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**Strong impact of daily minimum temperature on the green-up date and summer  
greenness of the Tibetan Plateau**

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## Abstract

Understanding vegetation responses to climate change on the Tibetan Plateau (TP) helps in elucidating the land-atmosphere energy exchange, which affects air mass movement over and around the TP. Although the TP is one of the world's most sensitive regions in terms of climatic warming, little is known about how the vegetation responds. Here we focus on how the spring phenology and summertime greenness respond to the asymmetric warming, i.e., stronger warming during nighttime than during daytime. Using both *in situ* and satellite observations, we found that vegetation green-up date showed a stronger negative partial correlation with daily minimum temperature ( $T_{\min}$ ) than with maximum temperature ( $T_{\max}$ ) before growing season (“preseason” henceforth). Summer vegetation greenness was strongly positively correlated with summer  $T_{\min}$ , but negatively with  $T_{\max}$ . A 1-K increase in preseason  $T_{\min}$  advanced green-up date by four days ( $P < 0.05$ ), and in summer enhanced greenness by 3.6% of the mean greenness of 2000-2004 ( $P < 0.01$ ). In contrast, increases in preseason  $T_{\max}$  did not advance green-up date ( $P > 0.10$ ) and higher summer  $T_{\max}$  even reduced greenness by 2.6%  $K^{-1}$  ( $P < 0.05$ ). The stimulating effects of increasing  $T_{\min}$  were likely caused by reduction in low temperature constraints, and the apparent negative effects of higher  $T_{\max}$  on greenness were probably due to the accompanying decline in water availability. The dominant enhancing effect of nighttime warming indicates that climatic warming will probably have stronger impact on TP ecosystems, than on apparently similar Arctic ecosystems where vegetation is controlled mainly by  $T_{\max}$ . Our results are crucial for future improvements of dynamic vegetation models embedded in the Earth System Models which are used to describe

38 the behavior of the Asian monsoon. The results are significant because the state of the  
39 vegetation on the TP plays an important role in steering the monsoon.

40

41 **Key words:** Asymmetric warming, climate change, plant phenology, Tibetan Plateau,  
42 vegetation growth

43

## Introduction

Changes in vegetation activity substantially modify the land surface energy balance of the Tibetan Plateau (Gu *et al.*, 2008, Ma *et al.*, 2015, Shen *et al.*, 2015c). These changes can affect the atmospheric circulation over the Tibetan Plateau and, further, the strength of the Asian monsoon as well as the climate of the wider Asian continent (Wu *et al.*, 2015). Knowledge of the climatic controls on Tibetan Plateau vegetation growth is thus needed for improving our understanding of: the role of the Tibetan Plateau in the monsoon system; ecosystem responses to climate change; and how to manage the Tibetan Plateau ecosystem sustainably. Vegetation growth at high latitudes and in alpine regions is sensitive to climatic warming (Lucht *et al.*, 2002). Both *in situ* and satellite observations in these regions have revealed substantial responses in vegetation growth over the past few decades, such as earlier vegetation green-up date and greening trends (Bhatt *et al.*, 2010, Hinzman *et al.*, 2005, Kerby & Post, 2013, Parmesan, 2007, Post *et al.*, 2009, Wang *et al.*, 2015b, Xu *et al.*, 2013, Zeng *et al.*, 2011).

However, the underlying mechanisms of spring phenology and vegetation growth responses to climatic warming are not yet well understood. Recent studies reported that spring phenology and vegetation growth were more strongly and positively associated with daily maximum, rather than daily minimum, temperature in the Northern Hemisphere (Peng *et al.*, 2013, Piao *et al.*, 2015). This matters because the Earth's temperature is increasing more rapidly at night than during the daytime (IPCC, 2013). The greater dependency on daily maximum versus daily minimum temperatures may, however, not hold true in cold and dry

65 areas, where higher maximum temperatures could exacerbate drought effects, while higher  
66 minimum temperatures could alleviate frost damage. It is thus crucial to investigate the  
67 separate effects of daily increases in maximum and minimum temperature on the spring  
68 phenology and vegetation growth on the cold and dry Tibetan Plateau.

69 The Tibetan Plateau, sometimes known as the “Earth’s third pole”, has a cold climate  
70 with mean annual temperature ranging from  $-15^{\circ}\text{C}$  to  $5^{\circ}\text{C}$  (You *et al.*, 2013). Yet, because it  
71 is at a relatively low latitude the Tibetan Plateau is very different from the poles in its annual  
72 cycle of daylength and solar radiation. It has a dry climate, because in most areas annual  
73 precipitation is less than 500 mm (Piao *et al.*, 2006), whereas potential evapotranspiration is  
74 higher than 600 mm (Chen *et al.*, 2006). Growth of the alpine vegetation on the Tibetan  
75 Plateau is considered highly sensitive to temperature, and the climatic warming during the  
76 past few decades has resulted in a widespread enhancement of vegetation growth and  
77 advancement of vegetation green-up date across the plateau (Chen *et al.*, 2013, Kato *et al.*,  
78 2006, Shen *et al.*, 2015b, Wang *et al.*, 2012, Zhang *et al.*, 2013). Nevertheless, a debate is  
79 ongoing about how the vegetation spring phenology is responding to climate warming (Yu *et*  
80 *al.*, 2010, Zhang *et al.*, 2013) — mainly because of our poor understanding of the mechanisms  
81 by which temperature controls vegetation green-up date.

