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

3

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16

17 **Abstract**

18 Understanding vegetation responses to climate change on the Tibetan Plateau (TP) helps in
19 elucidating the land-atmosphere energy exchange, which affects air mass movement over and
20 around the TP. Although the TP is one of the world's most sensitive regions in terms of
21 climatic warming, little is known about how the vegetation responds. Here we focus on how
22 the spring phenology and summertime greenness respond to the asymmetric warming, i.e.,
23 stronger warming during nighttime than during daytime. Using both *in situ* and satellite
24 observations, we found that vegetation green-up date showed a stronger negative partial
25 correlation with daily minimum temperature (T_{\min}) than with maximum temperature (T_{\max})
26 before growing season (“preseason” henceforth). Summer vegetation greenness was strongly
27 positively correlated with summer T_{\min} , but negatively with T_{\max} . A 1-K increase in preseason
28 T_{\min} advanced green-up date by four days ($P < 0.05$), and in summer enhanced greenness by
29 3.6% of the mean greenness of 2000-2004 ($P < 0.01$). In contrast, increases in preseason T_{\max}
30 did not advance green-up date ($P > 0.10$) and higher summer T_{\max} even reduced greenness by
31 2.6% K^{-1} ($P < 0.05$). The stimulating effects of increasing T_{\min} were likely caused by
32 reduction in low temperature constraints, and the apparent negative effects of higher T_{\max} on
33 greenness were probably due to the accompanying decline in water availability. The dominant
34 enhancing effect of nighttime warming indicates that climatic warming will probably have
35 stronger impact on TP ecosystems, than on apparently similar Arctic ecosystems where
36 vegetation is controlled mainly by T_{\max} . Our results are crucial for future improvements of
37 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

44 **Introduction**

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

58 However, the underlying mechanisms of spring phenology and vegetation growth
59 responses to climatic warming are not yet well understood. Recent studies reported that spring
60 phenology and vegetation growth were more strongly and positively associated with daily
61 maximum, rather than daily minimum, temperature in the Northern Hemisphere (Peng *et al.*,
62 2013, Piao *et al.*, 2015). This matters because the Earth's temperature is increasing more
63 rapidly at night than during the daytime (IPCC, 2013). The greater dependency on daily
64 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 $-15\text{ }^{\circ}\text{C}$ to $5\text{ }^{\circ}\text{C}$ (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

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

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

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

108 **Materials and methods**

109 **Datasets**

110 ***In situ* phenological observation data**

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

122 **Greenness vegetation index data**

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

126 phenology and growth (Myneni *et al.*, 1997, Tucker *et al.*, 1986, Xu *et al.*, 2013) because they
127 have been shown to be indicative of variations in canopy biophysical parameters such as leaf
128 area index and aboveground biomass (Di Bella *et al.*, 2004, Shen *et al.*, 2008, Wylie *et al.*,
129 2002). The MODIS NDVI and EVI data (MOD13A1, Collection 5) have a spatial resolution
130 of 500 m and temporal resolution of 16 days. The spatial and temporal resolutions of the
131 SPOT NDVI are 1 km and 10 days, respectively. All the NDVI and EVI data have been
132 calibrated for errors caused by adverse atmospheric, radiometric, and geometric conditions.
133 These vegetation index datasets have been reported to have higher data quality than the
134 GIMMS (Global Inventory Modeling and Mapping Studies) NDVI on the Tibetan Plateau
135 (Zhang *et al.*, 2013).

136 **Climate data**

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

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

148 **Analyses**

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

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

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

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

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

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

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

188 **Results**

189 **Response of green-up date to temperature**

190 We found that the species-level green-up date in seven out of the eight stations were
191 negatively correlated with pre-season T_{\min} with an average correlation coefficient of
192 -0.42 ± 0.19 (mean \pm SD), and four correlation coefficients were significantly negative ($P <$
193 0.05 , Fig. 1). In contrast, a significant ($P < 0.05$) negative correlation between species-level
194 green-up date and pre-season T_{\max} was observed at only one station. The sensitivity of
195 species-level green-up date to pre-season T_{\min} ranged from -5 days K^{-1} to -2.5 days K^{-1} with
196 mean values of -4.0 ± 1.1 days K^{-1} at the four stations with significantly negative partial
197 correlations between species-level green-up date and T_{\min} ($P < 0.05$, Fig. 1). That a majority of
198 stations have a negative relationship between T_{\min} and species-level green-up date suggests
199 that the increase in pre-season T_{\min} could substantially advance species-level green-up timing,
200 much more than the increase in T_{\max} . Nevertheless, it should be noted that these *in situ*
201 species-level green-up date observations were conducted in a limited number of stations,
202 covering a small fraction of the climate gradients and geographic ranges of the Tibetan
203 Plateau (Table S1).

