be sufficient to avoid spatial autocorrelation effects in these meadows with low  $\beta$  diversity and the high levels of soil homogeneity. Each replicate plot was divided into two parts: a  $5 \times 5$  m subplot for measurement of plant traits and a  $5 \times 3$  m subplot for community monitoring, counting of individual ramets and soil sampling (cf. Niu et al., 2015b).

### 2.3. Trait and abundance measurements

In July 2009 and 2010, mature leaves of 7–10 individuals at vegetative stage were randomly sampled for all but a few very infrequent species in the  $5 \times 5$  m subplots in grazed and ungrazed plots at each site. We measured specific leaf area (SLA,  $\text{mm}^2 \text{mg}^{-1}$ ),

leaf dry matter content (LDMC,  $\text{mg g}^{-1}$ ), leaf carbon concentration ( $\text{mg g}^{-1}$ ), leaf nitrogen concentration ( $\text{mg g}^{-1}$ ) and leaf phosphorus concentration ( $\text{mg g}^{-1}$ ) (Niu et al., 2015b). All measurements of functional traits followed standardized methods (Cornelissen et al., 2003; He et al., 2008; He et al., 2010). The sampled species accounted for 90–98% of the aboveground biomass and 95–99% of vegetation cover in the meadow community.

From mid-August to early September 2009 and 2010, we harvested all plants within each of the  $5 \times 3$  m subplots in a  $0.5 \times 0.5$  m quadrat at each site. Individual ramets were counted and harvested by species (Niu et al., 2010; Niu et al., 2014) to calculate trait distribution. After aboveground biomass was harvested in each quadrat, we collected and pooled three soil samples from the 0–15 cm soil layer, which were sieved (2-mm mesh) for further analyses. The sieved soil was dried for measurement of soil carbon and nutrient; the recovered root biomass was washed and dried to measure aggregate root biomass as well as root carbon and nitrogen. The total carbon and nitrogen concentrations ( $\text{mg g}^{-1}$ ) in soil and in root were measured using an elemental analyzer, and soil organic carbon concentrations ( $\text{mg g}^{-1}$ ) using the Walkley–Black method (Nelson and Sommers, 1982). Soil available phosphorus concentrations for plants (Olsen-P) ( $\text{mg kg}^{-1}$ ) were determined by the molybdate colorimetric test after perchloric acid digestion (Sommers and Nelson, 1972). Data of plant traits and abundance are presented in Appendix of Supplemental Materials.



**Fig. 2.** Effect of grazing on community biomass (a and b) and leaf C:N:P stoichiometry (c and d, in term of community weighted mean, CWM) at five sites. Bars and whiskers indicate mean value and its standard error. Significant differences between grazed and ungrazed plots tested by nested linear-mixed modelling (nested in sites) are indicated by different letters.

2.4. Data analysis

2.4.1. Trait distribution

For each 0.25 m<sup>2</sup> quadrat in grazed and ungrazed plots, we calculated the relative abundance of each species as the percentage ramet numbers of a given species relative to the total ramet numbers in the local plant community (i.e. each 0.25 m<sup>2</sup> quadrat). We calculated the means of SLA and LDMC (7–10 replicates) as well as leaf C, leaf N and leaf P (3 replicates) for each species in grazed and ungrazed plots in each of five sites. We used community weighted mean (CWM) and functional dispersion (FDis) of each trait to quantify the mean and variance of the distribution of each trait values, respectively.

The community weighted mean was calculated by summing the trait values for each species weighted by the species' relative abundance. Within various indices of FD, functional dispersion (FDis) is conceptually similar to the commonly used Rao's quadratic entropy (Mouchet et al., 2010), but is better for testing differences between communities through a distance-based test for homogeneity of multivariate dispersion (Laliberté and Legendre, 2010). We calculated a functional dispersion index (FDis) for each trait using the 'FD' package in R (Laliberté and Shipley, 2010). Additionally, we calculated species richness and Shannon entropy of true species diversity based on species number and relative abundance (Jost, 2006) using the 'vegetarian' package (Charney and Record, 2009) in R (R Core Team 2014).

