1 **Title:** Nonlinear response of community stability to ambient climate determines

2 response direction of community stability to warming and grazing

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Abstract: The impacts of human-driven environmental changes on the stability of natural grasslands have been assessed by comparing differences between manipulative warming and grazing plots and reference plots. However, little is known about whether or how ambient climate regulates the effects of manipulative treatments. A 36-year observational dataset shows that there is a nonlinear response of community stability to ambient climate. Manipulative warming and grazing decrease community stability with experiment duration through an increase in legume coverage and/or decrease in species asynchrony, due to exceeding the threshold of background annual mean air temperature with decreasing background annual mean air temperature through time during the 10-year experiment period. Moreover, the temperature sensitivity of community stability is more sensitive under the ambient treatment than under the manipulative treatments. Therefore, our study emphasizes the importance of the context dependency of the response of community stability to human-driven environmental changes.

INTRODUCTION

In recent years, the impacts of manipulative warming and grazing on the temporal stability (i.e., the inverse of variability over time) of aboveground net primary productivity (ANPP) (hereafter called as ANPP stability) have been assessed through experiments in the field by observing changes in plant composition and diversity (Post 2013; Zelikova *et al.* 2014; Hautier *et al.* 2015; Shi *et al.* 2016; Ma *et al.* 2017; Yang *et al.* 2017). However, these studies have focused on the differences between manipulated and reference plots. In fact, a key feature of ecological research is context dependence (Smith-Ramesh & Reynolds 2017; Blonder *et al.* 2018). Understanding the context dependence of responses to human-driven environmental changes provides new insights that can support generalization of the observed responses (Hanson & Walker 2020). To date, it remains unclear whether or how ambient climate regulates the effects of manipulative warming and grazing on ANPP stability in natural grasslands.

To date, there is no consensus about the effects of manipulative warming and grazing on ANPP stability (Post 2013; Zelikova *et al.* 2014; Shi *et al.* 2016; Ma *et al.* 2017), probably at least in part because studies derived from different ambient climates. For example, changes in species abundance over time in ambient treatments are often larger than the responses to manipulation in global change experiments (Langley *et al.* 2018), and background precipitation variability is likely a key factor influencing variability in results from various drought experiments (Hoover *et al.* 2018). Furthermore, a meta-analysis also showed that first flowering advanced more for long-term observations than for manipulative warming experiments (Wolkovich *et al.* 2012).

94   Together, these results suggest a hypothesis that ambient climate may control the

95   response direction, while manipulative treatments may determine the response

96   magnitude of the variables measured relative to the ambient treatment. Therefore, it is

97   critical that both the drivers and the response of ANPP stability are evaluated with

98   respect to context dependency.

99   To test the above hypothesis and its underlying mechanisms, we used two datasets,

100   one a 36-year long-term observational dataset from 1983 to 2018, and the other a 10-

101   year manipulative asymmetric warming and grazing experiment using infrared heaters

102   with moderate grazing from 2006 to 2015 in an alpine meadow on the Tibetan Plateau.

103   Our objectives were to determine (1) how ANPP stability responded to long-term

104   ambient climate variation; (2) whether effects of manipulative warming and grazing on

105   ANPP stability were regulated by the ambient climate; and (3) what main factors

106   affecting ANPP stability were for the manipulative treatments in the alpine meadow on

107   the Tibetan Plateau.

108

109   **METHODS**

110   **Study site**

111   The study site has been reported in a previous study (Zhao & Zhou 1999). The

112   experiment was conducted at the Haibei Alpine Meadow Ecosystem Research Station

113   (HBAMERS; 37°37′N, 101°12′E; 3200 m a.s.l.). The plant community at the study site

114   is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex*

115   *scabrirostris*, *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Blysmus*

sinocompressus and *Potentilla nivea*.

Mean annual precipitation at the station was 484 mm from 1983 to 2018, which was similar to the mean from 2006 to 2015 (476 mm) during the experimental period, but interannual differences were substantial, ranging from 382 mm in 2012 to 573 mm in 2014. Mean annual air temperature during the experimental period was −0.8 °C (ranging from −1.4 °C in 2014 to −0.4 °C in 2010), which was higher than the long-term mean from 1983 to 2018 (−1.1 °C).

Long-term observations

Aboveground net primary productivity (ANPP) has been monitored since 1983, and plants were clipped monthly from May to September to calculate community biomass, and peak biomass was regarded as yearly ANPP. The sampling method was reported in a previous study (Liu *et al.* 2018). In brief, 5 to 10 quadrats were randomly clipped within an area of 250 m × 230 m from 1983 to 2004. However, from 2005 to 2018 a systematic sampling method was used within an area of 150 m × 150 m. First, this area was divided into 25 equal blocks (30 m × 30 m) and 5 blocks on a diagonal were selected. Then, each of these 5 blocks was further divided into 25 cells (6 m × 6 m). Five quadrats (0.25 m × 0.25 m) were randomly clipped from a cell in each of the five blocks on the diagonal, and plant samples were oven-dried at 65 ºC to constant weight after clipping. The long-term meteorological data (air temperature and precipitation) were provided by HBAMERS.