204 To assess whether the advancing effect of the increasing pre-season T_{\min} on vegetation
205 green-up date is prevalent over the whole Tibetan Plateau, we investigated the impacts of
206 pre-season T_{\min} and T_{\max} on satellite-derived vegetation green-up date. Viewed at regional
207 level, vegetation green-up date was negatively correlated with pre-season T_{\min} ($P < 0.05$, [Table](#)
208 [1](#)), whereas no significant correlation with pre-season T_{\max} was found ($P > 0.10$). In addition,

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

218 We further examined the spatial pattern of partial correlation between vegetation
219 green-up date and preseason T_{\min} and T_{\max} . For 78% of the pixels, vegetation green-up date
220 was negatively correlated with preseason T_{\min} , with 37% being significantly correlated at the
221 $P < 0.05$ level, mostly distributed in the eastern, northeastern, and central parts of the plateau
222 (Fig. 2). Significant ($P < 0.05$) positive correlations between vegetation green-up date and
223 preseason T_{\min} were observed in less than 5% of the pixels. In contrast, vegetation green-up
224 date showed a diverse range of responses to preseason T_{\max} . In 45% of the pixels, a positive
225 correlation was observed, mostly in the northeastern and southwestern parts of the plateau,
226 with 14% being significant ($P < 0.05$) (Fig. 2). Negative correlations between vegetation
227 green-up date and preseason T_{\max} were mostly found in the central and middle-western parts
228 and eastern edge of the plateau, and 22% of the total pixels exhibited a statistically significant
229 negative correlation ($P < 0.05$). More widespread and stronger negative partial correlations

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

238 The sensitivity of vegetation green-up date to temperature increase further showed a
239 stronger impact of T_{\min} on vegetation green-up date than T_{\max} . The regression between
240 vegetation green-up date and preseason T_{\min} , T_{\max} , and precipitation showed that a 1 K
241 increase in the regionally averaged preseason T_{\min} would advance average vegetation
242 green-up date by four days ($P < 0.05$), while the coefficient of T_{\max} was not significant ($P >$
243 0.10) (Table 1). The east and northeast of the plateau exhibited sensitivities to T_{\min} with a
244 negative sign (i.e., increasing preseason T_{\min} advances vegetation green-up date), mostly with
245 magnitude larger than 4 days K^{-1} (Fig. 2). In the southwest and southeast of the plateau, the
246 temperature sensitivities varied widely from less than -10 days K^{-1} to more than $+10 \text{ days}$
247 K^{-1} . vegetation green-up date sensitivity to preseason T_{\max} showed greater negative values,
248 lower than -4 days K^{-1} , in the central plateau and highly variable values, on average greater
249 than 2 days K^{-1} , in the southwest, northeast, and southeast (Fig. 2). In general, nighttime
250 warming is likely to have advanced vegetation green-up date in more areas of the Tibetan

251 Plateau and with a greater magnitude than daytime warming.

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

253 Summer GVI showed a strong positive partial correlation with summer T_{\min} ($R = 0.87$, $P <$
254 0.01 , [Table 1](#)). The positive correlations were mainly observed in the northeast and central
255 parts of the plateau, and in 22% of the total pixels this positive correlation was marginally
256 significant at $P < 0.10$ level (Fig. 3). Only in about 3% of the pixels was there a statistically
257 significant negative correlation between GVI and summer T_{\min} (at $P < 0.10$). In contrast to
258 T_{\min} , the regionally averaged GVI showed a significant negative correlation with summer T_{\max}
259 ($P < 0.05$, [Table 1](#)), indicating a negative impact of increasing summer T_{\max} on summer
260 greenness. The relationship between GVI and summer T_{\max} showed substantial spatial
261 variation (Fig. 3). In the western half and the northeast of the plateau, correlations were
262 mostly negative, with 11% of the total pixels being significant at the $P < 0.10$ level, while in
263 the center and southeast the correlations were mostly insignificantly positive.