2.4.2. Grazing effect on community functional parameters and soil attributes

To assess whether grazing promotes forage digestibility and rangeland quality but depletes soil fertility, we first examined the effect of grazing on community functional parameters and soil attributes across our five study sites using a linear mixed model; then we used a generalized canonical discriminant analyses (gCCA)

to graphically illustrate the relationships between the community parameters and soil attributes in response to grazing across the five sites. The community functional parameters considered were community species diversity, the CWM and the FDis of each trait, the CWM of leaf C:N:P stoichiometry, aboveground biomass, root biomass, and root C and N concentrations. The soil C, N and P concentrations were used to characterize soil fertility.

Our linear-mixed model with residual maximum likelihood (REML) had the form: response ~ Site/Grazing, random = ~1|plot. The response variables included the community functional parameters and soil attributes along with 'Grazing' and were treated as nested, fixed factors within each site. Individual community samples (i.e. the 0.25 m<sup>2</sup> quadrats) were treated as a random factor to take account of any spatial autocorrelation due to their having been sampled in one larger area at each site. Given the distance between quadrats and the spatial homogeneity of soils at the sites (cf. Niu et al., 2015b), it is unlikely that there would be spatial autocorrelation in the replicate community samples (quadrats), but to be safe we opted for this statistically conservative formulation of the linear model. Some data were log-transformed to meet assumptions of normality and homogeneity of variance. We used the lme4 package in R to perform the mixed models (Bates et al., 2011). The gCCA with a nested linear model (grazing nested in site effect) was employed to examine and visualize linkages among community and soil parameters in grazed and ungrazed plots across the five study sites. The gCCA was performed using the candisc package (Friendly and Fox, 2013).

3. Results

3.1. Effect of grazing on community attributes and ecosystem services

As expected, grazing decreased aboveground biomass at all sites although not significantly at the QH site (Fig. 2a). Both root biomass (Fig. 2b) and the CWM of leaf C:N (Fig. 2c) decreased at wet sites (AZ and HY), but increased at dry sites (QH and NQ) in grazed relative to ungrazed plots. In term of CWM, both community leaf N:P (Fig. 2a) and C:P (not shown) declined significantly in grazed relative to ungrazed plots at all sites (but increased at WLK site, where community leaf N:P was below 25) due to significant increases in the CWM of leaf P (Fig. 3).

Species richness and Shannon index of species diversity tended to increase in grazed plots relative to ungrazed at most sites (significantly at the HY and QH sites), but both measures of diversity declined significantly with grazing at the AZ site (Table 1, Fig. 3). Carbon and nutrient in soil and root tended to decline in grazed relative to ungrazed plots (Table 1, Fig. 3), although the decrease in root C concentration was not significant due to large variation in replicate samples. The decrease in root N concentration, soil organic C, soil total N and soil available P was significant at either four or all five sites (Table 1, Fig. 3).

3.2. Effect of grazing on trait distribution

In term of the community weighted mean characteristics, grazing significantly increased rangeland community-wide LPC and SLA but decreased community LDMC at most sites (Table 1, Fig. 3); this is apparent on the first axis of the gCCA, which accounted for 46% of the variation in these data (Fig. 3). The CWM of leaf N increased in grazed relative to ungrazed plots at a wet and warm (AZ) site but decreased at dry and cold (QH and NQ) sites (Table 1, Fig. 3). In contrast, the CWM for leaf C tends to decline with grazing at the AZ and HY sites, but increase at the WLK and NQ sites (Table 1, Fig. 3).

In term of functional dispersion (FDis), the diversity of leaf P significantly increased, but FDis of leaf C, leaf N, SLA and LDMC

