

This is a repository copy of *Grazing and climate change have site-dependent interactive effects on vegetation in Asian montane rangelands*.

White Rose Research Online URL for this paper: https://eprints.whiterose.ac.uk/170407/

Version: Accepted Version

Article:

Kohli, M, Mijiddorj, TN, Suryawanshi, KR et al. (3 more authors) (2021) Grazing and climate change have site-dependent interactive effects on vegetation in Asian montane rangelands. Journal of Applied Ecology, 58 (3). pp. 539-549. ISSN 0021-8901

https://doi.org/10.1111/1365-2664.13781

© 2020 British Ecological Society. This is the peer reviewed version of the following article: Kohli, M, Mijiddorj, TN, Suryawanshi, KR et al. (3 more authors) (2020) Grazing and climate change have site-dependent interactive effects on vegetation in Asian montane rangelands. Journal of Applied Ecology. ISSN 0021-8901, which has been published in final form at 10.1111/1365-2664.13781. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk https://eprints.whiterose.ac.uk/

1	Grazing and climate change have site-dependent interactive effects on
2	vegetation in Asian montane rangelands
3	
4	Kohli, Mayank ^{1*} , Mijiddorj, Tserennadmid Nadia ^{2,3} , Suryawanshi, Kulbhushansingh Ramesh ^{4,5} ,
5	Mishra, Charudutt ^{4,5} , Boldgiv, Bazartseren ² , Sankaran, Mahesh ^{6,7}
6	
7	¹ Department of Ecology, Evolution and Behavior, University of Minnesota, Twin Cities, St Paul, MN,
8	USA
9	² Ecology Group, Department of Biology, School of Arts and Sciences, National University of
10	Mongolia, Ulaanbaatar 14201, Mongolia
11	³ Snow Leopard Conservation Foundation, P.O. Box 774, 44 Peace Avenue, Ulaanbaatar, Mongolia
12	⁴ Nature Conservation Foundation, Mysore, India
13	⁵ Snow Leopard Trust, Seattle, USA
14	⁶ National Center for Biological Sciences, Tata Institute of Fundamental Research, Bangalore 560065,
15	India
16	⁷ School of Biology, University of Leeds, Leeds LS2 9JT, UK
17	* Correspondence: 1987 Upper Buford Circle, Saint Paul, MN, USA 55108;
18	mayankkohli22@gmail.com; +1-651-703-1362

19 Abstract

41

20 1. Climate over Asian montane rangelands is changing faster than the global average, posing serious threats to the future of the region's livestock-based 21 22 economies and cultures. Effects of climate change on rangeland vegetation likely depend on grazing by herbivores but the potential responses of 23 24 vegetation to such changes in climate and grazing regimes remains unclear. 25 2. We examined vegetation responses to experimentally simulated climate 26 change (warming, drought and increased rainfall) and grazing (clipping 27 vegetation) between 2015-2018 at two mountain rangeland sites: Spiti valley, 28 in the Indian Trans-Himalaya and Tost, in the Gobi-Altai Mountains in 29 Mongolia. 30 3. Clipping and climate change manipulations interactively reduced vegetation 31 cover and biomass but did not affect species richness. Treatment effects and 32 their interactions varied between sites. In ungrazed plots, vegetation cover 33 and biomass declined sharply in response to warming (18-35%) and drought 34 (20-50%) at the two sites, and, surprisingly also declined slightly in response 35 to increased rainfall (20%) at Tost. While the effects of climate treatments were largely similar in the grazed and ungrazed plots in Tost, they were larger 36 37 in the ungrazed plots in Spiti. The decline in vegetation cover was driven by a 38 decline in the cover of both forbs and grasses. 39 4. In combination, grazing and warming (Tost) or drought (Spiti) had sub-additive 40 effects, i.e., the decrease in vegetation cover in response to grazing and

42 greater than the effect of either manipulation alone. Of the two, warming had a

warming/drought was less than the sum of their independent effects but

- 43 greater effect than drought at the more arid site (Tost), while drought had a
 44 larger effect at the more mesic site (Spiti).
- 45 5. Synthesis and applications. Our findings show that future changes in climate, 46 including just over 1°C of warming, could undermine the sustainability of pastoral economies and the persistence of wildlife across Asian montane 47 48 rangelands. Further, grazing by herbivores will play an important role in mediating rangeland responses to climate change; thus, pasture management 49 in concert with local pastoralists will be crucial in mitigating the adverse 50 51 effects of climate change on rangelands, pastoral livelihoods and wildlife populations. 52 53 Keywords 54 rangeland vegetation, dry steppe, climate change, montane grassland, global warming,
- 55 pastoral livelihood, trans-Himalayas, Gobi-Altai mountains

56 Introduction

57 Rangelands occupy nearly 45% of the Earth's terrestrial surface (Reid et al. 2008). They are vital for global food security and livelihoods of millions of pastoralists, and 58 59 provide ecosystem services such as soil erosion control, biodiversity maintenance and carbon sequestration. Because rangeland vegetation dynamics and functioning 60 are jointly shaped by climate and grazing by herbivores (Milchunas et al. 1988; Frank 61 62 et al. 1998; Liang & Gornish 2019), changes in climate and grazing (e.g., due to loss or replacement of native with domestic herbivores, or changes in the size or 63 64 composition of livestock) could interactively impact the ability of rangelands to 65 provide food, livelihoods and other ecosystem services (Dangal et al. 2016; Eldridge 66 et al. 2016).

67

68 Asian montane rangelands are a part of the largest contiguous grassland system in 69 the world, and despite being historically important for pastoralism are still relatively 70 understudied. This rangeland system stretches over central Asia (Kyrgyzstan, Turkmenistan, Uzbekistan, Tajikistan and Kazakhstan), trans-Himalaya (Pakistan, 71 72 India, Nepal and Bhutan), Tibetan Plateau (China) and steppe and Gobi regions in Mongolia, occupying between 40-65% of land area over this region (Angerer et al. 73 74 2008; Gintzburger et al. 2005). The bulk of this region's livestock-based economies 75 and cultures, and a vast majority of this region's mostly rural population, are 76 dependent on these rangelands for nomadic and agro-pastoralism. Further, these 77 rangelands are home to several endangered species of wildlife (e.g., Saiga Saiga 78 tatarica, Tibetan antelope Pantholops hodgsonii, and snow leopard Panthera uncia) 79 (Berger et al. 2013), and comprise a globally important carbon reservoir (e.g., Genxu 80 et al. 2002).

