Science Bulletin

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Citation: Science Bulletin **64**, 446 (2019); doi: 10.1016/j.scib.2019.03.012

View online: http://engine.scichina.com/doi/10.1016/j.scib.2019.03.012

View Table of Contents: http://engine.scichina.com/publisher/scp/journal/SB/64/7

Published by the Science China Press

Science Bulletin 64 (2019) 446–454

Contents lists available at ScienceDirect

Science Bulletin

journal homepage: www.elsevier.com/locate/scib

Article

Deciphering impacts of climate extremes on Tibetan grasslands in the last fifteen years

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ARTICLE INFO

Article history:
Received 2 January 2019
Received in revised form 6 March 2019
Accepted 7 March 2019
Available online 13 March 2019

Keywords:
Drought
Extreme cold
Extreme hot
Growth response
Alpine grasslands
Tibetan Plateau

ABSTRACT

Climate extremes have emerged as a crucial driver of changes in terrestrial ecosystems. The Tibetan Plateau, facing a rapid climate change, tends to favor climate extremes. But we lack a clear understanding of the impacts of such extremes on alpine grasslands. Here we show that extreme events (drought, extreme wet, extreme cold and extreme hot) occurred at a frequency of 0.67–4 months decade^{-1} during 2001–2015, with extreme precipitation predominantly occurring in June-to-August and extreme temperatures in May. Drought and extreme wet cause opposite and asymmetric effects on grassland growth, with drought-induced reductions greater than increases due to extreme wet. Grassland responses to extreme temperatures, which predominantly occur in May, show a dipole-like spatial pattern, with extreme hot (cold) events enhanced (reduced) growth in the eastern plateau but slightly reduced (enhanced) growth in the western plateau. These opposite responses to extreme temperatures over the eastern plateau are explained by the possibility that the occurrence of extreme cold slows the preseason temperature accumulation, delaying the triggering of spring phenology, while extreme hot hastens the accumulation. In the western plateau, in contrast, positive responses to extreme cold are induced by accompanying high precipitation. Furthermore, high extremeness of climate events generally led to a much lower extremeness in growth response, implying that the Tibetan grasslands have a relatively high resistance to climate extremes. The ecosystem models tested could not accurately simulate grassland responses to drought and extreme temperatures, and require re-parameterization before trust can be placed in their output for this region.

1. Introduction

There is high confidence that anthropogenic activities have not only led to a gradual change in mean climate state, but have also altered the variability of temperature and precipitation, resulting in an observed increased intensity and frequency of climate extremes (e.g. drought, extreme wet, extreme cold and extreme hot) in the past several decades [1–6]. Furthermore, these climate extremes are projected to become more intense and more frequent with stronger increases at higher levels of global warming [7]. Evidence gleaned from remote sensing, tree rings and global-change manipulative experiments have clearly shown that the occurrence of climate extreme events could trigger profound impacts on ecosystem carbon cycling [8–10], which would, in turn, accelerate or limit climate change through climate-carbon cycle feedbacks [11,12]. Climate extremes are therefore becoming an increasingly important driver of changes in terrestrial ecosystem carbon cycling, and their impacts on terrestrial ecosystems are reported to be one of the largest uncertainties in carbon cycling [8,10,12].

Nearly two-thirds of the Tibetan Plateau, also known as the "Third Pole", are covered by alpine grasslands, which provides forage for grazing livestock and is the major vegetation type covering the headstream regions of the major Asian rivers. The stability of Tibetan grassland production is crucial to local herders and for downstream water resources. Observations from Tibetan meteorological stations indicate that the occurrence of climate extreme events generally increased over the last several decades [13–15]. But our current understanding of Tibetan grassland responses to climate extremes is mainly derived from ecosystem-level manipulative experiments which artificially impose extreme conditions

SPECIAL TOPIC: The Second Tibetan Plateau Scientific Expedition and Research (I).

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https://doi.org/10.1016/j.scib.2019.03.012

(e.g. precipitation exclusion and heating) [16]. These manipulation experiments can improve our mechanistic understanding of grassland growth responses, but they do not adequately represent grasslands located in different climate regimes, nor do they consider realistic extreme conditions in an historical sense [17]. We therefore still lack a full description of the occurrence of climate extremes and an estimate of the relative magnitude of growth deviations induced by climate extremes over Tibetan grasslands.

Various lines of evidence indicate that reduced precipitation due to a weakened Indian summer monsoon [18,19] has been a crucial driver of grassland browning in southern Tibet since 2000 [20], suggesting that water availability is the main limiting factor for plant growth over the Tibetan Plateau. It has been presumed that droughts, with severe departures from normal precipitation, have strong negative impacts on grassland growth in the region [20,21]. Besides water availability, temperature is also recognized as an important constraint on plant growth in relatively cold environments [22]. In the last few decades, the warming rate over the Tibetan Plateau has been twice as fast as the global average [23], and the occurrence of temperature extremes, especially extreme hot spells, have become much more frequent [13,24]. These temperature extremes are generally expected to exert negative impacts on the carbon cycle, since the optimum temperature for plant photosynthesis could be exceeded during periods of extreme heat, and, during extreme cold, frosts could cause damage to plants [8,25–27]. However, grasslands that have adapted to the cold, alpine environment over the Tibetan Plateau might differ from other ecosystems with respect to carbon-cycle responses to temperature extremes. Quantifying the impacts and mechanisms of climate extremes over alpine grasslands could provide a comparison to studies of grasslands in other regions, culminating in a better understanding of the role of climate extremes in grassland carbon cycling.