82 Very few studies have been conducted into the effects of daytime and nighttime warming  
83 on the Tibetan Plateau vegetation spring phenology and summer growth, although  
84 observations showed that the daily minimum temperature on the Tibetan Plateau has increased

significantly faster than the daily maximum temperature, during the past few decades (Liu *et al.*, 2006). The air temperature over the Tibetan Plateau has a wide diurnal range ('four seasons in one day'), with low temperatures close to freezing during the night even in the growing season, and high temperatures during the daytime. This large diurnal temperature range coupled with a dry climate could result in more complex impacts of daytime and nighttime warming on Tibetan Plateau vegetation than vegetation in Arctic regions, especially because growing season nights are much shorter on the Tibetan Plateau than in the Arctic.

In this study, we investigated the effects of daily maximum and minimum temperatures ( $T_{\max}$  and  $T_{\min}$ ) on *in situ* observed species-level plant green-up date (China-Meteorological-Administration, 1993) and on satellite-derived vegetation green-up date and summer (June, July, and August) greenness on the Tibetan Plateau. Three satellite-derived vegetation greenness datasets were used to determine vegetation green-up date and to indicate summer greenness, namely Normalized Difference Vegetation Index (NDVI) from MODerate resolution Imaging Spectroradiometer (MODIS; onboard the NASA Earth Observing System's satellite Terra), and from VEGETATION (onboard the satellite Système Pour l'Observation de la Terre; SPOT), and Enhanced Vegetation Index (EVI; from MODIS). Vegetation green-up date was firstly determined from each of these three datasets using four methods separately, and then averaged over the resulting 12 combinations of datasets and methods (*Methods*). This average was used for all further analyses. The average of the three greenness vegetation indices (GVI) including two NDVIs and the EVI was used as a proxy for summer vegetation activity. A temporal partial correlation analysis was applied

to determine the correlation between vegetation green-up date and greenness and climatic variables.

## **Materials and methods**

### **Datasets**

#### ***In situ* phenological observation data**

We collected species-level green-up date data at eight phenology stations on the Tibetan Plateau (Table S1). Phenological observations were made every two days for 10 individual herbaceous plants per species at each station. The species-level green-up date was defined as the date when 50% of the individuals display green leaves that have grown up to 10 mm in spring (March, April, and May) or early summer (Chen *et al.*, 2015, China-Meteorological-Administration, 1993). Only green-up date data of the dominant species at each station were selected, which means, one species per station according to the vegetation map (Editorial-Board-of-Vegetation-Map-of-China, 2001). The stations included were restricted to those with longer than 10 years observations during 1981 to 2011. For each phenological station,  $T_{\min}$  and  $T_{\max}$  and precipitation were recorded at nearby national meteorological stations (Chen *et al.*, 2015).

#### **Greenness vegetation index data**

The three satellite-derived vegetation greenness index datasets for the period 2000–2012 comprised MODIS and SPOT NDVIs (Huete *et al.*, 2002, Maisongrande *et al.*, 2004) and MODIS EVI (Huete *et al.*, 2002). NDVI and EVI are widely used to infer vegetation



phenology and growth (Myneni *et al.*, 1997, Tucker *et al.*, 1986, Xu *et al.*, 2013) because they have been shown to be indicative of variations in canopy biophysical parameters such as leaf area index and aboveground biomass (Di Bella *et al.*, 2004, Shen *et al.*, 2008, Wylie *et al.*, 2002). The MODIS NDVI and EVI data (MOD13A1, Collection 5) have a spatial resolution of 500 m and temporal resolution of 16 days. The spatial and temporal resolutions of the SPOT NDVI are 1 km and 10 days, respectively. All the NDVI and EVI data have been calibrated for errors caused by adverse atmospheric, radiometric, and geometric conditions. These vegetation index datasets have been reported to have higher data quality than the GIMMS (Global Inventory Modeling and Mapping Studies) NDVI on the Tibetan Plateau (Zhang *et al.*, 2013).

#### **Climate data**

For analyzing the relationships between temperatures and vegetation green-up date,  $T_{\max}$ ,  $T_{\min}$ , and precipitation were provided by the Data Assimilation and Modeling Center for Tibetan Multi-spheres, Institute of Tibetan Plateau Research, Chinese Academy of Sciences (Chen *et al.*, 2011). These data have a spatial resolution of  $0.1^{\circ} \times 0.1^{\circ}$ . Air temperature at 1.5 m was produced by merging the observations from operational stations of the China Meteorological Administration (CMA) with the corresponding Princeton meteorological forcing data (Sheffield *et al.*, 2006). Precipitation was produced by combining three datasets: the precipitation products (code 3B42) derived from Tropical Rainfall Measuring Mission (TRMM) (Huffman *et al.*, 2007), precipitation observations from operational stations of CMA, and the Asian Precipitation – Highly Resolution Observational Data Integration Toward

Evaluation of the Water Resources (APHRODITE) precipitation data (Yatagai *et al.*, 2009).

