

Temperature leads to annual changes of plant community composition in alpine grasslands on the Qinghai-Tibetan Plateau

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Abstract In most grassland ecosystems, the effects of mean temperature increase on plant communities have been investigated; however, the effects of climate fluctuations on local plant community metrics are much less well understood. We conducted a nine-year survey in alpine meadow and alpine steppe to investigate the effects of inter-annual temperature and precipitation variation on plant community composition, species richness, and species diversity on the central Qinghai-Tibetan Plateau, China. We unexpectedly found that annual variability of growing season temperature, and not precipitation, is a driver of plant composition and species diversity in both habitats. Generally, increasing temperature had a negative effect on species diversity in meadow ($r^2 = 0.94$) and steppe ($r^2 = 0.95$). In the

meadow habitat, the proportion of grass decreased with increasing temperature and ultimately had positive impacts on the proportion of sedges. In steppe habitat, legumes increased and forbs decreased with the increase of growing season temperature; both legumes and forbs negatively affected proportion of grass and resulted in grass remaining stable under temperature change. Our results provide evidence that responses of functional group composition and species richness to temporal change of temperature are very different from those responses to mean temperature increase on the central Qinghai-Tibetan Plateau. In our results, temperature is a main regulator for annual variation of functional group composition and species richness, while soil water content is a dominant regulator for community responses in other experimental warming studies.

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Introduction

Climate warming is one of the dominant drivers of global change. Warming can alter relative species abundances, competition-interaction, and coexistence of species (Klein et al. 2008; Dieleman et al. 2015; Shi et al. 2015; Mokany et al. 2016; Dawson et al. 2011; Gruner et al. 2017) due to differential responses of species to changing temperatures (Ganjurjav et al. 2016). In grassland systems, warming-induced

reductions of biodiversity—which is largely regulated by community composition (Gruner et al. 2017)—may result in a decrease of ecosystem functions and services (Hautier et al. 2015).

Although researchers have primarily focused on investigating the effects of increasing average temperatures on plant community composition, climate change is also characterized by an increase of inter-annual variation in temperature (Thornton et al. 2014; Mulder et al. 2017). This climate variability also has significant effects on ecosystem functions and services (Seddon et al. 2016), because interactions can occur among environmental fluctuation, species richness, and ecosystem services (Oliver et al. 2015). For example, climate variability drives plant phenology (Adler et al. 2012) and species competition (Mulder et al. 2017), which can alter ecosystem functions, such as productivity, diversity, and carbon uptake capacity of ecosystem (Galvagno et al. 2013; del Río et al. 2017). Clearly, understanding how plant communities respond to changes in inter-annual variation rather than only to changes in average trends can provide critical perspective on the relationship between ecosystem function and environmental conditions.

The Qinghai-Tibetan Plateau is a highest region in the world and known as “the third pole” ranked after the Arctic and Antarctic (Qiu 2008). This harsh region is characterized by low temperature, low air pressure, and high solar radiation. The Qinghai-Tibetan Plateau is a main climate regulator of Asia and a headwater region of major Asian rivers, including the Yangtze River, the Yellow River, the Salween River, and the Mekong River (Gao et al. 2013; Liu et al. 2016). Large areas of the Qinghai-Tibetan Plateau are covered by grassland ecosystems, which are predominantly characterized by alpine meadow and alpine steppe. Since the 1960s, the plateau experienced significant warming and precipitation change (Chen et al. 2013). The grasslands on the plateau have also recently experienced widespread degradation due to climate change and human activities (Gao et al. 2013). These changes severely threaten ecosystem function and service, as well as the livelihood of herders.

On the Qinghai-Tibetan Plateau, both temperature and precipitation are the main driving forces for grassland community change (Liu et al. 2015). Researchers have experimentally manipulated warming to evaluate how temperature increases might affect grassland communities on the plateau (Klein et al. 2008; Li et al. 2011;

Zhang et al. 2015; Wang et al. 2012; Ganjurjav et al. 2016). Much of this work demonstrates that soil water is a dominant driver of community response to warming, where species with high water uptake ability may increase in grassland communities under future warming scenarios. For example, some studies concluded that increased temperatures resulted in a decrease of plant diversity (Klein et al. 2008; Zhang et al. 2015). Klein et al. (2008) explained that shallow-rooted plants demonstrated a greater decrease than deep-rooted plants for plant diversity decrease under warming. Li et al. (2011) found that the relative abundance of silverweed (*Potentilla anserina*), a tap-rooted plant with high water uptake ability, increased under warming in an alpine meadow. Finally, Ganjurjav et al. (2016) has shown that on alpine steppe, deep-rooted legumes increased after 3 years of experimental warming. Despite the clear relationship between plant communities and warming on the Qinghai-Tibetan Plateau, few researchers have formally investigated inter-annual climate variation on community composition and species richness or diversity.