81

82 Understandably then, there is concern about the degradation of these rangelands in recent times. This degradation has been linked with rapid changes in livestock 83 84 grazing regimes arising from ongoing socio-economic changes (Miller 1990; Angerer 85 et al. 2008; Harris 2010; Berger et al. 2013). For example, livestock numbers have 86 increased nearly 9-fold in over a 50-year period in Inner Mongolia (Angerer et al. 87 2008) and similar rapid increases have been reported from the Gobi region in Mongolia (Berger et al. 2013), Indian trans-Himalayas (Namgail et al. 2007), 88 89 Qinghai-Tibetan Plateau (Lu et al. 2017), and central Asia (Gintzburger et al. 2005). 90 This intensification of livestock holding and a shift towards smaller bodied livestock 91 has been accompanied by a decline in native herbivores and a large decline in 92 rangeland productivity across the Asian steppes (Angerer et al. 2008; Kerven et al. 93 2011).

94

95 In addition to changes in patterns of grazing, these rangelands are experiencing 96 some of the most rapid climatic changes globally (Christensen et al. 2007). For 97 example, average winter temperature over Qinghai-Tibet Plateau (QTP) has increased by more than 1.5°C in over two decades (Du et al. 2004), and projections 98 99 suggest a further increase of 2-5°C in the coming decades (Christensen et al. 2007). 100 Similarly, both summer and winter precipitation patterns are changing, although 101 changes in precipitation are harder to project and vary greatly over this region. 102 especially due to local orographic features in mountainous regions (Xu et al. 2008; 103 Christensen et al. 2007). Together with changes in livestock production systems, 104 these climatic changes are likely to influence rangeland vegetation and various 105 aspects of ecosystem functioning, including carbon cycling and storage, hydrological

cycles, and forage production. Furthermore, the effects of grazing are likely to be
influenced by changes in climate and vice-versa (Klein et al. 2004), making it
necessary to study these factors together to better predict future rangeland
functioning.

110

111 Thus far, most experimental research in these Asian montane rangelands has 112 focused on the effects of warming and has been predominantly conducted on the 113 Tibetan plateau (Klein et al. 2004; Ganjurjav et al. 2015; Lu et al. 2017). However, 114 the effects of changing climatic regimes and grazing systems on rangeland 115 vegetation in other regions of Asia have been less well studied experimentally. 116 Furthermore, most experimental studies manipulate a single climate variable (by imposing either warming or drought) at a single site, making comparisons across 117 118 different drivers and across sites with different environmental conditions difficult.

119

120 To address this gap, we experimentally manipulated growing-season temperature 121 and precipitation, and simulated changes in grazing over 3 years at two sites (Spiti 122 valley, India and Tost, Mongolia) in semi-arid Asian montane rangelands that have a 123 long history of livestock grazing. We examined changes in the cover and 124 composition of the vegetation community in response to these treatments. Previous 125 research from the region suggests that site-level precipitation regimes and micro-site 126 differences in soil moisture influence the direction of vegetation response to warming 127 (Klein et al. 2004; Liancourt et al. 2012; Ganjurav et al. 2016). As our study sites are 128 dry (see Methods: average rainfall in the growing season is <200 mm), and 129 vegetation is typically moisture limited (Bagchi & Ritchie 2011; Liancourt et al. 2013), 130 we expected warming to lower soil moisture and thus lower overall vegetation cover.

131 Further, we expected that vegetation cover would decline with reduced rainfall and 132 increase with supplemental rain. We also expected vegetation cover and biomass to 133 decline in response to simulated grazing. Finally, we expected that the effects of 134 grazing would be contingent on climate manipulations and vice-versa. Specifically, 135 we expected grazing to exacerbate the effects of warming and drought on vegetation 136 cover because of its negative effects on soil moisture status by increased 137 evaporation (although grazing could also ameliorate soil moisture by reducing 138 transpiration, e.g., see Veron, Paruelo & Oesterheld 2011). We also expected that 139 vegetation decline in response to grazing would be lower in plots with supplemental 140 watering due to a greater capacity for compensatory growth in irrigated plots.

141

142 Materials and Methods

143 Site description

Our two study sites were located in Spiti valley, India and Tost, Mongolia (details
follow). Total annual precipitation (rain + snow) between 2013-17 in Spiti varied
between 509 and 816 mm whereas in Tost it ranged between 66 and 207 mm (Table
S1).

148

149 Spiti valley, India

150 The Spiti valley is a part of the Trans-Himalayan region in the rain-shadow of the

151 Greater Himalayas. It spans an area of roughly 12000 km² in the catchment region of

the Spiti river and ranges between 3350-6700 m in altitude (Mishra 2001). The

climate is arid, with a mean annual precipitation of ~500 mm with most precipitation

154 occurring in the form of winter snow (mean precipitation during the growing season is

about ~ 200 mm). Temperature ranges between -30°C during winter and 28°C

156 during summer (Rana 1994). Despite being a low productivity landscape, livestock 157 density is high (Mishra 2001), and the livestock assemblage comprises of yaks, 158 cattle, cattle-yak hybrid (*dzo*), horses, donkeys, sheep and goats. The vegetation is 159 characterized as dry steppe rangeland vegetation comprising a mix of short shrubs 160 (Caragana versicolor, Lonicera sp., Eurotia sp.) and forbs and graminoids including 161 several species of Potentilla, Oxytropis, Poa, Stipa and Festuca. The experimental 162 plots were set up in a representative pasture at an altitude of ~5000 m 163 (32°19'49.12"N, 78° 4'28.70"E). Dominant species in the pasture included sedges 164 like Carex sp., Kobresia sp., graminoids including Elymus sp., Festuca sp., and forbs including *Potentilla* sp. Free-ranging domestic vaks graze the area seasonally in 165 166 addition to native herbivores bharal (Pseudois nayaur) and wooly hares (Lepus 167 oistolus).

