Received: 15 September 2017 | Accepted: 28 November 2017
DOI: 10.1111/1365-2664.13066

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Experimentally simulating warmer and wetter climate additively improves rangeland quality on the Tibetan Plateau

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Funding information
National Basic Research Program of China, Grant/Award Number: 2014CB954000; National Natural Science Foundation of China, Grant/Award Number: 31630009, 31570394 and 31621091; 111 Project of China, Grant/Award Number: B14001; The University Research Priority Program "Global Change and Biodiversity" of the University of Zurich.

Handling Editor: Johan du Toit

Abstract

1. The vast expanses of rangeland on the Tibetan Plateau, which support the livelihood of *c.* 9.8 million local inhabitants, have experienced rapid climate warming over the past 50 years. At the same time, precipitation has increased in large parts of the Plateau but decreased in other parts, particularly in the northwest. These trends are predicted to continue into the future. However, their potential effects on rangeland quality remain unclear.
2. We conducted a two-factor field experiment in which we manipulated temperature (control or warming by 1.5–1.8°C) and precipitation (control or 50% reduction or increase in rainfall) in an alpine grassland on the northeastern Tibetan Plateau, starting in 2011. From 2014 to 2016, we measured forage production and community composition, and in 2015 forage quality (crude protein, cell-soluble contents, hemicellulose, cellulose, lignin and digestibility) was represented by seven abundant species.
3. Overall, warming did not change total forage production at plant community level, but increased legume production and decreased non-legume forb production. Increased and reduced precipitation enhanced and decreased forage production by 18.2% and 12.9% respectively. Increased precipitation in particular increased grass and sedge production, but not legume production.
4. Forage quality showed species-specific responses to the simulated climate changes. At community level, warming and reduced precipitation improved forage quality, which were mainly caused by a shift in community composition towards more legumes, rather than the direct effects of simulated climate changes. Meanwhile, increased precipitation did not reduce forage quality, despite the precipitation-induced increase in forage production.
5. Integrating forage production and quality into nutrient production as a measure of rangeland quality, we found that warming and increased precipitation additively improved rangeland quality, while reduced precipitation decreased it.
6. *Synthesis and applications.* Rangeland quality, an important ecosystem provisioning service, will benefit from a warmer climate on the Tibetan Plateau in the regions with a predicted increase in precipitation, but not in those regions where precipitation might be reduced in the future. We suggest management strategies, including reseeding native legumes, establishing sustainable pastures and assisting the

exchange of harvested forage, to cope with the challenges posed by these different climate change scenarios.

KEYWORDS
alpine rangeland, climate change, ecosystem services, forage production, forage quality, global warming, precipitation, rangeland quality, Tibetan grasslands

1 | INTRODUCTION

Climate change will not only affect ecosystem structure and functioning (Ponce-Campos et al., 2013; Reichstein et al., 2013) but also the provisioning of ecosystem services such as forage production (Pettorelli, 2012; Polley et al., 2013). These changes could be particularly profound in high-elevation ecosystems (Chen et al., 2013). The Tibetan Plateau has experienced a rapid climate change over the past 50 years (Dong, Jiang, Zheng, & Zhang, 2012). Air temperatures have been rising at a rate of 0.4°C per decade, that is far more rapidly than the global average (0.06°C per decade; IPCC, 2013). At the same time, overall annual precipitation on most of the Plateau is also increasing (Chen et al., 2015), albeit with a large regional heterogeneity (Chen et al., 2013). If these climatic trends continue, then the previously very cold and relatively dry ecosystems on the Tibetan Plateau will experience an unprecedentedly large environmental change, affecting the homeland for millions of native people with a traditional nomadic life style (Shang et al., 2014) and the habitat of more than 50 million Tibetan sheep (Xin et al., 2011), 13 million yaks (Shang et al., 2014) and various endangered native species (Zhang, Chen, Li, & Yao, 2002).

While a number of studies have investigated the effect of climate warming on rangeland quality (Klein, Harte, & Zhao, 2007; Li, Liu, Frelich, & Sun, 2011), few studies have examined the effects of altered precipitation in combination with warming. Rangeland quality assessment generally considers forage production and quality as two important variables (Kawamura, Watanabe, Sakanoue, & Inoue, 2008; Shi et al., 2013). Forage production is the total forage biomass available to livestock over a whole year (Kawamura et al., 2008). Forage quality is represented by the chemical constituents of forage plants that determine the feeding value of forage (Cherney & Hall, 2000). Most studies on the Tibetan Plateau so far have focused on the effects of climate change on forage production, that is, above-ground net primary production (Li et al., 2011; Ma et al., 2017). In contrast, very few studies in these regions have investigated the effects of climate change on forage quality or combined measures of forage production and forage quality, that is, nutrient production here used as a measure of rangeland quality.

Climate warming can directly and indirectly affect rangeland quality. Several meta-analyses suggest that warming can increase forage production in cold ecosystems (Lin, Xia, & Wan, 2010; Lu, Zhou, Luo, & Li, 2013). The mechanism of this effect can be attributed to a stimulation of plant growth (Lin et al., 2010; Polley et al., 2013) and enhanced availability of soil nutrients (Bai et al., 2013). However, the increased forage production may be compromised by decreased forage quality via nutrient-dilution effects (Shi et al., 2013). Thus, some studies have shown that warming will not only enhance forage production but also increase structural carbohydrates and lignification, resulting in lower forage quality (Cherney & Hall, 2000; Dumont et al., 2015). Furthermore, warming may also affect both forage production and quality by inducing shifts in plant community composition. For example, warming is reported to stimulate legume growth on the Tibetan Plateau (Wang et al., 2012), which in turn may improve forage quality (Dumont et al., 2015). Such indirect effects of climatic factors on rangeland quality may be profound, but they have often been overlooked in previous studies.