Manipulative experiment design

We designed a two-factorial experiment with asymmetric warming and moderate grazing or clipping from 2006 to 2015 (Wang *et al.* 2012; Lv *et al.* 2020). The experiment had four treatments: a control with no warming and no grazing (C), no warming and grazing (G), warming and no grazing (W) and warming and grazing (WG). Each treatment had four replicates, making a total of 16 plots with diameters of 3 m each, which were completely randomly distributed within a 40 m × 40 m fenced block. Eight infrared heaters (1000 W, 240 V; Mor Electric Heating Association, Comstock Park, USA) were used for eight warming plots in hexagonal arrays 1.2 m above the vegetation canopy, with eight dummy arrays over the control plots. The heaters were controlled using a proportional-integral-derivative-outputs control system to ensure consistent warming between the heated and control plots (Kimball *et al.* 2008). Asymmetric warming was used, with 1.2 °C during daytime and 1.7 °C at night in summer and 1.5 °C during daytime and 2.0 °C at night in winter between the heated and corresponding control plots. Warming was applied throughout the year from 2006 to 2010 and only during the growing season from April to October from 2011 to 2015.

One (2006) or two (2007-2010) adult Tibetan sheep were fenced for approximately 1-2 h in each of the grazing plots, and grazing was conducted 2-3 times depending on the amount of aboveground biomass in July and August each year during the growing season. The total rate of forage use was about 50% from 2006 to 2010[15]. About 50% of the total litter biomass in the grazing plots was removed in winter by clipping from 2011 to 2015 (Lv *et al.* 2020) to simulate the rotational grazing system between summer and winter grasslands.

160   Soil temperature at a depth of 10 cm was monitored using type-K thermocouples

161   connected to a CR1000 datalogger (Campbell Scientific, Logan, U.S.A). Soil-water

162   content (SWC) at a depth of 10 cm was manually measured through a tube in the ground

163   that extended to a depth of 40 cm using a Model Diviner-2000 frequency domain

164   reflectometer (Sentek Pty Ltd., Australia) at 8:00, 14:00 and 20:00 each day during the

165   growing seasons, because the soils were frozen during the winter. SWC was expressed

166   as a volume percentage (%) or millimeters per 10 cm. Warming generally increased

167   annual mean soil temperature at a depth of 10 cm by 1.6 °C, while summer grazing only

168   increased mean annual soil temperature by 0.7 °C (Lv *et al.* 2020). Warming generally

169   decreased mean seasonal SWC at 10 cm by about 8% during the growing season, but

170   grazing had no significant effect on SWC (Lv *et al.* 2020).

171   Measurements of plant species composition and aboveground net primary

172   productivity (ANPP) have been described in a previous study (Wang *et al.* 2012). A 1

173   × 1 m quadrat was permanently fixed in the center of each plot for monitoring the

174   composition of plant species. The quadrats were divided into four hundred 5 cm × 5 cm

175   grids, and the mean height and mean cover of the vegetation canopy were measured

176   using the pin-point method. This process was also used outside the plots in non-grazed

177   and grazed fields, after which we clipped, dried, separated and weighed the vegetation

178   during the growing seasons and then defined a regression equation between

179   aboveground biomass, mean height and mean coverage for the community (Wang *et al.*

180   2012). Maximum aboveground biomass was used for ANPP in the plots without grazing.

181   Intake by sheep during each grazing period was estimated using the difference between

182 the biomass inside and outside the cage after each period of grazing. The cage (50 cm

183 × 50 cm) was set up before grazing. The sum of the maximum aboveground biomass

184 and total intake by sheep was used for ANPP in the grazing plots. All plant species in

185 each plot were recorded, and their coverages were calculated as the total coverage in

186 the 5 cm × 5 cm squares containing a species divided by the total number of squares in

187 each plot (400) (Wang *et al.* 2012). These species were then classified into four plant

188 functional groups (PFGs): grass, sedge, non-legume forb and legume.

189 **ANPP stability measurements**

190   In order to determine whether the individual effects of warming and grazing and

191 their interaction on ANPP stability depended on climate context or not, we used two

192 datasets in combination: a 36-year long-term observational dataset from 1983 to 2018

193 and a 10-year dataset from the manipulative asymmetric warming and grazing

194 experiment using infrared heaters and moderate grazing from 2006 to 2015. We

195 calculated ANPP stability over a minimum of 3 consecutive years. First, observational

196 periods of 3-36 consecutive years were defined based on the long-term dataset (i.e., 3-

197 year during 1983-1985, 4-year during 1983-1986, …, 36-year during 1983-2018), and

198 ANPP stability, annual mean air temperature (AT) and humidity index (HI) were

199 calculated for each period defined. Second, experimental periods of 3-10 consecutive

200 years were defined based on the 10-year manipulative dataset, and ANPP stability, mean

201 annual ANPP, standard deviation of ANPP, mean annual biodiversity (based on

202 principal component analysis), mean annual coverages of different PFGs, annual mean

203 AT and HI were calculated for each experimental period defined (i.e., 3-year during

204   2006-2008, …, 10-year during 2006-2015).

Data calculation

206   The temporal stabilities of ANPP in each plot were defined as μ/σ (Tilman 1999;

207   Hautier *et al.* 2015), where μ is the temporal mean of ANPP and σ is the standard

208   deviation of ANPP for a given period. It is a natural rule that stability (inverse of

209   coefficient of variation) is closely correlated with sample size. Hence, for further tests

210   (e.g., on the relationships between ANPP stability and background air temperature and

211   humidity index), we calculated the residual of ANPP stability after controlling for

212   sample size (i.e., observational duration or experimental duration) to eliminate the

213   effects of sample size.