Nearly real-time satellite remote sensing, with a short return interval to the same locations, offers the research community unprecedented information to detect terrestrial biosphere responses resulting from climate extremes in a consistent way [8]. Here, we used climate data and remote sensing proxies of vegetation growth to characterize spatio-temporal patterns of climate extremes (drought, extreme wet, extreme cold and extreme hot) and their impacts on grassland growth over the Tibetan Plateau since 2001. The knowledge gained from such satellite-based studies can provide invaluable information for improving the model representation of climate-extreme induced perturbations in ecosystem carbon cycling. With this in mind, we used the satellite-derived results to assess how state-of-the-art process-oriented ecosystem models simulate grassland responses to naturally occurring climate extreme events over the Tibetan Plateau.

2. Data and methods

2.1. Study area

The Tibetan Plateau is one of the largest and highest plateau in the world, with an average altitude of over 4,000 m. The climate of the Tibetan Plateau is controlled by the Indian summer monsoon in the summer and westerlies in the winter [28–30]. Precipitation in the region mainly occurs in the summer with the total amount of annual precipitation varying from over 1,000 mm in the southeast to less than 50 mm in the northwest [30]. The temperature over the Tibetan Plateau is generally very low, with the annual average temperature being below 0 °C almost everywhere in the region [31]. Grasslands cover about 60% of the Tibetan Plateau, while shrubs and a small fraction of sub-tropical forests are located on the southeastern edge [32,33]. The grassland type varies along the precipitation gradient from alpine meadow in the east, to alpine steppe in the central area, and desert grassland in the west.

2.2. Climate and satellite-based data sets

To detect climate extreme events, we used monthly climate data from the Climate Research Unit, University of East Anglia (CRU TS4.1) data set. The specific data used were temperature, precipitation and potential evapotranspiration data with a spatial resolution of 0.5° for the period 2001–2015. We used normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) to analyze the response of vegetation growth to climate extremes. The NDVI, which is used as a proxy for vegetation productivity, is calculated from the normalized reflectance difference between the near infrared band and the visible red band [34,35]. NDVI has been widely used in ecological studies, but it has long been suffered from the "mixed pixel" problem which occurs because most of land surface consists of open canopies for which significant canopy background signals affect the canopy reflectance properties [36,37]. This problem is most severe in semi-arid regions such as the desert grasslands of the western Tibetan Plateau, where the vegetation cover is relatively sparse. To address this problem, we have additionally used EVI in this study, as the calculation of EVI includes a canopy background adjustment term, and is therefore better able to decouple the canopy signal from the background noise [38]. The NDVI and EVI data from the MODIS MOD13C1 data set for the period 2001–2015 were used. Both vegetation indices (VI) were resampled to a spatial resolution of 0.5° using linear extrapolation.

2.3. Terrestrial ecosystem models

We also evaluated the performance of current state-of-the-art ecosystem models. Such models are important tools for estimating and projecting ecosystem response to a warmer climate and intensified climate extreme events in the future. We used simulated net primary productivity (NPP) from eight of the ecosystem models which participated in the TRENDY carbon cycle model comparison project (http://dgvm.ceh.ac.uk/files/Trendy_protocol%20_Nov2011_0.pdf). These eight models were: the Community Land Model Version 4.5 (CLM4.5); the Integrated Science Assessment Model (ISAM); the Joint UK Land Environment Simulator (JULES); the Lund-Postam-Jena DGVM (LPJ); the Lund-Postam-Jena General Ecosystem Simulator (LPJ-GUESS); the Land Surface Processes and eXchanges (LPX); the O-CN land surface model; and the Organizing Carbon and Hydrology in Dynamic Ecosystem (ORCHIDEE). All these terrestrial ecosystem models were forced by the CRU-NCEP climate dataset, and the simulation setup followed the standard protocol described in the intercomparison project. In this study, we used the results from the S2 experiment, which includes the impacts of climate change and rising CO_2 concentration on NPP. We used model output with a spatial resolution of 0.5°, covering the period from 2001 to 2012.

2.4. Detection of climate extreme events and corresponding grassland responses

Here, we define climate extreme events based upon monthly climatic statistics. We first detrended the monthly time series at each pixel to remove the long-term trend. As monthly variables contain both a seasonal cycle and a long-term trend, we calculated the trend at the annual scale and then replicated it for each month. This trend was then subtracted from the monthly time series to obtain the monthly detrended anomaly. To remove the seasonal cycle of each climate variable, we then calculated the standardized anomalies of monthly temperature and precipitation at each pixel following Eq. (1):

$$x_{i,j,k} = \frac{X_{i,j,k} - \bar{X}_{i,k}}{std(X_{i,k})}, \quad (1)$$

where x is the standardized anomaly, $X_{i,j,k}$ is the value of the climate variable at month i of year j at pixel k. $\bar{X}_{i,k}$ is the multi-year average of the variable at month i at pixel k. This procedure ensures that the standardized anomalies are comparable across seasons and space.

