RESEARCH ARTICLE

Daily minimum temperature and precipitation control on spring phenology in arid-mountain ecosystems in China

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Abstract

Climate anomaly has caused substantial shifts in phenology of mountain ecosystems, but the underlying mechanism of phenological responses to climate change is still not well understood. In essence, the abundance of vegetation communities increases the complexity of phenology-climate relationships, leading to a certain limitation in predictions of future dynamics among different vegetation types using a unified model. In this study, we focused on the climatic constraints on spring phenology in arid mountains (AMs) of China, and emphasis was laid on accurate representation of mechanisms that control phenology across different vegetation types. We Firstly explored spatio-temporal variations in satellite-derived estimates of starting date of vegetation growing season (SOS) over the period 2000–2015 using moderate-resolution imaging spectro-radiometer (MODIS) normalized difference vegetation index (NDVI). Phenological models in response to climate variability were then established by using mixed-effect models based on satellite observations and an extensive dataset of climatic measurements. Our results showed that the climatic regulation on SOS varied greatly over vegetation types. More climatic factors that regulate phenological development were found in grassland than forest and shrubland. At ecosystem level, two critical climate factors, daily minimum temperature (T_{min}) and precipitation, explained 74–95% of total variability in predicted SOS. The observed sensitivity to T_{min} is expected to be closely linked with the risk of frost damage, while preseason precipitation determines water availability in spring. The varying ecosystem sensitivity revealed the different resilience and adaptability to changing climate among vegetation types, which have been linked to their eco-physiological characteristics (e.g., water use efficiency) and environmental conditions (e.g., elevation). Overall, our results indicate a strong dependence of spring phenology on T_{min} and precipitation, and create an opportunity for a more realistic representation of vegetation phenology and growth of AM plants in China in land surface models.

KEYWORDS
arid mountain ecosystems, climate change, daily minimum temperature, NDVI, precipitation, spring phenology

1 | INTRODUCTION

Alterations in the temporal niche of vegetation phenophases as a consequence of climate change increase the uncertainties of ecosystemic structure and functioning, because of their strong controls of biochemical cycles, such as energy exchange, water balance, and carbon sequestration (Menzel, 2002; Peñuelas and Filella, 2009; Richardson *et al*., 2013; Keenan *et al*., 2014). Numerous studies in temperate, boreal, and tropical regions have documented strong responses in plant phenology, notably advances in the spring growth onset coupled with patterns of temperature increases (Walther *et al*., 2002; Borchert *et al*., 2005; Jeong *et al*., 2011; Zhang *et al*., 2013; Fu *et al*., 2014; Ge *et al*., 2015). As sensitive indicators of climate change, shifts in the timing of plant phenology provide valuable information about the responses of terrestrial vegetation, and potential feedbacks to climate anomalies (Schwartz and Chen, 2002; Cleland *et al*., 2007; Richardson *et al*., 2013). Thus, it is imperative to develop a better knowledge of climatic controls on vegetation phenology to understand future ecosystem dynamics (Badeck *et al*., 2004; Zhang *et al*., 2004; Pau *et al*., 2011).

However, the underlying mechanisms of plant phenological responses to climate change are not well understood. Generally, it has been accepted that temperature triggers the visible progress in phenology; nevertheless, the modulation of temperature is not invariable under environmental changes, and temperature alone does not explain well vegetation phenological variation (Marchin *et al*., 2015). For example, using the observation data in the European Alps, Vitasse *et al*. (2018) reported that the tree leaf-out onset along elevational gradient exhibited asynchronous responses to global warming with the reduction of the elevation-induced phenological shift over the past 50 years. Moreover, recent studies revealed a gradual decrease of temperature sensitivity of plant phenology in arid/semi-arid areas where preseason water availability is often limited (Chen *et al*., 2014; Forkel *et al*., 2015). Hence, Shen *et al*. (2015) argued that precipitation controls spring water availability and, therefore, affects SOS in the Tibetan Plateau. Cong *et al*. (2013) also found that the increase in preseason precipitation enhanced the temperature sensitivity of vegetation spring phenology in temperate China. These findings indirectly suggest an important cue of precipitation for phenological development. Nevertheless, less attention has been devoted to the dependence of plant growth on precipitation (Chen *et al*., 2014; Forkel *et al*., 2015), probably due to lack of clear association between phenology and precipitation that are normally obtained with temporal analysis conducted at regionally aggregated levels (Shen *et al*., 2015). Instead, the real impacts of climate change on the SOS could be benefited from a synthetical method, which may need spatial

response analysis to be involved (Liang and Zhang, 2016), because the differences of some climatic variables like precipitation in space are often more obvious than interannual variations. For example, Zhang *et al*. (2005) found that the spatial variation in SOS closely tracked the onset of the rainy season in Africa. Therefore, an essential step in enhancement for accurately mechanistic understanding of the role of climate change on vegetation phenology is to focus on the synthetical analysis of spatio-temporal responses, as that has received insufficient attention in previous studies.