## **Analyses**

### **Determination of vegetation green-up date**

Before determining vegetation green-up date from NDVI or EVI, we first eliminated the effects of snow cover on NDVI or EVI for each pixel using the median value of the uncontaminated winter NDVI or EVI values (Mod13a1-Quality, 2011, Vgt-Faq, 2012) between November and the following March (Zhang *et al.*, 2006, Zhang *et al.*, 2007). After that, because clouds and poor atmospheric conditions usually depress NDVI or EVI values, when NDVI or EVI dropped abruptly during the NDVI or EVI ascending period from the beginning of a year and the occurrence of the annual NDVI or EVI maximum in summer, the measured values were replaced by the values reconstructed using the Savitzky–Golay filter (Chen *et al.*, 2004). We then determined vegetation green-up date on each of the three vegetation indices using each of the four methods respectively, including two inflection point-based methods ( $CCR_{max}$  and  $\beta_{max}$ ) and two threshold-based methods ( $G_{20}$  and  $CR_{max}$ ). In general, those methods determine the vegetation green-up date around the time when NDVI or EVI begins to increase in spring or early summer. Details of those methods are given by (Shen *et al.*, 2015a). The vegetation green-up dates calculated from 12 combinations of dataset and method were then averaged before being used for further analyses.

### **Relationships between temperature and green-up date**

To assess the impact of  $T_{min}$  on the interannual variations in green-up date, we calculated

partial correlation coefficient between time series of green-up date (species-level green-up date or vegetation green-up date) and preseason  $T_{\min}$ , setting  $T_{\max}$  and precipitation as the controlling variables. Here the preseason length was determined for  $T_{\min}$  as the period preceding multiyear averaged green-up date in which mean  $T_{\min}$  has the largest partial correlation coefficient (absolute value) with the green-up date, referred to as the preseason for  $T_{\min}$ . While determining the length of the preseason period, we used a step of 10 days to smooth potential extreme  $T_{\max}$  or  $T_{\min}$  values. We did not constrain the preseason length for precipitation to be identical to that for temperature. To assess the magnitude of the impact of preseason  $T_{\min}$  on green-up date, we determined the apparent sensitivity of green-up date to preseason  $T_{\min}$  as the coefficient in the multiple linear regressions in which the green-up date was regressed against  $T_{\min}$ ,  $T_{\max}$ , and precipitation in the preseason for  $T_{\min}$ . The impact of preseason  $T_{\max}$  on the green-up date was assessed in a similar way, and the preseason for  $T_{\max}$  was determined similarly.

## **Relationships between temperature and vegetation summer growth**

We used the average of MODIS and SPOT NDVIs and MODIS EVI as the GVI as a surrogate of vegetation summer growth. To reduce the noise in the NDVI and EVI data, maximum values were used for each month. While assessing the impacts of summer  $T_{\min}$  on summer GVI, partial correlation analysis was used to account for the impacts of summer  $T_{\max}$  and precipitation. The impact of summer  $T_{\max}$  on GVI was assessed in a similar way. Sensitivity of vegetation growth to temperature was defined as the coefficients in the multiple regression between GVI and summer  $T_{\min}$ ,  $T_{\max}$ , and precipitation.

## Results

### Response of green-up date to temperature

We found that the species-level green-up date in seven out of the eight stations were negatively correlated with preseason  $T_{\min}$  with an average correlation coefficient of  $-0.42 \pm 0.19$  (mean  $\pm$  SD), and four correlation coefficients were significantly negative ( $P < 0.05$ , Fig. 1). In contrast, a significant ( $P < 0.05$ ) negative correlation between species-level green-up date and preseason  $T_{\max}$  was observed at only one station. The sensitivity of species-level green-up date to preseason  $T_{\min}$  ranged from  $-5$  days  $K^{-1}$  to  $-2.5$  days  $K^{-1}$  with mean values of  $-4.0 \pm 1.1$  days  $K^{-1}$  at the four stations with significantly negative partial correlations between species-level green-up date and  $T_{\min}$  ( $P < 0.05$ , Fig. 1). That a majority of stations have a negative relationship between  $T_{\min}$  and species-level green-up date suggests that the increase in preseason  $T_{\min}$  could substantially advance species-level green-up timing, much more than the increase in  $T_{\max}$ . Nevertheless, it should be noted that these *in situ* species-level green-up date observations were conducted in a limited number of stations, covering a small fraction of the climate gradients and geographic ranges of the Tibetan Plateau (Table S1).

To assess whether the advancing effect of the increasing preseason  $T_{\min}$  on vegetation green-up date is prevalent over the whole Tibetan Plateau, we investigated the impacts of preseason  $T_{\min}$  and  $T_{\max}$  on satellite-derived vegetation green-up date. Viewed at regional level, vegetation green-up date was negatively correlated with preseason  $T_{\min}$  ( $P < 0.05$ , Table 1), whereas no significant correlation with preseason  $T_{\max}$  was found ( $P > 0.10$ ). In addition,

we performed partial correlation analyses between vegetation green-up date and pre-season  $T_{\min}$  and  $T_{\max}$  respectively, adding winter temperature as an extra controlling variable to exclude its impacts. We found similar results (Fig. S1a). We also studied the partial correlation between vegetation green-up date, and  $T_{\max}$  and  $T_{\min}$  using the pre-seasons for  $T_{\min}$  and  $T_{\max}$ , respectively; we again produced similar results (Fig. S2a). The stronger negative correlation between pre-season  $T_{\min}$  and vegetation green-up date to that between pre-season  $T_{\max}$  and vegetation green-up date, indicates that the advancement of vegetation green-up date on the Tibetan Plateau over the past few decades was more associated with nighttime, rather than daytime warming.