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

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

275 **Discussion**

276 **Asymmetric effects of T_{\max} versus T_{\min} on vegetation green-up date and summer** 277 **greenness**

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

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

296 In contrast to the clear relation with T_{\min} , we did not find a statistically significant partial
297 correlation between regionally averaged preseason T_{\max} and vegetation green-up date. This
298 may be related to the confounding effects of water availability and T_{\max} on the green-up dates
299 on the Tibetan Plateau. Alpine steppe and alpine meadow comprise most of the vegetation on
300 the Tibetan Plateau, and spring growth of these vegetation types is suggested to be limited by
301 low water availability (Dorji *et al.*, 2013, Pangtey *et al.*, 1990, Shen *et al.*, 2015a, Shen *et al.*,
302 2011). In the areas with less preseason precipitation and high T_{\max} , daytime warming may be
303 associated with higher evaporation and reduced soil water availability, and thus lead to a
304 positive or weak correlation between T_{\max} and vegetation green-up date (Figs. S6, S7a and
305 S7b). In contrast, in the wetter areas where there is less water stress, such as the central and
306 middle-eastern plateau, T_{\max} increase could effectively advance green-up date. For instance,
307 ground-based observations showed that moisture appeared to be growth limiting for of a
308 dwarf shrub species in a dry area Tibetan Plateau, particularly the moisture loss due to high
309 maximum temperature in May and June (Liang *et al.*, 2012). Preseason T_{\max} is higher than 5
310 °C in most areas of the Tibetan Plateau (Figs. S3-S5). The high T_{\max} and dry climate in the
311 Tibetan Plateau may both, therefore, cause a weak correlation between the T_{\max} and green-up
312 dates. However, the mechanisms through which T_{\max} and precipitation co-determine

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

316 Besides temperatures and precipitation, photoperiod and snow melting date may
317 potentially be the drivers of the plant spring phenology in cold climates (Körner, 2007, Keller
318 & Körner, 2003, Sedlacek *et al.*, 2015). For photoperiod-sensitive plants, photoperiod
319 should be above a threshold to permit temperature-driven development (Basler & Körner,
320 2012, Körner, 2007). However, a previous study showed that the internannual variations in
321 vegetation green-up date were not related to sunshine duration in most areas of the Tibetan
322 Plateau (Wang *et al.*, 2015a). This suggests that the vegetation may be not sensitive to
323 photoperiod or photoperiod threshold is fulfilled during the study period. As to the effect of
324 snow cover changes, plants in concave terrain with secure snow cover may track temperature
325 whenever snow melts (Sedlacek *et al.*, 2015). On the Tibetan Plateau, however, an earlier
326 study suggest that the interannual variations in green-up date averaged over the Plateau seems
327 unlikely to result from changes in snow melt dates (Yu *et al.*, 2010). This could be a result of
328 the low fraction of snow cover during the period preceding green-up date (Fig. S8). Therefore,
329 the stronger effect of T_{\min} on the green-up date was not likely caused by the changes in
330 photoperiod and snow melting date.

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

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

340 Unlike in boreal ecosystems where increases in summer T_{\max} have been observed to
341 stimulate summer vegetation growth (Tan *et al.*, 2015), on the Tibetan Plateau the positive
342 correlation between summer GVI and summer T_{\min} suggests that vegetation growth was likely
343 still constrained by low T_{\min} . As given in Fig. S9a, in most areas of the plateau, the mean
344 summer T_{\min} is still below 5 °C, and such a low temperature allows little growth (Körner,
345 2003, Körner, 2015). This explanation is also consistent with the stronger positive correlation
346 between GVI and T_{\min} in areas with lower summer T_{\min} (Fig. S9b). Previous ground-based
347 observations have also found positive effects of higher summer T_{\min} on plant growth on the
348 Tibetan Plateau (Liang *et al.*, 2009, Zhu *et al.*, 2011). Higher summer T_{\min} may thus promote
349 vegetation growth by reducing the constraints of low temperature and such benefit would be
350 greater in the areas with lower summer T_{\min} (Fig. S9b). On the other hand, under high summer
351 T_{\max} (Fig. S10), further temperature increases may not enhance vegetation growth, but instead
352 depress it by reducing root zone water content on the Tibetan Plateau (Peng *et al.*, 2013). This
353 also helps to explain the stronger negative impact of higher summer T_{\max} on the vegetation

354 growth in more arid areas (Fig. S11).