We conducted a 9-year ground survey in alpine meadow and alpine steppe habitat on the central Qinghai-Tibetan Plateau, to evaluate the effects of annual variations of temperature and precipitation on grassland community. To avoid the effects of human activities on grasslands, we fenced the experimental areas and excluded grazing. We measured community data, including: biomass, height, species richness, functional group relative abundances, and species diversity. Our previous work highlighted that soil water content is a dominant regulator for community response to an increase in average temperature (Ganjurjav et al. 2016). Therefore, we expected annual variations of precipitation to be a main factor influencing inter-annual community dynamics and the abundance of tap-rooted legumes or the species with high water uptake capacity would show higher degree of dominance in warm years compared to that in cold years.

Materials and methods

Site description

The experimental sites are located in the Nagqu prefecture, Tibet Autonomous Region, China. The meadow site is located in Nagqu County (31.441° N, 92.017° E; 4460 m above sea level), and the steppe site is located in

Baingion County (31.389° N, 90.028° E; 4725 m above sea level). The annual mean temperatures in meadow and steppe between 2006 and 2014 were -0.3 and -0.7 °C, respectively. During the same time period, annual total precipitation is 506.4 and 428.1 mm, respectively, in meadow and steppe (Fig. 1). In the meadow site, the dominant species are sedges, including *Carex moorcroftii* Falc. ex Boott, *Kobresia humilis* (C. A. Mey. ex Trautv.) Sergiev, and *Kobresia pygmaea* C. B. Clarke; the dominant grasses are *Poa pratensis* L. and *Stipa purpurea* Griseb.; the dominant legumes are *As-tragalus membranaceus* (Fisch.) Bunge and *Oxytropis microphylla* (Pall.) DC.; and the dominant forbs are *Lancea tibetica* Hook. f. et Hsuan, *Potentilla bifurca* L., and *Potentilla tanacetifolia* Willd. ex Schlecht. In the steppe site, the dominant species are grasses, including *Festuca ovina* L., *P. pratensis* L., *Roegneria thordiana* (Oliv.) Keng, and *S. purpurea* Griseb.; the main sedge is *C. moorcroftii* Falc. ex Boott; the dominant legumes are *A. membranaceus* (Fisch.) Bunge and *O. microphylla* (Pall.) DC.; and the dominant forbs are *Leontopodium*

nanum (Hook. f. et Thoms.) Hand.-Mazz., *Potentilla saundersiana* Royle and *Saussurea japonica* (Thunb.) DC. The experimental areas were fenced 1 year before the experiment was initiated in 2006 to exclude large herbivores during the experimental period.

Data measurements

Climate data The climate data of the experimental regions (Nagqu County and Baingoin County) were obtained from the China Meteorological Data Sharing Service System of the China Meteorological Administration. To clarify the correlation of community composition with climate data, we calculated annual mean temperature and total precipitation using the data September of the previous year to August of the current year. We also calculated temperature and precipitation in each month using climate data from May to August to represent growing season mean temperature and growing season total precipitation. The temperature and precipitation