214   The humidity index was calculated as the ratio of precipitation to potential

215   evapotranspiration (PET) (Liu *et al.* 2018). PET was based on air temperature and

216   relative humidity and was calculated as:

217    $$PET=0.0018\times(25+T_{air})^2\times(100-RH) \tag{1}$$

218   where T_{air} is monthly air temperature and RH is monthly relative humidity.

219   Species richness (S) in each plot was the number of species in a 1×1 m square, and

220   the Shannon-Wiener diversity index (H') and evenness (E) were calculated as:

221    $$H'=-\Sigma_{p_i}\times \ln(Pi) \tag{2}$$

222   and

223    $$E=H'/\ln(S) \tag{3}$$

224   where P_i is the relative coverage of species *i*.

225   An index of community-wide species asynchrony was calculated as (Loreau & De

226   Mazancourt 2008):

$$1-\varphi_x = 1 - \sigma^2 \big/ \big(\Sigma_{i=1}^{S}\sigma_i\big)^2 \qquad (4)$$

228   where φ_x is species synchrony, σ^2 is the interannual variance of community

229   coverage and σ_i is the interannual standard deviation of the coverage of species i in a

230   plot with S species during a specific period. This index would equal one if species

231   fluctuation were perfectly asynchronized and would equal zero if species fluctuation

232   were perfectly synchronized.

233   **Statistical analyses**

234   Aboveground net primary productivity (ANPP), ANPP stability, mean annual

235   ANPP (μ) and standard deviation of ANPP (σ) were logarithm 10 transformed to ensure

236   normality and homogeneity. To find the fitted model for the response of ANPP stability

237   to climate factors, seven equations were introduced with function lm() in R :

238     $$y \sim x1 + x2;$$

239     $$y \sim x1 * x2;$$

240     $$y \sim x1 + x2 + x1 * x2;$$

241     $$y \sim x1^2 + x2^2;$$

242     $$y \sim x1 + x2 + x1^2 + x2^2;$$

243     $$y \sim x1 * x2 + x1^2 + x2^2;$$

244     $$y \sim x1 + x2 + x1 * x2 + x1^2 + x2^2,$$

245   where y indicates ANPP stability under different observational durations, $x1$ and $x2$

246   indicate annual mean air temperature (AT) and annual mean humidity index (HI) based

247   on observational durations of 3-36 consecutive years from the long-term dataset.

248   Akaike's information criterion (AIC) was calculated for each regression model to detect

249   the fit of these models, and the model with the lowest AIC was selected to predict the

250   response of ANPP stability to background AT and HI. Modeled values (surface with

251   contour lines) are predictions from models fitted with observations spanning the

252   environmental space. Annual mean AT and HI were the average annual mean AT and

253   HI, respectively, during the corresponding observational period (3-36 years).

254   To detect the time series of annual mean AT and HI, variations in ANPP stability

255   with increasing observational duration, and relationships between ANPP stability and

256   climate factors (annual mean AT and HI), linear and segmented linear regression were

257   fitted in R. A segmented linear regression approach with one breakpoint was applied

258   based on observational durations of 3-36 consecutive years. The linear and segmented

259   linear regressions were fitted using the functions lm() and segmented(), respectively.

260   Akaike's information criterion (AIC) was calculated for the simple regression model

261   and the segmented linear regression model to detect the fitness of these two models,

262   and a regression model with ΔAIC >2 indicates a better model (Meng *et al.* 2018). The

263   davies.test() was introduced to detect the existence and significance (<0.05) of the

264   breakpoint, which indicates a significant difference in slopes before and after the

265   breakpoint.

266   We conducted a principal component analysis (PCA) of species richness, the

267   Shannon-Wiener diversity index and species evenness based on 10 consecutive

268   experimental years from 2006 to 2015, and only the first component (PC1) of the PCA

269   (hereafter called 'biodiversity') was introduced as a new variable into the subsequent

270 structural equation model (SEM) to avoid close correlations. This proxy of biodiversity

271 explained 91.31% of the variation in the data, and its eigenvalue (2.74) exceeded 1. The

272 Shannon-Wiener diversity index contributed the largest loading to the proxy of

273 biodiversity, followed by evenness and species richness (Fig. S4).

274 Relationships between ANPP stability and experimental duration, background

275 annual mean AT and HI through 3 to 10 consecutive experimental years, and interannual

276 variation of ANPP, coverage of PFGs and biodiversity based on 10 consecutive

277 experimental years from 2006 to 2015 were tested by function lm() in R. Then, function

278 sma() was used to detect slope heterogeneity among the 4 treatments, in which the H_0

279 was that there is a common slope among treatments.

280 In addition, simple linear regression was used to test the relationships between

281 abiotic and biotic ecological factors (soil temperature, soil water content, biodiversity,

282 species asynchrony and coverages of the PFGs) and ANPP stability using data from 10

283 consecutive experimental years from 2006 to 2015 (n=16). To identify the direct and

284 indirect effects of warming and grazing on ANPP stability, a SEM was constructed to

285 understand the relationships among warming, grazing, biodiversity, species asynchrony

286 and coverages of PFGs based on data from 10 consecutive experimental years from

287 2006 to 2015. We constructed an *a priori* conceptual SEM based on potential

288 relationships among the drivers of ANPP stability, in which mean annual ANPP (μ) and

289 the standard deviation of ANPP (σ) were treated as response variables, whereas

290 biodiversity, species asynchrony and coverages of PFGs were treated as explanatory

291 variables. The SEM should be simplified for the small sample size (n=16) (Jiang *et al.*

292 2020). Hence, we only considered those explanatory variables that had significant

293 relationships with response variables, and eliminated nonsignificant explanatory

294 variables until we attained the final model (Fig. 4). We used maximum-likelihood

295 estimation to obtain the path coefficients and the χ^2 goodness-of-fit test, normed fit

296 index (NFI), root mean square error of approximation and AIC to evaluate the model.