Arid mountains (AMs) constitute a special geomorphic unit that develops in arid/semi-arid climate zones at high altitudes. The environmental components are affected by the climate type of baseband, and exhibit characteristics of vertical zonality (He *et al*., 2018). In AMs, ongoing occurrences of climatic anomalies have become extraordinarily frequent (Lin *et al*., 2017). For example, temperature records in Qilian Mountains of China indicated an average rise of 0.26°C per decade during the past 50 years, with the violent fluctuation of precipitation (Du *et al*., 2014). It is expected to increase the frequency of droughts due to preseason warming and precipitation reduction (Shen *et al*., 2016). Drought-induced tree growth decline can be interpreted as an early-warning signal of mountain forest vulnerability in semi-arid environments (Tognetti *et al*., 2019). Moreover, elevated spring temperature generally results in a shorter snow cover period as well as earlier snowmelt (Clow, 2010), which acts as a critical factor that regulate the spring onset of growth and flowering in subalpine meadow ecosystem (Inouye, 2008). Additionally, recent studies have reported a reduction of the chilling accumulation to some tree species in high-latitude and high-altitude ecosystems during exceptionally warm winters, leading to increasing forcing requirement and/or later dormancy break (Schwartz and Hanes, 2010; Vitasse *et al*., 2018). These climatic changes will inevitably impose great environmental stresses on AM ecosystems. Although climate warming is generally associated with a lengthening of the growing season due to advances in the spring onset of growth and/or delays in autumn senescence (Wang *et al*., 2014b; He *et al*., 2015; Dai *et al*., 2018), individual responses vary greatly over different vegetation types (Ge *et al*., 2015). As observed in a recent study in the Santa Catalina Mountains in the United States, phenological sensitivity of annual forbs to a changing climate can differ from that of woody plants by more than onefold (Crimmins *et al*., 2010). Across a semi-arid mountain region in China, Zhou *et al*. (2016) found varying degrees of correlation in vegetation phenology with climatic factors among functional groups, and different magnitude of sensitivity to temperature increase. It follows that the individualistic responses of phenology to climate change are likely to arise from different mechanisms acting within AM biomes (He *et al*., 2015);

therefore, the abundance of vegetation communities increases the complexity of phenology-climate relationships (Crimmins *et al*., 2010). Predicting the seasonal trajectory of vegetation activities in AM ecosystems in a future climate remains a great challenge, as it requires accurate representation of mechanisms that control phenology across a diverse range of plant taxa.

In this study, we aimed to investigate the climatic constraints on spring phenology in an AM region of China, and emphasis was laid on accurate representation of mechanisms that control phenology across different vegetation types. To that end, we retrieved satellite-based time series (2000–2015) of the SOS dates from the normalized difference vegetation index (NDVI) records obtained from the moderate-resolution imaging spectro-radiometer (MODIS). We considered an extensive dataset of climatic observations including the potential influencing factors reported previously in temperate zones. We examined the spatio-temporal pattern of phenological changes and the associated climate variability. The synthetical analysis of spatio-temporal responses were then performed to unveil potential differential effects of climate factors on SOS for three vegetation types, and the possible underlying mechanisms were further elucidated.