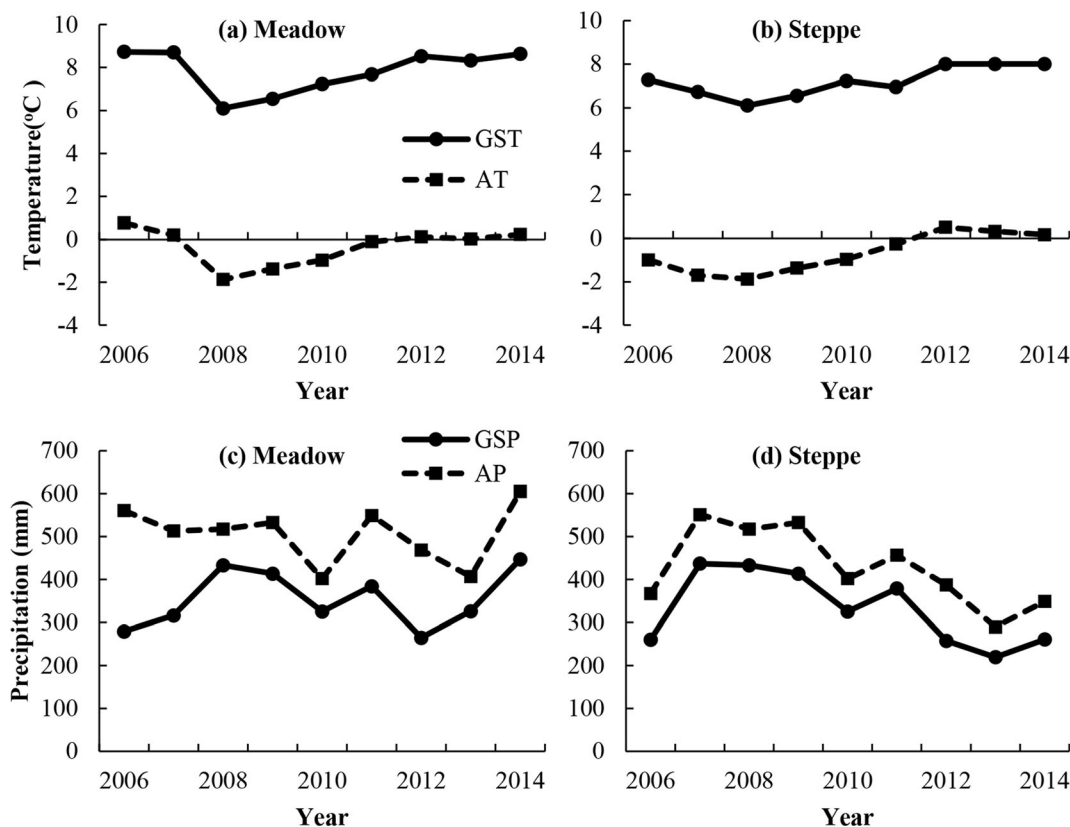


Fig. 1 Annual mean temperature (AT), growing season temperature (GST), annual total precipitation (AP), and growing season precipitation (GSP) changes from 2006 to 2014 in the central Qinghai-Tibetan Plateau

anomalies (the difference between climate value in given time and the value in long-term average) across different timescales (year, growing season, and month) were used to quantify the annual variations of climate at the site.

Community data We used a quadrat sampling method to investigate community characteristics in late July or early August in each year. We randomly selected five plots (10 m × 10 m) in each site and three subplots in each plot. In each subplot (0.5 m × 0.5 m), we used quadrat sampling method to record species number, species height, and species cover. We randomly selected five individuals of each species and measured their height and used the average height of the five individuals to estimate average species height in each quadrat. The average height of all species was used to estimate average community height. The relative height of each species was calculated by the proportion of species height to the sum of all species height. The total coverage and species coverage were measured visually. The relative coverage of each species was expressed by the proportion of species coverage to sum of all species coverage. We used the average value of relative height and coverage of each species to present the proportion of each species in the community. The proportion of each functional group (sedge, grass, legume, and forb) in the community was represented by the sum of each species in the same functional group. The species richness was represented by the total species number in the quadrat. The species diversity was represented by Shannon-Weiner index.

Data analysis

We wanted to identify contributions of environmental factors to community composition using permutational multivariate analysis of variance (PERMANOVA), a non-parametric method that operates on distance matrices, allowing for multivariate analysis. To maintain parsimony, we only included factors in our PERMANOVA models that demonstrated significant correlations with the community ordination scores. To do this, we investigated the fit of environmental factors including year, plot, growing season temperature, growing season precipitation, average precipitation, and average temperature onto the NMDS ordination. Significant factors were included in PERMANOVA models.

Data from the two sites (steppe and meadow) were modeled separately.

We investigated the fixed effects of environmental variables (and the random effects of plot) on species richness, the proportion of grass, the proportion of legumes, the proportion of sedges, and the proportion of forbs using a repeated measures ANOVA. Again, data were modeled separately for the two habitats and Bonferroni corrections were applied to account for multiple comparisons. These analyses were conducted in R version 3.1.1 (R Development Core Team 2012) using the MASS and vegan packages.

We used structural equation modeling (SEM, using IBM SPSS AMOS 24) to conduct path analysis on relationships among climate factors, community composition and species diversity. The indices we used to model selection including chi-squared discrepancy function, the Tucker-Lewis Index (TLI), and the root mean square error of approximation (RMSEA). A selected best model for path analysis was examined by a non-significant chi-square test ($p > 0.05$), TLI (> 0.95), and low RMSEA (< 0.05) (Hu and Bentler 1999).

Results

Changing trends of temperature and precipitation

The annual mean temperature and growing season temperature initially decreased and then increased from 2006 to 2014 at both sites (Fig. 1a, b). There were no consistent changing trends in annual total precipitation and growing season precipitation in the meadow site from 2006 to 2014 (Fig. 1c). At the steppe site, both annual total precipitation and growing season precipitation decreased significantly in the past decade (Fig. 1d).

The temperature and precipitation showed annual variation in both sites. In the meadow habitat, the annual mean temperatures from 2008 to 2010 were lower than the mean value across years (from 2006 to 2014) (Fig. 2a). In the steppe site, the annual mean temperatures from 2006 to 2010 were lower than the mean value across all years, while the mean temperatures from 2011 to 2014 were higher than average (Fig. 2b). The annual total precipitation and growing season precipitation had high variation in both meadow and steppe (Fig. 2).