Realistic climate change scenarios should include possible changes in precipitation as well as temperature because soil humidity is one of the most important factors affecting rangeland quality. It is well known that forage production generally increases with mean annual precipitation along environmental gradients (Bai, Han, Wu, Chen, & Li, 2004; Knapp & Smith, 2001; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012), including those on the Tibetan Plateau (Shi et al., 2013; Yang, Fang, Pan, & Ji, 2009). For forage quality, a recent meta-analysis based on 75 studies suggested that forage nitrogen content nonlinearly decreases with increasing water availability, while structural carbohydrate showed an opposite trend (Dumont et al., 2015). Furthermore, similar to warming, altered precipitation regimes may lead to shifts in plant community composition and thus indirectly affect forage production and quality. For instance, some studies reported that increased precipitation can stimulate grass growth (Collins et al., 2012), which may result in lower forage quality (Deak, Hall, Sanderson, & Archibald, 2007).

Little is known whether expected effects of changes in temperature and precipitation are additive or if they interact, such that the effect of one factor is increased or reduced at a particular level of the other factor (Hoeppner & Dukes, 2012; Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011; Xu, Sherry, Niu, Li, & Luo, 2013). For instance, warming has been reported to affect plant production only in combination with drought in a grassland in the Alps (De Boeck, Bassin, Verlinden, Zeiter, & Hiltbrunner, 2016). In contrast, as will be shown in the present paper, effects of warming and altered precipitation may be more or less additive in Tibetan rangelands. Such knowledge is essential for the development of rangeland adaptation strategies that cope with climate change in the coming decades.

In our study, we assessed the potential effects of warming, altered precipitation and their interaction on rangeland quality by using a two-factor manipulative field experiment in a meadow at 3,200 m altitude on the Tibetan Plateau. Our goal was to find out how forage production and quality on Tibetan rangelands responded to warming and altered precipitation regimes, particularly reduced or increased rainfall. Using our experimental results, we propose region-specific rangeland management strategies to adapt to predicted climate change scenarios and maintain rangeland quality into the future.

2 | MATERIALS AND METHODS

2.1 | Experimental site and design

The experimental site is located at the Haibei Alpine Grassland Ecosystem Research Station on the northeastern Tibetan Plateau, China (101°12′E, 37°37′N, 3,250 m above sea level, Figure S1). The local climate is characterized by strong solar radiation with cold winters and cool summers. The growing season generally starts in mid-April and ends in late October (Wang et al., 2014). In the 1980–2014 period, mean annual temperature was −1.2°C and mean annual precipitation was 486 mm. More than 80% of the annual precipitation falls in the growing season. The alpine meadow vegetation is dominated by *Kobresia humilis* (C. A. Meyer ex Trautvetter) Sergievskaja in Komarov, *Elymus nutans* Grisebach and *Stipa aliena* Keng. The soil is classified as Mat-Gryic Cambisol (Chinese Soil Taxonomy) with a pH of 7.8 at 0–10 cm depth (Lin et al., 2016).

In July 2011, we set up a two-way factorial experiment with a randomized block design to study the effects of increased annual temperature and increased or decreased annual precipitation and their interaction on the alpine meadow vegetation. The two levels of the factor temperature were control and warming and the three levels of the factor precipitation were control and reduced or increased rainfall (see below). These six treatment combinations were applied to plots of 1.8 × 2.2 m and replicated in six blocks for a total of 36 plots; the positions of the different treatment combinations were separately randomized in each block. There were 3.2-m buffer belts between blocks and 2.5-m buffer belts between plots.

We use overhead infrared heaters to simulate warming. In each warmed plot, two medium-wave (1,200 W, 220 V, 1,000 mm long and 22 mm wide) infrared heaters were suspended 1.6 m above-ground. In each control plot, two "dummy" arrays were suspended to mimic shading and other non-warming effects of the heaters. Soil temperature and moisture at 5, 10 and 20 cm were automatically recorded per hour by data loggers (EM 50; Decagon Devices Inc., Pullman, WA, USA). Compared to the control, warming increased soil temperature by *c.* 1.5–1.8°C at 5 cm depth (Lin et al., 2016; also see Figure S2). To manipulate precipitation, we used rainout shelters consisting of four transparent panlite sheet channels (PC-1151; Teijin Chemicals, Tokyo, Japan) at an angle of 15°, covering 50% of the plot area. In the reduced-precipitation treatment, the shelter intercepted 50% rainfall, which flowed into a white plastic rain collector. The rainfall withheld from a reduced-precipitation plot was added to an increased-precipitation plot, providing it with 50% additional rainfall. In control–precipitation plots, four "dummy" channels with holes were installed to mimic shading and other non-precipitation-related effects of the channels. Our treatments should be compared with an observed 50-year increase by 245 mm in the localities with the largest increase and an observed 50-year decrease by 170 mm in the localities with the largest decrease in precipitation on the Tibetan Plateau (Chen et al., 2013).

2.2 | Response variables

We used total above-ground live biomass at the peak of the growing season (late August) to represent forage production, because peak above-ground live biomass is a good approximation of forage production in this ecosystem (Klein et al., 2007). Within each plot, we randomly sampled three 0.15 × 0.15 m quadrats and clipped all live plant material. We harvested 24 plots in 2014 and 36 plots in 2015 and 2016. Plants in each plot were sorted to species and dried in the oven at 65°C for 48 hr to achieve constant weight in the laboratory. Plant species were classified into the four functional groups: grasses, sedges, legumes and non-legume forbs. This classification into functional groups is directly linked to their ecological niches or functions in the ecosystem. Grasses and sedges, although they both have fibrous roots, differ in rooting depths. The rooting depth of sedges is generally less than 25 cm, while grasses have deeper roots that can reach down to 85 cm in soil depth, thus they can use soil moisture in deeper soil layers and have higher drought tolerance. Legumes have tap root systems and root nodules with nitrogen-fixing bacteria. Non-legume forbs have broader leaves than grasses and sedges and lack the ability to fix nitrogen with symbiotic bacteria. We did not classify plant species into palatable and non-palatable species, because most plants in our experiment site were eaten by livestock (Wang, 2007).