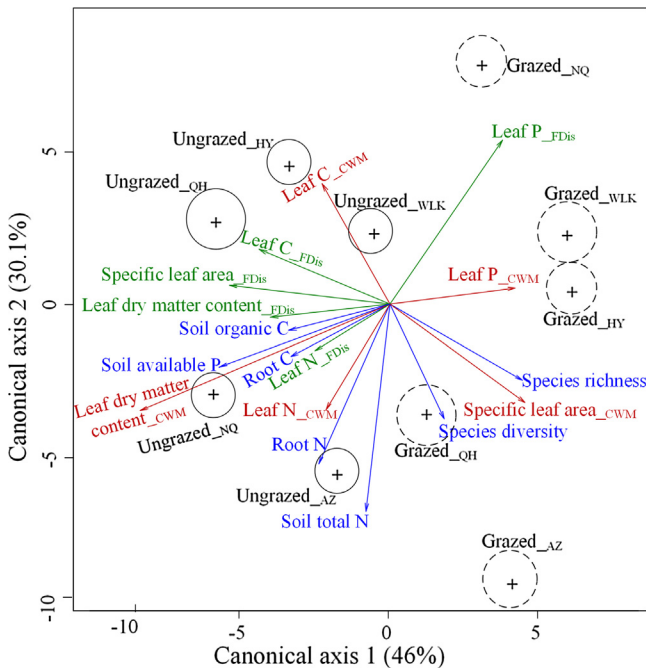


Fig. 3. Generalized canonical discriminant analysis showing the influence of tradeoffs between forage quality and soil fertility for species within and among the grazed and ungrazed communities at each of the five study sites. The broken lines at each site bound the 95% confidence interval around the site-treatment mean. Both grazing and sites effect are significant at P < 0.01 by Wilks' lambda multivariate test. The forage quality was indicated by community weighted mean (CWM) and functional dispersion (FDis) of foliar traits.

**Table 1**

Results of nested linear-mixed modelling for effect of grazing (nested in sites) on community-wide trait mean values and functional dispersion of key functional traits, species diversity as well as nutrient concentration in aggregate root biomass and soil. Value = slope value + standard error with bold entries indicating  $p < 0.05$ , \* indicating  $p < 0.01$ . Positive and negative values indicate increased and decreased the indices, respectively, in grazed plots relative to ungrazed plots. The tabulated values indicate the strength of the grazing effect gauged by the slope of the relationship. AIC: Akaike information criterion, BIC: the Schwarz's Bayesian Information Criteria. Degrees of Freedom = 60.

	AIC/BIC	Strength and direction of the grazing effect				
		AZ site	HY site	WLK site	QH site	NQ site
Community weighted mean (CWM) of functional traits						
Leaf carbon concentration	19.56/44.68	-0.070 ± 0.107	<b>-0.572 ± 0.102*</b>	<b>0.404 ± 0.107</b>	0.077 ± 0.114	<b>0.289 ± 0.102</b>
Leaf nitrogen concentration	-55.9/-30.78	<b>0.141 ± 0.057</b>	0.047 ± 0.055	0.080 ± 0.057	<b>-0.176 ± 0.061</b>	<b>-0.305 ± 0.055*</b>
Leaf phosphorus concentration	-322.1/-296.9	<b>0.016 ± 0.006</b>	0.010 ± 0.006	<b>0.017 ± 0.006</b>	0.007 ± 0.006	<b>0.012 ± 0.006</b>
Specific leaf area	500.5/525.6	<b>55.73 ± 5.894*</b>	<b>19.64 ± 5.649*</b>	-8.092 ± 5.894	-7.90 ± 6.301	<b>25.32 ± 5.649*</b>
Leaf dry matter content	-238.2/-213.1	<b>-0.075 ± 0.012*</b>	<b>-0.09 ± 0.012*</b>	<b>-0.062 ± 0.013*</b>	0.005 ± 0.013	<b>-0.211 ± 0.012*</b>
Functional dispersion (FDIs) of functional traits						
Leaf carbon concentration	-217.9/-192.8	0.012 ± 0.015	<b>-0.047 ± 0.014*</b>	<b>-0.097 ± 0.015*</b>	<b>-0.054 ± 0.016*</b>	<b>-0.053 ± 0.014*</b>
Leaf nitrogen concentration	-176.1/-151.0	0.015 ± 0.020	-0.034 ± 0.02	<b>-0.046 ± 0.020</b>	<b>-0.064 ± 0.022*</b>	<b>-0.067 ± 0.02*</b>
Leaf phosphorus concentration	-224.3/-199.1	<b>0.057 ± 0.014*</b>	0.002 ± 0.013	<b>0.070 ± 0.014*</b>	0.024 ± 0.015	<b>0.091 ± 0.013*</b>
Specific leaf area	-207.9/-182.7	-0.002 ± 0.016	<b>-0.078 ± 0.015*</b>	<b>-0.072 ± 0.016*</b>	<b>-0.070 ± 0.017*</b>	<b>-0.031 ± 0.015</b>
Leaf dry matter context	-197.4/-172.2	<b>-0.104 ± 0.017*</b>	0.019 ± 0.016	<b>-0.034 ± 0.017</b>	0.004 ± 0.018	-0.015 ± 0.017
Species diversity						
Species richness	349.8/375.9	1.792 ± 1.680	<b>10.52 ± 1.61*</b>	2.542 ± 1.680	<b>11.00 ± 1.796</b>	<b>-3.267 ± 1.610</b>
Shannon species diversity	16.89/42.02	0.181 ± 0.105	<b>0.363 ± 0.101*</b>	0.024 ± 0.105	<b>0.333 ± 0.112</b>	<b>-0.535 ± 0.101*</b>
Root carbon and nitrogen concentration						
Root carbon concentration	314.6/339.7	0.836 ± 1.252	-1.374 ± 1.20	-0.398 ± 1.253	-0.831 ± 1.339	-1.161 ± 1.201
Root nitrogen concentration	-46.71/-21.57	<b>-0.231 ± 0.062*</b>	<b>-0.208 ± 0.059*</b>	<b>-0.198 ± 0.062*</b>	<b>-0.122 ± 0.061</b>	-0.099 ± 0.059
Soil carbon and nutrient concentration						
Soil organic carbon	28.60/53.73	<b>-0.663 ± 0.116*</b>	<b>-0.461 ± 0.111*</b>	<b>-0.3093 ± 0.115*</b>	<b>-1.665 ± 0.124*</b>	<b>-0.412 ± 0.111*</b>
Soil total nitrogen	-94.66/53.73	<b>-0.160 ± 0.412*</b>	-0.033 ± 0.39	-0.052 ± 0.413	<b>-0.227 ± 0.044</b>	-0.053 ± 0.039
Soil available phosphorus	-71.02/-45.89	-0.013 ± 0.050	<b>-0.115 ± 0.048*</b>	<b>-0.178 ± 0.05*</b>	<b>-0.138 ± 0.054</b>	<b>-0.163 ± 0.048*</b>