We further examined the spatial pattern of partial correlation between vegetation green-up date and pre-season  $T_{\min}$  and  $T_{\max}$ . For 78% of the pixels, vegetation green-up date was negatively correlated with pre-season  $T_{\min}$ , with 37% being significantly correlated at the  $P < 0.05$  level, mostly distributed in the eastern, northeastern, and central parts of the plateau (Fig. 2). Significant ( $P < 0.05$ ) positive correlations between vegetation green-up date and pre-season  $T_{\min}$  were observed in less than 5% of the pixels. In contrast, vegetation green-up date showed a diverse range of responses to pre-season  $T_{\max}$ . In 45% of the pixels, a positive correlation was observed, mostly in the northeastern and southwestern parts of the plateau, with 14% being significant ( $P < 0.05$ ) (Fig. 2). Negative correlations between vegetation green-up date and pre-season  $T_{\max}$  were mostly found in the central and middle-western parts and eastern edge of the plateau, and 22% of the total pixels exhibited a statistically significant negative correlation ( $P < 0.05$ ). More widespread and stronger negative partial correlations

between  $T_{\min}$  and vegetation green-up date compared with correlations between  $T_{\max}$  and vegetation green-up date, were also observed when we statistically excluded the effect of winter temperature (Figs. S1b and S1c) and when we used different definitions of preseason (that is, using preseason for  $T_{\max}$  for correlation between  $T_{\min}$  and vegetation green-up date and preseason for  $T_{\min}$  for correlation between  $T_{\max}$  and vegetation green-up date; Figs. S2b and S2c). These results suggest that nighttime warming is likely to advance vegetation green-up date in widespread areas of the Tibetan Plateau, while the advancing effect of daytime warming is limited mainly to the central and middle-eastern plateau.

The sensitivity of vegetation green-up date to temperature increase further showed a stronger impact of  $T_{\min}$  on vegetation green-up date than  $T_{\max}$ . The regression between vegetation green-up date and preseason  $T_{\min}$ ,  $T_{\max}$ , and precipitation showed that a 1 K increase in the regionally averaged preseason  $T_{\min}$  would advance average vegetation green-up date by four days ( $P < 0.05$ ), while the coefficient of  $T_{\max}$  was not significant ( $P > 0.10$ ) (Table 1). The east and northeast of the plateau exhibited sensitivities to  $T_{\min}$  with a negative sign (i.e., increasing preseason  $T_{\min}$  advances vegetation green-up date), mostly with magnitude larger than 4 days  $K^{-1}$  (Fig. 2). In the southwest and southeast of the plateau, the temperature sensitivities varied widely from less than  $-10$  days  $K^{-1}$  to more than  $+10$  days  $K^{-1}$ . vegetation green-up date sensitivity to preseason  $T_{\max}$  showed greater negative values, lower than  $-4$  days  $K^{-1}$ , in the central plateau and highly variable values, on average greater than 2 days  $K^{-1}$ , in the southwest, northeast, and southeast (Fig. 2). In general, nighttime warming is likely to have advanced vegetation green-up date in more areas of the Tibetan

Plateau and with a greater magnitude than daytime warming.

### **Responses of vegetation greenness to temperature in summer**

Summer GVI showed a strong positive partial correlation with summer  $T_{\min}$  ( $R = 0.87$ ,  $P < 0.01$ , [Table 1](#)). The positive correlations were mainly observed in the northeast and central parts of the plateau, and in 22% of the total pixels this positive correlation was marginally significant at  $P < 0.10$  level (Fig. 3). Only in about 3% of the pixels was there a statistically significant negative correlation between GVI and summer  $T_{\min}$  (at  $P < 0.10$ ). In contrast to  $T_{\min}$ , the regionally averaged GVI showed a significant negative correlation with summer  $T_{\max}$  ( $P < 0.05$ , [Table 1](#)), indicating a negative impact of increasing summer  $T_{\max}$  on summer greenness. The relationship between GVI and summer  $T_{\max}$  showed substantial spatial variation (Fig. 3). In the western half and the northeast of the plateau, correlations were mostly negative, with 11% of the total pixels being significant at the  $P < 0.10$  level, while in the center and southeast the correlations were mostly insignificantly positive.

We further determined the sensitivity of summer GVI to summer  $T_{\min}$  and  $T_{\max}$  by regressing GVI against  $T_{\min}$ ,  $T_{\max}$ , and precipitation. As expected, the GVI averaged for the Tibetan Plateau was more sensitive to summer  $T_{\min}$  than to  $T_{\max}$  ([Table 1](#)). A 1-°C increase in summer  $T_{\min}$  enhanced GVI by 3.6% of the mean GVI of 2000-2004 ( $P < 0.01$ ). In contrast, increases in higher summer  $T_{\max}$  reduced GVI by 2.6%  $K^{-1}$  ( $P < 0.05$ ). The spatial pattern of the sensitivity was slightly different to that of correlation, but they shared the same sign. The majority of pixels with a high sensitivity ( $> 0.03$  GVI units per K) of GVI to summer  $T_{\min}$

were found in the plateau center, and the northeast part had slightly lower sensitivity (Fig. 3). On the other hand, greater negative impacts of summer  $T_{\max}$  on GVI ( $< -0.03$  GVI units per K) were found in the south of the plateau. For the rest of the plateau, the sensitivity of GVI to temperature change was much lower (Fig. 3).