2 | DATA AND METHODS

2.1 | Study area and biomes

The study area is the Qilian Mountains (QLMs) in northwestern China (Figure 1). The area covers 1.93×10^5 km^2, spanning a latitudinal range of 35.8°–40.0°N, and longitudinal extent of 93.5°–104.0°E, with an average altitude up to 3,660 m above sea level (a.s.l.) (Figure S1). Climate across the QLMs is characteristic of temperate continental plateau in that it is cool and arid (Du *et al*., 2014). According to observational records from meteorological stations, the mean annual temperature across the QLMs is 4.1°C (for years 2000–2015), and annual cumulative precipitation is 340 mm, mainly concentrated in May to September. As one of the major AMs in China, QLM is the source of three inland river basins (the Shiyang, Hei, and Shule Rivers). Vegetation in the QLMs has an important influence on regional ecological security, because of its role in water conservation and regulation (He *et al*., 2012). A rasterization map of vegetation types across QLMs was extracted from 1:1000000 Vegetation Map of China (Figure 1), which was produced by Chinese Academy of Sciences from the land resource investigation (Hou, 2001). We grouped the vegetation into forest, shrub, and grass covers in our analysis. The cropland was not considered because of intense human disturbance. To match the MODIS NDVI products, the vegetation data were then resampled to a spatial resolution of 1 km. Considering the possible classification errors caused by this downscaling method, we further refined it with the help of Landsat images (http://www.landcover.org/data/, Du *et al*., 2014). In this process, some necessary preprocessing steps of remote sensing images are involved, including image correction and radiation enhancement. The purpose is to eliminate the influence of radiation noises (such as cloud shadow, topographic effect) on image interpretation. Through field sampling validation, the overall classification accuracy of the final vegetation map is more than 85%, which is acceptable for our analysis. To be
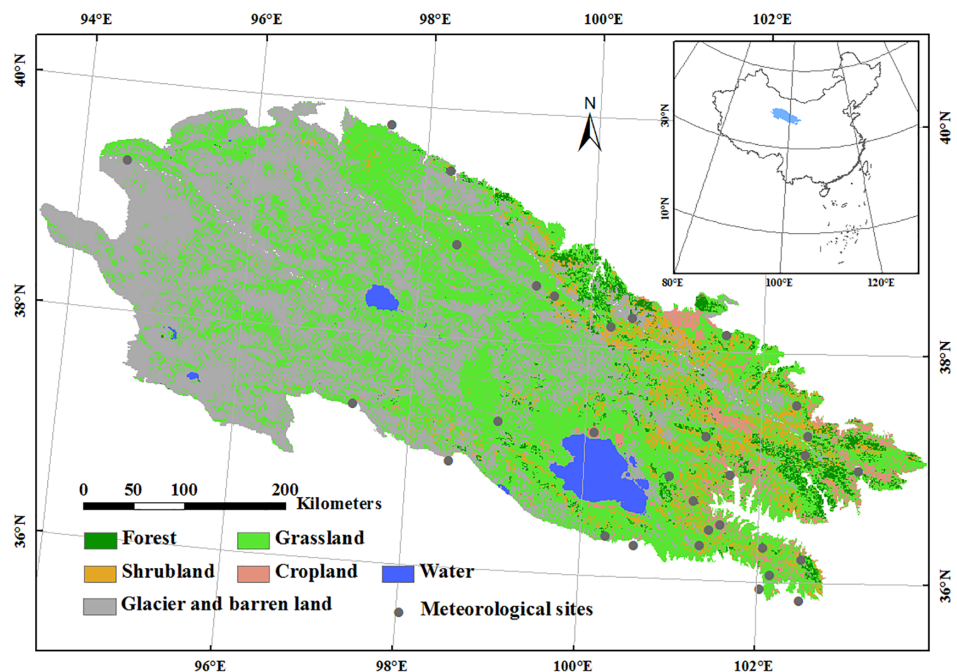

FIGURE 1 Location of the QLMs and spatial distributions of meteorological stations [Colour figure can be viewed at wileyonlinelibrary.com]

specific, the forest is dominated by Qinghai spruce (*Picea crassifolia*), and mainly distributed in the northern and eastern part of the QLMs, at a mean altitude of 3,160 m (a.s.l.) (-Figure S1). Shrubland is primarily located in the subalpine zones of the QLMs above the treeline. Common shrub species are *Salix gilashanica*, *Caragana jubata*, and *Potentilla fruticosa* (He *et al*., 2015). Grassland has a wide geographical distribution at altitudes ranging from 2,500 to 4,600 m. Several constructive species, such as *Stellera chamaejasme Linn*. and *Potentilla multifida*, are collectively present at QLMs (He *et al*., 2018).

2.2 | In situ phenological monitoring

On-the-ground phenological data were collected at meteorological stations in the QLM. There exists the case that spring phenology of the three vegetation types around a meteorological station was simultaneously observed. The temporal and spatial coverage of green-up observations for each site is not in complete accord with others, with time series length of at least 5 years since 2001 and ranging from 1 to 5 km^2 in space area (see He *et al*. (2015) for more descriptions of the observational sites). In total, the observed phenology data from 20 sites for forest, 22 sites for shrub, and 27 sites for grass, were available (-Figure S2), with a combination of sequences of spring events (e.g., bud burst, beginning of flowering, and full flowering) from different dominant species. Unlike satellite-derived phenology, ground observations of green-up date are based on the survey at species scale. In spring, each site was visited every 2–5 days, and the developmental status of all dominant species was recorded. The species-level green-up was defined as the date when 50% of leaves have unfolded, as shown in previous studies (e.g., Dai *et al*., 2014; Shen *et al*., 2016). For each vegetation type, the weighted average for green-up dates for dominant species by the frequency of occurrence was calculated annually in each site. Given the limited monitoring length (of time) of ground data, the spatial correlation analysis was conducted to compare with satellite-based phenology. Specifically, take the case of shrubland, we first calculated the mean ground-based values for all monitoring years at each site. Likewise, the mean of satellite-derived SOS measures from 2000 to 2015 for shrubland pixels in the 20 km buffer around each site was calculated. The spatial pattern of ground observations and satellite-derived SOS measures was then compared by exploring the Pearson's correlation coefficient between them across sites (Wang *et al*., 2014a). Similar methods were used for the other two vegetation types.

