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Field-based observations of regional-scale, temporal variation in net primary production in Tibetan alpine grasslands

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Abstract

Net primary production (NPP) is a fundamental property of natural ecosystems. Temporal variation of NPP not only reflects how communities respond to environmental fluctuations, but it also has important implications for regional carbon assessment. Unfortunately, studies based on field measurements to directly address this issue in the extreme environment of alpine grasslands are rare. In this study, we measured aboveground NPP (ANPP) and species richness in 40 sites across the Tibetan alpine grasslands from 2006 to 2009 to investigate the regional pattern of temporal variation in ANPP and to quantify the effects of climate fluctuation and biodiversity on this variation. The results showed that, during the four-year period, the average ANPP varied 1.5-fold, from 83.9 to 125.7 $g\,m^{-2}$, with a mean coefficient of variation of temporal variation of 36.6 % across the 40 sites. Due to the regionally similar climatic fluctuations caused by South Asian monsoons, aboveground NPP exhibited synchronous temporal variation and consistent spatial patterns over the four-year period. Moreover, rainfall fluctuation had a more profound effect on the ANPP dynamics than temperature variation, which suggests that production in the Tibetan alpine grasslands is primarily driven by precipitation. Therefore, the Tibetan alpine grasslands are mainly constrained by water availability. Finally, we found that species richness negatively correlates with variation in aboveground NPP, which might provide evidence that diversity can stabilize community production in high-altitude grasslands.

1 Introduction

Net primary production (NPP) is the initial step and the most variable part of the carbon biogeochemical cycle (Huston and Wolverton, 2009; Zhao and Running, 2010). In natural ecosystems, NPP shows year-to-year dynamics that accord with environmental fluctuations such as climate variation, resource heterogeneity, and disturbance (Briggs and Knapp, 1995; Knapp and Smith, 2001; Muldavin et al., 2008). The characteristics of the plant community, particularly species richness and composition, also influence the temporal variability of NPP (Bai et al., 2004; Flynn et al., 2008; Roscher et al., 2011). Therefore, investigating and quantifying the interannual dynamics of NPP will provide insight into the processes by which plant communities respond to external variations (Knapp and Smith, 2001; Oesterheld et al., 2001; Weber et al., 2009) and improve predictions of the potential responses of ecosystem function to global change (Ma et al., 2010b; La Pierre et al., 2011).

Temporal dynamics of NPP may challenge the robustness of large-scale patterns of vegetation productivity that have been described based on one-time surveys. In ecological research, transect sampling designs can amass considerable data and are often used for large-scale field surveys (e.g., Williams and Rastetter, 1999; Yang et al., 2009; Ma et al., 2010a). However, temporal dynamics could potentially induce significant changes in the spatial patterns of NPP, thus reducing the validity of generalizing across years from one-year transect sampling. For example, highly productive communities may be susceptible to climatic fluctuations and thus experience lower production in response to drought or cold damage. Even if such incidents affect only a subset of sites during a one-year transect survey, biased conclusions might be reached. Hence, it is necessary to use methods, such as multi-year surveys, that incorporate temporal variation into investigations of large-scale patterns of ecosystem productivity.

Worldwide, grasslands are dominant ecosystems that cover nearly 25 % of the earth's land surface (Scurlock and Hall, 1998; Hui and Jackson, 2006). Moreover, grasslands are mainly distributed across arid and semi-arid regions and exhibit high sensitivity to environmental change as well as temporally dynamic production (Knapp et al., 2002; Shaw et al., 2002; Nippert et al., 2006). Thus, a number of studies of grasslands have investigated temporal variability in production and the factors that influence it (e.g., Briggs and Knapp, 1995; Niklaus et al., 2001; Oesterheld et al., 2001; Weber et al., 2009). However, most of these studies have been conducted in temperate and tropical grasslands; very few have focused on alpine grasslands where difficulties with accessibility can make re-visiting the sampling sites challenging.

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Alpine grasslands are the main vegetation types at high altitudes (Körner, 2003). Due to the extreme environmental conditions they face, especially low temperature, alpine grasslands are often considered more sensitive to environmental variation than other ecosystems because temperature should be primarily responsible for vegetation growth (Theurillat and Guisan, 2001; Cui and Graf, 2009; Gao et al., 2009). Nevertheless, studies on temporal variability in alpine grasslands remain very limited and are mostly based on modeling and remote sensing (e.g., Piao et al., 2006; Gao et al., 2009; Zhong et al., 2010) rather than directly observed data. Therefore, studies based on field surveys are necessary to improve our understanding of alpine grasslands.

The Tibetan Plateau is the highest and largest plateau in the world, and over 60 % of the area is covered by alpine grasslands (Zhang et al., 1988; Yang et al., 2009). Moreover, a large part of the plateau has not been strongly disturbed by many anthropogenic activities such as mineral exploration, industrial pollution, and farmland reclamation. Therefore, the Tibetan Plateau is an ideal location to investigate the climate-driven, year-to-year dynamics of alpine grasslands. In a previous study, we addressed large-scale patterns of plant richness and productivity across Chinese grasslands (Ma et al., 2010a). Here, we extend those results to investigate the interannual variability of the Tibetan alpine grasslands based on a four-year, 2006–2009, repeated survey of 40 sites across the plateau. We attempted to investigate whether (1) annual ANPP of alpine grasslands would vary in accordance with variation in climate like other grassland types, as alpine grasslands in Tibet are supposed to be more sensitive to climate change than elsewhere, (2) fluctuation in temperature would be more responsible for temporal variation in alpine vegetation growth than other factors, because high altitude plants are often considered to be temperature-constrained, and (3) sites with high species diversity would be less vulnerable to climate change.