To assess the effects of treatments on forage quality, we measured nutrient content and digestibility of the one to three dominant species in each functional group in 2015. These species were: *E. nutans* (grass), *Helictotrichon tibeticum* (Roshevitz) J. Holub (grass), *S. aliena* (grass), *K. humilis* (sedge), *Medicago archidutis-nicolai* Sirjaev (legume), *Oxytropis subfalcata* Hance (legume) and *Saussurea superba* J. Anthony (non-legume forb), which account for 6.3%, 6.6%, 41.9%, 5.8%, 5.1%, 4.0% and 1.4% of total forage production respectively. For each treatment combination and target species, we collected all above-ground plant tissues (leaves plus stems) from the same three randomly selected blocks in late August, because livestock on the Tibetan Plateau eat both leaf and stem (Cao, Xiong, Sun, Xiong, & Du, 2011). We analysed crude protein, neutral detergent fibre, acid detergent fibre and acid detergent lignin of all these species. We only chose one species from each functional group (*S. aliena*, *K. humilis*, *M. archidutis-nicolai* and *S. superba*) to examine digestibility because this measurement required large amounts of sample material. Crude protein was determined with an Automatic Kjeldahl Nitrogen Determination Apparatus (Kjeltec 8100; FOSS, Höganäs, Sweden). Neutral detergent fibre, acid detergent fibre and acid detergent lignin were determined by a sequential detergent fibre analysis (Goering & Van Soest, 1970). We calculated indices for cell-soluble contents, cellulose and hemicellulose (Goering & Van Soest, 1970). The digestibility of plant species was determined by *in vitro* digestive experiments (Tilley & Terry, 1963).

To assess the nutrient content at community level (NC_c), we first calculated nutrient content at functional group level (NC_f) using production-based weightings as explained in Equation 1; and then calculated community nutrient content using Equation 2:

$$NC_{fij} = \sum_{k=1}^{n} p_k s_{ik} \quad (1)$$

where NC_{fij} is the content of nutrient *i* in functional group *j*, p_k is the relative production in 2015 of species *k* in functional group *j* and s_{ik} is the content of nutrient *i* of species *k*. *n* is the total number of the representative species in functional group *j*.

$$NC_{ci} = \sum_{j=1}^{4} p_j NC_{fij} \quad (2)$$

where NC_{ci} is the content of nutrient *i* at community level, p_j is the relative production in 2015 of functional group *j* and 4 is the number of functional groups. The community digestibility was assessed by the same method.

To synthesize forage production and forage quality, we calculated community nutrient production (*NP*) to assess rangeland quality as explained in Equation 3:

$$NP_i = NC_{ci} F \quad (3)$$

where NP_i is the production of nutrient *i*, NC_{ci} is the content of nutrient *i* at community level and *F* is the forage production in 2015.

2.3 | Statistical analyses

We used repeated-measures ANOVA to examine the main and the interactive effects of experimental warming, altered precipitation and sampling year (2014–2016) on the forage production of the total plant community and the four functional groups separately. Two-way ANOVA was used to examine the main and the interactive effects of experimental warming and altered precipitation on the digestibility, nutrient content and nutrient production in 2015. In the repeated-measures analysis, warming and altered precipitation were treated as fixed-effects between-subject factors and tested against the random-effects factor plot (subject), which was nested within the random-effects factor block. We used Tukey's test to compare individual treatments with each other. Square root or log transformations were used for response variables if this improved residual distributions with regard to homoscedasticity and normality (Schmid, Baruffol, Wang, & Niklaus, 2017). Variation in community nutrient content was decomposed into two categories according to the influencing explanatory variables, that is, climatic factors (experimental treatments of warming and altered precipitation) and community composition (production of grasses, sedges, legumes and non-legume forbs), by partial regression with a redundancy analysis ("vegan" package in the R software; Oksanen et al., 2013). The variables to characterize community composition were previously identified by forward selection. All statistical analyses were conducted in R 3.2.2 (R Core Team, 2015).

3 | RESULTS

3.1 | Effects of warming and altered precipitation on forage production

Forage production significantly responded to warming and altered precipitation (see Table 1). The effects of warming and precipitation were additive, that is, their interaction was statistically not significant for either total production or functional group productions (Table 1). Although warming had no detectable effect on total forage production, it significantly increased legume production by 96.7% and decreased non-legume forb production by 25.6% (Figure 1a). Increased precipitation enhanced total forage production by 18.2%, while reduced precipitation decreased it by 12.9% (Figure 1b). At the level of the different plant functional groups, increased precipitation enhanced grass production by 28.7% compared to the control treatment, while reduced precipitation decreased grass and sedge production by 19.5% and 27.9% respectively. In contrast to the other functional groups, legumes reduced forage production from dry to control to wet along the precipitation treatments (Figure 1b; for 2015 see Figure S3). Besides, the inter-annual variation in forage production was paralleling the variation in annual precipitation (Figure S4), an observation made previously for vegetation on the Tibetan Plateau (Yang et al., 2009).

3.2 | Effects of warming and altered precipitation on nutrient content

Forage quality components in terms of plant nutrient contents (amounts per unit biomass) and digestibility highly varied among plant

TABLE 1 Results of repeated-measures ANOVAs for responses of forage production (g/m^2) of the total plant community and plant functional groups to warming and altered precipitation from 2014 to 2016

	Warming (W)	Precipitation (P)	W × P	Year (Y)	W × Y	P × Y	W × P × Y
Total	1.140	20.419***	0.054	10.275**	0.513	1.302	3.281*
Grass	0.626	25.811***	0.224	14.417***	0.444	0.236	2.585
Sedge	2.509	3.273*	2.737	0.305	0.548	0.717	0.628
Legume	36.307***	6.496**	0.754	1.842	0.002	1.245	0.604
Non-legume forb	12.078***	3.839*	2.536	0.789	1.248	3.113*	0.046

Table entries are *F* values and their significances: *$p < .05$; **$p < .01$; ***$p < .001$.