A drought or an extreme cold event is defined as when the monthly standardized precipitation or temperature anomaly, respectively, is lower than twice the standard deviation (σ) of the standardized anomalies for the study period 2001–2015. Similarly, an event with monthly standardized climatic anomaly above 2σ for temperature or precipitation anomalies is identified as extreme heat or wet, respectively. The frequencies of climate extreme events during the chosen period were then calculated as the ratio of the total number of climate extreme months, to the total number of months during the study period. The definition of drought based on the monthly precipitation amount only partly reflects the water availability, because water availability is also determined by potential evapotranspiration [39]. Therefore, we also used monthly climatic water deficit (CWD), computed as the difference of monthly precipitation and monthly potential evapotranspiration, as an index to detect the drought events.

To analyze the responses of grassland growth to climate extremes, we first detrended the VI time series at each pixel to remove the long-term trend. This trend is not required because it may include the influence of non-climatic factors, such as the fertilization effect of increasing CO_2 concentration on grassland growth. We then calculated the standardized VI anomaly following Eq. (1). The normalized VI anomalies corresponding to climate extreme months are regarded as climate extreme event-induced VI changes. The model-simulated net primary productivity was processed following the same steps. As we are focused on the response of vegetation growth to climate extremes, we only consider events that occur during the growing season (May to October).

3. Results and discussion

3.1. Frequency of climate extremes

The identified drought frequency at the pixel level is around 1.5 months decade^{-1}, ranging from 0.5 months decade^{-1} in the southwestern plateau to 3.5 months decade^{-1} in the central plateau (Fig. 1a). Higher drought frequency occurs in the central plateau, and lower frequency in the northeastern and southwestern plateau areas. The distribution of drought frequency shows a clear altitude dependence, with an increase with altitude until 4,500 m and then a decrease at higher altitudes (Fig. 1b). The same pattern is observed if drought events are defined in terms of water availability (precipitation minus evapotranspiration), rather than simply precipitation (Fig. S1 online). The identified droughts mainly occur in the summer (June to August, 95.0%), with only 4.9% occurring in spring (May) and 0.1% in autumn (September to October). The seasonal and altitudinal distributions of extreme wet are similar to those of drought, except for the high frequencies of extreme wet observed in the southwestern plateau. As with the droughts, most of extreme wet events occur in the summer months (86.3% in the period from June to August) with only 6.6% in spring and 7.1% in autumn (Fig. 1c).

There is a high frequency of extreme cold, of around 3.5 months decade^{-1}, in the southwestern plateau, but, in contrast to the distribution of extreme precipitation, the central region has a low frequency (0.7 months decade^{-1}). The frequency of extreme cold events increases slightly with elevation and peaks at an altitude of around 5,550 m (Fig. 1f). Most of the extreme cold events occur in the spring (47.4%), with only 26.6% in summer and 26.0% in autumn (Fig. 1e). In contrast to extreme cold, extreme hot events mainly occur in the northeastern plateau while the central and southern plateau areas are less affected. The extreme hot events do not have a significant dependence on altitude, which may be due to the uniform warming across the entire Tibetan Plateau in recent decades [31]. The extreme hot events mainly occur in spring (40.0% in May) and autumn (35.1% in October), with only 24.9% occurring in the summer months.

3.2. Effects of climate extremes on grassland growth

To quantify the overall impact of climate extreme events on grassland growth, we considered all extreme months in the 15-year VI record at each pixel for each climate extreme event type. For each pixel and each event type, we averaged the corresponding standardized VI anomalies (see Methods) of all the extreme months in the 15-year period. This procedure enables us to compare climate extreme-induced VI deviations across pixels of differing growth status and among different event types.

3.2.1. Drought and extreme wet events

Our results showed that the different event types have contrasting effects on grassland growth. Following drought stress, alpine grasslands exhibit an obvious decline in growth, with an average standardized NDVI anomaly of −0.5 and an average standardized EVI anomaly of −0.4. The largest reductions in NDVI and EVI are found in the northeastern Tibetan Plateau with negative NDVI and EVI anomalies exceeding twice the standard deviation. Alpine grasslands in the central region show the least response to drought. The vegetation response to drought shows a clear altitude dependency, with low-elevation regions having large negative responses and high-elevation regions having small negative or even slightly positive responses (Fig. 2a–c).