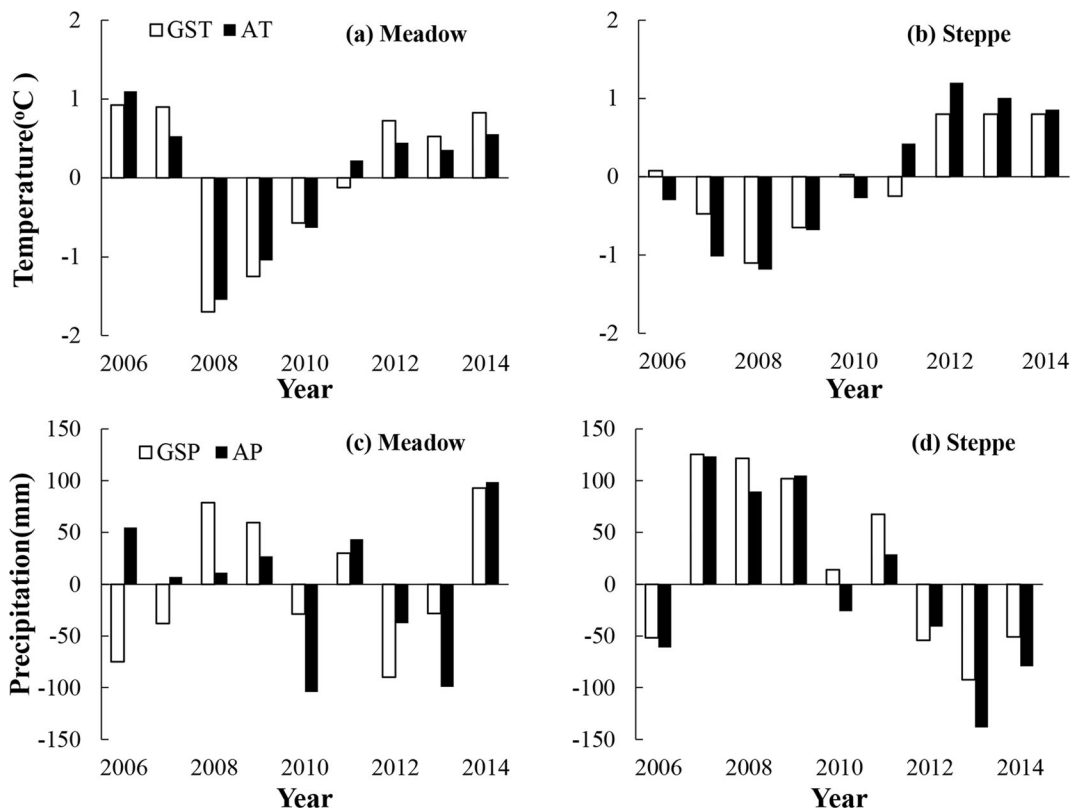


Fig. 2 Anomalies of annual temperature (AT), growing season temperature (GST), annual precipitation (AP), and growing season precipitation (GSP) from 2006 to 2014 in the central Qinghai-Tibetan Plateau

Effects of climate on community composition

Out of the seven factors tested for correlations with the community data, only year ($r^2 = 0.48, p < 0.001$), growing season temperature ($r^2 = 0.38, p < 0.001$), and average temperature ($r^2 = 0.23, p < 0.001$) demonstrated significant fit. These factors were included in the PERMANOVA models.

In the meadow habitat, year ($F = 41.17, p = 0.001$), average temperature ($F = 21.30, p = 0.001$), growing season temperature ($F = 5.84, p = 0.003$), the interaction between year and growing season temperature ($F = 5.04, p = 0.003$), the interaction between annual mean temperature and growing season temperature ($F = 7.38, p = 0.002$), and the interaction between all three factors ($F = 12.50, p = 0.001$) contributed to differences in community composition. In the steppe habitat, year ($F = 8.45, p = 0.001$), average temperature ($F = 7.17, p = 0.001$), growing season temperature ($F = 2.59, p = 0.03$), and the interaction between year and average temperature ($F = 3.28, p = 0.005$) contributed to differences in community composition (Tables 1 and 2).

Effects of climate on species richness

In the meadow habitat, species richness declined with average temperature ($F = 60.99, p < 0.001$, Fig. 3). There was also an interaction between average temperature and growing season temperature ($F = 27.93, p < 0.001$), where species richness had a negative relationship with growing season temperature at lower than average temperatures, but a generally positive relationship with growing season temperature at higher than average temperatures in the meadow site (Fig. 3, Table 3). In the steppe habitat, species richness declined with increasing temperature ($F = 36.71, p < 0.001$, Fig. 3, Table 4).

Effects of climate on functional groups

In the meadow habitat, the proportion of grass declined as year ($F = 19.03, p < 0.001$), average temperature ($F = 63.79, p < 0.001$), and growing season temperature ($F = 20.61, p < 0.001$) increased (Fig. 4a, e). There was also an interaction between average temperature and

Table 1 PERMANOVA output for explanatory variable effects on the meadow plant community.