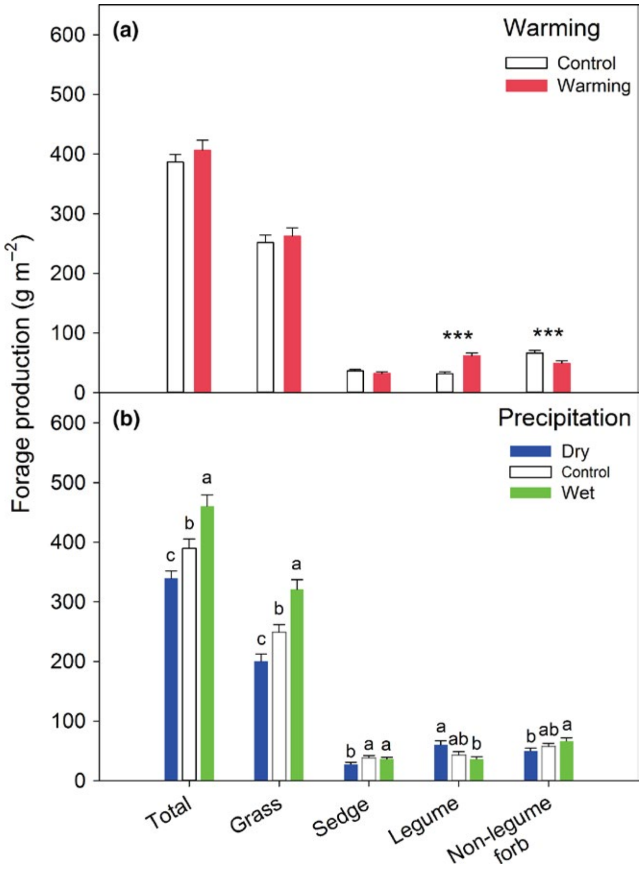

FIGURE 1 Main effects of warming (a) and altered precipitation (b) on forage production of the total plant community and of four plant functional groups. Bars represent *M* ± *SE* values averaged across 2014–2016. Different letters or asterisks represent significant differences: different letters, $p < .05$; ***$p < .001$

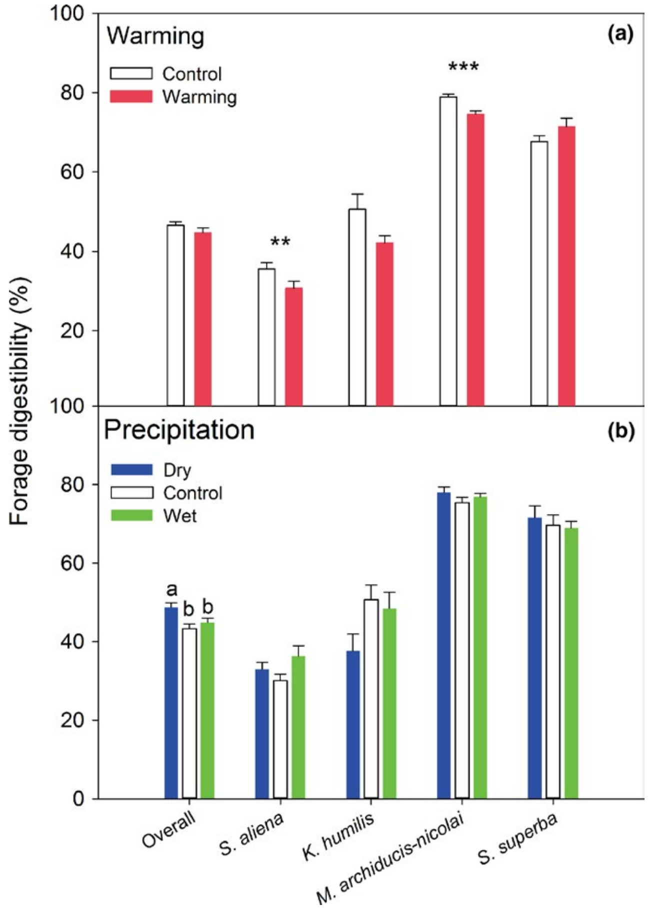

FIGURE 2 Main effects of warming (a) and altered precipitation (b) on the digestibility of the total plant community and of representative species from the four plant functional groups (from left to right the four species represent grasses, sedges, legumes and non-legume forbs). Bars represent *M* ± *SE* values. Different letters or asterisks represent significant differences: different letters, $p < .05$; **$p < .01$; ***$p < .001$

species (Figure 2 and Figure S4). According to the nutrient content ranking, legumes had the highest nutritive value, followed by non-legume forbs, sedges and grasses (Figure S5). As expected, the response direction and magnitude of quality components to warming, altered precipitation and their interactions were specific to different plant species (Tables S1 and S2; Figures 2 and 3).

Despite these different specific responses of plant species to warming and precipitation treatments, there were also several consistent overall effects of these treatments on nutrient contents at community level (Table 2 upper part, Figure 4a,b). Thus, warming increased crude protein content from 8.6% to 9.2%. In addition, crude protein content declined from dry to control to wet along the precipitation treatments and a significant interaction between warming and precipitation treatments indicated that the positive effect of warming was lost under increased precipitation (Figure S6). From the reduced- to the control–precipitation treatment, increased water availability reduced cell-soluble contents, lignin content and digestibility from 42.6% to 39.3%, 7.9% to 7.2% and 48.8% to 43.3%, respectively, and increased cellulose content from 21.3% to 24.1%. Overall, warming and reduced precipitation, especially under a concurrent condition, increased forage quality in terms of nutrient contents. However, although nutrient production increased with increasing precipitation as shown below, this was at the expense of reduced forage quality.

Using variation partitioning analysis, we further quantified the contributions of climate change and community composition to the variation of forage quality in terms of nutrient contents. The amount of variation captured by all selected variables was 93.5% for overall nutrient content (from 89.4% to 94.2% for individual nutrients; Figure 5). The pure effects of community composition accounted for 69.1% of variation (from 32.6% to 81.4% for individual nutrients), while the pure effects of climatic factors only account for 3.3% of variation (from 0.2% to 15.5% for individual nutrients). In addition, the joint effects of climate and community composition accounted for 21.1% variation (from 7.5% to 58.9% for individual nutrients). Therefore, the variation in nutrient contents was mainly explained by differences in community composition, which was, however, itself affected by the climatic factors, that is, warming and precipitation treatments (see Table 1 and Figure 1).