In contrast, extreme wet events generally increase grassland growth (Fig. 2d, e). A meta-analysis of grassland precipitation experiments suggested that the impact of extreme wet events on grassland growth has a significant dependence on site aridity, with xeric biomes showing positive responses and mesic biomes displaying negative responses [40]. The observed positive response is in accord with the wide recognition that plant available water is a crucial limiting driver of grassland growth over the Tibetan Plateau [41,42]. We further show that there is stronger stimulation effect of extreme wet events on grassland growth in low-elevation regions than in high-elevation regions (Fig. 2f). This relationship to altitude might be expected since temperature becomes increasingly important to plant growth at relatively high altitudes [43,44]. It is interesting to note that there is an asymmetric response of grassland growth to drought and extreme wet (Fig. 2 a, b, d, e). Over 76.34% of the area had a negative NDVI anomaly under drought, with 21.21% having a negative NDVI anomaly of greater than 1 standard deviation and a regional average standardized NDVI anomaly of −0.5. For extreme wet events, however, only 14.76% of the area had a positive NDVI anomaly greater than 1 standard deviation, and the average NDVI anomaly is 0.3, which is smaller than the absolute value for drought events. This asymmetric response is in line with the previously reported asymmetric vegetation response to extreme climate events based on global satellite-based GPP and ecosystem models [45,46]. The underlying mechanisms are suggested to be saturation of the positive effect of wetting in extreme wet years [47], and a collapse of the community and ecosystem functions in extreme drought [48]. Our finding

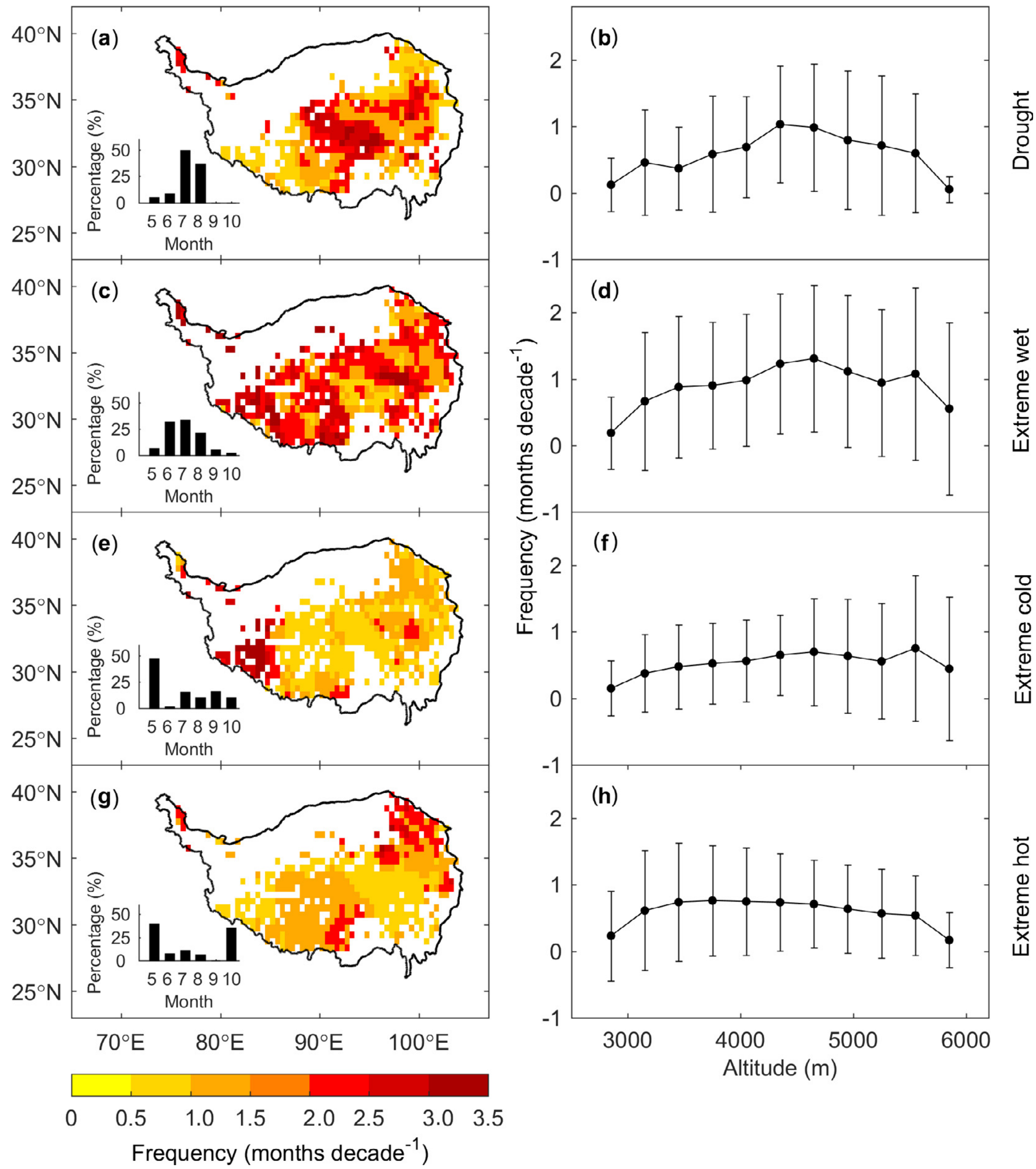

Fig. 1. Spatial and altitudinal distributions of the frequency of climate extreme events during the period 2001–2015. The frequency denotes the average number of months that are identified as climate extremes. The (a), (c), (e), and (g) show the spatial distribution of the frequency of climate extremes, with the subplot showing its seasonal distribution. The (b), (d), (f) and (h) illustrate the frequency of climate extremes at different altitudes. Drought and extreme wet were detected using precipitation anomalies.

therefore implies that there is a relatively high probability of grassland productivity over the Tibetan Plateau suffering losses if it is facing frequency increases at both ends of the spectrum of precipitation extremes.