decreased, in grazed plots relative to ungrazed plots at most sites (Table 1, Fig. 3). Grazing induced an increase in diversity of species and in the CWM of leaf P coupled with decreases in community LMDC and belowground nutrients, significantly discriminating grazed from ungrazed plots at all five sites (Fig. 3).

## 4. Discussion

### 4.1. Grazing induced tradeoffs between forage digestibility and soil fertility

Overall, the decrease in LDMC coupled with increase in SLA and enrichment of leaf nutrient content lends some support to the view of traditional pastoralists that rotational grazing will not only ensure biodiversity but also promote forage quality (Table 1 and Fig. 3). These changes in community-wide foliar traits, however, mostly result from re-growth (i.e. a plastic response to grazing) in perennial herbaceous species, rather than changes in species composition induced by continuous moderate grazing. On the other hand, the result supports our hypothesis that plant (re) growth coupled with removal of aboveground biomass by grazing can exhaust soil available P in Tibetan rangeland to the point of deficiency. For instance, the increase of root biomass (Fig. 2b) and nutrients in community-wide leaf biomass, but coincident decline of nutrients in root and soil (Table 1) indicate a decrease in soil available P following grazing. Our results suggest there is a grazing induced tradeoff between forage quality and soil fertility in these Tibetan alpine meadows that arises through shifts in plant community structure and function in poorly managed grazing systems.

An increase in forage quality under grazing might initially be viewed as an advantage for livestock production, e.g. producing high-quality yak milk (Cincotta et al., 1991; Roche et al., 2009), but in the longer term with a lack of compensation for losses in soil available P, this will not necessarily be the case. First, the increased

consumption of soil available P by plant (re)growth could potentially exhaust soil available P, in turn depressing plant growth and rangeland productivity. Second, an open rangeland with low plant height but high quality forage will favor smaller wild animals (e.g. pika, marmots) over larger domesticated livestock (Wise and Abrahamson, 2007), thus reducing forage availability. In short, grazing-induced increases in forage quality occur at the expense of depletion of soil available P, which can lead to declines in yield of forage and livestock production and accelerate degradation of the rangeland if the situation is not well-managed. Hence, there is a pressing need to consider rangeland management strategies that weigh the tradeoffs between forage quality and soil fertility in order to achieve a truly sustainable grazing system.