Temp = average temperature, growing season temp = average temperature of growing season, DF = degree of freedom, mean sq. = mean square

	DF	Mean sq.	<i>F</i>	<i>R</i> ²	<i>p</i>
Year	1	2.02	41.17	0.34	0.001
Temp.	1	1.05	21.30	0.18	0.001
Growing season temp.	1	0.29	5.84	0.05	0.003
Year * temp.	1	0.04	0.82	0.01	0.500
Year * growing season temp.	1	0.25	5.04	0.04	0.003
Temp * growing season temp.	1	0.36	7.38	0.06	0.002
Year * temp * growing season temp.	1	0.61	12.50	0.10	0.001

growing season temperature ($F = 10.99$, $p = 0.002$), where the proportion of grass had a negative relationship with growing season temperature at lower than average temperatures, but demonstrated a positive relationship with growing season temperature at higher than average temperatures. In the meadow habitat, the proportion of legumes declined through time ($F = 14.70$, $p = 0.001$). The proportion of sedges appeared to increase as both year ($F = 29.69$, $p < 0.001$) and average temperature ($F = 44.28$, $p < 0.001$) increased (Fig. 4b, f). There was also an interaction between average temperature and growing season temperature ($F = 12.16$, $p = 0.001$), where the proportion of sedges had a positive relationship with growing season temperature at lower than average temperatures, but demonstrated a negative relationship with growing season temperature at higher than average temperatures. We found no effect of any explanatory variables on the proportion of forbs at the meadow site (Fig. 4d, h).

In the steppe habitat, the proportion of grass declined with increasing average temperature ($F = 15.97$, $p < 0.001$, Fig. 4a). Proportion of legumes increased with year ($F = 23.82$, $p < 0.001$). There was also an interaction between average temperature and growing season temperature ($F = 12.16$, $p = 0.001$), where the

proportion of legumes had a negative relationship with growing season temperature at lower than average temperatures, but demonstrated a positive relationship with growing season temperature at higher than average temperatures (Fig. 4c, g). There was no effect of any of the explanatory variables on proportion of sedges (Fig. 4b, f). Finally, there was a decline in the proportion of forbs with increasing annual temperature and growing season temperature ($F = 10.49$, $p = 0.004$, Fig. 4h).

Relationships among climate variation, community composition, and species diversity

In the meadow site, growing season temperature had both direct and indirect effects on species richness and diversity (Table 5). Growing season temperature had a positive direct effect on species diversity ($p < 0.05$). Grasses responded directly to variation of growing season temperature. Annual growing season temperature negatively impacted the proportion of grass ($p < 0.001$). The proportion of grass was negatively correlated to the proportion of sedge ($p < 0.001$), while positively correlated to proportion of species richness ($p < 0.05$). The proportion of sedge has negative effects on both species richness ($p < 0.05$) and diversity ($p < 0.001$). Thus,

Table 2 PERMANOVA output for explanatory variable effects on the steppe plant community.

Temp = average temperature, growing season temp = average temperature of growing season, DF = degree of freedom, mean sq. = mean square

	DF	Mean sq.	<i>F</i>	<i>R</i> ²	<i>p</i>
Year	1	0.39	8.45	0.18	0.001
Temp.	1	0.33	7.17	0.15	0.001
Growing season temp.	1	0.12	2.59	0.05	0.032
Year * temp.	1	0.15	3.28	0.07	0.005
Year * growing season temp.	1	0.08	1.83	0.04	0.125
Temp * growing season temp.	1	0.09	2.05	0.04	0.073
Year * temp * growing season temp.	1	0.08	1.70	0.04	0.146

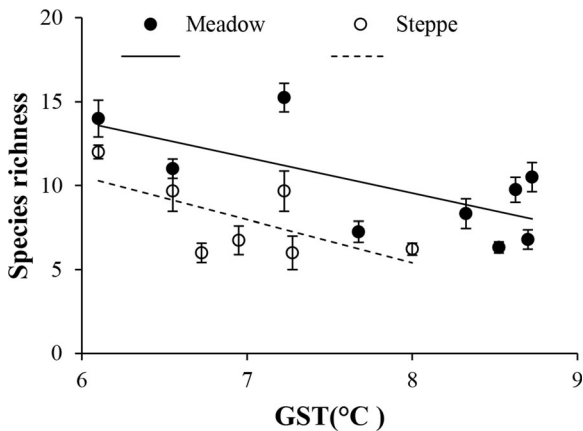


Fig. 3 Relationships between growing season temperature (GST) and species richness in meadow and steppe habitats. The solid circle and hollow circle indicate meadow and steppe, respectively; the solid line and dotted line indicate the relationships between each parameters in meadow and steppe habitat, respectively

growing season temperature had a negative indirect effect on species richness and diversity. Finally, the total effects of growing season temperature on species richness and diversity were negative (Table 5). The annual variations of growing season temperature, proportion of grass, and proportion of sedge accounted for 64 and 94% variation of species richness and species diversity, respectively, in the alpine meadow (Fig. 5a).