We used the satellite-derived results to evaluate the performance of state-of-the-art terrestrial ecosystem models from the TRENDY project. Since the model simulation period ends at the year 2012, the model-data comparison was performed for the period 2001–2012. Our results showed that the models appeared to correctly simulate an increase in net primary productivity in response to extreme wet, but failed to capture a widespread decline in productivity under drought (Fig. S2 online). We calculated the spatial correlation coefficient between simulated changes in standardized NPP anomalies and observed changes in VI anomalies across pixels. This diagnostic metric is useful for assessing the overall agreement between model simulations and satellite-derived observations (Fig. 3). For most of the models and for the multi-model ensemble mean, the simulations had a positive correlation with the observations, but none of them passed the significance test at the 0.05 significance level, suggesting that the current models are still not sufficiently able to represent alpine grassland responses to precipitation extremes. Specifically, in response to drought, the multi-model ensemble mean simulated a positive response in most pixels, highlighting the fact that current ecosystem models perform poorly when it comes to simulating water stress on alpine grasslands. As we used a "one model-one vote" approach to calculate the multi-model ensemble mean, it is hard to say if the result is biased by any specific model or if most of the models perform poorly. Previous model evaluation studies have suggested that there are predictability limits on carbon metabolism for all models [49]. For grassland ecosystems, a large proportion of model uncertainties arise from factors controlling water stress (e.g. precipitation, humidity and air temperature) [50]. The uncertainties may originate in limited schemes for