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2 Materials and methods

2.1 Site description

This study was conducted in the alpine grasslands of the Tibetan Plateau during four separate expeditions that occurred in late July and early August from 2006 to 2009. Forty field sites along an approximately 1200 km long and 200 km wide transect in the central-eastern part of the plateau (latitudes from 30.31 to 37.28° N, longitudes from 90.80 to 101.48° E, and altitudes from 2925 to 5105 m a.s.l.) were selected for plant community surveys. All of the sites were selected by visual inspection of the vegetation with the aim to sample sites subjected to minimal grazing and other anthropogenic disturbances. For this purpose, sites were established either in deferred grazing areas or on winter pastures inside fences to minimize livestock-induced disturbances.

Across the sites and in the 50 yr from 1960 to 2009, mean annual air temperature (MAT) ranged from −5.8 to 2.6 °C, and mean annual precipitation (MAP) ranged from 218 to 604 mm. The vegetation represented natural zonal grassland and included two main vegetation types: alpine steppe (18 sites) and alpine meadow (22 sites). Alpine steppes are dominated by short, dense tussock grasses such as *Stipa purpurea* and *S. subsessiliflora*, whereas alpine meadows consist mainly of perennial tussock sedges such as *Kobresia pygmaea*, *K. humilis*, and *K. tibetica* (Zhang et al., 1988).

2.2 Data collection

We collected data on plant community biomass and species richness from all of the sites for each year from 2006 to 2009. The geographical coordinates, elevation and vegetation type of each site were recorded. Sampling sequence was consistent between years.

During the 2006 expedition, we positioned a 10 m × 10 m quadrat at each site and established three plots along the diagonal line of each quadrat. In each plot, one sampling square (1 m × 1 m) was randomly selected to measure aboveground plant community biomass and species richness. Previous studies have proved that this survey method is sufficient to represent the biomass and biodiversity of alpine grasslands on the Tibetan Plateau (Wang et al., 2006; Fan et al., 2009; Ma et al., 2010a). All of the vascular plant species in each sampling square were counted to obtain a measure of species richness (SR). After the community survey, we collected the aboveground biomass in all three squares. The harvested biomass was measured by first oven-drying the sample at 60 °C and then weighing it to the nearest 0.1 g. This late July/early August, aboveground biomass was used as a proxy for aboveground NPP (Sala et al., 2000). In the following three expeditions, from 2007 to 2009, we used the same protocol in the same 10 m × 10 m quadrats but located sampling squares away from the previous ones to eliminate the influences of the harvest.

Climate data used in this study included annual temperature (AT), annual precipitation (AP), growing season temperature (GST, from April to August) and growing season precipitation (GSP) from 2006 to 2009. Like in our previous articles, these data were calculated based on a cokriging method that uses a 2 km resolution digital elevation model (DEM) from monthly temperature and precipitation records (2006 to 2009) at 752 well-distributed climate stations across China as a covariate (Yang et al., 2008a; He et al., 2009).

2.3 Statistical analyses

The mean ANPP and species richness of three plots for each year were taken as site-level data and used in the analysis. For each site, the coefficient of variation (CV) of ANPP (abbreviated to CV_{ANPP}) over the four-year period was used to express the interannual variation in aboveground NPP, and the four-year average SR was taken as the measurement of species richness.

A repeated measures ANOVA was used to detect the effect of vegetation type on ANPP and to compare the differences across years in ANPP for the whole study region or within a vegetation type. To detect whether the spatial pattern of aboveground NPP changed over time, we performed type-II regressions (major axis regressions) and rank regressions (Culver et al., 2003; Stoch et al., 2009) between the ANPP of different years. We assumed that the rank of ANPP for each site would remain the same over all four years if the spatial pattern did not change. If both regression relationships were significant and slopes of the rank regression lines did not strongly differ from one, we could conclude that the temporal variation in the spatial pattern of ANPP was weak.

Further, analysis of covariance (ANCOVA) was conducted to test for temporal changes in the relationships between climate factors, species richness and aboveground net primary production across the study region. Ordinary least squares (OLS) regression was used to investigate the relationships between climatic fluctuations, species richness and temporal variation of aboveground NPP. Finally, general linear models (GLMs) were used to quantify effect strengths. Climate factors used in our analysis included AT, AP, GST, and GSP. The magnitudes of these factors were measured by their CVs, following the same method as for temporal variation of ANPP (abbreviated as CV_{AT}, CV_{AP}, CV_{GST}, and CV_{GSP}, respectively). Due to collinearity between AT/GST and AP/GSP, both ANCOVAs and GLMs were built using either the annual climate data or the growing season climate data.

All statistical analyses were performed using R 2.13.2 (2011). The tests of slope in rank regression were achieved using the R package *smatr*.

3 Results

3.1 General patterns of ANPP over the four study years

According to the observed climate data from 49 meteorological stations across the Tibetan alpine grasslands, the temporal fluctuations in temperature and precipitation during the study period represented more than 80 % of the ranges of the climate records over the past three decades, from 1980 to 2009 (Fig. 2). Thus, our study could well reflect recent past climate fluctuations.

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Across all 40 sites, the mean annual ANPP was 109.9, 91.2, 83.9, and 125.7 $g\,m^{-2}$ in 2006, 2007, 2008, and 2009, respectively, with corresponding standard deviations (SD) of 75.13, 54.32, 61.62, and 72.01. Interannual variation of aboveground NPP (CV_{ANPP}) over the four-year period for each site averaged 36.6 % with a range of 6.3 to 70.3 % (Table 2).

On the whole, alpine meadows had higher production (with mean ANPP of 133.3, 107.9, 100.8, and 138.5 $g\,m^{-2}$ from 2006 to 2009) than alpine steppes (78.3, 68.6, 60.9, and 108.4 $g\,m^{-2}$, $P < 0.01$). Across the study region, ANPP values in 2006 and 2009 were significantly higher than those in 2007 and 2008 ($P < 0.05$). This pattern was also evident for alpine meadows, but ANPP in 2009 was highest in alpine steppes (Table 2).