## Discussion

### Asymmetric effects of $T_{\max}$ versus $T_{\min}$ on vegetation green-up date and summer greenness

In most middle and high latitude areas in the Northern Hemisphere, plant leaf onset is determined mainly by preseason  $T_{\max}$  (Piao *et al.*, 2015). In contrast to this general pattern, our results for the Tibetan Plateau clearly show greater control by preseason  $T_{\min}$  over vegetation green-up date than by preseason  $T_{\max}$ . There are several reasons why vegetation in the Tibetan Plateau could be more sensitive to  $T_{\min}$  than to  $T_{\max}$ . First is the very low  $T_{\min}$  and the associated risk of frost damage. On the Tibetan Plateau, the preseason  $T_{\min}$  is commonly below  $-5^{\circ}\text{C}$  (Figs. S3-S5), which may put a strong constraint on plant developmental processes (such as break of ecodormancy, bud growth, and leaf unfolding) associated with green-up onset (Horvath *et al.*, 2003, Körner, 2015). Low temperatures may also directly injure cell structures. To mitigate the high risk of freezing injury at low temperatures, plants may slow or postpone developmental processes and thus retard spring leaf unfolding (Vitasse *et al.*, 2014). In addition, the frozen soil water under low temperature could also limit water absorption by the roots of the alpine plants (Pangtey *et al.*, 1990). On the Tibetan Plateau where winter and early spring is dry, soil water availability is largely dependent on the spring



thaw. Whereas, the spring thaw on the plateau was constrained by the low soil temperature (Wan *et al.*, 2012, Yang *et al.*, 2013, Yi *et al.*, 2013, Zhang *et al.*, 2005). Increasing nighttime temperature may, therefore, help to remove such constraints and thus advance green-up onset. Such a process would explain the observed correlations with  $T_{\min}$ .

In contrast to the clear relation with  $T_{\min}$ , we did not find a statistically significant partial correlation between regionally averaged preseason  $T_{\max}$  and vegetation green-up date. This may be related to the confounding effects of water availability and  $T_{\max}$  on the green-up dates on the Tibetan Plateau. Alpine steppe and alpine meadow comprise most of the vegetation on the Tibetan Plateau, and spring growth of these vegetation types is suggested to be limited by low water availability (Dorji *et al.*, 2013, Pangtey *et al.*, 1990, Shen *et al.*, 2015a, Shen *et al.*, 2011). In the areas with less preseason precipitation and high  $T_{\max}$ , daytime warming may be associated with higher evaporation and reduced soil water availability, and thus lead to a positive or weak correlation between  $T_{\max}$  and vegetation green-up date (Figs. S6, S7a and S7b). In contrast, in the wetter areas where there is less water stress, such as the central and middle-eastern plateau,  $T_{\max}$  increase could effectively advance green-up date. For instance, ground-based observations showed that moisture appeared to be growth limiting for of a dwarf shrub species in a dry area Tibetan Plateau, particularly the moisture loss due to high maximum temperature in May and June (Liang *et al.*, 2012). Preseason  $T_{\max}$  is higher than 5 °C in most areas of the Tibetan Plateau (Figs. S3-S5). The high  $T_{\max}$  and dry climate in the Tibetan Plateau may both, therefore, cause a weak correlation between the  $T_{\max}$  and green-up dates. However, the mechanisms through which  $T_{\max}$  and precipitation co-determine

vegetation green-up date still remain unclear. Further experimental studies are thus needed to identify the physiological mechanisms underlying the asymmetric impacts of  $T_{\min}$  and  $T_{\max}$  on vegetation green-up date.

Besides temperatures and precipitation, photoperiod and snow melting date may potentially be the drivers of the plant spring phenology in cold climates (Körner, 2007, Keller & Körner, 2003, Sedlacek *et al.*, 2015). For photoperiod-sensitive plants, photoperiod should be above a threshold to permit temperature-driven development (Basler & Körner, 2012, Körner, 2007). However, a previous study showed that the internannual variations in vegetation green-up date were not related to sunshine duration in most areas of the Tibetan Plateau (Wang *et al.*, 2015a). This suggests that the vegetation may be not sensitive to photoperiod or photoperiod threshold is fulfilled during the study period. As to the effect of snow cover changes, plants in concave terrain with secure snow cover may track temperature whenever snow melts (Sedlacek *et al.*, 2015). On the Tibetan Plateau, however, an earlier study suggest that the interannual variations in green-up date averaged over the Plateau seems unlikely to result from changes in snow melt dates (Yu *et al.*, 2010). This could be a result of the low fraction of snow cover during the period preceding green-up date (Fig. S8). Therefore, the stronger effect of  $T_{\min}$  on the green-up date was not likely caused by the changes in photoperiod and snow melting date.

In addition, we also observed spatially varying sensitivity of vegetation green-up date to preseason  $T_{\max}$  (Fig. 2) and we have shown that such variability was associated to the

preseason precipitation (Fig. S7b) (but note that the water availability is also dependent on soil water holding capacity). In comparison, there was lower spatial variability in the sensitivity of green-up date to  $T_{\min}$  and we are still unclear what environmental factor dominates such variability or how interactions between multiple environmental factors resulted in the variability. Moreover, the different phenological strategies and varying species compositions across the communities in the Tibetan Plateau should also contribute to variability in the observation relationships between green-up date and temperatures.

Unlike in boreal ecosystems where increases in summer  $T_{\max}$  have been observed to stimulate summer vegetation growth (Tan *et al.*, 2015), on the Tibetan Plateau the positive correlation between summer GVI and summer  $T_{\min}$  suggests that vegetation growth was likely still constrained by low  $T_{\min}$ . As given in Fig. S9a, in most areas of the plateau, the mean summer  $T_{\min}$  is still below 5 °C, and such a low temperature allows little growth (Körner, 2003, Körner, 2015). This explanation is also consistent with the stronger positive correlation between GVI and  $T_{\min}$  in areas with lower summer  $T_{\min}$  (Fig. S9b). Previous ground-based observations have also found positive effects of higher summer  $T_{\min}$  on plant growth on the Tibetan Plateau (Liang *et al.*, 2009, Zhu *et al.*, 2011). Higher summer  $T_{\min}$  may thus promote vegetation growth by reducing the constraints of low temperature and such benefit would be greater in the areas with lower summer  $T_{\min}$  (Fig. S9b). On the other hand, under high summer  $T_{\max}$  (Fig. S10), further temperature increases may not enhance vegetation growth, but instead depress it by reducing root zone water content on the Tibetan Plateau (Peng *et al.*, 2013). This also helps to explain the stronger negative impact of higher summer  $T_{\max}$  on the vegetation

growth in more arid areas (Fig. S11).