297 SEM analyses were conducted in SPSS Amos 22.0 (IBM Corporation, New York

298 USA), and all other analyses were conducted in R V.3.5.3 (R Foundation for Statistical

299 Computing, Vienna, Austria, 2013). We used the 'segmented' package to conduct the

300 segmented linear regression, the 'SMART' package to analyze slope heterogeneity, the

301 'nlme' package to construct the linear mixed models, the 'psych' package to conduct

302 the correlation test, and the 'vegan' package to conduct the PCA.

303

304 **RESULTS**

305 **Ambient climate and variability of ANPP stability**

306 We found that in general there was a period with a trend of increasing annual mean

307 air temperature (AT) from 1983 to 2005 (increase by 0.61 ℃ per decade) with a

308 decreasing trend in annual mean AT of -0.41 ℃ per decade from 2006-2018 (i.e.,

309 nonlinear variability through time with a breakpoint in the year 2006) (Fig. 1a and Table

310 S1 and S2). However, the annual mean humidity index (HI) linearly decreased through

311 time (Fig. 1b and Table S1 and S2). Accordingly, there was a nonlinear variability in

312 ANPP stability with experimental duration (Fig. S1a, Table S1 and S2), and annual

313 mean AT and HI co-determined ANPP stability (Fig. S1b and Table S3). Moreover,

314 when controlling for experimental duration and annual mean HI, we still found that

315 there was a nonlinear response of ANPP stability to background annual mean AT (Fig.

316 1c, Table S1 and S2). A similar nonlinear response was found to background annual

317 mean HI (Fig. 1d, Table S1 and S2). ANPP stability significantly increased by 0.21 $°C^{-1}$

318 with temperature increase when background annual mean AT was lower than the

319 breakpoint of -1.4 $°C$, whereas it decreased by -0.16 $°C^{-1}$ with temperature increase

320 when background annual mean AT was higher than the breakpoint (Fig. 1c and Table

321 S1 and S2). ANPP stability increased by 0.57 HI^{-1} with drying when annual mean HI

322 was higher than the breakpoint of 1.11, and decreased by 1.18 HI^{-1} with drying when

323 annual mean HI was lower than the breakpoint (Fig. 1d, Table S1 and S2). Therefore,

324 ANPP stability increased with warming and drying below the thresholds of annual mean

325 AT, and decreased with cooling and drying beyond the thresholds of background annual

326 mean AT in the alpine meadow.

327 **Responses of ANPP stability to manipulative warming and grazing**

328 We noticed that the background annual mean AT and HI during the manipulative

329 warming and grazing experiment from 2006 to 2015 were -0.75 $°C$ and 0.89 (Fig. 1a

330 and 1b), which were higher than the thresholds of annual mean AT and HI which

331 determine response direction of ANPP stability (Fig. 1c and 1d). Moreover, background

332 annual mean AT decreased by -0.84 $°C$ per decade through time (i.e., cooling ambient

333 climate), while background annual mean HI did not alter during the experimental period

334 (Fig. 1a and 1b, Table S2). Thus, as hypothesized, we found that ANPP stability

335 significantly decreased with experimental duration for all treatments (Fig. 2a and Table

S4). Moreover, when controlling for experimental duration and annual mean HI, we still found that there were negative relationships between ANPP stability and background annual mean AT during the experimental period, except for in the warming with no-grazing treatment (Fig. 2b and Table S4). These results supported the findings of analysis of the 36-year long-term observation when cooling in ambient air temperature (Fig. 1c and Fig. S1a). However, analysis showed no significant effects of background annual mean HI on ANPP stability (Fig. 2c and Table S4), suggesting that background annual mean AT was the primary controlling factor influencing ANPP stability due to the lack of significant variability in annual HI during the experimental period from 2006 to 2015 (Table S2). More importantly, there were significant differences in duration sensitivity (i.e., the slope of the regression equations between ANPP stability and experiment duration) (Fig. 2a and Table S4) and temperature sensitivity of ANPP stability (i.e., the slope of the regression equations between ANPP stability and background annual mean AT) between the manipulative treatments and their controls (Fig. 2b and Table S4). These results suggested that negative effects of warming and grazing on ANPP stability could vary with experiment duration and temperature increase due to greater sensitivity to ambient treatment than to manipulative treatments (Table S4). Therefore, together, our study suggested that background annual mean AT during the experiment period (i.e., higher than the threshold of background annual mean AT) could control the response direction of ANPP stability to manipulative warming and grazing, and that manipulative treatments could determine the response magnitude relative to ambient climate, which supported our

358 hypothesis.

Factors affecting ANPP stability

360 There were negative relationships between ANPP stability and soil temperature

361 (Fig. 3a) and variability of ANPP (σ) (Fig. 3b), but the relationships were positive

362 between ANPP stability and species asynchrony (Fig. 3c) and biodiversity (Fig. 3d).

363 Principal component analysis of species richness, diversity and evenness was

364 performed[4] and biodiversity mainly derived from species diversity rather than from

365 richness (Fig. S2). Moreover, warming decreased ANPP stability mainly through the

366 net effect of a direct positive effect of warming on ANPP (μ) and an indirect positive

367 effect of legume coverage on σ (Fig. 4). The negative effect of grazing on ANPP

368 stability was primarily through an indirect positive effect of species asynchrony on σ.