3.2 Temporal variation of the spatial pattern of ANPP

To detect temporal changes in the spatial pattern of aboveground NPP, a type-II regression was first used to examine the linear relationships between net primary production data from different years. The results indicated that annual ANPP from different years was highly correlated across years ($P < 0.001$, Table 3). Further, rank regression analysis produced significant regression lines between different years ($P < 0.001$, Fig. 3a–f); the slopes were close to one, and none of them differed significantly from one ($P > 0.1$, Fig. 3a–f).

These results demonstrate that the spatial sequence of annual ANPP was maintained during the period of 2006–2009. Despite climate fluctuations and changes in mean ANPP, the sites with relatively high productivity in one year maintained relatively high productivity in other years. Thus the spatial pattern in aboveground NPP variation between sites did not change over the four-year period.

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3.3 Influences of climatic fluctuation and species richness on the interannual variation of ANPP

ANCOVA revealed that, across the whole region, AP, GSP, and SR all had significant relationships with ANPP. AT and GST did not have significant relationships with ANPP, and neither interacted significantly with year (Table 4).

In the OLS regression analysis, CV_{AT}, CV_{AP}, and CV_{GSP} all showed significant positive relationships with CV_{ANPP} ($P < 0.05$, Fig. 4a and b), but the site-specific $SR_{average}$ over the four-year period was negatively correlated with CV_{ANPP} (Fig. 5).

Give that temperature was not a significant driver of aboveground NPP and that CV_{GST} was not significantly related to CV_{ANPP}, we entered rainfall factors into the GLMs first. The analysis indicated that both the model incorporating annual climate factors and species diversity (entered in sequences as CV_{AP}, CV_{AT}, and $SR_{average}$) and the one incorporating growing season climate factors and diversity (CV_{GSP}, CV_{GST}, and $SR_{average}$) were significant ($P < 0.001$) with multiple R^2 values of 53.3 % and 32.9 %, respectively (Table 5).

Both models showed that climate fluctuations had relatively high explanatory power for the interannual variation in ANPP. For the model with annual climate factors as independent variables, CV_{AP}, CV_{AT}, and their interaction were all significant and explained 15.0 %, 9.9 % and 6.1 % of the variation in ANPP, respectively. For the second model, CV_{GSP} explained 22.8 % of the total variation, whereas neither CV_{GST} nor the interaction of the two CVs were significant (Table 5).

Finally, average species richness significantly accounted for 9 % of the variation in the temporal CV of ANPP when CV_{AP} and CV_{AT} were fitted into the model. However, the influence of diversity was not significant when CV_{GSP} and CV_{GST} were entered as explanatory variables (Table 5).

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4 Discussion

Based on a transect survey performed using standard protocols over four consecutive years, we found that aboveground NPP in the Tibetan alpine grasslands had an interannual CV of 36.6 % on average with a range of 6.3–70.3 %. Over four years of measurements, we observed a synchronous temporal variation of ANPP across the 40 sites. Moreover, we found that temporal variation of ANPP increases with rising climatic fluctuations, and precipitation fluctuations had more obvious influence on the ANPP dynamics, suggesting such temporal dynamics of the Tibetan alpine grassland production are mainly driven by variations in rainfall. Finally, we found CV of ANPP decreases with increasing plant species richness, providing evidence that species richness played a role in stabilizing community production.

4.1 Are ecosystems at high altitudes vulnerable to climatic fluctuation?

Our research found that, across four years from 2006 to 2009, aboveground NPP in the Tibetan alpine grasslands varied significantly from 6.3 to 70.3 % at different sites with a mean of 36.6 %. Gao et al. (2009) reported a nearly equivalent result in that the interannual variation of NPP in Northern Tibetan grasslands from 1981 to 2004 was 35.2 % using MODIS remote sensing data. Considering the fact that climatic fluctuations during our study period could reflect climatic fluctuations in the past, this similarity suggests that our study could be comparable to the long-term study on the Tibetan Plateau.

Generally, high-altitude vegetation is believed to be much more vulnerable and sensitive to climate fluctuations than other ecosystems due to the extreme environments and severe stresses, especially cold temperature (Körner et al., 1997; Theurillat and Guisan, 2001; Cui and Graf, 2009). For instance, Sala et al. (2000) used models to point out that small changes in climate could induce large changes in community composition and biodiversity in alpine and arctic ecosystems. Studies in alpine ecosystems of the European Alps have shown obvious and unexpected changes in vegetation cover-

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age with climate change (Pauli et al., 2003; Cannone et al., 2007). Moreover, warming and biodiversity experiments in the Tibetan alpine grasslands have reported rapid and strong responses of aboveground biomass to artificial warming and species invasion (e.g., Zhang and Welker, 1996; Pfisterer et al., 2004).

Nevertheless, compared with studies in other types of grasslands, our results suggest that the Tibetan alpine grasslands are not more vulnerable than other grassland types in terms of community production. By collecting long-term production records from 118 grasslands sites across the world, Yang et al. (2008b) reported that at the global scale, the interannual CV of ANPP in grasslands had a range of 3.6–101.0 %, and CV of precipitation ranged between 3.0 to 40.0 %. Hu et al. (2007) reported that the temporal variation of ANPP in the Inner Mongolian temperate steppes had a mean of 32.8 % with a range of 13.2–80.8 %, and temporal variation of rainfall was approximately 7 to 28 %. Obviously, the temporal variability of aboveground net primary production in our study is similar to that found in previous studies, whereas environmental fluctuation, mainly expressed by variation in precipitation, is similar to or greater than that in prior studies.