355 **Implications**

356 Vegetation green-up date on the Tibetan Plateau advanced by 15-18 days during the 1980s and
357 1990s (Piao *et al.*, 2011, Yu *et al.*, 2010, Zhang *et al.*, 2013). This is about 2-3 times the
358 average for the latitude band 40 °N–70 °N (6.4 days for Eurasia and 7.7 days for North
359 America) (Zhou *et al.*, 2001), despite the smaller climatic warming on the Tibetan Plateau on
360 the basis of mean daily temperature (Hansen *et al.*, 2010). The stronger response of phenology
361 is probably due to the dependence of Tibetan Plateau vegetation green-up date on preseason
362 T_{\min} (while in the Arctic and in other northern middle and high latitude regions, vegetation
363 green-up date is mainly cued by preseason T_{\max} (Piao *et al.*, 2015)), but also because
364 preseason T_{\min} has increased more rapidly than preseason T_{\max} during this period. During the
365 past decade, the decrease in preseason precipitation and daytime warming-induced soil water
366 loss may have counteracted the advancing effect of warming on the green-up date on the
367 Tibetan Plateau. In general, the controls of T_{\min} on both the vegetation green-up date and
368 summer growth indicate that the ongoing climate change, in which nighttime warming is
369 more intensive than daytime, could impose stronger impacts on the Tibetan Plateau
370 ecosystems than on Arctic ecosystems.

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

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

384 Based on the projected higher precipitation and temperature (Diffenbaugh & Field,
385 2013, Su *et al.*, 2013), we may expect that climate change will impact the alpine vegetation
386 growth in a positive way. Yet, the dominant role of T_{\min} warming suggests that the future
387 impacts could continue to be greater on the Tibetan Plateau than on other regions which are
388 more responsive to T_{\max} . The enhancement of vegetation activity could strengthen the
389 influence of vegetation on ecosystem structure and processes, and on surface energy
390 partitioning; these influences could further strengthen the regional atmospheric circulation
391 that affects Asian climate. The evidence provided in this study improves our understanding of
392 how the Tibetan Plateau vegetation responds to climate change and creates the opportunity for
393 a more realistic representation of vegetation phenology and growth in land surface models —
394 an improvement which is urgently needed for reducing uncertainty in Earth-atmosphere

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

396 Such modeling efforts will include interpreting the satellite retrievals of vegetation
397 phenology and growth from ecophysiological findings at species level. In this study, green-up
398 dates at both species and community levels were used to assess the phenological response to
399 T_{\min} and T_{\max} . The two datasets are in accordance with each other regarding the stronger effect
400 of pre-season T_{\min} on green-up date than T_{\max} . To know how well they correlated with each
401 other, we calculated the Pearson's correlation coefficient between the time series of the
402 satellite-derived vegetation green-up date and *in situ* species-level green-up date of the
403 dominant species at each of the 8 phenological stations for the overlapped years (10-12 years).
404 We found that vegetation green-up date was positively correlated with species-level green-up
405 date at 7 out of the 8 stations, and that 42.9% of the positive correlations were significant at P
406 < 0.05 level. No significant correlation ($P = 0.19$) between vegetation green-up date and
407 species-level green-up date was found (Table S2). Vegetation green-up date is determined on
408 the greenness vegetation indices NDVI and EVI which are well related to leaf area index or
409 aboveground green biomass over pixel-sized area where there could be dozens of species
410 exhibiting different leafing stages, while species-level green-up date is based on leaf length
411 for a limited number of individuals for one species. Therefore, vegetation green-up date
412 should differ from species-level green-up date unless the species-level green-up date of a
413 limited number of individuals for one species could indicate the seasonal change of greenness
414 for the pixel-sized area where the station locates. We call for higher representativeness of
415 ground phenological observations regarding large number plant species and a variety of

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

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604

605

606 **Table 1**

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

615

	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**

616

617

618

619 **Figure captions**

620

621 **Fig. 1.** Top, Partial correlation coefficient between species-level green-up date of dominant
622 species and preseason T_{\min} and T_{\max} , setting respectively preseason T_{\max} and T_{\min} and
623 precipitation as controlling variables at each of eight phenological stations (Table S1) on the
624 Tibetan Plateau. For correlation between green-up date and T_{\min} , preseason for T_{\min} was used,
625 and for correlation between green-up date and T_{\max} , preseason for T_{\max} was used. Bottom,
626 Sensitivities of species-level green-up date to preseason T_{\min} and T_{\max} . Significance: *** $P <$
627 0.01 ; ** $P < 0.05$; * $P < 0.10$. Correlations with no asterisk are not significant ($P > 0.10$).