168

169 Tost mountains, Mongolia

170 Our study site was situated in the Tost mountains at an elevation of 1450-2550m in 171 Gurvantes soum, South Gobi (43°13'27.7"N, 100° 37'57.1"E), which is part of the 172 south-eastern Altai mountainous landscape. Climate in the region is semi-arid, with 173 low mean annual precipitation (~110 mm at the lower pediments), and high year to year variability. Temperature ranges between -15.4 to 24.4°C. Vegetation, 174 175 characterized as desert steppe, is dominated by the grass Stipa glareosa, and small 176 shrubs and forbs such as Caragana leucophloea, Allium polyrrhizum, Ajania spp., 177 Artemisia spp..

178

According to local statistical information from 2017, Tost *bag* [administrative unit] is home to about 90 herder families who owned 55,229 heads of livestock of which

49,201 were goats, 3461 sheep, 1499 camels, 900 horses and 168 cattle, with 80 to
1200 heads of livestock per family. Except goat and sheep that are herded daily, the
rest of the livestock are free ranging (Mijiddorj et al., 2019).

184 Experimental design

185 At each site, 5 experimental blocks, each 10 m × 10 m, were established (in 2015 in 186 Spiti, and 2016 in Tost) within 50 m of each other to minimize spatial heterogeneity 187 in soil and vegetation. The blocks were fenced to a height of 2.5 m to exclude large 188 mammals. Within each block, 2 plots each for warming, reduced rainfall and 189 increased rainfall treatments and 2 control plots, each measuring approximately 2 m 190 × 2m and separated by 1-m walkways, were established for a total of 40 plots at 191 each site (Fig. S1 in Supporting Information). Treatments were randomly assigned to 192 plots. We built hexagonal open-top chambers (OTC, dimensions: 170 cm across at 193 the top, 60 cm high) with sides made of transparent acrylic sheets. In a pilot study 194 preceding this experiment, we found that this OTC warmed plots by almost 3°C. 195 Thereafter, we left one side of the hexagon open, and this reduced the warming 196 effect to an average of 1.2°C (±0.25) (P<0.0001, Fig. S2), a degree of warming 197 expected to occur in this region within the next 3 decades (Xu et al. 2017). We 198 deployed temperature loggers (iButton DS1921G by Maxim Integrated) taped to 199 wooden pegs ~10 cm above ground to measure air temperature difference between 200 warmed and control plots at 30-min interval over 85 days between June and August. 201 Ten loggers were deployed in Tost, and 8 in Spiti, distributed over the unmanipulated 202 and warmed plots. We constructed rainout shelters with channels made of clear, 203 transparent polyvinyl assembled on a steel pipe frame such that the shelters 204 intercepted 50% of rainfall (because they covered 50% of the ground area) and 205 diverted it away from the plot. We dug channels around all plots to ensure that runoff

206 from the rainout shelters did not irrigate other plots. Precipitation runoff from 207 additional rainout shelters (dimensions 1 m × 2 m equaling 50% of plot area) was 208 collected in 20L cans and this collected rainwater was uniformly sprinkled on the 209 increased rainfall plots once every two weeks (Fig. S1). Therefore, the increased 210 rainfall treatment plots received ~50% more water. Once or twice over a season in 211 Spiti during a large rain event (but never in Mongolia), the cans were too small to 212 collect all the rain. To examine the effects of intensive biomass removal by grazers, 213 one out of each pair of climate treatment and ambient plots in each block was 214 randomly assigned to a clipping treatment. In these 'grazed' plots, aboveground 215 plant biomass was clipped once every two weeks to 2-3 cm above ground using 216 hand-held clippers (Fig. S1). Although we did not weigh clipped biomass to quantify 217 offtake, our clipping treatment simulates a very high intensity of grazing similar to 218 what is prevalent at these sites. In Spiti, for example, pastoralists graze each pasture 219 once or twice every week. Previous studies have estimated that grazers remove 220 nearly 75% of plant production (Bagchi & Ritchie 2010), leading to a five-fold 221 difference in standing plant biomass between intensively and moderately grazed 222 areas (Mishra et al. 2004). Care was taken to remove the clipped biomass from the 223 plots.

224

225 Vegetation sampling

At each site, we monitored vegetation in all plots annually at peak biomass (July in Gobi, early August in Spiti), by visually estimating the percent cover of each species rooted within permanent 1 m × 1 m quadrats, and the percent cover of bare ground. The 1 m² quadrat was located in the center of each treatment plot, allowing for a buffer area from the plot edges; this also allowed us to avoid sampling any

vegetation under the sloping sides of the hexagonal OTCs. Each species was

assigned to one of the following plant functional groups: grass, sedge, non-

leguminous forb, leguminous forb, or shrub. Data presented here were collected

234 between 2015-2017 (Spiti), and 2016-2018 (Tost).

235

236 Live plant biomass

237 At both sites, we calibrated the relationship between percent cover, height and 238 aboveground biomass for the most common species and by plant functional group. 239 In Spiti, independent calibration measurements were performed in summer 2016. In 240 178 plots across the site, we estimated the percent cover of species rooted in the 241 plot and subsequently harvested all aboveground biomass. This biomass was then 242 sorted to species, dried and weighed. In Tost, all aboveground biomass inside the 1 m² permanent vegetation cover guadrats was harvested in October 2018, sorted by 243 244 species, dried and weighed. Thus, species cover and biomass could be directly 245 correlated. The details of calibration are provided in a supplement (Tables S2, S3): 246 to summarize, species cover (% cover) was a better predictor of plant biomass than 247 volume (% cover * height). In Spiti, *R*-squared values (correlation) between cover 248 and biomass ranged between 0.75-0.98, and in Tost, from 0.47-0.95. We used these 249 calibrations to estimate the effects of treatments on total plant biomass as well as by 250 plant functional group.