Such relative stability in productivity in the face of environmental variation could arise from the large amount of underground biomass, the long preformation of buds, and the widespread asexual clonal propagation in alpine ecosystems (Diggle et al., 1998), all of which could dampen the impacts of environmental fluctuations on ecosystem production. Thus, despite possible changes in community composition or diversity, alpine grasslands do not exhibit a high amplitude response to climatic variation in terms of NPP.

4.2 Monsoon drives synchronous regional-scale dynamics of ANPP

Regardless of the variation in mean aboveground NPP over the four-year period, we found that temporal changes were synchronized among sites in the current study, as indicated by the significant correlations of per-site ANPP across the four-year period

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and the slope of rank regression lines not significantly different from 1. As mentioned above, these results reflect consistent spatial patterns of ANPP during the time series.

We speculate that this similarity in the spatial pattern of ANPP across sites over the four-year period could stem from parallel climatic regimes across the whole study region. In general, environmental factors, such as climate and soil properties, are the main drivers of plant community productivity at large spatial scales (Briggs and Knapp, 1995; Knapp and Smith, 2001; Jobbagy et al., 2002; Bai et al., 2004). Particularly, climatic factors are important drivers of net primary productivity in most biomes (Sala et al., 1988; Briggs and Knapp, 1995; Tian et al., 1998; Chapin et al., 2002; Jobbagy et al., 2002). For the Tibetan Plateau, the unique plateau monsoon system that derives from changes in atmospheric pressure and circulation direction with changes in season, governs the climate on the plateau surface, and characterizes a relatively independent climate zone (Qian and Zhu, 2001; Lu et al., 2004). During the summer season, the southwest monsoon from the Indian Ocean brings more than 80 % of the annual rainfall and forms a gradient of decreasing precipitation on the plateau from southeast to northwest (Lu et al., 2004; Tian et al., 2007). In winter, the high pressure on the Tibetan Plateau drives the flow of atmospheric currents toward its surroundings and induces a cold and dry climate (Loewen et al., 2007). This monsoon climate system would generate synchronous climatic fluctuations across the plateau. Records show that over the past several decades, temperature variations have been spatially consistent across the plateau (Lin and Zhao, 1996), and rainfall has also had similar temporal trends and fluctuations in most regions (Xu et al., 2008). In addition, by using climate data from 66 meteorological stations from 2006 to 2009 in our study region, we found that climate variables (AT, AP, GST and GSP) changed synchronously between stations over the years (Fig. 6). Thus, the similar dynamics of aboveground NPP during the four-year period at the different sites were most likely caused by a similar climate pattern.

Our analysis also answers the questions of whether temporal variation could induce significant changes in the spatial pattern of ANPP, and if it is necessary to make re-

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peated, multi-year investigations for all large-scale field studies. Our study showed that if the climatic regime does not change significantly during a study period, such as on the Tibetan Plateau, interpretations based on one-time transect surveys can be representative of the pattern of net primary production even if the productivity values might vary substantially between years. Conversely, one-year transect surveys might bias community production patterns if they are conducted across more than one climatic region, and interannual variation would have to be considered a potential caveat in the interpretations of the results.

4.3 Precipitation overrides temperature in shaping patterns of ANPP

At high altitudes, plant growth is often considered to be mainly limited by low growing season temperature (Körner, 2003), so consequently, fluctuation in temperature should be more important than precipitation in determining the temporal variation in alpine vegetation (Shaver and Jonasson, 1999; Wielgolaski and Karlsen, 2007). A number of experiments in alpine and arctic ecosystem also presented that warming, either due to nature or treatment, would induce significant increases in plant biomass (Schäppi, 1996; Schäppi and Körner, 1996; Van Wijk et al., 2004; Walker et al., 2006). However, our ANCOVA showed that on the Tibetan Plateau, temperature factors do not significantly predict ANPP, and variation in precipitation has higher explanatory power in GLMs than that of temperature, as CV_{GST} was not significant. Given the large spatial scale of this investigation and the relatively high explanatory power of rainfall in the GLMs, these results indicate that precipitation overrides temperature in driving patterns of aboveground NPP. A question naturally follows: why does temporal variation in rainfall, but not in temperature, play a key role in driving aboveground fluctuation in NPP?

It is well known that water is usually a limiting factor for plant growth in grasslands (Sala et al., 1988; Jobbagy et al., 2002; Huxman et al., 2004). Previous studies have demonstrated that the productivity of alpine grasslands is highly responsive to rainfall (Ram et al., 1989; Walker et al., 1994; Song et al., 2008; Yang et al., 2009), indicating

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the importance of water condition in constraining alpine vegetation production. Particularly, the quantity of rainfall during the growing season greatly influences grassland production (Lauenroth and Sala, 1992; Yang et al., 1998; Nippert et al., 2006; La Pierre et al., 2011). In addition, many alpine species are well adapted to extremely low temperatures and large diurnal temperature ranges (Zhang et al., 1988; Walker et al., 1994; Elmendorf et al., 2012). As several studies have shown, alpine plants are often characterized by low optimal temperature, high temperature adaption, and strong resilience to short-term temperature fluctuations (Billings and Mooney, 1968; Chapin, 1983; Billings, 1987; Beck, 1994; Theurillat and Guisan, 2001; Erschbamer et al., 2009). Hence, as our analysis showed, production in Tibetan alpine grassland ecosystems would be quite constrained by rainfall, especially growing season precipitation, and the temporal variation in precipitation surpasses that of temperature in determining the spatial patterns of NPP. In view of the fact that rainfall on the plateau surface is mainly brought by the warm and humid monsoon from South Asia, we could conclude that the interannual variation in monsoon activity drives the temporal dynamics of community production in the Tibetan alpine grasslands.

Recently, Geng et al. (2012) reported that the large-scale patterns of soil respiration in the Tibetan alpine grasslands are best explained by belowground biomass and soil moisture but not temperature, which affects respiration indirectly by influencing belowground biomass and soil moisture. Considering that decomposition processes are very sensitive to temperature, the results of Geng et al. (2012), together with ours, suggest that differing with other alpine ecosystems, Tibetan alpine grassland ecosystems might be more constrained by water conditions than temperature.