## Implications

Vegetation green-up date on the Tibetan Plateau advanced by 15-18 days during the 1980s and 1990s (Piao *et al.*, 2011, Yu *et al.*, 2010, Zhang *et al.*, 2013). This is about 2-3 times the average for the latitude band 40 °N–70 °N (6.4 days for Eurasia and 7.7 days for North America) (Zhou *et al.*, 2001), despite the smaller climatic warming on the Tibetan Plateau on the basis of mean daily temperature (Hansen *et al.*, 2010). The stronger response of phenology is probably due to the dependence of Tibetan Plateau vegetation green-up date on preseason  $T_{\min}$  (while in the Arctic and in other northern middle and high latitude regions, vegetation green-up date is mainly cued by preseason  $T_{\max}$  (Piao *et al.*, 2015)), but also because preseason  $T_{\min}$  has increased more rapidly than preseason  $T_{\max}$  during this period. During the past decade, the decrease in preseason precipitation and daytime warming-induced soil water loss may have counteracted the advancing effect of warming on the green-up date on the Tibetan Plateau. In general, the controls of  $T_{\min}$  on both the vegetation green-up date and summer growth indicate that the ongoing climate change, in which nighttime warming is more intensive than daytime, could impose stronger impacts on the Tibetan Plateau ecosystems than on Arctic ecosystems.

Same to the most of the other regions on the Earth (Easterling *et al.*, 1997), the Tibetan Plateau is warming faster during night than during day, resulting in a decreasing diurnal temperature range. Such decrease in diurnal temperature range has been attributed to changes

in cloud cover, soil moisture, precipitation, solar radiation, and vegetation activity (e.g. leaf area index), but it remains unknown whether nighttime warming and daytime warming will interact with each other. The stronger positive effects of nighttime warming on vegetation growth in the summer and the net cooling effect of enhanced vegetation growth during daytime because of stronger effect of evaporative cooling over warming effect of albedo decrease (Shen *et al.*, 2015c) suggest that nighttime warming may dampen daytime warming on the Tibetan Plateau, thus contributing to the decreases in diurnal temperature range. Moreover, the advance in vegetation green-up caused by the increase in pre-season  $T_{\min}$  could also result in higher greenness in late spring or early summer, suggesting that pre-season nighttime warming may have a cooling effect on growing season  $T_{\max}$ .

Based on the projected higher precipitation and temperature (Diffenbaugh & Field, 2013, Su *et al.*, 2013), we may expect that climate change will impact the alpine vegetation growth in a positive way. Yet, the dominant role of  $T_{\min}$  warming suggests that the future impacts could continue to be greater on the Tibetan Plateau than on other regions which are more responsive to  $T_{\max}$ . The enhancement of vegetation activity could strengthen the influence of vegetation on ecosystem structure and processes, and on surface energy partitioning; these influences could further strengthen the regional atmospheric circulation that affects Asian climate. The evidence provided in this study improves our understanding of how the Tibetan Plateau vegetation responds to climate change and creates the opportunity for a more realistic representation of vegetation phenology and growth in land surface models — an improvement which is urgently needed for reducing uncertainty in Earth-atmosphere

interaction modeling (Shen *et al.*, 2015c).

Such modeling efforts will include interpreting the satellite retrievals of vegetation phenology and growth from ecophysiological findings at species level. In this study, green-up dates at both species and community levels were used to assess the phenological response to  $T_{\min}$  and  $T_{\max}$ . The two datasets are in accordance with each other regarding the stronger effect of pre-season  $T_{\min}$  on green-up date than  $T_{\max}$ . To know how well they correlated with each other, we calculated the Pearson's correlation coefficient between the time series of the satellite-derived vegetation green-up date and *in situ* species-level green-up date of the dominant species at each of the 8 phenological stations for the overlapped years (10-12 years). We found that vegetation green-up date was positively correlated with species-level green-up date at 7 out of the 8 stations, and that 42.9% of the positive correlations were significant at  $P < 0.05$  level. No significant correlation ( $P = 0.19$ ) between vegetation green-up date and species-level green-up date was found (Table S2). Vegetation green-up date is determined on the greenness vegetation indices NDVI and EVI which are well related to leaf area index or aboveground green biomass over pixel-sized area where there could be dozens of species exhibiting different leafing stages, while species-level green-up date is based on leaf length for a limited number of individuals for one species. Therefore, vegetation green-up date should differ from species-level green-up date unless the species-level green-up date of a limited number of individuals for one species could indicate the seasonal change of greenness for the pixel-sized area where the station locates. We call for higher representativeness of ground phenological observations regarding large number plant species and a variety of

climate regimes on the plateau and further study to bridge the two kinds of phenological observations.