2.3 | Satellite NDVI data

NDVI, based on the differential reflectance of green vegetation in the infrared and near-infrared bands, has been widely used in monitoring of vegetation dynamics and plant phenology because it is strongly related to the strength of photosynthetic activity and the amount of green-leaf productivity (Pettorelli *et al*., 2005; Jeong *et al*., 2011). In this study, the timing of SOS in the QLMs from 2000 to 2015 was retrieved from a MODIS NDVI dataset. The 16-day maximum-value composite MODIS NDVI data (product MOD13A2) at a spatial resolution of 1 km were generated from atmospherically corrected bi-directional surface reflectances that had been masked for water, clouds, heavy aerosols, and cloud shadows (Zhang *et al*., 2013), and obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LPDAAC) (http://LPDAAC.usgs.gov).This dataset has been widely used and tested in the retrieval of remote-sensing phenology across diverse vegetation biomes and in different climatic regions, and their robustness for SOS trend analyses were validated (Zhang *et al*., 2004; Delbart *et al*., 2006; Kross *et al*., 2011).

2.4 | Climate data

To comprehensively investigate the correlation between SOS dynamics and climate change, the potential climatic drivers of phenology were considered in our analysis, including variations in preseason temperatures (Richardson *et al*., 2013), winter chilling (WC) (Clark *et al*., 2014), snow melt (SM) (Clow, 2010), and preseason precipitation (P) (Shen *et al*., 2015). Thus, an extensive dataset of daily climatic observations at 31 national meteorological stations (26 inside of the study area and 5 outside, but in the immediate vicinity of the boundary) from 2000 to 2015 was obtained from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn) (Figure 1 and Table S1). As the length of the phenologically relevant period (preseason) for temperatures (including T_{max}, T_{mean}, and T_{min}) and precipitation could vary at different sites and among vegetation types, we did not use a fixed period. Instead, the preseason period length was determined separately with an optimization method based on a partial correlation analysis. Here, we calculated partial correlation coefficients between SOS time series and each variable (setting others as control factors) during different preseason lengths preceding the 2000–2015 average SOS. This procedure used a step of 10 days when changing the preseason length to smooth potential extreme values (Shen *et al*., 2015). Then the optimal preseason length for the four climatic parameters for different vegetation types at each station was identified by exploring the largest partial correlation coefficient (Wang *et al*., 2016), and the corresponding preseason temperature and precipitation were determined. When we computed the winter chilling accumulation necessary for triggering leaf-out, an alternative model

was used to calculate the time period of days during which temperatures were below a base threshold (Dantec *et al.*, 2014), following Equation (1):

$$WC_{req}(t) = \sum_{t_0}^{t_{sos}} 1, T_t \leq T_b \qquad (1)$$

where t_{sos} was the day of vegetation green-up (day of year, DOY), t_0 was the starting date for chilling accumulation (DOY), and T_b was the base threshold value. Most previous studies have reported that temperatures slightly above freezing are the most effective in satisfying the chilling requirement and suggested a temperature of 5°C as the base threshold (Schwartz and Hanes, 2010; Polgar and Primack, 2011). Hence, we fixed the starting day on the date as first September in the previous year (Dantec *et al.*, 2014). As for the timing of snowmelt, we did not have adequate observations. Nevertheless, since land surface temperature is closely associated with observed snowmelt (Høye *et al.*, 2007), we estimated the timing of snowmelt as the date when daily mean temperature at ground level rose above 0°C for seven consecutive days (Wang *et al.*, 2015b). A comparison between simulated and observed snowmelt dates at some of the meteorological stations validated the efficacy of this method, with average absolute error of 3 days. In this study, we did not take photoperiod into account because photoperiod, mainly determined by latitude and time of year, is expected to be insensitive to climate change. Moreover, the maximum difference in spatio-temporal pattern of sunshine duration was only 0.4-hour across the QLM (Wang *et al.*, 2015a).

2.5 | Retrieval of remote sensing SOS

Before retrieval of remote sensing SOS, typical preprocessing procedures were used with the time series of NDVI values. First, the effect of snow cover on NDVI was eliminated for each pixel; snow cover in winter and early-spring often depresses NDVI values, possibly leading to biases of the seasonality reconstruction in vegetation greenness (Delbart *et al.*, 2006). With the support of the flag file (snow free records from MOD13A2 dataset) for data quality, we identified pixels where snow cover possibly existed, and interpolated values by the spline method on the basis of uncontaminated pixels. If negative outliers in the time series remained, we further applied the median-filter method for each pixel using the nearest-interpolation algorithm. Additionally, clouds and poor atmospheric conditions in the course of vegetative growth can also result in abnormally high or low NDVI values. To remove these spikes, the Savitzky–Golay filter with a five-point moving window was used in each NDVI cycle (e.g., Shen *et al.*, 2015).