4.4 Community stability tends to increase with species richness on the Tibetan Plateau

In addition to fluctuations in abiotic conditions, we also found that biodiversity can be associated with the interannual variation of production in alpine grasslands. In previous research, we observed that mean ANPP was positively affected by species richness

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in these high-altitude grasslands of the Tibetan Plateau (Ma et al., 2010). Here, we found a negative correlation between average species richness and CV_{ANPP}, and after considering annual climatic fluctuations, the effects of SR were still significant in the first GLM. This contrasts with some experimental studies in which diversity-dependent production decreases the stability of ecosystem functioning (e.g., Pfisterer and Schmid, 2002). To some extent, these results provide field evidence for a positive diversity–stability relationship as has been reported in most studies (e.g., Bai et al., 2004; Tilman et al., 2006; Flynn et al., 2008; Roscher et al., 2011).

Both local processes, due to asynchronous population responses (Tilman et al., 2006; Loreau and de Mazancourt, 2008), and regional processes, such as species immigration (Loreau et al., 2003; Staddon et al., 2010), could contribute to the species richness–stability relationship at a large scale. However, considering that the dominant species in alpine ecosystems are perennial (Zhang et al., 1988; Godfree et al., 2004), processes necessary for the spatial insurance effect, such as species dispersal and turnover, would be very slow and unlikely to be observed in a four-year study. Thus, local processes are probably the main cause of the stabilizing effect of species richness on community productivity in our study.

Furthermore, the R^2 of the linear regression between species richness and CV_{ANPP} was relatively low, and species richness did not have a significant effect in the GLM that used growing season climate data. These results suggest that diversity does not strongly influence community stability. Several studies have reported that in addition to richness, species composition and evenness would also affect community stability (Hector et al., 2011; Sasaki and Lauenroth, 2011). Therefore, it is necessary to choose other aspects of biodiversity to effectively study the diversity–stability relationship at large spatial scales.

4.5 Limitations of the current study

In the present study, transect surveys over four consecutive years were conducted to investigate the interannual variation in community production in the Tibetan alpine grass-

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lands. The results show that, due to the parallel climatic regimes across the plateau, these alpine grasslands are not more vulnerable than other grassland types in terms of community production. Tibetan alpine grasslands represent synchronous, regional-scale dynamics of ANPP. However, although climate variations during our study period could represent more than 80 % of the climate fluctuations observed over the past 30 yr, our study period might still be too short to explore some characteristics of the temporal variations, such as the spatial insurance effect, in the alpine grasslands. Additionally, although the plateau monsoon could generate parallel climate patterns in different years, extreme climate events may occur and induce deviations from the synchronous pattern. Therefore, the magnitude of uncertainty in the studies based on a one-year transect surveys is still unclear.

Another potential limitation in our study could stem from excluding the influences of grazing incompletely. Due to herbivorous behavior has major effect on the measurement of ANPP, we located our survey sites either in deferred grazing areas, or on the winter pastures which are free from grazing in growing seasons. However, even if no domestic animals exist, there are still wild animals such as Mongolian gazelle (*Procapra gutturosa*) and Tibetan antelope (*Pantholops hodgsonii*) that appear in a number of study sites. Because of the absence of the data, it is very difficult to evaluate the intensity of herbivory rising from wild animals. To what extent grazing may have the impact on the interannual variation of ANPP in our study region is still difficult to quantify.

Further, studies are needed to explore the temporal dynamics of the Tibetan alpine grasslands, in particular, the effect of biodiversity on community stability in extreme environments. Site-specific, long-term observations along environmental gradients would test these results. Moreover, combining multiple approaches, such as field surveys, ecological modeling, and remote sensing, will likely be necessary to fully understand the temporal dynamics in the Tibetan alpine grasslands.

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5 Conclusions

Based on a transect survey that used the same protocols for four consecutive years, we found that the average ANPP in Tibetan alpine grasslands varied 1.5-fold with a mean temporal CV of 36.6 % across the 40 sites. Compared with other studies, the magnitude of temporal variation in the alpine grasslands is not larger than those in other grassland types, suggesting that alpine grasslands are not more vulnerable to climate fluctuations than other grasslands. Despite the variations in the average value, aboveground NPP suggested synchronous temporal variation and consistent spatial patterns over the four-year period because the plateau monsoon system generates parallel climate regimes on the plateau over time. Moreover, we found that rainfall fluctuation had a more profound effect on community production dynamics than temperature variation; variations in monsoon activity drive the interannual variations of aboveground NPP in the Tibetan grasslands. These results will improve our understanding of water deficiency in the Tibetan alpine grasslands. Meanwhile, high species richness significantly reduced variations in aboveground NPP, supporting that diversity can stabilize community production in high-altitude grasslands.

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Table 1. Description of the study region. Mean annual temperature (MAT), mean annual precipitation (MAP), mean growing season temperature (MGST) and mean growing season precipitation (MGSP) of the sampling sites are shown.

Parameters	Value/Range
No. of sites	40
Longitude (° E)	90.80–101.48
Latitude (° N)	30.31–37.28
Altitude (m)	2925–5105
MAT (°C)	−5.8–2.6
MGST (°C)	1.5–11
MAP ($mm\,yr^{-1}$)	218–604
MGSP ($mm\,yr^{-1}$)	133–402

Table 2. Aboveground net primary production (ANPP, $g\,m^{-2}$) and species richness in the Tibetan grasslands from 2006–2009. Mean, standard deviation (SD) and range of observations are shown. Different letters indicate statistically significant differences at $P < 0.05$. Temporal variations were calculated as the coefficient of variation of ANPP over the four-year period.