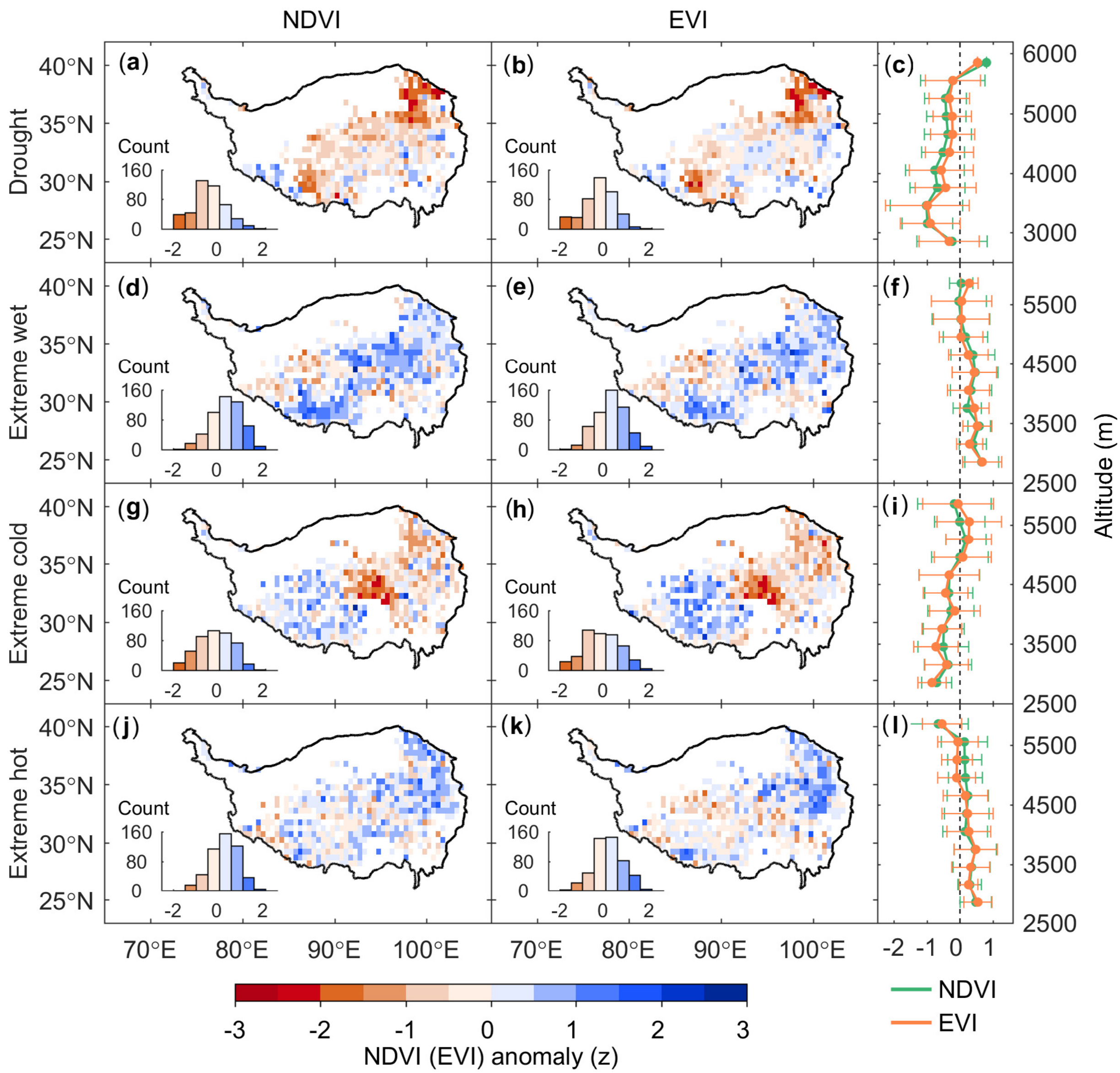

Fig. 2. Spatial distribution of climate extreme-induced changes in NDVI (a, d, g, j) and EVI (b, e, h, k) anomalies and their altitudinal distributions (c, f, i, l) for different types of climate extremes. The subplot shows the frequency distribution of NDVI (EVI) anomalies. The dot and errorbars in (c, f, i, l) illustrate the average and standard deviation within an elevation bin.

parameterization of water stress, or in inadequate descriptions of the root profile for grasslands that have shallow root depths and where roots may vary seasonally [51].

3.2.2. Temperature extremes

Extreme cold leads to a dipole pattern of both NDVI and EVI changes, with an obvious decline in both eastern and central plateau areas and an evident increase in the western plateau (Fig. 2g, h). The grassland growth responses to extreme hot also display a similar, but not so marked, dipole pattern, with a discernible increase in the eastern and central plateau and a non-significant change or minor decline in the western plateau (Fig. 2j, k). This dipole pattern is consistent with recently reported dipole patterns of phenology changes [52]. Since both extreme cold and extreme hot events mainly occur in May (Fig. 1e, g), when spring phenology plays an important role in VI changes, we suggest that the direction and magnitude of their impacts are determined by climate extreme-induced changes in spring phenology and subsequent spring grassland growth. In the eastern and central plateau, temperature was found to exert control over spring phenology [52,53]. Preseason temperature accumulation is the key forcing that influences spring phenology events [54], so the occurrence of extreme cold could slow the accumulation, resulting in a delay in spring phenology and a subsequent decline in spring NDVI. In contrast, extreme hot could hasten the temperature accumulation and result in an advance in spring phenology and an increase in spring NDVI. In the western plateau, however, the timing of spring phenology is mainly regulated by water availability [53]. We found that the occurrence of extreme cold in this region has been accompanied by higher precipitation than the average. Although the exact reason for this phenomenon goes beyond the scope of this study, the relatively high precipitation together with the control of precipitation on spring phenology explains the positive response of grassland growth to extreme cold in the western plateau.

There are other possible mechanisms for the observed responses of grassland growth to temperature extremes. Under extreme cold, the direct damage to plant tissues [55] could consti-

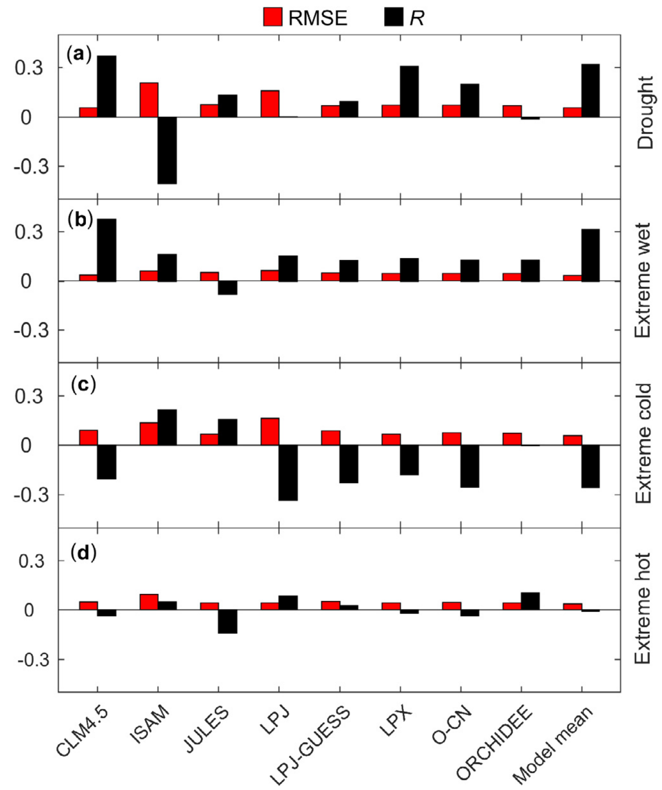

Fig. 3. Comparison of climate extreme-induced anomalies in models with satellite-derived observations. Smaller root mean squared error (RMSE) and larger correlation coefficient (R) indicate a better correlation between NPP and VI anomalies. The VI anomalies are calculated as the average of standardized anomalies of NDVI and EVI.