628

629 **Fig. 2.** Top, spatial pattern of partial correlation coefficient (R_p) between vegetation green-up
630 date and T_{\min} or T_{\max} . For correlation between green-up date and T_{\min} , preseason for T_{\min} was
631 used, and for correlation between green-up date and T_{\max} , preseason for T_{\max} was used.
632 $R=\pm 0.60$, $R=\pm 0.52$, $R=\pm 0.42$, $R=\pm 0.34$ correspond to the 5%, 10%, 20%, 30% significance
633 levels, respectively. Bottom, spatial patterns of sensitivities of vegetation green-up date to
634 preseason T_{\min} and T_{\max} , respectively. Inset in each panel shows the percentage of the pixels in
635 each interval of correlation coefficient or sensitivity with the interval value indicated by the
636 color in the legend in the right.

637

638

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

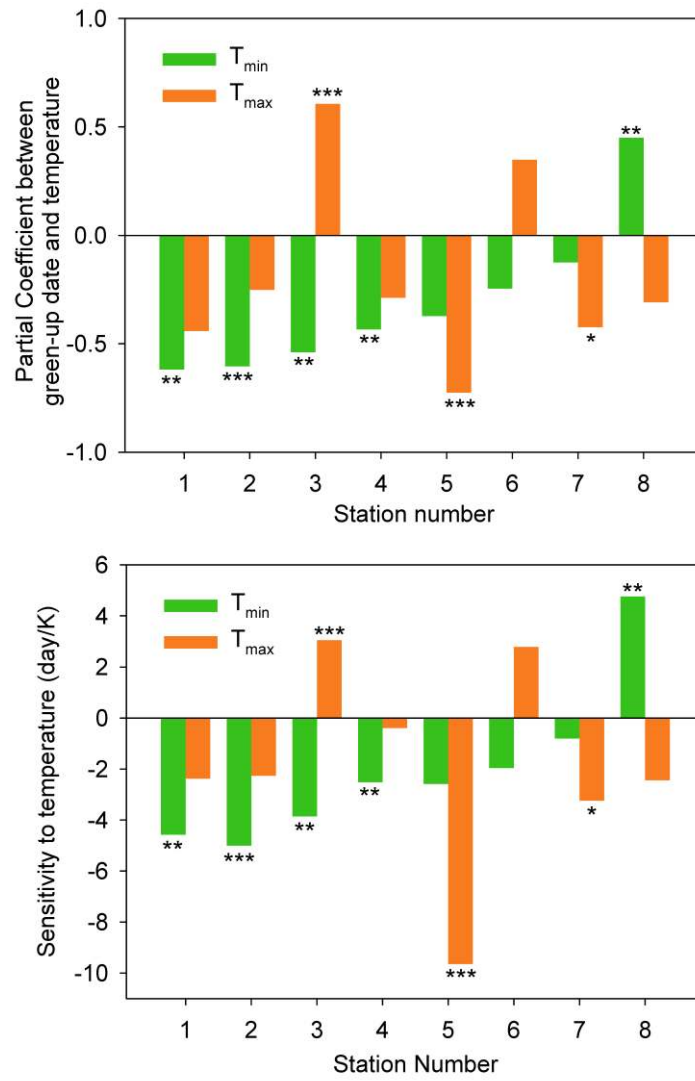
640 summer T_{\min} , and T_{\max} , respectively. $R=\pm 0.60$, $R=\pm 0.52$, $R=\pm 0.42$, $R=\pm 0.34$ correspond to the
641 5%, 10%, 20%, 30% significance levels, respectively. Bottom, spatial patterns of sensitivities
642 of summer GVI to summer T_{\min} and T_{\max} , respectively. Inset in each 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.