251

252 Statistical analysis

For each site separately, we analyzed vegetation cover and peak biomass (August in
Spiti, July in Tost), both total and aggregated by plant functional group, in response
to climate and grazing treatments. We applied linear mixed-effects models using the

Ime function in the *nlme* package in R software to analyze our data (Pinheiro et al. 2017). We also analyzed species richness (number of species rooted inside 1 m² permanent vegetation quadrats) using generalized linear mixed effects models using the *lme4* package (Bates et al. 2015). We modeled experiment year, climate manipulation and clipping treatments as fixed effects. We included experimental block as a random intercept to account for the spatial variability in the plant community due to factors not examined here such as abiotic drivers of vegetation.

264 **Results**

265 Site characteristics

On average, across the duration of the experiment and all replicate blocks, live vegetation cover was $32.57 (\pm 5.12)\%$ in Spiti, and $18.02 (\pm 2.68)\%$ in Tost. Average live biomass in control plots was $135.83 (\pm 19.38)$ g.m⁻² and $22.02 (\pm 3.30)$ g.m⁻² in Spiti and Tost, respectively. On average, there were 6.46 and 5.45 species m⁻² in Spiti and Tost, respectively.

271

272 Effects of climate and grazing manipulations

273 Where vegetation was not clipped, warming and drought greatly reduced vegetation 274 cover at both sites. The effects of warming were more pronounced than drought at 275 the more arid site (Tost), while the effects of drought were more pronounced at the 276 more mesic site (Spiti). Averaged across treatment years, warming reduced 277 vegetation cover and biomass in the unclipped plots by 17.5% and 26.5% (or 36 g.m⁻ ²) in Spiti and by 35 and 37% (8.1 g.m⁻²) in Tost (Fig. 2). Reducing rainfall reduced 278 279 vegetation cover and biomass by 50% and 55% (74 g.m⁻²) in Spiti and by 20 and 280 23% (1.67 g.m⁻²) in Tost (Fig. 2). Supplemental watering had no impact on total

vegetation cover in Spiti but, surprisingly, reduced vegetation cover and biomass by
21 and 26% (5.82 g₋m⁻²) in Tost (Figs 1-2; Tables 1, S4-S5). Neither climate
manipulations nor grazing treatment affected species richness at either of the two
sites (Table 1, Fig. 2) suggesting that the decline in vegetation cover and biomass
was not caused by an overall decline in the number of species present but instead
due to a decline in their growth.

287

288 Simulated grazing reduced vegetation cover and biomass at both sites, but had 289 larger impacts at the more productive site (Spiti). In Spiti, grazing alone (no climate 290 manipulation) reduced vegetation cover by 40% and 47% (64 g.m⁻²) while in Tost, 291 grazing alone reduced vegetation cover and biomass by 25% and 38% (8.32 g.m⁻², 292 Fig. 2). Grazing and climate treatments together had sub-additive effects on 293 vegetation cover (Tables 1, S4-S5): in Spiti, decline in vegetation cover in plots that 294 were grazed and had reduced rainfall was less than the sum of the independent 295 effects of treatments on vegetation cover. Likewise, in Tost, the combined effect of 296 warming and grazing on vegetation cover was lower than the sum of their 297 independent effects (Table 1, S5; Figs. 1-2). It is worth pointing out that although the 298 combined impacts of grazing and climate manipulations on vegetation cover were 299 sub-additive, they were often greater than the impact of either climate or grazing 300 manipulation alone (Figs. 1, 2, Table 1, S4-S5).

301

Comparing effect sizes of climate and grazing manipulations on vegetation cover
 offers further insights. First, the effects of climate manipulations varied by site: e.g.,
 warming effects were more pronounced at the drier site (Tost, Mongolia), whereas
 reducing rainfall had larger impacts at the relatively wetter site (Spiti, India) (Figs. 3

306 A, B). Second, grazing had a larger negative impact on vegetation in Spiti than in 307 Tost (Figs. 3 C, D). Third, the interactions between grazing and climate treatments 308 varied between sites: in Spiti, climate manipulations did not significantly impact 309 vegetation cover in grazed plots as shown by effect sizes that were not significantly 310 different from zero (Fig. 3A). In Tost, by contrast, the effects of climate treatments 311 were similar (and negative) across grazed and ungrazed plots (Fig. 3B). At both sites 312 the effects of grazing were largely similar (and negative) across ambient, warmed 313 and watered plots. However, in plots where rainfall was reduced, intensive grazing 314 had no overall impact on vegetation cover (Fig. 3D).

315

316 Effects on plant functional types

317 Dominant plant functional types responded differently to climate treatments and 318 simulated grazing, and the responses varied by site. In Spiti, forbs and grasses 319 declined in response to lowered rainfall (40% and ~75% decline in cover), warming 320 (30-35% decline in cover) and simulated grazing (50% and 70% decline in cover. 321 respectively, Fig. 4, Table S6). When rainfall was reduced, leguminous forbs were 322 completely lost from ungrazed plots, but almost doubled in abundance in grazed 323 plots. Sedges showed a weak decline in response to lowered rainfall although this 324 trend was not statistically significant (Fig. 4, Table S6).

325

In Tost, forbs and grasses declined in response to warming while shrubs declined in
plots where rainfall was reduced. Grasses were not affected significantly by
simulated grazing (Fig. 5, Table S7). The decline in forb cover in response to
warming depended on the grazing treatment – where plots were grazed, the decline

was lower. Shrubs declined in response to grazing and reduced rainfall and there
was no significant climate by grazing interaction (Fig. 5, Table S7).

332

333 Discussion

334 Our results indicate that, in Asian montane rangelands, overall vegetation cover and 335 biomass could decline significantly depending on the interaction between warming, 336 drought and grazing. Further, the magnitude of this decline, the relative importance 337 of warming and drought, and their interaction with grazing are likely to be site-338 specific. The combined effects of grazing and climate manipulations were sub-339 additive: they never exceeded the sum of their independent effects, but were almost 340 always larger than the effect of either factor alone. Taken together, our findings show 341 that pastoral livelihoods are likely to be undermined by future climatic changes, and 342 the effects of grazing and climate change need to be considered together in the 343 management of these pastures.