DISCUSSION

371 Our results indicated that warming in ambient climate increased ANPP stability

372 and cooling in ambient climate decreased it based on a 36-year long-term observation

373 (Fig. 1 and Fig. S1), suggesting that there was a positive relationship between ANPP

374 stability and ambient air temperature. The manipulative warming and grazing decreased

375 ANPP stability during the cooling in ambient air temperature of the experimental period

376 which further supported the finding of the long-term observation. Therefore, our results

377 supported our hypothesis that ambient temperature controlled the response direction of

378 ANPP stability to manipulative treatments in the alpine meadow.

379 We found that warming had direct positive effects on mean ANPP (μ) and indirect

18

380   positive effects on its variability (σ) through increased legume coverage (Fig. 4),

381   suggesting that decreased ANPP stability induced by warming through time could result

382   from a greater increase in σ relative to the increase in μ. On the one hand, warming

383   increased the optimal temperature for plant growth (Huang *et al.* 2019) and prolonged

384   the growing season (Li *et al.* 2016) and further increased ANPP (Wang *et al.* 2012) in

385   the alpine region. However, the increase in ANPP induced by warming decreased over

386   time (Fig. S3a) probably due to decreasing background AT during the experimental

387   period (Fig. 1a). Thus, the difference between warming and control treatments also

388   decreased with time because of the lack of significant change in ANPP of the control

389   treatment through time (Fig. S3a), which was also indicated by the lack of significant

390   difference in their slopes (Table S5). Different and even opposing trends in changes

391   among PFGs induced by warming could partly offset the positive effect of warming on

392   ANPP (Fig. S3b-3e), which was consistent with previous reports (Liu *et al.* 2018). On

393   the other hand, natural grasslands are usually deficient in nitrogen (N) needed for plant

394   production (LeBauer & Treseder 2008). In our study, warming greatly increased the

395   coverage of legumes (Fig. 4 and Fig. S3d), which would increase fixation of

396   atmospheric N in the community. Previous studies with experimental N addition

397   treatments (Zhang *et al.* 2016) and the manipulation of diversity containing legumes

398   (Spehn *et al.* 2005; Fargione *et al.* 2007) also found that increased N availability

399   decreased ANPP stability, probably because competition increased at higher

400   productivity, leading to more frequent competitive exclusions (Brooker & Kikvidze

401   2008). Meanwhile, warming in the alpine region typically shifts plant composition

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402 toward tall and deep-rooted grasses (Liu *et al.* 2018), which shades the forbs and

403 legumes and could further increase plant competition for light and N (Jiang *et al.* 2018;

404 Li *et al.* 2018), which in turn could further increase σ and thus reduce ANPP stability.

405   Consistent with previous studies (Hautier *et al.* 2015; Zhang *et al.* 2016; Ma *et al.*

406 2017; Craven *et al.* 2018), we also found a positive correlation between ANPP stability

407 and species asynchrony (Fig. 3c) because both warming and grazing reduced species

408 asynchrony which had a negative effect on σ (Fig. 4). A previous study reported that

409 species asynchrony promoted community stability by compensating growth between

410 species or plant functional groups (Song & Yu 2015). Our results thus indicated that

411 decreased species asynchrony, especially with grazing (Fig. 4), could reduce the

412 temporal complementarity between species or PFGs due to increases in plant

413 competition for resources.

414   Overall, there was a positive correlation between biodiversity and ANPP stability

415 (Fig. 3d) due to a decrease in biodiversity in all treatments (Fig. S3f and Table S5),

416 which supports the hypothesis that higher biodiversity leads to higher ANPP stability

417 (Hautier *et al.* 2015; Craven *et al.* 2018). In the structural equation model, biodiversity

418 had no direct or only indirect effects on μ or σ regardless of warming or grazing (Fig.

419 4). This suggests that biodiversity was not a main factor affecting ANPP stability under

420 warming conditions, which was consistent with a previous study (Ma *et al.* 2017), and

421 grazing in the alpine meadow. Our earlier study showed that decreased species richness

422 induced only by warming resulted from a decrease in rare species which had a small

423 contribution to ANPP (Wang *et al.* 2012), so changes in species diversity in experiments

424   that manipulate diversity in species-poor plant communities may have disproportionate

425   effects on ANPP and its stability compared with changes in species diversity in more

426   species-rich natural grasslands (Jiang *et al.* 2009).

427   In summary, we found that there was a nonlinear correlation between ANPP

428   stability and background annual mean AT and HI in a 36-year long-term observational

429   dataset, and a negative effect of manipulative warming and grazing on ANPP stability

430   during the 10-year long-term experiment when background annual mean AT exceeded

431   a given threshold. In particular, ambient climate-mediated effects on ANPP stability did

432   not depend either on manipulative warming or grazing, both of which caused shifts in

433   plant functional group composition or change in species asynchrony. In combination

434   with recent demonstrations that ambient climate is a major determinant of measured

435   ecological variables (e.g., species abundance, ANPP and phenology) (Wolkovich *et al.*

436   2012; Hoover *et al.* 2018; Langley *et al.* 2018), these findings suggest that there may

437   be a universal regulation of ambient climate (e.g., temperature or precipitation-

438   limitation) on variables measured in response to human-driven environmental changes.