tute another cause of reduced grassland growth. Frost damage has been reported to be an important risk for vegetation growth in northern hemisphere ecosystems, especially in Europe where the advances in spring phenology increase the number of frost days during the growing season [56]. The influence of frost damage is greater in wet regions than in dry regions, as low leaf wettability in dry climates can hinder the formation of ice on the leaf surface and protect the leaf from frost damage [57,58]. Extreme cold induced frost damage could also be a possible mechanism for the reduced NDVI observed in the eastern and central plateau areas. In the main growing season, the direction of the impact of extreme hot on grassland growth depends on whether the high temperature exceeds the optimal photosynthetic temperature [26,59]. Recent research has highlighted the negative effect of extreme high temperatures on ecosystem carbon sinks during the mega heatwave events in 2003 and 2010 in Europe [60,61], in 2015 in tropical regions [62], and in 2012 in Australia [63]. High temperatures in excess of the photosynthetic optimum temperature, which is between 20 and 30 °C across boreal, temperate and tropical species [64,65], could suppress the activity of Robisco activase, increase photorespiration, and therefore lead to a decline in the net photosynthesis [66,67]. However, the Tibetan Plateau has an extremely cold climate, with a climatological growing season temperature of around 5.5 °C, and therefore, the extreme hot events identified by our method (see Methods) have a very small possibility of exceeding the locally-adapted optimal photosynthetic temperature. On the contrary, the extreme hot events in this region could enhance alpine grassland growth.

In terms of the multi-model ensemble mean, the spatial distributions of simulated NPP changes in response to extreme hot and extreme cold are opposite to the distributions of VI changes (Figs. 2 and S2 (online)). Six out of the eight models showed a negative correlation coefficient between simulated NPP change and VI change across pixels (Fig. 3), suggesting that these current terrestrial ecosystem models wrongly represent the impacts of temperature extremes on alpine grassland growth. Since climate extreme-induced changes in spring phenology was suggested to be an important factor regulating grassland responses to extreme temperatures, the common model deficiency could be mainly due to unrealistic simulation of the effect of climatic factors on spring phenology. Current terrestrial ecosystem models use a prognostic phenological curve or a growing degree day model to simulate vegetation phenology [68]. The former scheme uses a fixed phenological curve derived from remote sensing datasets for each vegetation type, and therefore does not have the ability to simulate spring phenology changes in response to climate extremes. The latter scheme calculates the date of spring phenology from growing degree days, and its performance is highly reliant on the calibration and parameterization of the model [54]. Our results over the Tibetan Plateau highlight the importance of the parameterization of current models in simulating phenology in the alpine grasslands.

3.3. Decadal change in climate extremes and their impacts on grassland responses

We examined the decadal change of climate extremes and the resultant changes in grassland growth responses between the 2000 s (2001–2007) and 2010 s (2008–2015). Fig. 4 displays spatial distributions of changes in frequencies of drought and extreme wet. The frequency of extreme wet has an overall mean increase of 0.5 months decade^{-1} over the plateau, with the increase accounting for more than 57.7% of the plateau during the last 15 years. Correspondingly, this increase in frequency leads to a widespread increase of grassland growth, with an average increase of 0.4 in both NDVI and EVI anomalies over the plateau. In contrast, the drought frequency decreased in over 60.9% of the region and increased in the remaining 39.1% in the last 15 years, resulting in an overall increase of 0.1 months decade^{-1} over the whole plateau. This change in drought frequency led to concurrent decreases of 0.1 in NDVI and 0.3 in EVI anomalies.

Fig. 4g, j also shows the spatial patterns of frequency change for both extreme cold and extreme hot. There is an almost plateau-wide increase in the frequency of extreme cold events in the last 15 years and a similar scale decrease in extreme hot events over the same period. Classification into different altitudinal bands indicates that extreme cold has seen an increase in frequency at altitudes below 4,000 m, but a decline at higher altitudes (Fig. S3 online). This result can be explained by the recent finding that the rapid warming rate before the late 1990s slowed down at altitudes below 4,000 m but has continued to persist at higher altitudes since the late 1990s [69].

Following decadal-scale increases in the frequency of extreme cold and extreme hot, the change in grassland growth response displayed a dipole-like pattern in both cases. For extreme cold (Fig. 4h, i) there was a decline in the growth response in the central and eastern plateau and an increase in the western plateau. For extreme hot the pattern was largely reversed (Fig. 4k, l), with an increase in the central plateau and a minor change in the west. As stated above, the main mechanism triggering the observed change pattern in the central and eastern plateau is attributed to the possibility that an increase in the frequency of extreme cold events could counteract the accumulation of forcing units in initiating spring phenology. Conversely an increase in the frequency of extreme hot events could speed up the accumulation thus bringing spring phenology forwards. In contrast, over the western plateau, spring phenology and plant growth is much more sensitive to precipitation than to temperature, and grassland growth responses to