In steppe habitat, both direct and indirect effects of growing season temperature on species richness and diversity were negative (Table 5). Legumes and forbs were directly impacted by annual growing season temperature. The proportion of legumes ($p < 0.01$) was positively correlated to annual variation of growing season temperature, while the proportion of sedges was negatively correlated to variation of growing season temperature ($p < 0.001$). Both legumes and forbs demonstrated negative effects on grass. Legumes ($p < 0.01$) positively impacted species diversity while grass ($p < 0.001$) had a

negative effect on species diversity. Moreover, the variation of growing season temperature directly impacted species richness and diversity in steppe site (Fig. 5b). In steppe, 50 and 95% of the variation in species richness and diversity were explained by growing season temperature, legume, forb, and grass.

Table 5 Effects (path coefficient) of growing season temperature on species diversity in alpine meadow and alpine steppe habitat.

Discussion

Inter-annual variation of climate has a significant effect on plant community composition in grassland ecosystems. Based on 9-year survey in alpine meadow and alpine steppe, we found that growth season temperature rather than precipitation was the main regulator for plant community composition and species richness in meadow and steppe. These results do not support our hypothesis that precipitation should be more important to influence plant community composition.

Temperature rather than precipitation: the regulator of annual community variation

Temperature and precipitation are characterized as the main regulators for variations of species composition and richness in grasslands across spatial and temporal scales (Cleland et al. 2013; Jonas et al. 2015). Research highlights that species richness and composition are sensitive to annual precipitation in water-limited ecosystems, such as desert steppe (Xia et al. 2010). For example, Harrison et al. (2015) stated that a decrease of midwinter precipitation was a main driver of loss of species with low drought tolerance. In our study precipitation had no direct or indirect effects through time on

Table 3 ANOVA output for explanatory variable effects on species richness in the meadow habitat. Temp = average temperature, growing season temp = average temperature of growing season, DF = degree of freedom, mean sq. = mean square

	DF	Mean sq.	F	p
Year	1	9.56	3.82	0.061
Temp.	1	152.48	60.99	<0.001
Growing season temp.	1	1.17	0.47	0.501
Year * temp.	1	1.22	0.49	0.491
Year * growing season temp.	1	3.65	1.46	0.238
Temp * growing season temp.	1	69.84	27.93	<0.001
Year * temp * growing season temp.	1	80.31	32.12	<0.001

Table 4 ANOVA output for explanatory variable effects on species richness in the steppe habitat. Temp = average temperature, growing season temp = average temperature of growing season, DF = degree of freedom, mean sq. = mean square

	DF	Mean sq.	<i>F</i>	<i>p</i>
Year	1	12.48	5.49	0.295
Temp.	1	83.4	36.71	<0.001
Growing season temp.	1	16.07	7.01	0.150
Year * temp	1	6.97	3.07	0.950
Year * growing season temp.	1	0.81	0.36	0.556
Temp * growing season temp.	1	9.13	4.02	0.587
Year * temp * growing season temp.	1	8.66	3.81	0.650

plant community composition and species richness in meadow and steppe, two habitats with different water availabilities. These results indicate that the response of species richness and diversity to inter-annual climate in the central Qinghai-Tibetan Plateau is dissimilar to what has been found in other water-limited temperate grasslands. Some researchers confirmed that the cover of generally drought intolerant species is strongly correlated to precipitation (Harrison et al. 2015; Yan et al. 2015). Other than temperate grasslands, the species of our sites are mainly restricted by low temperature (Li et al. 2016). Therefore, plant composition may be a main factor that decides response of species richness and diversity to precipitation on the long time scale. For example, Wu et al. (2012) found that, across space, the variation of species richness was mainly explained by precipitation distribution in the Qinghai-Tibetan Plateau. Therefore, the driver of species richness and diversity variation across temporal scale and spatial scale are distinct from one another.

Currently, effects of inter-annual temperature variation on species richness and diversity are significant, but there is still a lack of rigorous formal studies of this dynamic, especially in the Qinghai-Tibetan Plateau. In central Northern America, Jonas et al. (2015) found that temperature acted as an important regulator for inter-annual variation of species richness and diversity. Moles et al. (2014) also summarized that plant community composition was strongly correlated to annual mean temperature rather than precipitation on the global scale. We found that inter-annual variation of plant community composition, species richness, and diversity are strongly correlated with growing season temperature (Fig. 5). The high variation in inter-annual temperature can increase productivity variation on the Qinghai-Tibetan Plateau (Ye et al. 2013), which significantly affects

ecosystem stability and animal husbandry. Species richness and diversity are one of the decisive factors for productivity, biodiversity, and ecosystem stability (Loreau and Mazancourt 2013). Therefore, species richness and diversity responses to inter-annual temperature variation are very important for ecosystem functions on the Qinghai-Tibetan Plateau. Our results provide the first record that growing season temperature is a main regulator for inter-annual variation of species richness and diversity in alpine meadow and steppe habitats on the central Qinghai-Tibetan Plateau. These findings suggest that inter-annual variation of species richness and diversity may increase under future climate change.