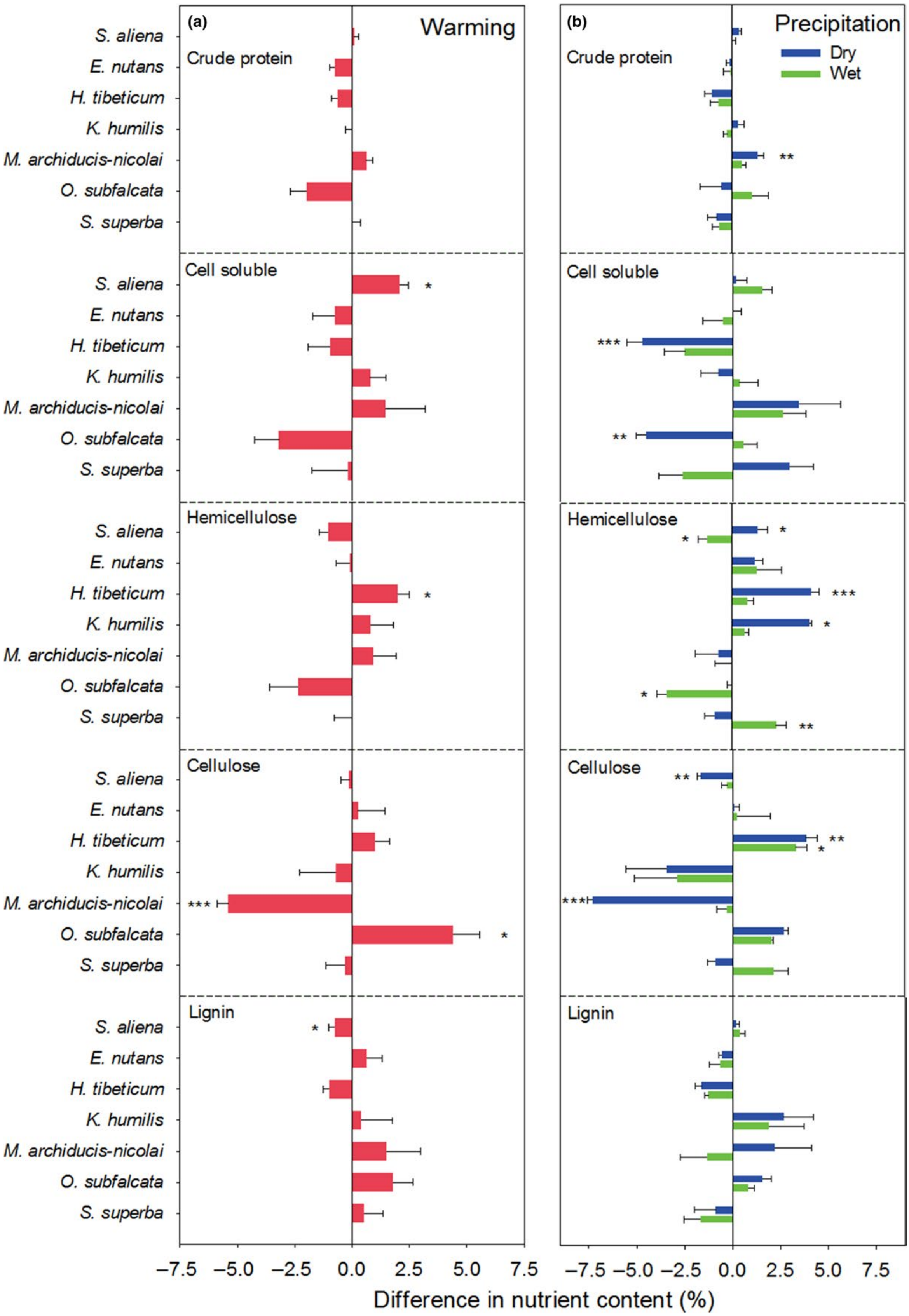

FIGURE 3 Main effects of warming (a) and altered precipitation (b) on nutrient contents of the dominant species *Stipa aliena*, *Elymus nutans*, *Helictotrichon tibeticum*, *Kobresia humilis*, *Medicago archiducis-nicolai*, *Oxytropis subfalcata* and *Saussurea superba*. Bars represent the difference between global change and control treatments. Significance: *$p < .05$; **$p < .01$; ***$p < .001$

3.3 | Effects of warming and altered precipitation on nutrient production

Rangeland quality was assessed by community nutrient production, which integrated forage production and forage quality. Warming and altered precipitation significantly affected nutrient production (Table 2 lower part, Figure 4c,d). Warming increased crude protein production by 11.7% but had no significant effects on the production of other nutrient components. Compared to the control treatment, increased precipitation enhanced cell-soluble contents, hemicellulose, cellulose and lignin production by 15.6%, 18.1%, 19.0% and 15.6%, respectively, and reduced precipitation decreased hemicellulose and cellulose production by 13.4% and 19.6% respectively. Overall, warming and increased precipitation improved Tibetan rangeland quality, while reduced precipitation decreased it.

TABLE 2 ANOVA results for responses of community nutrient content (%) and nutrient production (g/m^2) to warming and altered precipitation

	Crude protein	Cell-soluble contents	Hemicellulose	Cellulose	Lignin
Content (%)					
Warming (W)	18.250***	0.901	0.423	0.262	2.050
Precipitation (P)	32.410***	5.879**	2.482	19.964***	21.909***
W × P	13.210***	2.454	1.501	1.661	0.543
Production (g/m^2)					
Warming (W)	5.910*	2.235	1.089	1.290	2.881
Precipitation (P)	2.813	4.331*	13.353***	20.952***	5.136*
W × P	1.010	0.523	0.626	0.189	0.272

Table entries are *F* values and their significances: **p* < .05; ***p* < .01; ****p* < .001.