	2006	2007	2008	2009	Temporal variation
ANPP ($g\,m^{-2}$)					
Alpine meadow ($n = 22$)					
Mean	133.3b	107.9a	100.8a	138.5b	31.3 %
SD	84.90	56.35	66.96	80.82	0.16
Range	40.7–330.4	32.4–244.6	16.3–297.8	45.6–415.7	6.3–70.3 %
Alpine steppe ($n = 18$)					
Mean	78.3b	68.6ab	60.9a	108.4c	42.4 %
SD	44.70	46.05	46.05	55.72	0.17
Range	29.9–160.5	13.4–177.4	8.0–158.1	28.6–220.6	18.0–68.6 %
Overall ($n = 40$)					
Mean	109.9b	91.2a	83.9a	125.7b	36.6 %
SD	75.13	54.32	61.62	72.01	0.17
Range	29.9–330.4	13.7–244.6	8.0–297.9	28.6–415.7	6.3–70.3 %
Species richness					
Alpine meadow ($n = 22$)					
Mean	16.9b	15.0a	14.7a	17.6b	14.9 %
SD	5.08	5.10	4.41	3.82	0.09
range	9–26.3	8–26	7.3–24.7	11–25.7	0.8–30.8 %
Alpine steppe ($n = 18$)					
Mean	10.9a	10.2a	10.0a	12.5b	17.5 %
SD	4.42	4.34	3.64	3.72	0.06
range	5.3–21.3	5.3–24.3	5–20.7	7.3–23	7.4–30.5 %
Overall ($n = 40$)					
Mean	14.2b	12.9a	12.5a	15.3c	16.1 %
SD	5.62	5.29	4.67	4.52	0.08
range	5.3–26.3	5.3–26	5–24.7	7.3–25.7	0.8–30.8 %

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Table 3. Type II regression between ANPP of different years. Slope of regression line, 95 % lower limit of slope, and 95 % upper limit of slope are shown. All regression lines are extremely significant ($P < 0.001$).

Dependent variable	Independent variable	Slope	95 % lower limit	95 % upper limit
2006	2007	1.38	1.09	1.75
	2008	1.22	1.02	1.45
	2009	1.04	0.84	1.29
2007	2006	0.72	0.57	0.91
	2008	0.88	0.71	1.09
	2009	0.75	0.58	0.98
2008	2006	0.82	0.69	0.98
	2007	1.13	0.91	1.41
	2009	0.86	0.71	1.03
2009	2006	0.96	0.78	1.78
	2007	1.32	1.02	1.72
	2008	1.17	0.97	1.4

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Table 4. Summary of ANCOVA for the effects of year, climate and species richness on above-ground net production (ANPP).

Term	Df	MS	*F* value	*P* value
Using annual climate data				
Year	3	2.19	5.76	< 0.001[c]
AT	1	0.18	0.47	0.496
AP	1	5.23	13.76	< 0.001[c]
SR	1	8.47	22.27	< 0.001[c]
Year: AT	3	0.14	0.36	0.785
Year: AP	3	0.61	1.61	0.189
Year: SR	3	0.15	0.39	0.758
Using growing season climate data				
Year	3	2.19	5.62	0.001[b]
GST	1	0.30	0.76	0.384
GSP	1	3.61	9.26	0.003[b]
SR	1	9.20	23.60	< 0.001[c]
Year: GST	3	0.22	0.57	0.634
Year: GSP	3	0.34	0.87	0.461
Year: SR	3	0.14	0.36	0.786

[a] $P < 0.05$;
[b] $P < 0.01$;
[c] $P < 0.001$;
[d] $P < 0.1$.

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Table 5. Summary of GLM for the effects of climate fluctuation and species richness (SR) on the interannual variation of aboveground primary production (ANPP).

Term	Df	MS	*F*	*P*	%SS
Using annual data					
CV_{AP}	1	0.17	10.24	0.003 [b]	15.0
CV_{AT}	1	0.11	6.77	0.014 [a]	9.9
$SR_{average}$	1	0.10	6.15	0.019 [a]	9.0
CV_{AP}: CV_{AT}	1	0.07	4.19	0.049 [a]	6.1
CV_{AP}: $SR_{average}$	1	0.07	4.08	0.052 [d]	6.0
CV_{AT}: $SR_{average}$	1	0.00	0.13	0.725	0.2
CV_{AP}: CV_{AT}: $SR_{average}$	1	0.08	4.90	0.034 [a]	7.2
Residuals	32	0.02			46.7
Using growing season data					
CV_{GSP}	1	0.25	10.89	0.002 [b]	22.8
CV_{GST}	1	0.00	0.05	0.829	0.1
$SR_{average}$	1	0.04	1.89	0.179	4.0
CV_{GSP}:CV_{GST}	1	0.05	2.09	0.158	4.4
CV_{GSP}: $SR_{average}$	1	0.01	0.62	0.436	1.3
CV_{GST}: $SR_{average}$	1	0.00	0.02	0.882	0.0
CV_{GSP}: CV_{GST}: $SR_{average}$	1	0.00	0.11	0.745	0.2
Residuals	32	0.02			67.1

AP: annual precipitation;
AT: annual temperature;
GSP: growing season precipitation;
GST: growing season temperature;
CV: coefficient of variation;
%SS: percentage of total sum of squares explained.
[a] $P < 0.05$;
[b] $P < 0.01$;
[c] $P < 0.001$;
[d] $P < 0.1$.