### 4.2. Is there evidence for phosphorus depletion in Tibetan rangeland?

Soil available P is an expected limitation on plant growth in grasslands on old, well-weathered soils, but not on the younger soils of the Tibetan Plateau (Walker and Syers, 1976; Lambers et al., 2008). Nonetheless, there is increasing evidence for limitation of plant productivity by soil available P in Tibetan rangeland: i) addition of P or mixed N and P fertilizer significantly increased aboveground biomass but not addition of N fertilizer alone (Yang et al., 2014a; Zhou et al., 2015); ii) field investigations along transects in Tibetan rangeland (Hong et al., 2014) as well as experiments manipulating soils and microbes have shown deficiency of soil available P (Liu et al., 2012) coupled with enrichment of P in plant tissues (He et al., 2008; Geng et al., 2011); and iii) the general increase in the soil N:P ratio in Chinese rangelands has been attributed to a decrease in soil P over the long term and at broad spatial scales (Yang et al., 2014b). Our results suggest a general mechanism for a grazing induced deficiency of soil available P that could explain these recent observations for rangelands on younger soils in the Tibetan Plateau.

### 4.3. Developing strategies for managing Tibetan rangelands for sustainability

In a narrow focus, supplementing soils depleted in phosphorus would be a reasonable response to ensure high levels of livestock production in depleted Tibetan rangeland. It is the case that fertilization in semi-natural grassland with inorganic P can significantly increase plant biomass production, but only at the cost of rapid loss of species diversity (Humbert et al., 2015; Stevens et al., 2015); properly managed removal of aboveground biomass by grazing can rescue part of the biodiversity loss (Yang et al., 2012; Borer et al., 2014). Organic fertilizers (Bi et al., 2009; Diacono and Montemurro, 2010) or the use of phosphate solubilizing microorganisms (Khan et al., 2009) provide similar alternatives. The establishment and net effects of any large-scale fertilization program in Tibetan rangeland, however, would require experimental tests prior to widespread adoption.

Such experiments should be carried out in the larger context of an adaptive management approach (Briske et al., 2011) designed to find a balance between the intensity and timing of the grazing rotation and the demands for sufficient yield of forage and livestock production. Identifying the efficacy of any supplemental fertilization program inevitably will be complicated by the many biotic and abiotic factors and interactions that need to be considered. For example, moderate grazing often promotes biodiversity and productivity in relatively wet grassland, but not in dry habitats (Diaz et al., 2007b; Bagchi and Ritchie, 2011; Addison et al., 2012; Eldridge et al., 2015; Török et al., 2016). Similarly, the effect of grazing by wild and domestic grazers differ (Bagchi and Ritchie, 2010b) and the effect of grazing on community structure, productivity and nutrient availability are more pronounced in long-grazed communities (e.g. WLK site in our study) than in short grazed communities (Semmartin et al., 2008; Smith et al., 2008). Finally, sociological factors can also play a role. Tibetan alpine pastures under rotational grazing jointly by three to seven families have significantly higher aboveground vegetation cover and species diversity than pasture grazed by livestock from a single family (Cao et al., 2013). Given these and other complications, an adaptive management approach (Briske et al., 2011) that considers the tradeoff between forage quality and soil fertility is most likely to ensure rangeland sustainability in the Tibet Plateau.

## 5. Conclusion

Our findings and a review of related literature suggest that traditional grazing practices in alpine meadows on the Tibetan Plateau involve a trade-off between short-term yield and sustainability. Moderate levels of grazing induce an increase in plant digestibility, nutrient concentrations, and nutrient diversity in these alpine meadows but this increase in forage quality comes at the cost of losses in both carbon stock and nutrient availability that can depress biomass production as grazing intensity increases. Hence market forces driving increased grazing intensity pose a serious challenge to sustainability on Tibetan rangelands with low soil fertility. Finding the combination of interventions and modulation of grazing intensity that will ensure sustainability calls for a program of adaptive management that can provide concrete evidence of the cost and benefits of alternative management regimes.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.04.023>.

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