344

345 Climate & grazing interactively influence vegetation cover & biomass

346 There has been uncertainty regarding the effects of future warming on vegetation 347 cover and biomass in Asian montane rangelands. Previous studies have reported 348 both a warming induced decline (Klein et al. 2007; Hopping et al. 2018) and increase 349 (Wang et al. 2012; Ganjurjav et al. 2015) in vegetation cover and biomass. Our 350 findings from two sites support the view that future warming will lead to significant 351 declines in vegetation. These divergent findings could be partially explained by 352 precipitation regimes at these sites: our field sites receive less summer precipitation (<200 mm in Tost, 200-300 mm in Spiti) than sites where positive effects of warming 353 354 on vegetation have been reported (~ 450 mm for sites in Wang et al. 2012, and

Ganjurav et al. 2015). Ganjurjav et al. (2016) found that total plant cover increased with warming at a more moist meadow site but declined with warming at a drier steppe site. Our finding that the drier of the two sites (Tost, Mongolia) experienced a greater warming induced decline in vegetation cover supports the view that the impacts of future warming over this region will vary with prevailing moisture regimes (Liancourt et al. 2012; Ganjurjav et al. 2016).

361

362 Considering that soil moisture constrains plant growth in this ecosystem (Bagchi & 363 Ritchie 2011; Liancourt et al. 2012) we expected rain manipulation treatments to 364 significantly influence plant growth. In support of our expectations and corroborating 365 previous findings from Asian highlands (He et al. 2017; Xu et al. 2018) and other 366 global dry steppes (Yahidjan & Sala 2006; Wu et al. 2011), reducing rainfall greatly 367 depressed forb, graminoid and overall vegetation cover at both sites. Contrary to our 368 expectations, however, increasing rain in plots also reduced rather than increased 369 vegetation cover, particularly impacting grasses (both sites) and leguminous forbs 370 (Spiti). Although surprising, previous studies lend support to these findings: He et al. 371 (2017) reported a decline in graminoid biomass in a Tibetan steppe when rain was 372 added to plots while Xu et al. (2018) reported a decline in legumes but an increase in 373 graminoids and forbs. Effects of precipitation manipulation could be affected by 374 topography, ecotype, and biotic interactions (e.g., plant competition), even over small 375 spatial scales, such that water addition may only benefit phenotypes that usually 376 grow in less water stressed areas (Liancourt et al. 2013). In addition to these 377 biological mechanisms, it is also possible that other reasons contributed to these 378 results. For example, although we sprinkled water on our plots as carefully as we 379 could, the rate of water addition was probably much greater than in a typical summer

380 rainfall. As a result, topsoil might have been impacted, and water would also have 381 moved through the soil column much faster than that with less potential for 382 contribution to plant growth. A previous study from a Mongolian grassland lends 383 support to this argument- supplemental watering rapidly influenced community 384 composition when watering interval was low (1 week) but has no effects when the 385 watering interval was high (3 weeks) (Spence et al. 2016). Finally, our water 386 additions were often performed in warm, sunny conditions leading to potentially 387 higher rates of evapotranspiration. The mechanisms underlying the observed decline 388 in vegetation cover upon supplemental watering need to be explored in future work. 389

390 Despite differences in site conditions (e.g., soil nutrient status, temperature and 391 precipitation), warming, drought and grazing treatments had gualitatively similar (and 392 negative) impacts on vegetation at our study sites. Differences in the magnitude of 393 climate and grazing induced impacts, and in the responses of plant functional types 394 between the two sites could occur because of differences in history of grazing. 395 edaphic conditions, prevailing climatic regimes and biotic interactions (Milchunas et 396 al. 1993, Liancourt et al. 2013). Perhaps most importantly, precipitation regimes at 397 the two sites are very different: Spiti valley receives more summer (and total annual) 398 precipitation than Tost mountains but Tost experiences higher inter-annual variability 399 in precipitation which could explain why vegetation response to lowered precipitation 400 was lower at this site (Knapp & Smith 2001; Nippert et al. 2006). Similarly, among site differences in climate could have led to the same amount of warming (~1 °C) 401 402 producing a greater amplification of the dry conditions in Tost relative to Spiti.

403

404 There has been much debate about the role of grazing versus abiotic factors on 405 structure and functioning of rangelands (Milchunas & Lauenroth 1993; Koerner & 406 Collins 2014; Liang & Gornish 2019). Our findings support the view that both grazing 407 and abiotic factors interactively shape rangeland vegetation (Koerner & Collins 2014; 408 Dangal et al. 2016; Lu et al. 2017); thus, prevailing grazing patterns will influence the 409 impact of climate change on rangelands. For example, at the less arid site (Spiti), 410 warming and rainfall manipulations had no or a slightly positive effect on vegetation 411 when plots were grazed compared to when they were not grazed. Further, at both 412 sites the effect of grazing was dampened when rainfall was reduced rather than 413 increased, and conversely the effect of drought was dampened under grazed 414 conditions. This supports findings from a defoliation experiment in Spiti wherein 415 plants compensated aboveground growth (ANPP) for defoliation more in the 416 absence of irrigation (Bagchi & Ritchie 2011). These results suggest that plant 417 community responses to climate and grazing are interlinked, possibly through 418 resource allocation between root and shoot growth. Finally, grazing mediated 419 vegetation compositional changes in response to climate manipulations. Taken 420 together, our results demonstrate that grazing will play a crucial role in mediating the 421 impacts of climate change on Asian montane rangelands, and that the interactive 422 effects of grazing and climate are not easily predicted from their independent effects. 423

Although temperature and precipitation patterns are changing simultaneously, we could only examine vegetation responses to these drivers independently. Previous studies suggest the combined effects of warming and precipitation changes could be additive (Xu et al. 2018) or interactive (Wu et al. 2011; Ronk et al. 2020). Future work should aim to understand their joint effects on ecosystems. Our experimental

429 rain addition simulates larger but less frequent rain events rather than a regular, 430 small increase in rainfall. While this matches the local inhabitants' perceptions of 431 climate change (Singh et al. 2015; informal accounts of residents of Kibber, Spiti) 432 and observed trends of increasing frequency and magnitude of large storm events 433 (Fu et al. 2013; Goulden et al. 2016), it leaves room to explore how other modes of 434 precipitation increase may impact vegetation. One shortcoming of our study is a lack 435 of soil moisture data; linking changes in soil moisture to changes in vegetation would 436 provide a clearer understanding of mechanisms underlying vegetation responses to 437 climate and grazing.