439   In this case, increased background annual mean air temperature (higher than a threshold

440   of -1.4 ºC) with decreasing annual mean air temperature through time during the

441   experiment period led to decreased ANPP stability regardless of manipulative warming,

442   which was also supported by a previous study (Ma *et al.* 2017), and grazing in the alpine

443   region.

444

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456

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557

Figures

Figure 1 Climate and community stability based on 36-year observational data.
Interannual variation in annual mean air temperature (**a**) and humidity index (**b**) from 1983 to 2018, relationship between mean annual air temperature (AT) and residuals of ANPP stability after controlling for both observational duration and mean annual humidity index (HI) effects (**c**) and relationship between mean annual HI and residuals of ANPP stability after controlling for both observational duration and mean annual AT effects (**d**) based on 3-36 consecutive observational years. Selection of regression model and regression equations are shown in Table S1 and S2 (see Materials and Methods). Grey shaded areas in Fig. 1**c** and **d** show 95% confidence intervals. ANPP stability was logarithm 10 transformed before analysis.

Figure 2 Community stability based on 10-year manipulative experimental data.
Relationship between ANPP stability and experimental duration (**a**), relationship between residuals of ANPP stability after controlling for both experimental duration and mean annual humidity index (HI) effects and mean annual air temperature (AT) (**b**), and relationship between residuals of ANPP stability after controlling for both experimental duration and mean annual AT effects and mean annual HI based on 3-10 consecutive experimental years between 2006 and 2015. C: no-warming with no-grazing; G: no-warming with grazing; W: warming with no-grazing; and WG: warming with grazing. Regression equations and test of slope heterogeneity are shown in Table S4. Data are means ± standard errors. ANPP stability was logarithm 10 transformed before analysis.

580 **Figure 3 Relationships between biotic or abiotic factors and community stability.**

581 Relationships between soil temperature (**a**), standard deviation of aboveground net

582 primary productivity (ANPP) (**b**), species asynchrony (**c**), biodiversity (**d**) and ANPP

583 stability based on 10 manipulative experimental years from 2006 to 2015. Grey shaded

584 areas show 95% confidence intervals. Here, biodiversity was the first component of a

585 principal component analysis with species richness, evenness and diversity (see Fig.

586 S4). ANPP stability was logarithm 10 transformed before analysis.

587 **Figure 4 Direct and indirect treatment effects on the two components of**

588 **community stability.** A structural equation model was fitted to infer the direct and

589 indirect effects of variables measured on the temporal stability of aboveground net

590 primary productivity (ANPP) based on 10 consecutive years of a warming and grazing

591 experiment from 2006 to 2015. Boxes indicate measured variables entered in the model.

592 Numbers adjacent to arrows are standardized path coefficients, analogous to partial

593 regression weights and indicative of the effect size of the relationship. Single-headed

594 and double-headed arrows represent causal relationships and covarying variables,

595 respectively. R^2 represents the proportion of variance explained for each dependent

596 variable in the model. Nonsignificant pathways were removed from the model until we

597 attained this final model. μ: mean annual ANPP, σ: standard deviation of ANPP. μ and

598 σ were logarithm 10 transformed before analysis. *, $p < 0.05$; **, $p < 0.01$; ***, $p <$