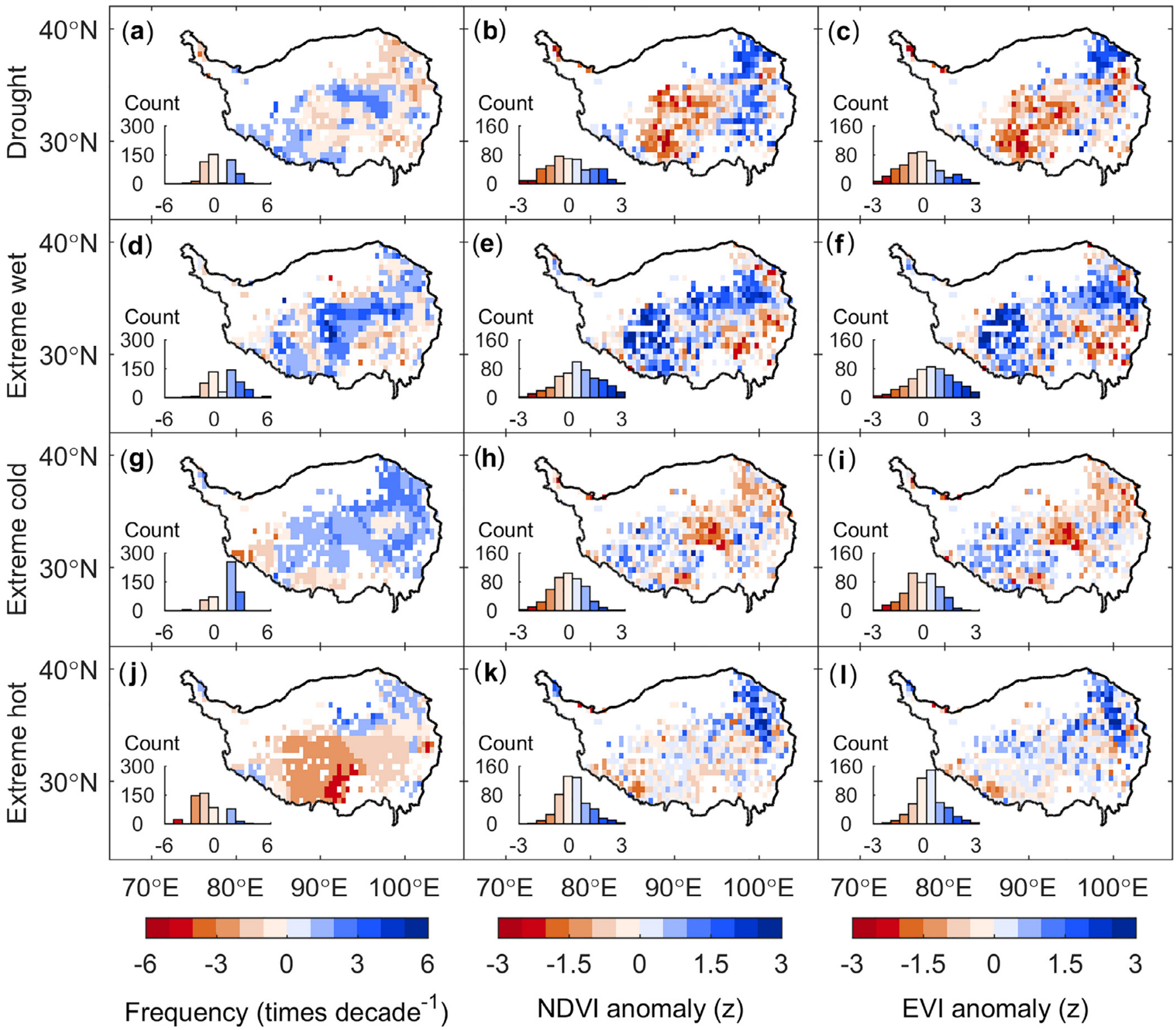

Fig. 4. Spatial patterns of decadal change in the frequency of climate extremes (a, d, g, j) and corresponding VI responses (b, e, h, k, c, f, i, l) between the period 2001–2007 and 2008–2015.

changes in temperature extremes in this area will become much more dependent on the accompanying change in water availability.

4. Conclusions

We have performed an overall assessment of the impacts of four types of climate extremes on alpine grassland growth over the Tibetan Plateau. Drought was recognized as the most severe extreme event that leads to a widespread decline in grassland growth in the region. The recent increase in frequency of extreme wet can potentially negate the negative impacts caused by drought. Extreme hot events, which mainly occur in May, generally stimulate grassland growth in this relatively cold environment. However, the increased occurrence of extreme cold could potentially cause direct damage to plant tissues and reduce grassland growth. In addition, we have clearly shown that current state-of-the-art terrestrial ecosystem models have a rather weak capability to model the impacts of climate extremes on Tibetan grasslands. Using these simulations to inform present and future impacts of climate extremes on Tibetan carbon cycling is likely to be misleading. Before considering the application of such models to Tibetan grasslands, re-parameterization of the processes relevant to impacts of climate extremes is required in most of the terrestrial ecosystem models that are generally designed for global simulations.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This work was supported by the Strategic Priority Research Program (A) of the Chinese Academy of Sciences (XDA20050101), the National Natural Science Foundation of China (41530528, 41871104), the Chinese Postdoctoral Science Foundation Project (Y7Gc011012), the Key Research and Development Programs for Global Change and Adaptation (2017YFA0603604), the Second

Tibetan Plateau Scientific Expedition and Research (STEP) Project and the Thousand Youth Talents Plan Project in China. Mr. Tao Yang performed the data analysis.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scib.2019.03.012.

Author contributions

T. Wang designed the research and led the drafting of this manuscript. D. Liu contributed to the drafting of this manuscript and the development and implementation of methodology. T. Yang performed data analysis and prepared figures. Z. Yan, Y. Liu, Y. Zhao and S. Piao contributed to the interpretation of results and the writing of this paper.

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