438

439 **Conclusions**

440 Pastoralists across the Asian highlands perceive that their rangelands are degrading 441 with changing climate, negatively impacting their livelihoods and influencing their 442 livestock production systems (Lkhagvadorj et al. 2013; Singh et al. 2015). Together 443 with previous findings from the Tibetan plateau (Klein et al. 2007) our study lends 444 support to these concerns. Considering that livestock production accounts for a 445 major portion of monetary income and a source of food and materials (Mishra 2001; 446 Lkhagvadorj et al. 2013), such degradation greatly risks the economic and food 447 security of the region's pastoralists. Although future climate will severely impact 448 rangeland functioning regardless of livestock grazing, based on our findings we 449 suggest that managing pastoral practices will be vital, both to prevent rangeland 450 degradation, and to mediate the impacts of climate change on rangeland functioning 451 and pastoral economies. Examining how different pastoral practices (e.g., rotational 452 grazing, low versus high intensity of grazing, diversification of livestock) influence the 453 responses of vegetation to climate change could help identify best practices.

454

455 Acknowledgments

- 456 The authors would like to acknowledge the support of MoEFCC, India, and the
- 457 Himachal Pradesh Forest Dept. We also acknowledge support provided to MS and
- 458 NCBS by the Department of Atomic Energy, Government of India, under project no.
- 459 12-R&D-TFR-5.04-0800, and the Science & Engineering Research Board,
- 460 Government of India (SERB/ DIA/ 2018/000038). MK was supported by grants from
- the University of Minnesota. BB was supported by the Taylor Family-Asia Foundation
- 462 Endowed Chair in Ecology and Conservation Biology. We thank two anyonymous
- reviewers, the editor, and Forest Isbell for constructive comments. We would like to
- thank Namgail, Rinchen Tobgye, Tandup Chhering, Tenzin Thukten, Tenzin
- 465 Chhewang 'Miranda,' Chhunit Kesang, Dorje Chhering, and Abhirup Khara for field
- 466 assistance in Spiti, Boldmaa, Oyuna and Mije for the same in Tost, and Chandan
- 467 Pandey and Chengappa SK for help with sample logistics. We also thank Wildlife
- 468 Conservation Network for financial support in Mongolia.

469

470 Authors' contributions

- 471 MK, CM, MS, BB and KS conceived and designed the experiment. MK and TM set
- 472 up, maintained and collected data. MK analyzed the data with inputs from MS and
- BB. MK wrote the first draft of the manuscript and all authors contributed
- 474 substantially to revisions. All authors gave final approval for publication.

475

476 Data availability statement

- 477 Data used here are available via the Dryad Digital Repository:
- 478 https://doi.org/10.5061/dryad.g4f4qrfnz

480 **References**

- Angerer, J., Han, G., Fujisaki, I., & Havstad, K. (2008). Climate change and ecosystems of Asia with
 emphasis on Inner Mongolia and Mongolia. *Rangelands*, *30*(3), 46-51.
- Bagchi, S., & Ritchie, M. E. (2011). Herbivory and plant tolerance: experimental tests of alternative
 hypotheses involving non-substitutable resources. *Oikos*, *120*(1), 119-127.
- 486
 487 Berger, J., Buuveibaatar, B., & Mishra, C. (2013). Globalization of the cashmere market and the
 488 decline of large mammals in Central Asia. *Conservation Biology*, 27(4), 679-689.
- 489 490 Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, R., ... & Magaña Rueda, V.
- 491 (2007). Regional climate projections. In *Climate Change, 2007: The Physical Science Basis.*
- 492 Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on
- 493 *Climate Change, University Press, Cambridge, Chapter 11* (pp. 847-940). 494
- Dangal, S. R., Tian, H., Lu, C., Pan, S., Pederson, N., & Hessl, A. (2016). Synergistic effects of
 climate change and grazing on net primary production of Mongolian grasslands. *Ecosphere*, 7(5),
 e01274.
- Dorji, T., Totland, Ø., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2013). Plant functional traits
 mediate reproductive phenology and success in response to experimental warming and snow addition
 in Tibet. *Global change biology*, *19*(2), 459-472.
- 503 Du, J., & Ma, Y. (2004). Climatic trend of rainfall over Tibetan Plateau from 1971 to 2000. Acta
 504 Geographica Sinica, 59(3), 375-382.
 505
- 506 Eldridge, D. J., Poore, A. G., Ruiz-Colmenero, M., Letnic, M., & Soliveres, S. (2016). Ecosystem
 507 structure, function, and composition in rangelands are negatively affected by livestock
 508 grazing. *Ecological Applications*, *26*(4), 1273-1283.
- Frank, D. A., McNaughton, S. J., & Tracy, B. F. (1998). The ecology of the earth's grazing
 ecosystems. *BioScience*, *48*(7), 513-521.
- Fu, Y., Chen, F., Liu, G., Yang, Y., Yuan, R., Li, R., ... & Sun, L. (2016). Recent trends of summer
 convective and stratiform precipitation in mid-eastern China. *Scientific reports*, *6*, 33044.
- 516 Ganjurjav, H., Gao, Q., Zhang, W., Liang, Y., Li, Y., Cao, X., ... & Danjiu, L. (2015). Effects of warming
 517 on CO2 fluxes in an alpine meadow ecosystem on the central Qinghai–Tibetan Plateau. *PLoS*518 *One*, *10*(7), e0132044.
- Ganjurjav, H., Gao, Q., Schwartz, M. W., Zhu, W., Liang, Y., Li, Y., ... & Guo, H. (2016). Complex
 responses of spring vegetation growth to climate in a moisture-limited alpine meadow. *Scientific reports*, *6*, 23356.
- 524 Genxu, W., Ju, Q., Guodong, C., & Yuanmin, L. (2002). Soil organic carbon pool of grassland soils on
 525 the Qinghai-Tibetan Plateau and its global implication. *Science of the Total Environment*, 291(1-3),
 526 207-217.
- 528 Gintzburger, G., Le Houérou, H. N., & Toderich, K. N. (2005). The steppes of Middle Asia: post-1991
 529 agricultural and rangeland adjustment. *Arid Land Research and Management*, *19*(3), 215-239.
 530
- Goulden, C. E., Mead, J., Horwitz, R., Goulden, M., Nandintsetseg, B., McCormick, S., ... & Petraitis,
 P. S. (2016). Interviews of Mongolian herders and high resolution precipitation data reveal an
 increase in short heavy rains and thunderstorm activity in semi-arid Mongolia. *Climatic Change*, *136*(2), 281-295.
- Harris, R. B. (2010). Rangeland degradation on the Qinghai-Tibetan plateau: a review of the evidence
 of its magnitude and causes. *Journal of Arid Environments*, 74(1), 1-12.