599 0.001. $\chi^2 = 6.54$, $p = 0.48$; NFI = 0.96; RMSEA < 0.001; AIC = 46.54.
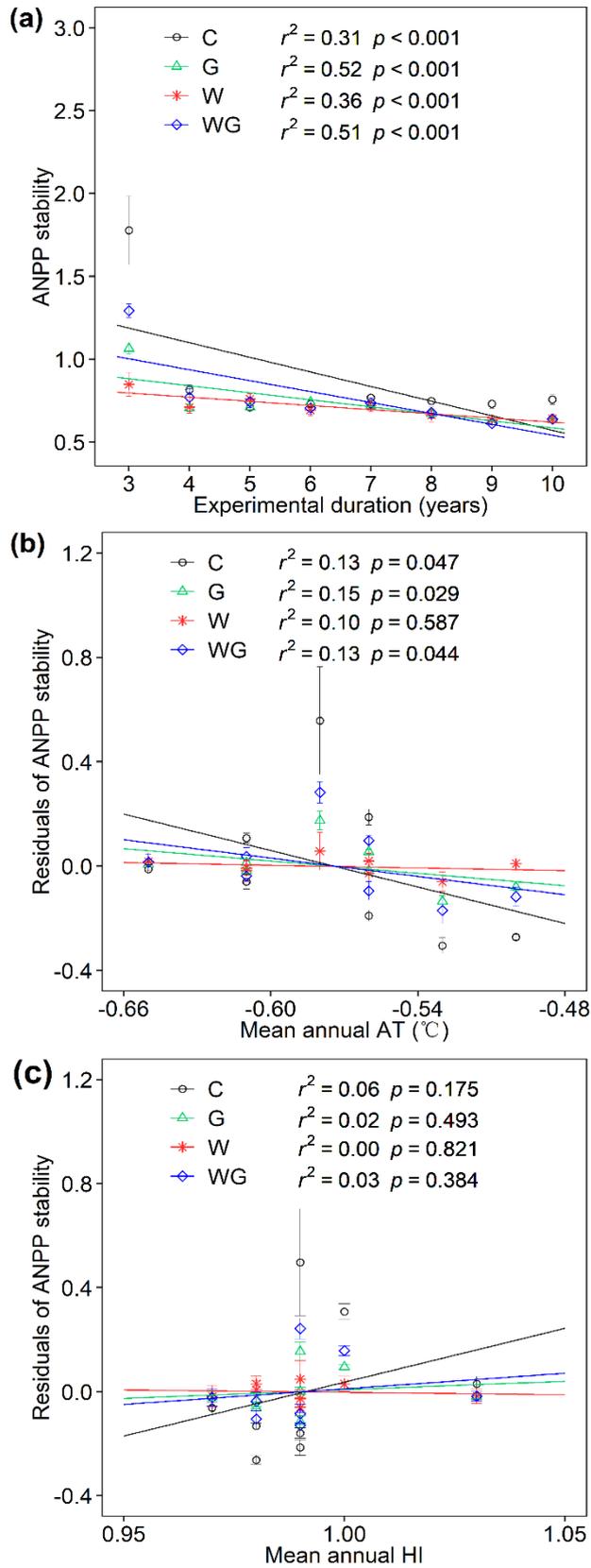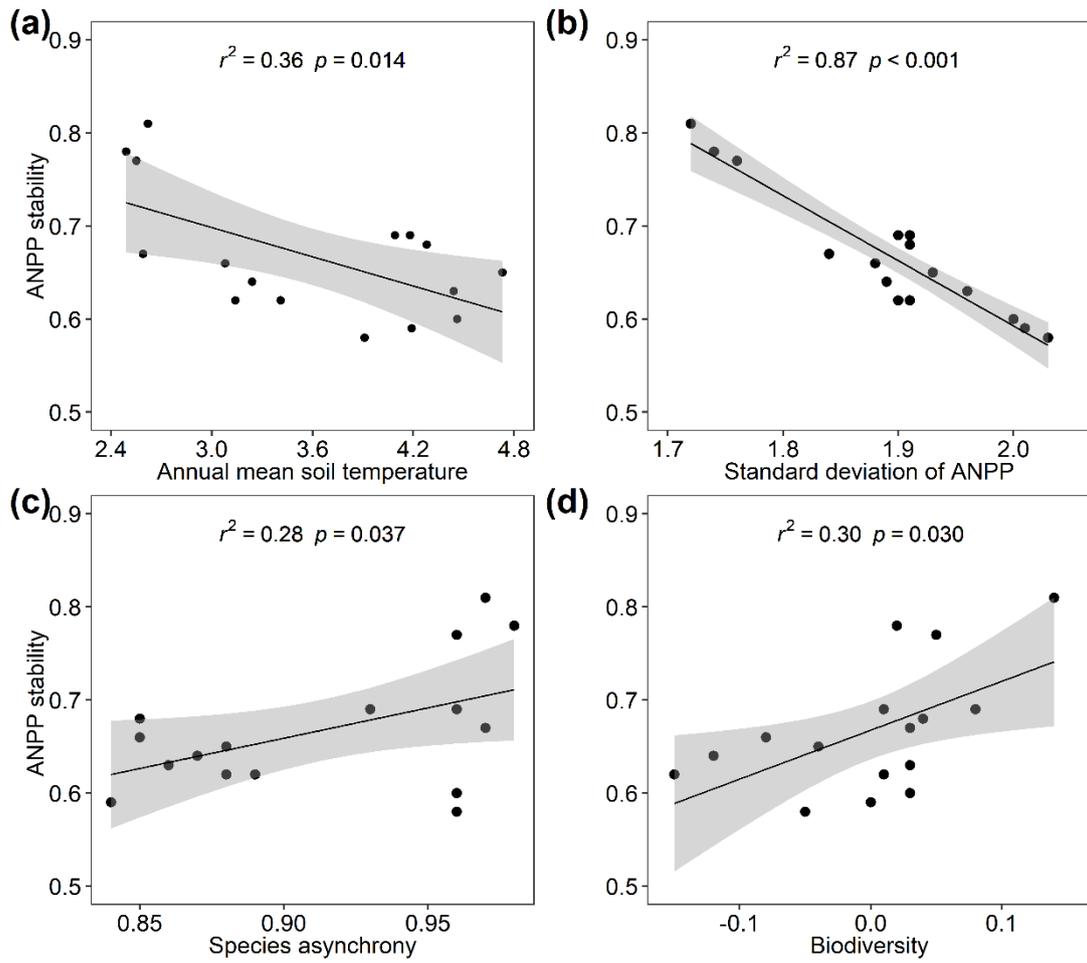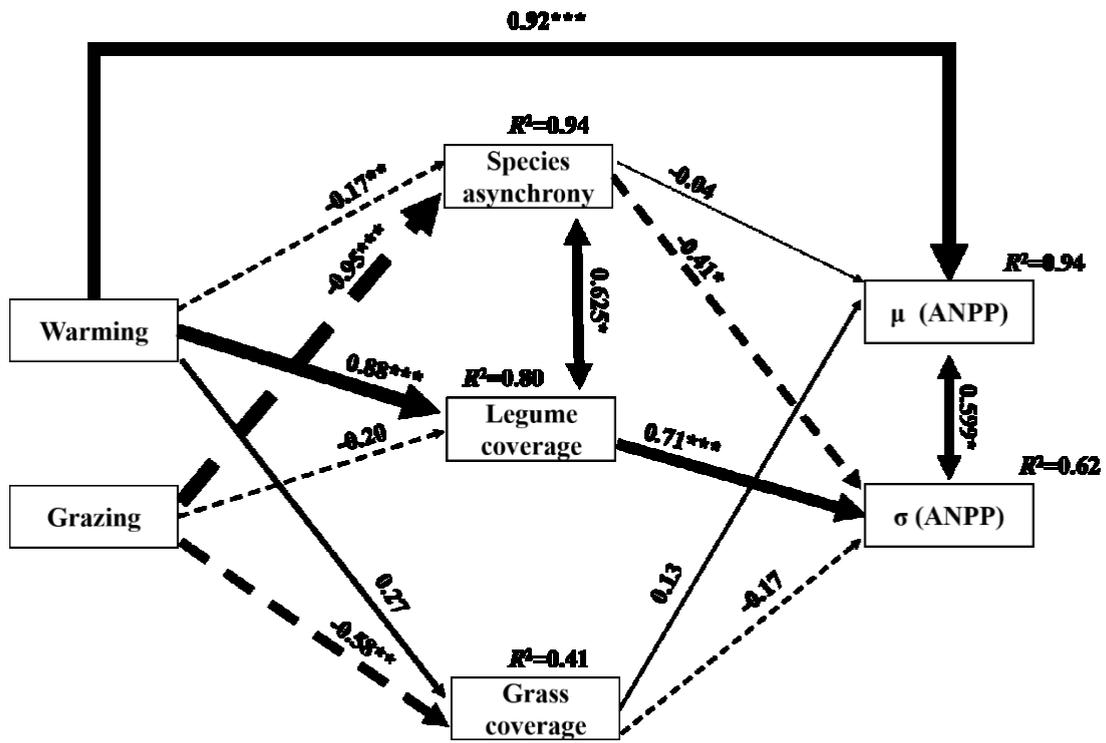