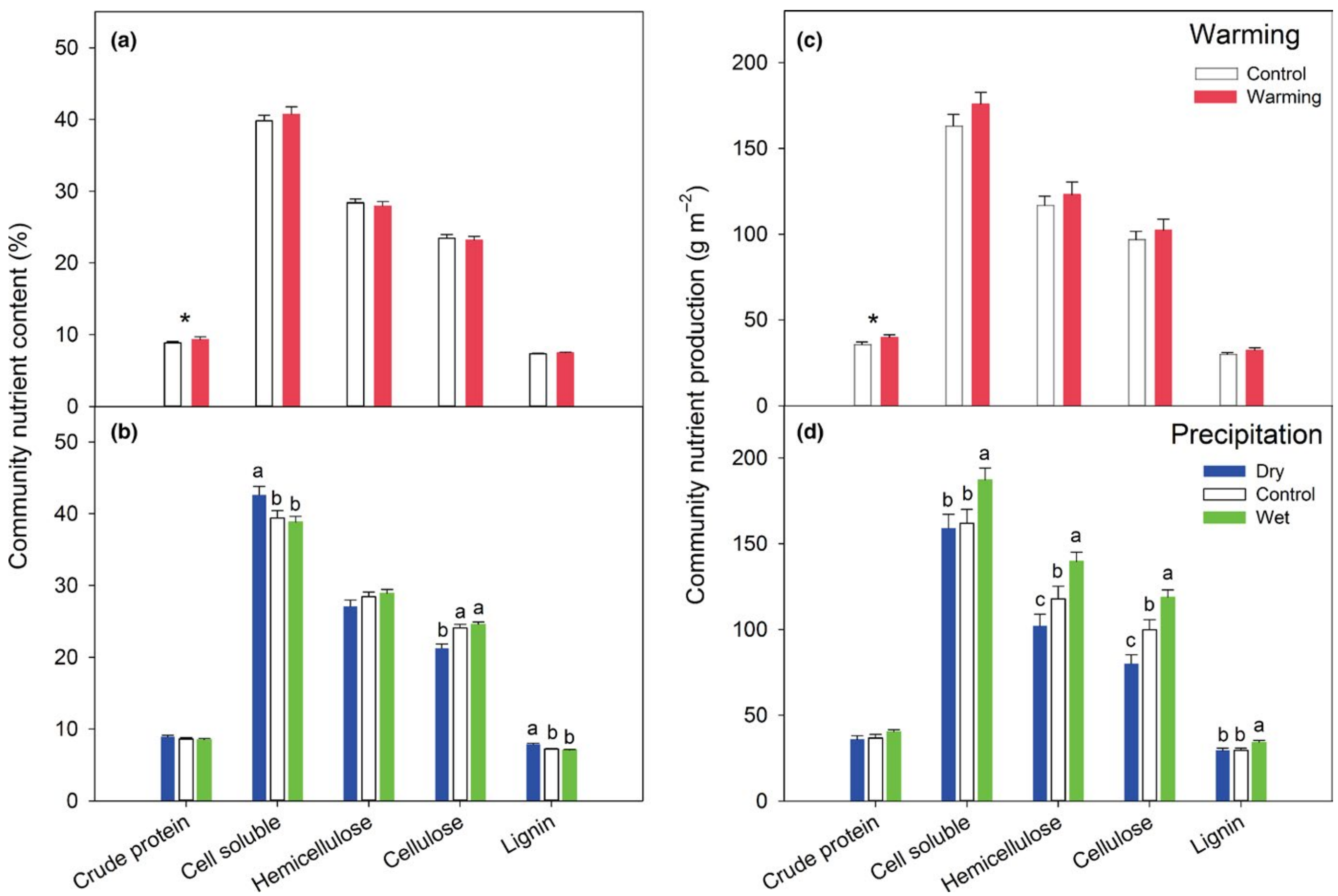

FIGURE 4 Main effects of warming and altered precipitation on community nutrient content (a, b) and community nutrient production (c, d). Bars represent *M* ± *SE* values. Different letters or asterisks represent significant differences (*p* < .05)

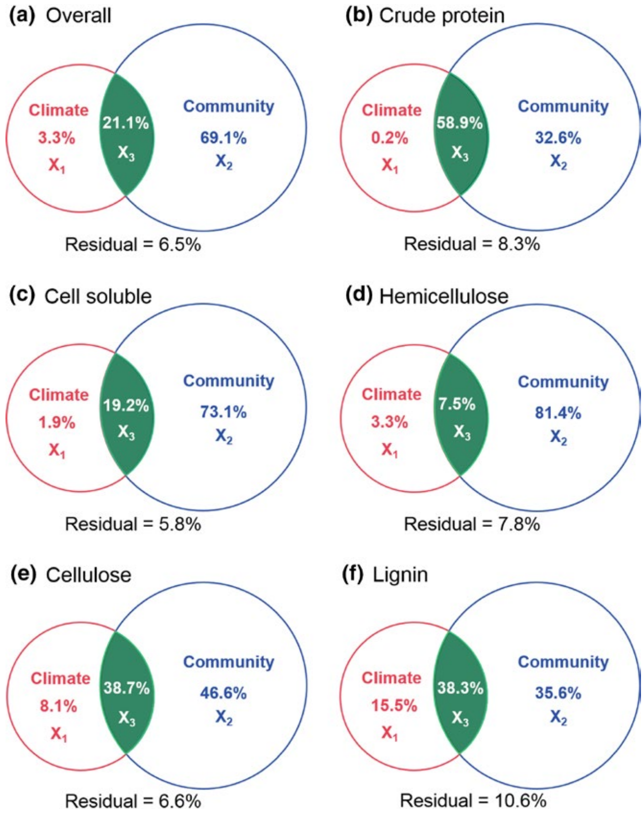

FIGURE 5 Results of variation partitioning for total plant community nutrient content (a), crude protein content (b), cell-soluble nutrient content (c), hemicellulose content (d), cellulose content (e) and lignin content (f) in terms of fractions of variation explained. Variation is explained by four categories: pure effects of experimentally manipulated climatic factors (X_1), pure effects of community composition (X_2), joint effect of climatic factors and community composition (X_3) and residual variation

4 | DISCUSSION

Rangeland quality is anticipated to potentially be strongly impacted by climate warming and altered precipitation (Briske et al., 2015). While increasing precipitation is widely reported to improve rangeland quality, the effects of warming generally depend on local temperature and precipitation regimes. Specifically, warming is expected to improve rangeland quality in cold and humid regions, but decrease it in warm and arid regions (Briske et al., 2015; Polley et al., 2013). Our study on the cold but relatively dry Tibetan Plateau suggest that, in comparison with these current climatic conditions, future warming together with increased precipitation will improve rangeland quality, whereas a less likely decrease in precipitation would decrease it. Furthermore, we found that warming and altered precipitation affected rangeland quality in different ways: warming improved rangeland quality mainly by increasing forage quality (see Figure 4a,c), whereas altered precipitation affected rangeland quality mainly by changing forage production (see Figure 4b,d). Given the important role of livestock husbandry on the Tibetan Plateau (Qiu, 2016), effective adaptation strategies are required to cope with challenges and opportunities of future climate change in this high-elevation grassland ecosystem.