539 He, F., Wang, K., Hannaway, D. B., & Li, X. (2017). Effects of precipitation and clipping intensity on 540 net primary productivity and composition of a Leymus chinensis temperate grassland steppe. PloS 541 one, 12(12), e0190450. 542 543 Hopping, K. A., Knapp, A. K., Dorji, T., & Klein, J. A. (2018). Warming and land use change 544 concurrently erode ecosystem services in Tibet. Global change biology, 24(11), 5534-5548. 545 546 Kerven, C., Steimann, B., Dear, C., & Ashley, L. (2012). Researching the future of pastoralism in 547 Central Asia's mountains: Examining development orthodoxies. Mountain Research and 548 Development, 32(3), 368-378. 549 550 Klein, J. A., Harte, J., & Zhao, X. Q. (2004). Experimental warming causes large and rapid species 551 loss, dampened by simulated grazing, on the Tibetan Plateau. Ecology Letters, 7(12), 1170-1179. 552 553 Klein, J. A., Harte, J., & Zhao, X. Q. (2007). Experimental warming, not grazing, decreases rangeland 554 quality on the Tibetan Plateau. Ecological Applications, 17(2), 541-557. 555 556 Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground 557 primary production. Science, 291(5503), 481-484. 558 559 Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland 560 plant communities in North America and South Africa. Ecology, 95(1), 98-109. 561 562 Kohli, Mayank et al. (2020), Grazing and climate change have site-dependent interactive effects on 563 vegetation in Asian montane rangelands, Dryad, Dataset, https://doi.org/10.5061/dryad.g4f4qrfnz 564 565 Liancourt, P., Spence, L. A., Boldgiv, B., Lkhagva, A., Helliker, B. R., Casper, B. B., & Petraitis, P. S. 566 (2012). Vulnerability of the northern Mongolian steppe to climate change: insights from flower 567 production and phenology. Ecology, 93(4), 815-824. 568 569 Liancourt, P., Spence, L. A., Song, D. S., Lkhagva, A., Sharkhuu, A., Boldgiv, B., ... & Casper, B. B. 570 (2013). Plant response to climate change varies with topography, interactions with neighbors, and 571 ecotype. Ecology, 94(2), 444-453. 572 573 Liang, M., & Gornish, E. S. (2019). Rainfall regulation of grazed grasslands. Proceedings of the 574 National Academy of Sciences, 116(48), 23887-23888. 575 576 Lkhagvadorj, D., Hauck, M., Dulamsuren, C., & Tsogtbaatar, J. (2013). Pastoral nomadism in the 577 forest-steppe of the Mongolian Altai under a changing economy and a warming climate. Journal of 578 Arid Environments, 88, 82-89. 579 580 Lu, X., Kelsey, K. C., Yan, Y., Sun, J., Wang, X., Cheng, G., & Neff, J. C. (2017). Effects of grazing on 581 ecosystem structure and function of alpine grasslands in Qinghai-Tibetan Plateau: a 582 synthesis. Ecosphere, 8(1), e01656. 583 584 Mijiddorj, T. N., Ahearn, A., Mishra, C., & Boldgiv, B. (2019). Gobi Herders' Decision-Making and Risk 585 Management under Changing Climate. Human Ecology, 47(5), 785-794. 586 587 Milchunas, D. G., Sala, O. E., & Lauenroth, W. (1988). A generalized model of the effects of grazing 588 by large herbivores on grassland community structure. The American Naturalist, 132(1), 87-106. 589 590 Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils 591 over a global range of environments: Ecological Archives M063-001. Ecological monographs, 63(4), 592 327-366. 593 594 Miller, D. J. (1990). Grasslands of the Tibetan Plateau. Rangelands Archives, 12(3), 159-163. 595 596 Mishra, C. (2001). High altitude survival: conflicts between pastoralism and wildlife in the Trans-597 Himalaya. 598