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**Table 1**

Impacts of  $T_{\min}$  and  $T_{\max}$  on vegetation green-up date and summer greenness (GVI). For partial correlation between green-up date and  $T_{\min}$ , preseason for  $T_{\min}$  was used, and for correlation between green-up date and  $T_{\max}$ , preseason for correlation was used. For sensitivity of green-up date to  $T_{\min}$ , preseason for  $T_{\min}$  was used, and for sensitivity to  $T_{\max}$ , preseason for  $T_{\max}$  was used. Here 0.015 GVI unit and 0.10 GVI units (the magnitude of the two sensitivities) are equivalent to about 3.6% and 2.6% of the mean GVI of 2000-2004, respectively. Significance: \*\*\* and \*\* indicate significance levels at  $P < 0.05$  and at  $P < 0.01$ , respectively. Correlation and sensitivity with no asterisk are not significant ( $P > 0.10$ ).

	$T_{\min}$	$T_{\max}$
Partial coefficient between vegetation green-up date and temperature	-0.64**	-0.48
Sensitivity of vegetation green-up date to temperature (day/K)	-4.17**	-2.56
Partial coefficient between GVI and temperature	0.87***	-0.65**
Sensitivity of GVI to temperature (1/K)	0.015***	-0.011**

## Figure captions

**Fig. 1.** Top, Partial correlation coefficient between species-level green-up date of dominant species and preseason  $T_{\min}$  and  $T_{\max}$ , setting respectively preseason  $T_{\max}$  and  $T_{\min}$  and precipitation as controlling variables at each of eight phenological stations (Table S1) on the Tibetan Plateau. For correlation between green-up date and  $T_{\min}$ , preseason for  $T_{\min}$  was used, and for correlation between green-up date and  $T_{\max}$ , preseason for  $T_{\max}$  was used. Bottom, Sensitivities of species-level green-up date to preseason  $T_{\min}$  and  $T_{\max}$ . Significance: \*\*\*  $P < 0.01$ ; \*\*  $P < 0.05$ ; \*  $P < 0.10$ . Correlations with no asterisk are not significant ( $P > 0.10$ ).

**Fig. 2.** Top, spatial pattern of partial correlation coefficient ( $R_p$ ) between vegetation green-up date and  $T_{\min}$  or  $T_{\max}$ . For correlation between green-up date and  $T_{\min}$ , preseason for  $T_{\min}$  was used, and for correlation between green-up date and  $T_{\max}$ , preseason for  $T_{\max}$  was used.  $R=\pm 0.60$ ,  $R=\pm 0.52$ ,  $R=\pm 0.42$ ,  $R=\pm 0.34$  correspond to the 5%, 10%, 20%, 30% significance levels, respectively. Bottom, spatial patterns of sensitivities of vegetation green-up date to preseason  $T_{\min}$  and  $T_{\max}$ , respectively. Inset in each panel shows the percentage of the pixels in each interval of correlation coefficient or sensitivity with the interval value indicated by the color in the legend in the right.

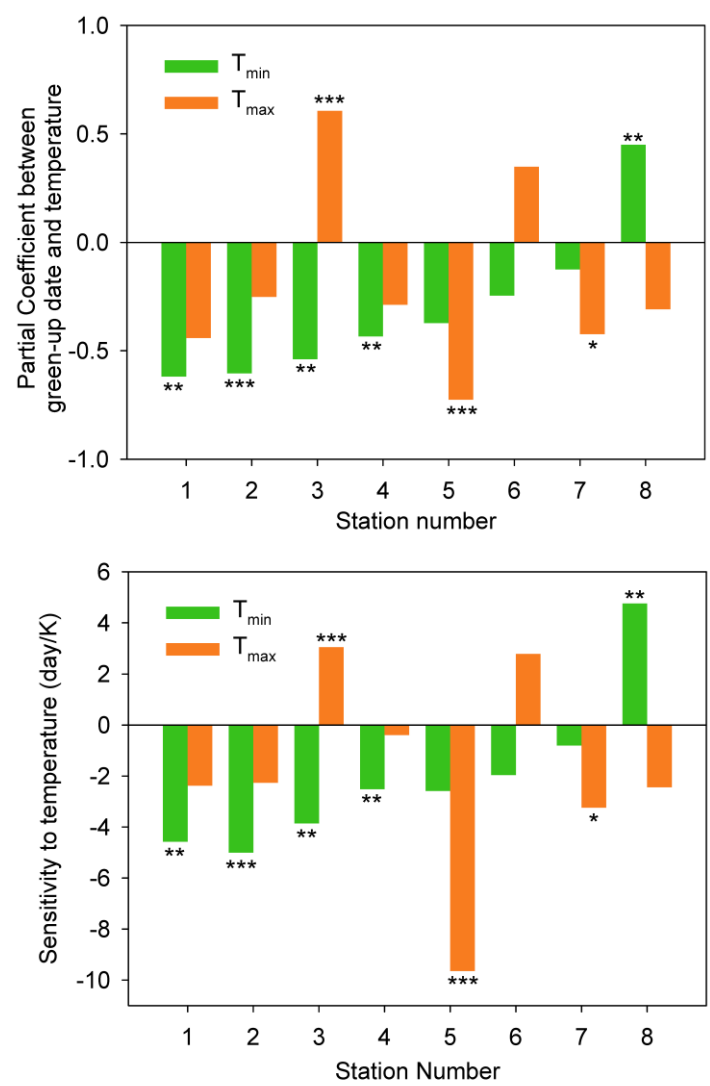
**Fig. 3.** Top, spatial patterns of partial correlation coefficient between summer GVI and

640 summer  $T_{\min}$ , and  $T_{\max}$ , respectively.  $R=\pm 0.60$ ,  $R=\pm 0.52$ ,  $R=\pm 0.42$ ,  $R=\pm 0.34$  correspond to the  
641 5%, 10%, 20%, 30% significance levels, respectively. Bottom, spatial patterns of sensitivities  
642 of summer GVI to summer  $T_{\min}$  and  $T_{\max}$ , respectively. Inset in each panel shows the  
643 percentage of the pixels in each interval of correlation coefficient or sensitivity with the  
644 interval value indicated by the color in the legend in the right.