Inter-annual climate variation impacts on community composition

Although temperature has a negative impact on species richness and diversity in meadow and steppe habitats (Table 5), different species have different responses to inter-annual temperature changes (Fig. 5). Generally, warming is expected to increase biotic interactions and competition among species (Olsen and Klanderud 2014). Our results support this by highlighting that the changes of subordinate species, like grasses in the meadow and legumes and forbs in the steppe, which directly responded to temperature change, drove change of dominant species (Fig. 5).

In steppe habitat, we found that forbs decreased and legumes increased with temperature, but grasses remained relatively stable. Other researchers also found that warming results in an increase of legumes (Ganjurjav et al. 2016; Meng et al. 2017) and a decrease of forbs (Klein et al. 2008) on the Qinghai-Tibetan Plateau. As the dominant species, change of grasses under temperature variation is very important for steppe community stability and

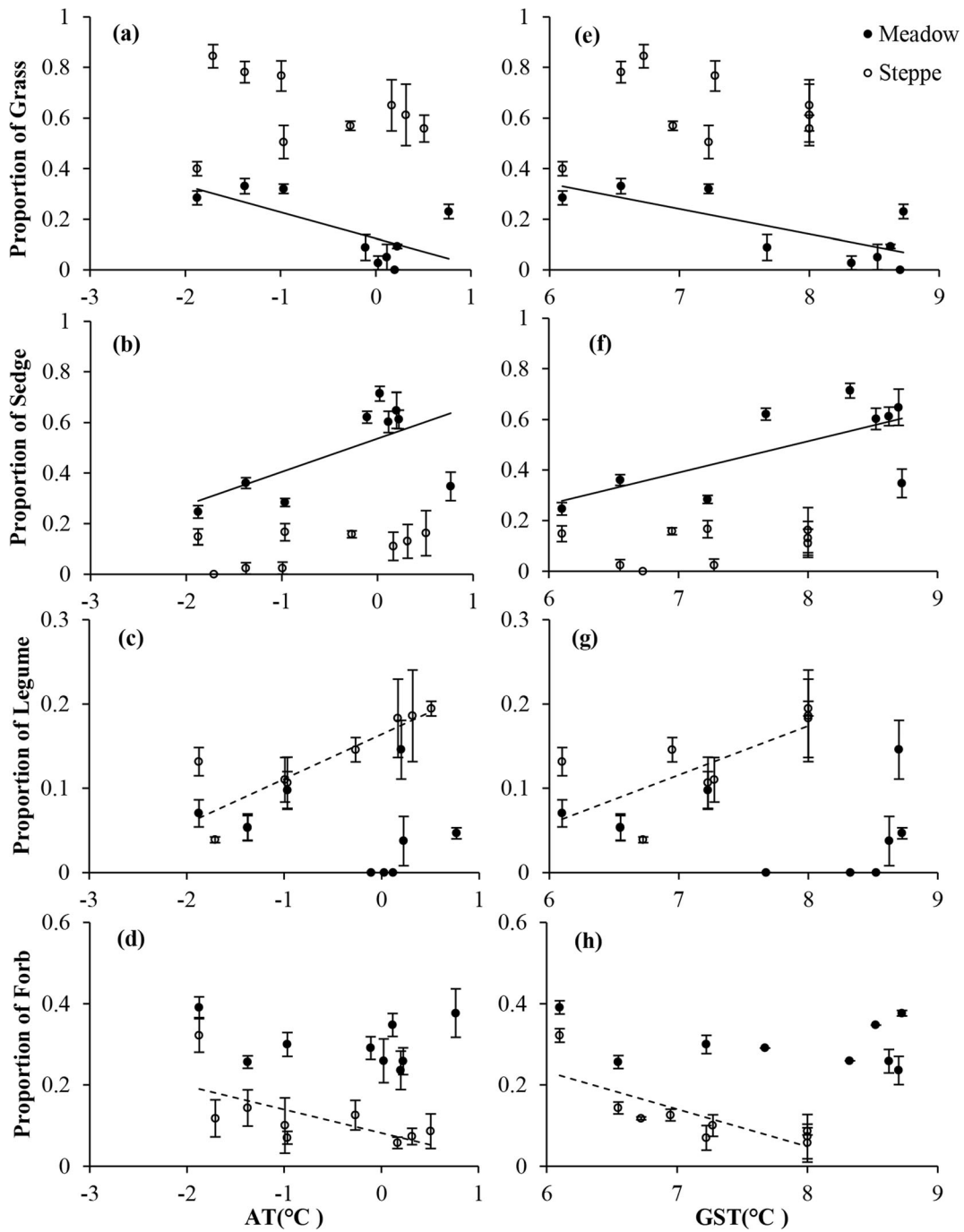


Fig. 4 Relationships among proportion of each functional group and annual temperature (AT) and growing season temperature (GST) in meadow and steppe from 2006 to 2014. The solid circle