- Namgail, T., Bhatnagar, Y. V., Mishra, C., & Bagchi, S. (2007). Pastoral nomads of the Indian
 Changthang: Production system, landuse and socioeconomic changes. *Human Ecology*, 35(4), 497.
- 601
 602 Nippert, J. B., Knapp, A. K., & Briggs, J. M. (2006). Intra-annual rainfall variability and grassland
 603 productivity: can the past predict the future?. *Plant Ecology*, *184*(1), 65-74.
- Rana, B.S. 1994. Management plan of Kibber Wildlife Sanctuary. Department of Forest Farming and
 Conservation, Wildlife Wing, Himachal Pradesh. 81 pp.
- Reid, R. S., Gichohi, H., Said, M. Y., Nkedianye, D., Ogutu, J. O., Kshatriya, M., ... & Bagine, R.
 (2008). Fragmentation of a peri-urban savanna, Athi-Kaputiei Plains, Kenya. In *Fragmentation in semi-arid and arid landscapes* (pp. 195-224). Springer, Dordrecht.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R.
 (2017). Package 'nlme'. *Linear and Nonlinear Mixed Effects Models, version*, 3-1.
- Ronk, A., Liancourt, P., Boldgiv, B., Petraitis, P. S., & Casper, B. B. (2020). Greater effect of warming
 on community composition with increased precipitation and in moister landscape location. *Journal of Vegetation Science*, *31*(1), 3-13.
- Singh, R., Sharma, R. K., & Babu, S. (2015). Pastoralism in Transition: Livestock Abundance and
 Herd Composition in Spiti, Trans-Himalaya. *Human ecology*, *43*(6), 799-810.
- Spence, L. A., Liancourt, P., Boldgiv, B., Petraitis, P. S., & Casper, B. B. (2016). Short-term
 manipulation of precipitation in Mongolian steppe shows vegetation influenced more by timing than
 amount of rainfall. *Journal of vegetation science*, 27(2), 249-258.
- Verón, S. R., Paruelo, J. M., & Oesterheld, M. (2011). Grazing-induced losses of biodiversity affect
 the transpiration of an arid ecosystem. *Oecologia*, *165*(2), 501-510.
- Wang, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., ... & Cui, X. (2012). Effects of warming and
 grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, *93*(11),
 2365-2376.
- Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial
- 634 ecosystems to temperature and precipitation change: a meta-analysis of experimental 635 manipulation. *Global Change Biology*, *17*(2), 927-942.
- Ku, Z. X., Gong, T. L., & Li, J. Y. (2008). Decadal trend of climate in the Tibetan Plateau—regional
 temperature and precipitation. *Hydrological Processes: An International Journal*, 22(16), 3056-3065.
- Ku, Y., Knudby, A., Ho, H. C., Shen, Y., & Liu, Y. (2017). Warming over the Tibetan Plateau in the last
 55 years based on area-weighted average temperature. *Regional environmental change*, *17*(8), 23392347.
- Ku, W., Zhu, M., Zhang, Z., Ma, Z., Liu, H., Chen, L., ... & He, J. S. (2018). Experimentally simulating
 warmer and wetter climate additively improves rangeland quality on the Tibetan Plateau. *Journal of applied ecology*, *55*(3), 1486-1497.
- Yahdjian, L., & Sala, O. E. (2006). Vegetation structure constrains primary production response to
- 649 water availability in the Patagonian steppe. *Ecology*, 87(4), 952-962.
- 650

Table 1. Model summaries describing response of total live vegetation cover,

biomass, and species richness to climate and clipping treatments in A) Spiti, India
and B) Tost, Mongolia. A random intercept for block was included. Live cover was
log-transformed. Generalized linear models were used for species richness with a

655 poisson distribution. Full model summaries are provided in Tables S4-S5.

A)

Source		Total cover		Live biomass		Species richness	
	df	χ ²	Р	χ ²	Р	χ ²	Р
Year	1	11.829	2.7e-03	0.51	0.47	2.44	0.11
Climate	3	12.884	4.8e-03	11.68	8.5e-03	3.26	0.35
Clipping	1	25.725	3.9e-07	23.21	1.4e-06	0.01	0.89
Year: Climate	3	0.5472	0.9972	0.21	0.97	0.26	0.96
Year: Clipping	1	6.6965	0.0351	2.59	0.10	0.11	0.74
Climate: Clipping	3	19.801	1.9e-04	21.01	0.00	1.16	0.76
Year: Climate:	3			1.37	0.72	0.13	0.98
Clipping		1.767	0.9398				

B)

Source		Total cover		Live biomass		Species richness				
	df	χ^2	Р	χ^2	Р	χ^2	Р			
Year	1	183.52	<2.2e-16	68.02	< 2.2e-16	22.86	1.7e-06			
Climate	3	45.066	8.9e-10	14.75	2.1e-03	4.12	0.24			
Clipping	1	11.715	6.2e-04	21.76	3.0e-06	0.01	0.93			
Year: Climate	3	79.165	5.3e-15	5.82	0.12	5.1	0.16			
Year: Clipping	1	8.4857	0.0143	0.03	0.85	0.1	0.75			
Climate: Clipping	3	2.4728	0.4802	6.28	0.10	0.25	0.96			
Year: Climate:	3			4.01	0.26	0.21	0.98			
Clipping		18.329	5.4e-03							

Figure 1. Total live vegetation cover across three years in response to climate
treatments in plots where vegetation was not clipped (A,C) and clipped to ~3 cm
once every two weeks (B,D) in Spiti (top panels) and Tost (bottom panels). Each
point is average (±1 SEM) across blocks at site.



Figure 2. Average species richness (A, B) and live biomass (C, D) in response to

674 simulated climate and grazing treatments in Spiti (A, C) and Mongolia (B, D). Each

point is average (±1 SEM) across years (within block), across all blocks at each site.



point is average (11 OLIVI) across years (within block), across an br



677 678 679

Figure 3. Effect sizes (log ratio of cover in treatment and control plot) of climate (A,
B) and grazing (C,D) manipulations. Thus, plots A, B show differences between
climate treatment (e.g., warmed) and control plots for both grazed and ungrazed
conditions. Plots C, D show differences between grazed and ungrazed plots for each
of the different climate manipulations and the control. Each point is mean (±1 SEM)
across years in a block, across blocks at a site.





Figure 4. Vegetation cover (% area) of dominant plant functional types in response to climate and clipping treatments at Spiti, India. Each point is average (±1 SEM) across years within block and across all blocks at site.



Figure 5. Vegetation cover (% area) of dominant plant functional types in response
 to climate and clipping treatments at Tost, Mongolia. Each point is average (±1 SEM)
 across years within block and across all blocks at site.