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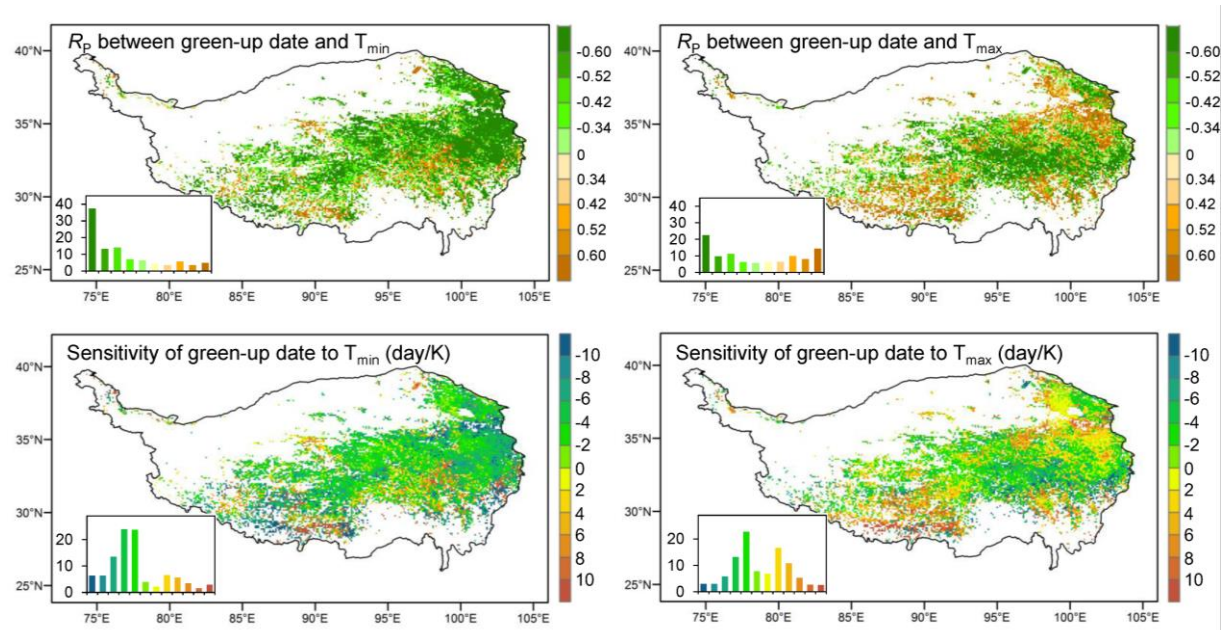
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647 **Figure 1**  
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651 **Figure 2**

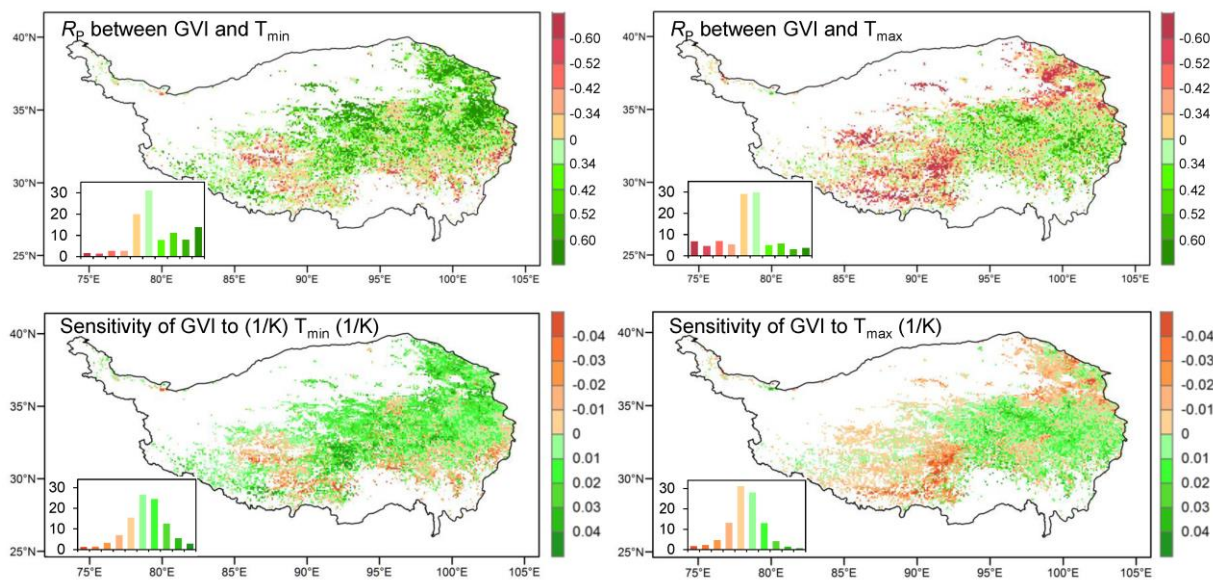


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654 **Figure 3**



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