Subsequently, a logistic model was employed to fit the temporal variation of the filtered NDVI data for an annual growth phase. The logistic model function has the form (Zhang *et al.*, 2004):

$$y(t) = \frac{c}{1 + e^{a+bt}} + d \qquad (2)$$

where $y(t)$ was NDVI at time t, the parameters a and b controlled the shape of the curve, c and d determined the amplitude values in a single year, and d represented the initial background NDVI value. Finally, the date of vegetation SOS was retrieved from the pre-processed NDVI data by using two different algorithms, the inflection point-based method (β_{max}), and the relative threshold method (R_{20}). Both methods have been described and widely tested across diverse vegetation biomes and in different climatic zones, and their robustness in extracting phenological metrics were validated (e.g., Studer *et al.*, 2007; Yu *et al.*, 2010). In the β_{max} method, the first derivative (β) of the fitted logistic function was calculated, and the date of SOS was defined as the time when NDVI increases at the first local maximum of β. In the R_{20} method, the SOS was considered to be the day on which NDVI values increased to 20% of the seasonal amplitude (i.e., subtraction from the maximum and minimum values) in late spring. The threshold value was determined according to the leaf unfolding date observed in situ to obtain the lowest absolute error with remote-sensing derived phenology (Shen *et al.*, 2015). Since a comparison of satellite-based SOS calculated from the two methods revealed a general consistency (Figure S3), these results were ultimately averaged before being used for subsequent analysis.

2.6 | Phenology-climate analysis

The phenology-climate analysis was conducted on pixels found in the 20 km-buffer area around meteorological stations. Remote sensing SOS of these pixels was further averaged in accordance with the station-level meteorological observations. Spatio-temporal shifts of remote sensing-based SOS were examined using mixed-effect models in relation to variation in climatic measurements. We used the mixed model in this analysis because our data was the repeated observations of multiple points in chronological sequence, which involve two dimensions of time series and cross section. The mixed model can not only overcome the trouble of multi-collinearity in time series analysis, but also consider the spatial response relationship (Freyermuth *et al.*, 2010). In the mixed model procedure, the following fixed effects were specified: vegetation types, and climatic factors including T_{max}, T_{min}, T_{mean}, P, WC, and SM; the meteorological sites were declared as random effects. Restricted maximum
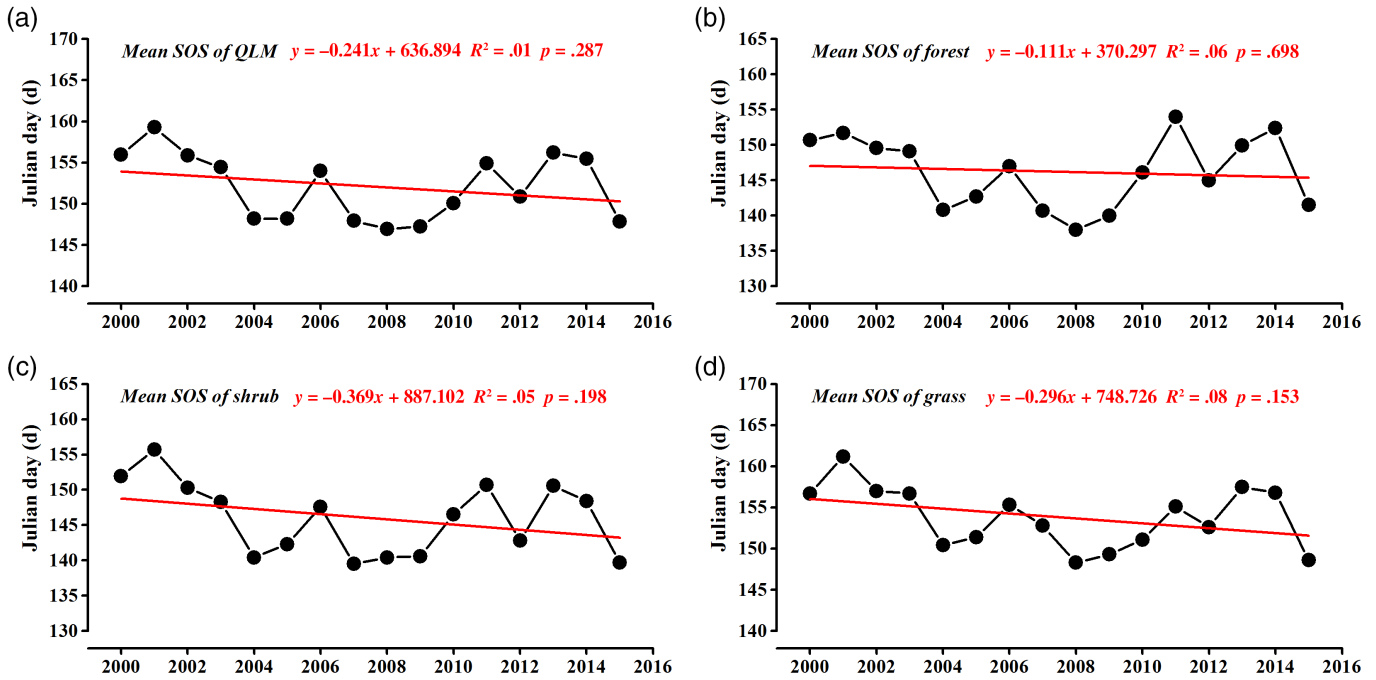
FIGURE 2 Interannual variation in satellite-derived SOS in the QLMs (a) and for different vegetation types (b–d) from 2000 to 2015 based on the MODIS datasets [Colour figure can be viewed at wileyonlinelibrary.com]
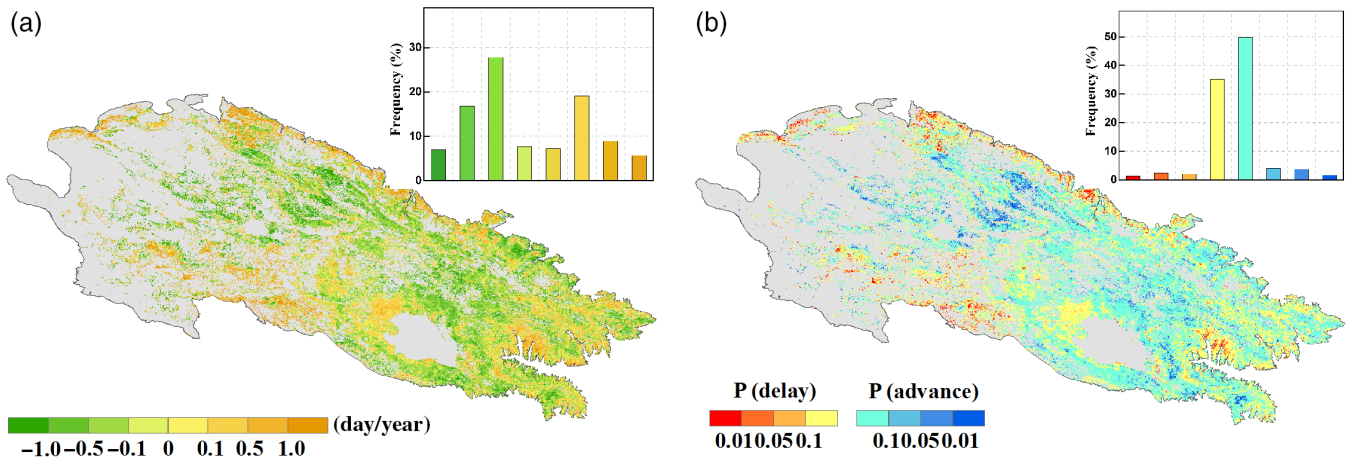