4.1 | Increased rangeland quality due to warming-induced community shifts to legumes

Our study showed that warming improved rangeland quality, through increased plant nutrient content (forage quality), rather than increased plant biomass (forage production). Similar observations have been made in other studies from the Tibetan plateau (Li et al., 2011; Shi et al., 2015) and Arctic tundra (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Welker, Fahnestock, Sullivan, & Chimner, 2005), however, the mechanisms were different. Warming improved forage quality mainly due to accelerated net nitrogen (N) mineralization and increased available soil nutrients in Arctic tundra (Natali, Schuur, & Rubin, 2012), but this was not the case in our system, where no detectable effect on net N mineralization under warming treatment has been observed (Wang et al., 2012). Rather, we found that a shift in community composition towards increased legume biomass with high-nutrient contents was responsible for the improved forage quality at community level (see Figure 6). In addition, other mechanisms might also have contributed to this effect, including warming-induced increases in N content during plant senescence as observed in other alpine grasslands (Shi et al., 2015).

Another study carried out in the same ecosystem found that warming decreased rangeland quality due to a reduction in both forage production and forage quality (Klein et al., 2007). These contrasting results might be attributed to the following two reasons: first, Klein et al. (2007) used open-top chambers to simulate warming, which in contrast to infrared heaters increase air temperature more than soil temperature and additionally reduce wind speed (Marion et al., 1997; Wan, Luo, & Wallace, 2002), further increasing air temperature up to 7°C (Klein, Harte, & Zhao, 2005). However, alpine plants, especially tall graminoids, are sensitive to heat stress (Wang et al., 2012). Second, the different species measured in these two studies may cause different results regarding forage quality. We found that legume forage had the highest quality among the studied four functional groups in the alpine meadow. Warming almost doubled legume production and consequently improved forage quality at community level. However, Klein et al. (2007) chose a non-legume forb, *Gentiana straminea*, to represent the quality of the combined legume plus non-legume functional group of forbs. Hence, they did not examine the potential effects of changes in legume production on forage quality under their warming treatment. In contrast, our study emphasizes the great importance of legume production for Tibetan rangelands.

The warming-increased legume production may be particularly relevant in this high-elevation ecosystem, because Tibetan rangelands under the current low-temperature climatic conditions have lower legume production than most natural grasslands around the world (Jin et al., 2013). Our results, along with previous studies (Jin et al., 2013; Wang et al., 2012), provide strong evidence that a warmer climate can benefit legumes and consequently improve Tibetan rangeland quality.

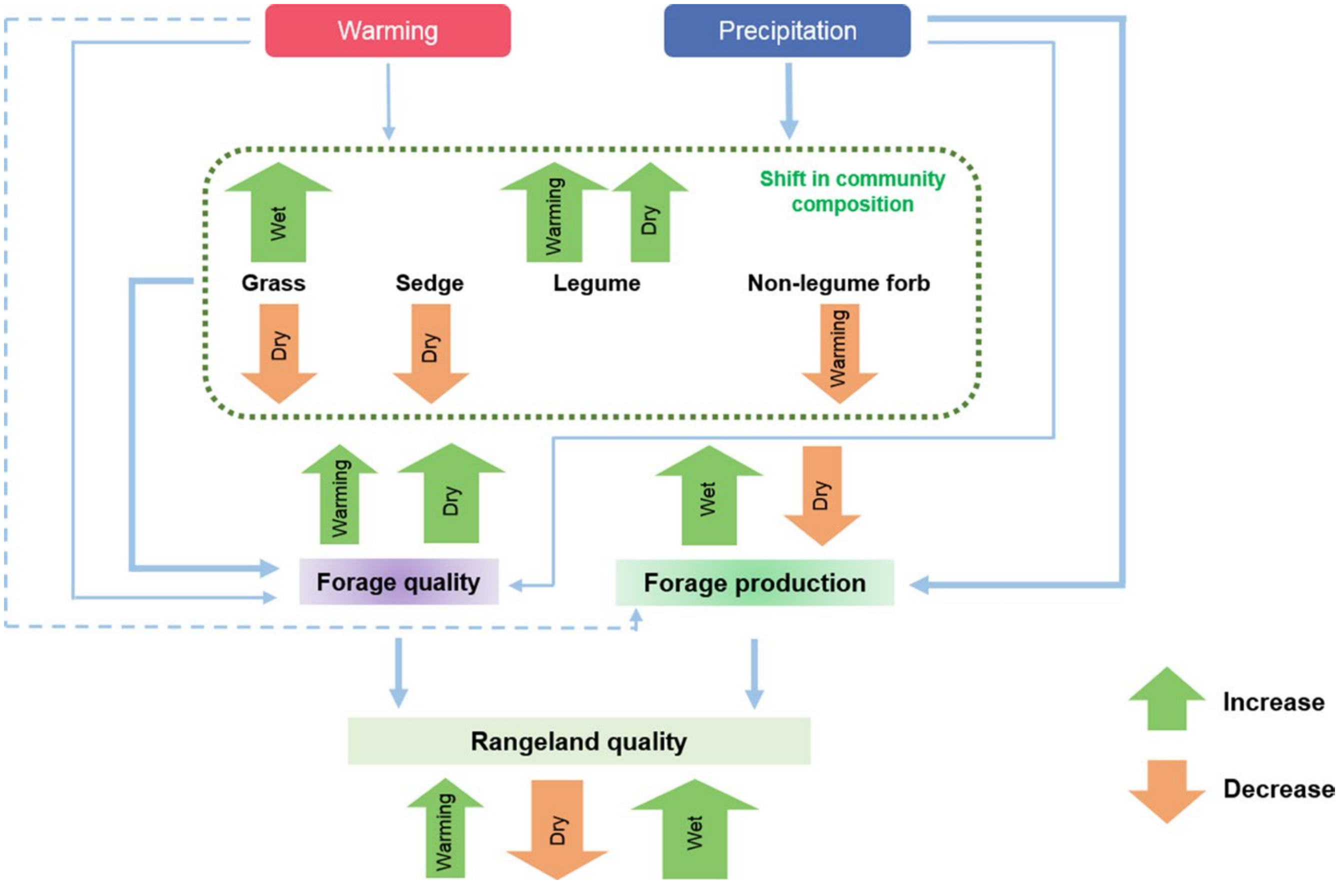

FIGURE 6 Summary of impacts of warming and altered precipitation on Tibetan rangeland quality, emphasizing the regulating paths. Warming and precipitation affect forage quality mainly by shifting community composition. Forage production is influenced by altered precipitation, but not by warming. The content in the box shows responses in community composition under climate change. The widths of lines and arrows correspond to effect sizes. Solid lines indicate significant effects and the dashed line indicates a non-significant effect