645

646

647 **Figure 1**

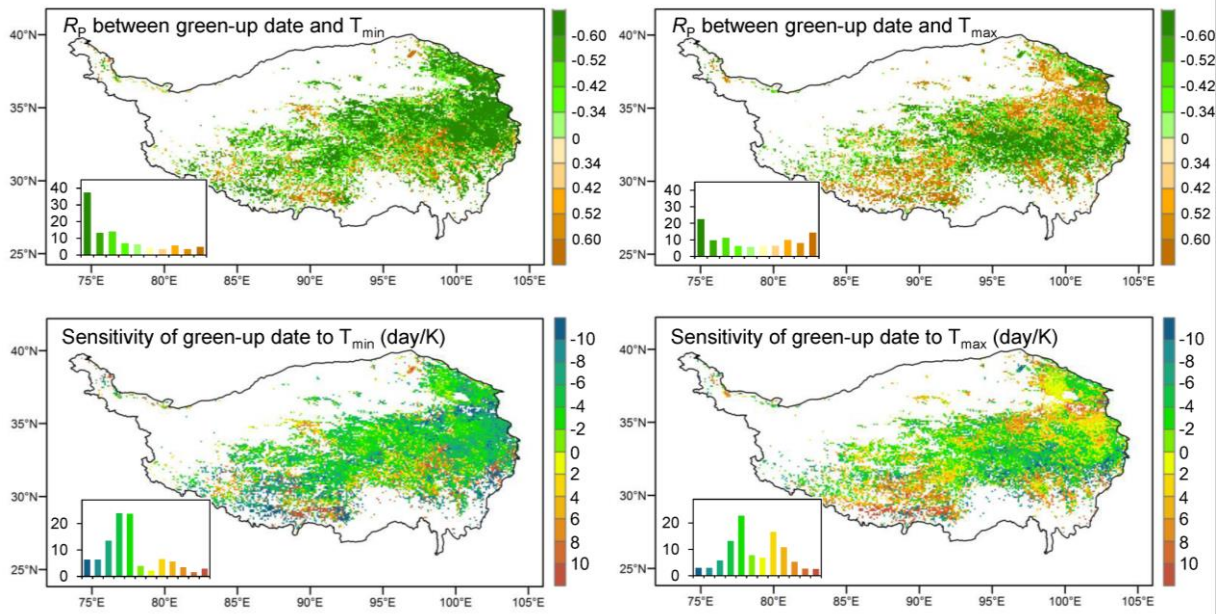
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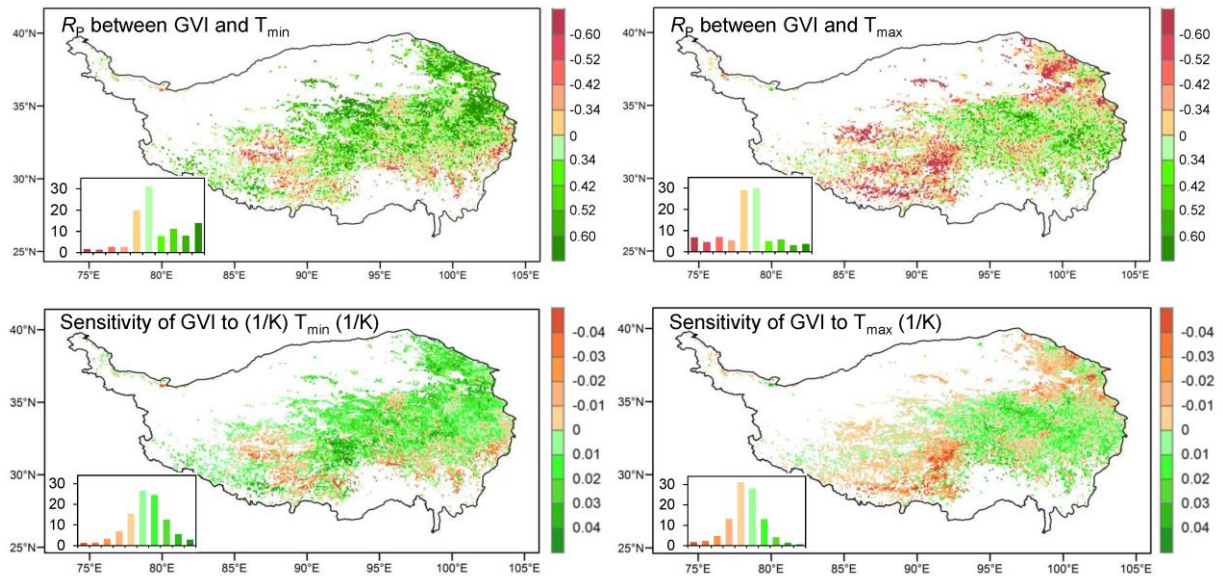
651 **Figure 2**



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653

654 **Figure 3**



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