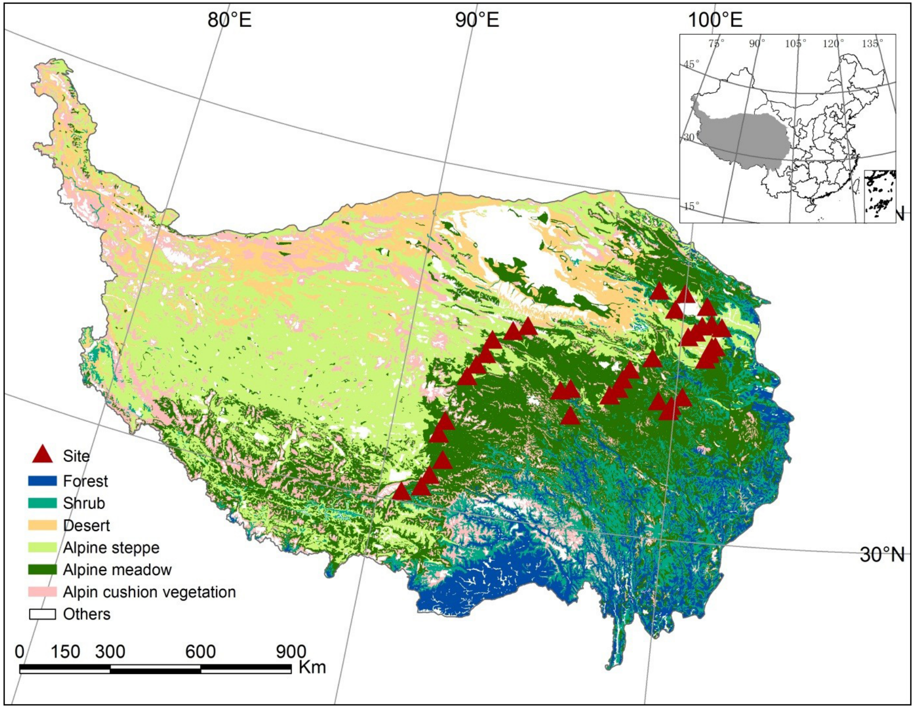

Fig. 1. Geographical distribution of the sampling sites against the background map of the vegetation types on the Tibetan Plateau (1 : 1 000 000) (Chinese Academy of Sciences, 2001).

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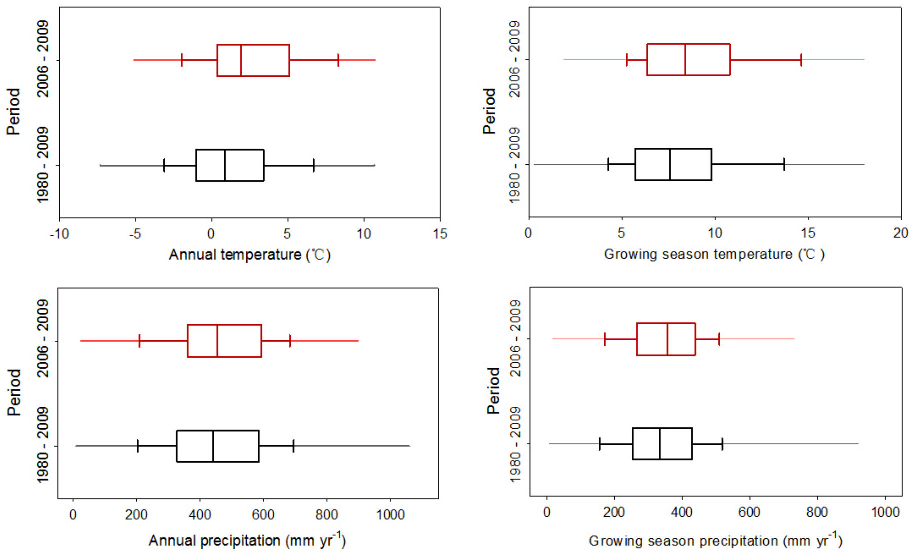

Fig. 2. Box plots of annual temperature, annual precipitation, growing season temperature and growing season precipitation collected from 49 meteorological stations during the current period of study (2006–2009) and 30 yr (1979–2009) in the past. The box plots show the median, quartiles and 10th and 90th percentiles of the climatic variables, and the red lines show their ranges.

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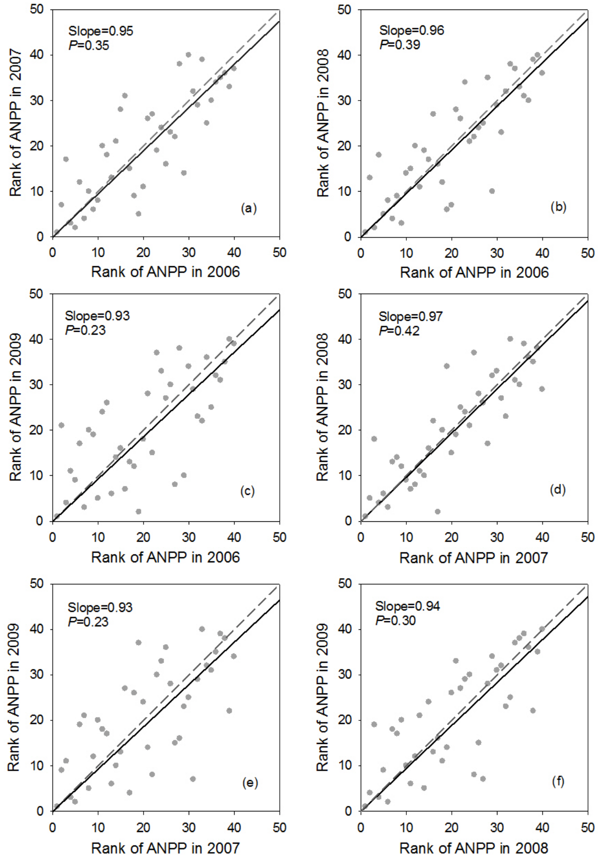
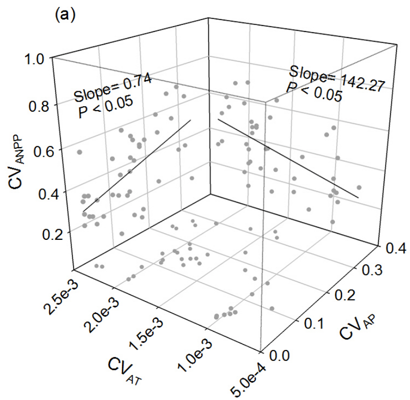


Fig. 3. The rank regression between aboveground net primary production (ANPP) for each pair of years from 2006–2009 **(a–f)**. The slopes of the regression lines are given, and none differ significantly from one.