FIGURE 3 Spatial patterns of temporal change rate in satellite-derived SOS (a) and the significance levels (b) from 2000 to 2015 based on MODIS data. The top right inset shows the frequency distributions of corresponding trends and significance levels [Colour figure can be viewed at wileyonlinelibrary.com]

likelihood was applied to compute the estimates of coefficients for models (Nakagawa and Schielzeth, 2013). To compare the climatic constraints on the timing of SOS across vegetation types, mixed models were separately constructed for forest, shrub, and grassland biomes with the same response variables. These procedures were performed in *SAS* 9.2 (SAS Institute Inc., Cary, NC).

Before modelling analysis, the SOS dates and all climatic variables except T_{min} were transformed via the square root algorithm to normalize distribution or to improve homogeneity of variances. Thus, the transformed data were used in the following model specification. To check whether there was multi-collinearity among explanatory predictors, variance inflation factors (VIFs) were also calculated through collinearity diagnostics. Generally, variables with VIF less than 4 represent weak collinearity (O'Brien, 2007). To quantify the performance of mixed models, we calculated the adjusted coefficient of determination (R^2_{adj}) for goodness of fit. All significance levels given were derived from Type III tests. Normality of the residuals was checked with Q-Q

plots, and homogeneity of variances with a scatterplot of standardized residuals and predicted values. In our analysis, we started from a null model that had no fixed predictors.

TABLE 1 Mixed model of the effects of climatic variables on vegetation SOS in the QLMs

Predictive variables	Estimated ($\times 10^{-2}$) [95%CI]	p	DOV (%)
Intercept (β_0)	1,193.89 [1,143.83, 1,243.96]	.000	
T_{max} (β_1)	−16.33 [−23.05, −9.60]	.000	9.33
T_{min} (β_2)	−4.96 [−6.18, −3.74]	.000	29.51
T_{mean} (β_3)	—[a]	—[a]	
P (β_4)	−3.64 [−4.33, −2.95]	.000	17.11
WC (β_5)	6.53 [3.81, 9.24]	.000	4.97
SM (β_6)	3.18 [1.13, 5.22]	.002	1.18
Type (G) (β_7)	22.27 [13.51, 31.04]	.000	37.90
Type (S)	13.98 [4.64, 23.33]	.004	
Type (F)	0		
−2 log likelihood	932.56		
AIC	938.56		
R^2_{adj}	.69	.000	

Abbreviations: T_{max}, the maximum air temperature; T_{min}, the minimum air temperature; T_{mean}, the mean air temperature; P, precipitation; WC, winter chilling; SM, snowmelt; G, grass; S, shrub; F, forest; AIC, Akaike Information Criterion; R^2_{adj}, the adjusted coefficient of determination for goodness of fit; β_0, β_1, … and β_7, the fitted parameters; DOV, the decomposition of the predicted variance.