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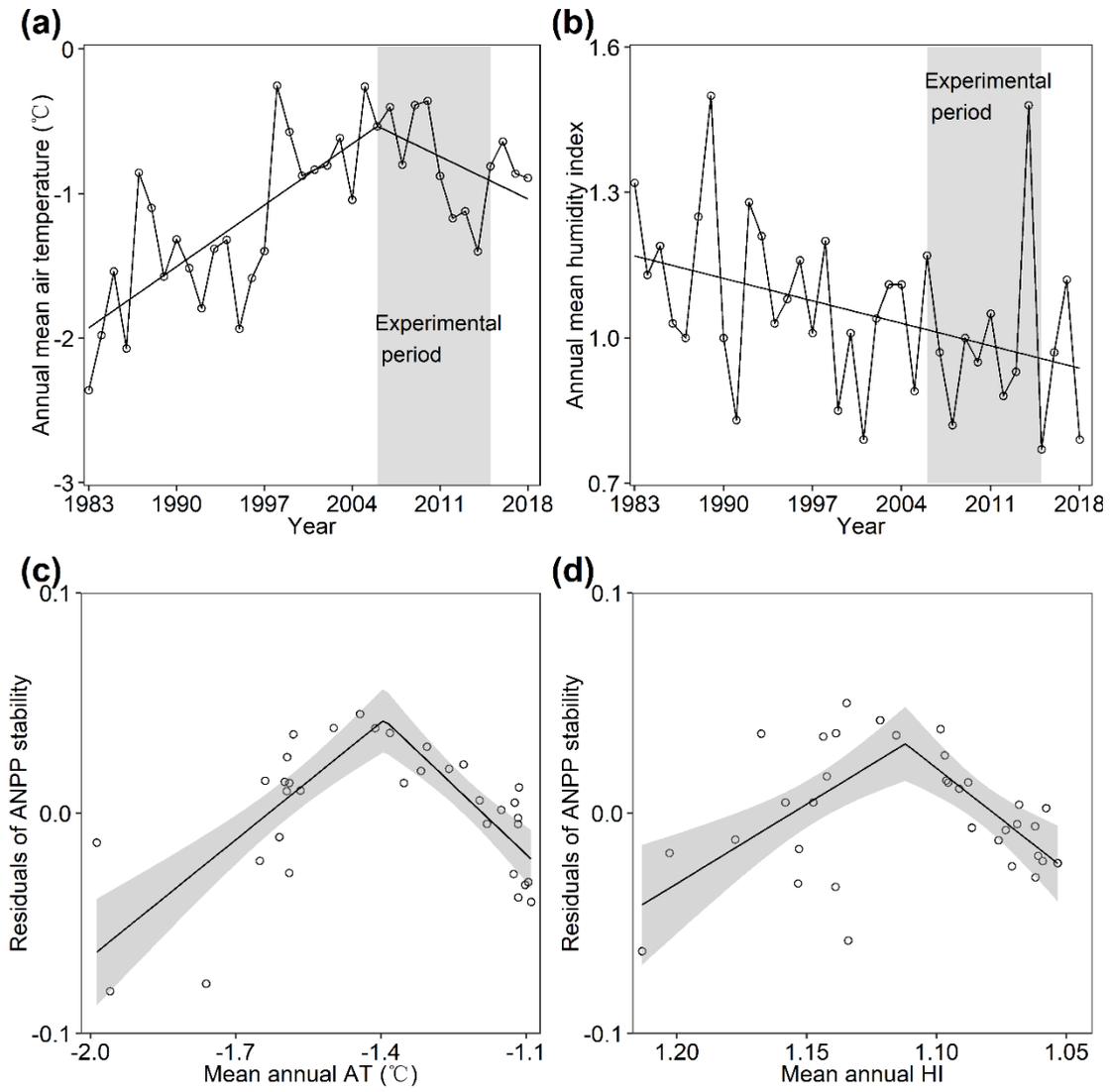
Figure 2

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