4.2 | Improved rangeland quality due to precipitation-induced forage production

A global meta-analysis reported that cold ecosystems are more responsive to altered precipitation than other ecosystems (Wu et al., 2011). In line with previous studies (Bai et al., 2004; Knapp & Smith, 2001; Ponce-Campos et al., 2013; Yang et al., 2009), we found that increased precipitation enhanced forage production. The positive response of forage production mainly resulted from a strong increase in grass production, which accounted for 63% of forage production in control plots and for 69% in wetter plots. Similar observations were made in long-term rainfall experiments in the steppes of Inner Mongolia (Yang et al., 2011) and Patagonia (Yahdjian & Sala, 2006) and in Kansas prairies (Collins et al., 2012). Reduced precipitation decreased forage production due to suppressed grass production. This result is comparable with similar findings in drought experiments in steppes in Colorado (Evans, Byrne, Lauenroth, & Burke, 2011) and high-elevation grassland in the Alps (De Boeck et al., 2016). Further evidence shows that forage production is generally more responsive to increased rather than reduced precipitation (Unger & Jongen, 2015; Wu et al., 2011) and this is also what we found in our study.

Forage quality was only weakly affected by altered precipitation, which therefore had similar effects on rangeland productivity and rangeland quality (see Figure 6). Nevertheless, the decreased forage production under reduced precipitation, after five consecutive years of treatment, was at least partly compensated by improved forage quality (see Figure 4b), thus maintaining relatively constant nutrient production (see Figure 4d). Other studies suggested that more severe drought over a long time can accelerate plant senescence, resulting in a decline not only of forage production but also of forage quality (Polley et al., 2013). A reason for the improved forage quality in our study was the shift in community composition towards higher legume abundance, a functional group with generally high quality (Deak et al., 2007), induced by long-term drought.

Our results suggest that a future wetter climate will be beneficial to rangeland quality, while a future dryer climate could induce forage deficiency. Without efficient adaptation strategies, overgrazing may be more frequent and severe in dryer regions, resulting in accelerated rangeland degradation (Li et al., 2013; Shang et al., 2014). Therefore, local governments should pay more attention to balance the stocking rate and forage production in reduced-precipitation regions on the Tibetan Plateau.

4.3 | Implications for rangeland management

Our study provides experimental evidence that a warmer and wetter climate, which is anticipated as a general trend in the coming decades (Chen et al., 2015), could improve rangeland quality, while a drier climate could decrease it. Although climate warming is widely observed throughout the Tibetan Plateau, there is large geographical heterogeneity of precipitation (Chen et al., 2015). In the central, northern and southeastern parts, precipitation has increased since 1960, however, in the western part and eastern periphery, opposite trends of precipitation have been observed (Chen et al., 2013, 2015; Xu, Gong, & Li, 2008). Here, we propose several adaptation strategies that can be effective supplements to the current strategies, such as the "Four-Package Project" (Yan, Wu, & Zhang, 2011), based on geographically specific predictions of climate change and the possible responses of alpine grassland as found in the present study.

First, in mesic and wet regions at lower elevations (<4,000 m a.s.l), reseeding native legumes such as *M. archiducis-nicolai* and *Astragalus tanguticus* Batalin can be a promising approach to improve the quality of degraded rangelands. A warmer climate can reduce low-temperature stress on legume growth (Jin et al., 2013) and make it possible to transform degraded grassland to higher quality rangeland. Reseeding legumes in degraded meadow grassland has been proved feasible in several cold ecosystems in northern China (Wang, Sun, An, Nuer, & Chen, 2011).

Second, the government can support the establishment of productive and sustainable pastures in humid regions such as southeast part of the Plateau (Xu et al., 2008) by providing information about locally optimal seed mixtures. Furthermore, the government should support the development of new varieties and species mixtures for rangeland in drier regions, which will become more humid under the projected precipitation increase in coming decades.

Third, the government should help the exchange of harvested forage between more humid and drier regions, particularly the few regions with predicted precipitation decreases (northwestern parts of the Plateau, Chen et al., 2013), to avoid overgrazing in those regions. This should be combined with incentives for pastoralists to reduce stocking rates and help them to diversify into other activities such as eco-tourism.

The success of implementing these management practices will rely on the involvement of local government staff in advising pastoralists, the support of agricultural research stations and adaptive monitoring. In addition, strengthening regional collaboration and raising public awareness of climate change issues should further contribute to develop livestock husbandry on the Tibetan Plateau in a direction that will maintain productivity and sustainability in the face of continued climatic change.

ACKNOWLEDGEMENTS

This research was funded by the National Basic Research Program of China (2014CB954000) and National Natural Science Foundation of China (31630009, 31570394 and 31621091). It was further supported by the 111 Project of China (grant no. B14001) and the University Research Priority Program "Global Change and Biodiversity" of the University of Zurich.

AUTHORS' CONTRIBUTIONS

J.-S.H. conceived the ideas and designed methodology; W.X., M.Z., Z.Z., Z.M. and H.L. collected the data; W.X. analysed the data; W.X., M.Z. and J.-S.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.sq539 (Xu et al., 2017).

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How to cite this article: Xu W, Zhu M, Zhang Z, et al. Experimentally simulating warmer and wetter climate additively improves rangeland quality on the Tibetan Plateau. *J Appl Ecol*. 2018;55:1486–1497. https://doi.org/10.1111/1365-2664.13066