[a]The T_{mean} was screened out of predictive variables in mixed modelling, because of a high multi-collinearity with other predictors (VIFs > 4).

Improvement in model fit was examined by adding the fixed predictors to null model using −2 log likelihood estimation, Akaike information criterion (AIC) (Nakagawa and Schielzeth, 2013). Additionally, to identify the relative contributions of the different regressors, decomposition of the predicted variance (DOV) was performed (Huang *et al.*, 2014).

3 | RESULTS

3.1 | Variability in the onset date of spring green-up

A comparison of satellite-based SOS with ground observations revealed a general consistency, with a high correlation coefficient of 0.92 (R_p) in average for the three vegetation types (Figure S2). Averaged over the entire period of 2000–2015, the onset dates of green-up over QLMs occur between DOY 120 and 191 (for 95% confidence interval), with the mean value of DOY 161 corresponding to July 10. The relatively late SOS was found at the central regions, whereas early SOS was mainly in the eastern part of QLMs (Figure S4). This spatial distribution of SOS date appears to be elevation dependent, suggesting temperature being the primary controlling factor. Meanwhile, it shows that the spatial pattern of SOS is roughly coupled with the pattern in SOS trend during the past 16 years. Although there was no statistically significant temporal trend at a regional scale (with the slope of −0.24 day per year, p = .287) (Figure 2a), 9.4% of the pixels of the study area, concentrated in central QLMs, displayed a significant shift in SOS toward an earlier
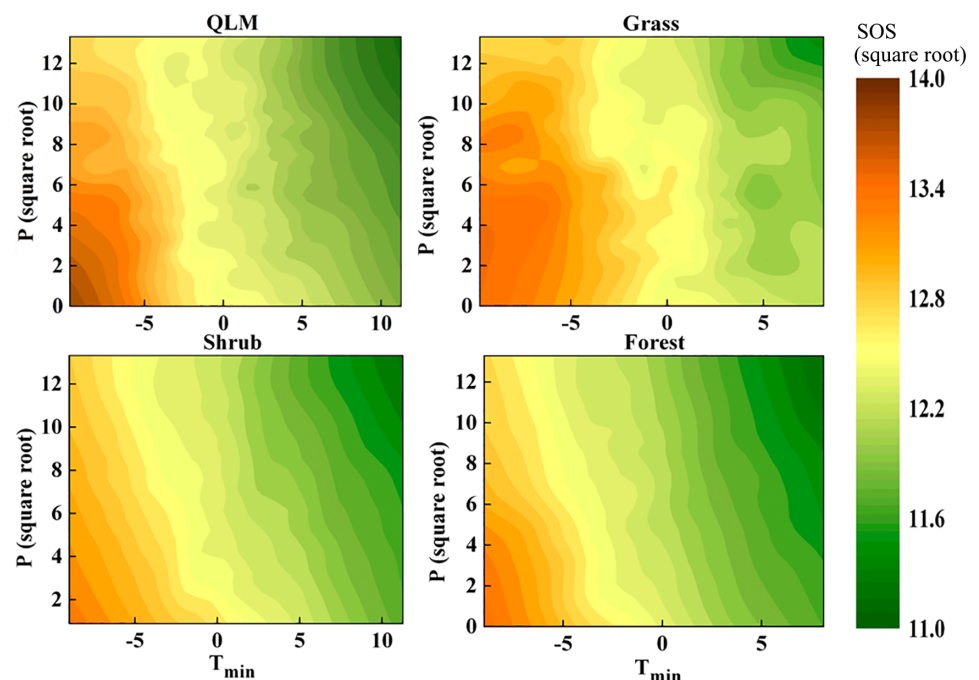

FIGURE 4 Spline-interpolated surface plot showing the relationships between the predicted SOS and T_{min} and precipitation in the QLMs for different vegetation types [Colour figure can be viewed at wileyonlinelibrary.com]

date ($p < .1$) (Figure 3). On the contrary, the advance of phenology in response to climate change was slackened or even inverted to delay in the eastern part of QLMs. When interannual variability in vegetation SOS was analysed for different vegetation types, the similar temporal trend was observed (Figure 2b-d).