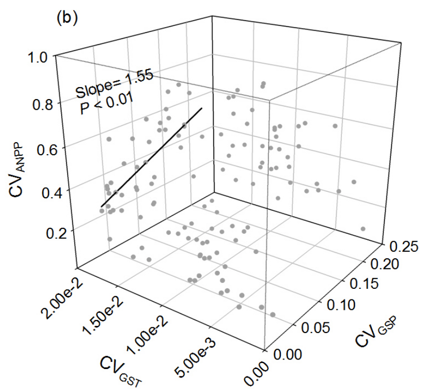


Fig. 4. Linear relationships for **(a)** annual climate fluctuation, CV of aboveground net primary production (ANPP) with CV of annual precipitation and CV of annual temperature and **(b)** growing season climate fluctuation, CV of aboveground net primary production (ANPP) with CV of growing season precipitation and CV of growing season temperature, from 2006–2009. Significant regression lines at $P < 0.05$ are shown.

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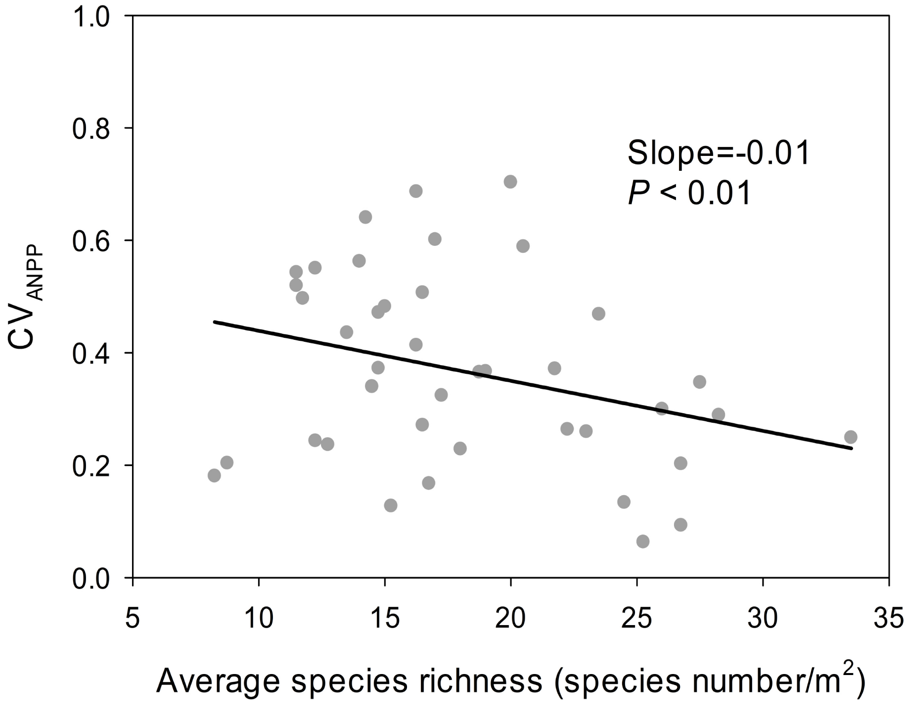

Fig. 5. Linear relationship between four-year average of species richness and CV of above-ground net primary production (ANPP).

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Regional-scale, temporal variation in net primary production

Y. Shi et al.

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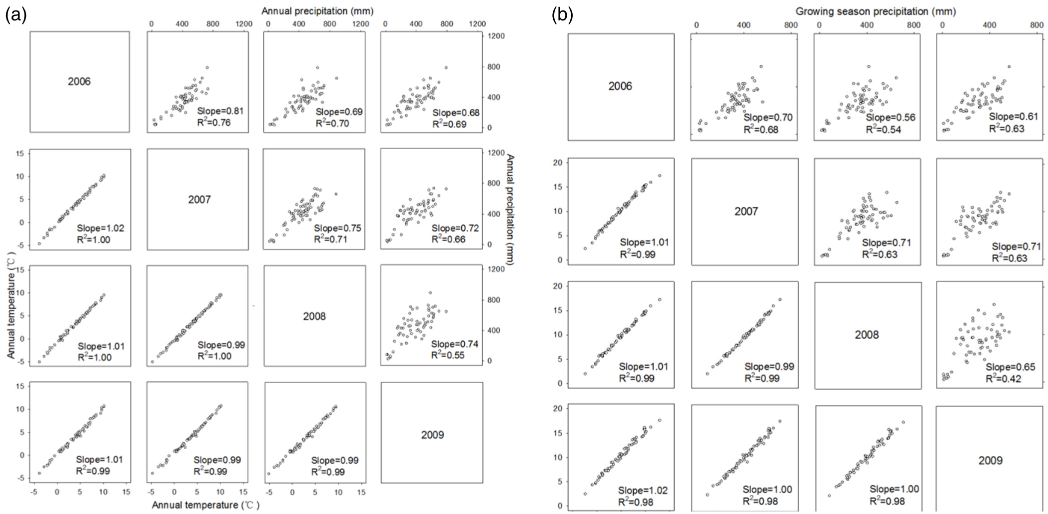

Fig. 6. The results from linear regressions of climate factors (**(a)** annual climate data; **(b)** growing season climate data) between different years. All relationships are very significant ($P < 0.01$).

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