and hollow circle indicate meadow and steppe respectively; the solid line and dotted line indicate the relationships between each parameter in meadow and steppe habitat, respectively

ecosystem productivity (Li et al. 2015; Yang et al. 2017). Therefore, our results highlight that grass stability is beneficial to ecosystem stability in steppe habitat and that increase of legumes may result in land degradation.

In meadow habitat, our findings showed that grasses decreased and sedges increased with temperature. But in other works in alpine meadow on the Qinghai-Tibetan Plateau, results were very different

Table 5 Standardized total, direct, and indirect effects of growing season temperature on species richness and diversity

Habitat	Richness and diversity	Total effect	Direct effect	Indirect effect
Meadow	Richness	-0.532	0	-0.532
	Diversity	-0.453	0.164	-0.617
Steppe	Richness	-0.608	-0.604	-0.004
	Diversity	-0.502	-0.121	-0.381

from each other as well as from our findings. For example, we previously found that warming had no significant effect on plant composition (Ganjurjav et al. 2016). Wang et al. (2012) showed that warming increased graminoids and legumes, while it decreased forbs and Peng et al. (2017) found that forbs and grasses increased and sedges decreased under warming. These studies showed a mean effect of short-term warming (2–5 year) on plant composition, but there exists significant annual variation (both magnitude and direction) in community response to warming (Wang et al. 2012; Ganjurjav et al. 2016; Peng et al. 2017). Our results just explain that growing season temperature is a driver of annual community variation on a long-term scale.

Climate change is characterized as increase of both mean temperature and inter-annual variation in temperature (Thornton et al. 2014; Mulder et al. 2017). However, our results showed that the responses of plant communities to inter-annual temperature change were very different from mean temperature increase.

Therefore, in a warmer future, the community responses to climate may be more complex than current estimation.

Conclusions

Our results highlight that inter-annual variation of growing season temperature, rather than precipitation, is a main regulator for yearly dynamics of species richness and diversity on the Qinghai-Tibetan Plateau. From our results, we conclude that species richness and diversity in warm years are lower than that in cold years in both meadow and steppe. In warm years, the decrease of grasses in meadow and forbs in steppe contribute to the reduction of species richness and diversity compared to cold years. In a warmer future, the species loss and diversity decrease may occur in both meadow and steppe on the Qinghai-Tibetan Plateau.

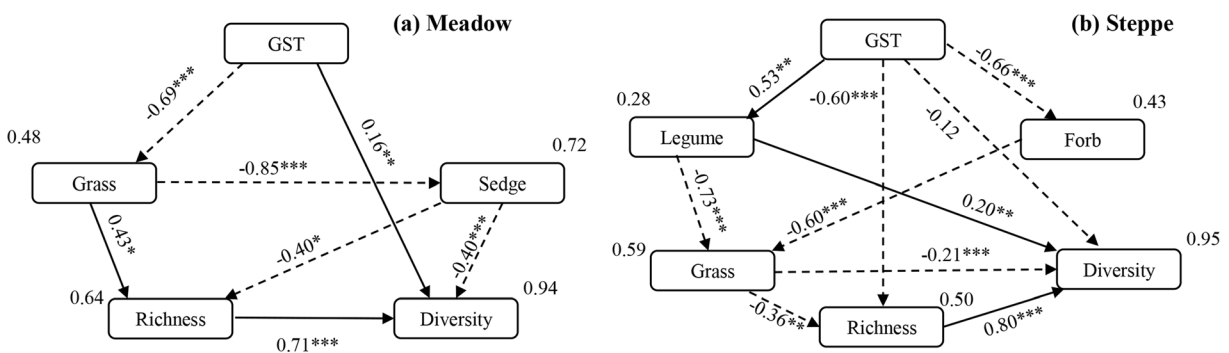


Fig. 5 Structural equation models for relationships among annual growing season temperature (GST), community composition, species richness, and species diversity in meadow (a chi-square = 3.060, $p = 0.382$, $LTI = 0.999$, $RMSEA = 0.024$) and steppe (b chi-

square = 4.235, $p = 0.516$, $LTI = 1.015$, $RMSEA < 0.001$). The solid line indicates positive correlation and the dotted line indicates negative correlation; “****” indicates $p < 0.001$, “***” indicates $p < 0.01$, and “**” indicates $p < 0.05$

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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