3.2 | Onset date of spring green-up in relation to climate

The mixed model results showed that the dynamics of vegetation SOS were closely related to the changes in climate variables (Table 1), suggesting that multiple climate factors act their respective roles in triggering the visible progress of spring phenology in the QLMs. However, such climatic regulation of timing of spring green-up varied with vegetation type. For example, in addition to T_{min} and precipitation, earlier snowmelt was significantly related to an advancement in the spring onset of growth for shrubland and grassland ecosystems at high altitudes (Tables S2a and 2b). Moreover, winter chilling conditions also served as an important cue for grassland phenology, with fewer chilling days corresponding to earlier SOS (Table S2a and Figure S5). For forest ecosystems at lower elevations, shifts in preseason maximum and minimum temperatures and cumulative precipitation were significantly and negatively correlated with changes in SOS, indicating that these variables were critical regulators of spring phenological responses to climate change in these systems.

To further quantify how much variance in the predicted SOS can be attributed to climatic predictors, a decomposition of the predicted variance was performed. We found that vegetation type accounted for 37.9% of the predicted variability, and ranked as a primary factor for consideration in forecasting of climate change impacts on plant phenology over entire QLMs (Table 1). The remaining variability was explained by T_{min} (29.5%), followed by precipitation (17.1%), T_{max} (9.3%), winter chilling (5.0%), and snowmelt (1.2%). At the level of ecosystem type, T_{min} and precipitation were two critical climate factors, which explained 74–95% of the total variability in predicted SOS (Table S2a-c). As shown in Figure 4, the SOS generally advanced when both preseason T_{min} and precipitation increased.

4 | DISCUSSION

4.1 | Responses of spring green-up onset dates to climate change

Our analysis of satellite NDVI records showed that over the past 16 years, there was no clear trend in SOS shifts for ecosystems in the QLMs, which generally agreed with the findings of previous studies (Cong *et al*., 2013; Wang *et al*., 2014b; Zhou *et al*., 2016). For example, although most of the temperate China experienced an overall advancing trend in SOS since the 1980s, such advancement SOS signals became weak after 2000 (Cong *et al*., 2013). Zhou *et al*. (2016) argued that the recent shift to a delay in SOS, especially since 2008, resulted in a deceleration of the advancing trend, as was indicated by the findings in the present study.

Phenological variability is considered to agree well with the signals of climate change (Cong *et al*., 2013; Richardson *et al*., 2013; Clark *et al*., 2014; Dai *et al*., 2014). In this study, most of the shifts in SOS could be explained by the variation in spring temperatures (T_{max} and T_{min}), preseason precipitation, winter chilling days, and the timing of snowmelt. Our results show that several climatic factors control spring onset of growth in AM plants. At ecosystem level, the common feature across the biomes was the leading control of T_{min} and precipitation on spring vegetation activity. However, the climatic regulation of other variables on SOS varied greatly over vegetation types. For example, we found that shift in grassland SOS was significantly and positively associated with winter chilling accumulations; in contrast, the timing of green-up onset for shrubs and forests exhibited relatively little dependence on chilling conditions. This varying response of ecosystems to chilling may be derived from a trade-off between decreasing the winter chilling accumulation and minimizing the risk of freezing injury with climate warming. Theoretically, warming-related reductions in chilling days could impede the fulfilment of chilling requirements, which may delay spring phenology (Yu *et al*., 2010; Clark *et al*., 2014; Dantec *et al*., 2014). Meanwhile, the decreased amount of exposure to cold temperatures could also decrease the risk of freezing injury to the sensitive growing tissues of AM plants, and thus promote green-up onset (Inouye, 2008; He *et al*., 2018). Our results may imply a balance between impediment and promotion of accumulated chilling reduction to spring green-up for forests and an imbalance toward to promotion for grasslands. Alternatively, our results of a shift to an earlier SOS of grassland indicated that the winter climatic conditions under the current state of warming can still meet the chilling requirement, and that the AM plants may have a relatively low chilling requirement.

Additionally, we found that in addition to T_{min}, the T_{max} also has an important contribution in explaining the total variance in predicted SOS in Qilian Mountains, especially for forest ecosystems. Although the individual influence of one of the two variables has been reported in several studies as well as the asymmetric effects of T_{max} versus T_{min} on vegetation SOS (e.g., Peng *et al*., 2013; Piao *et al*., 2015), the synergistic effect of both factors on vegetation growth is rarely involved. The possible mechanism of co-regulation by T_{min} and T_{max} in green-up onset in this study may work via

higher night time temperatures helping to mitigate the risk of frost and promoting spring thaw; this increases soil water availability for plant photosynthesis during the daytime (Shen *et al.*, 2016). Further, more energy available from higher daytime temperatures and insolation in turn enhances the ability of plants to withstand the freezing injury and water stress at night time (Piao *et al.*, 2015).

4.2 | Dependence of spring phenology on T_{min} and precipitation

In most high-latitude and high-altitude ecosystems, temperature has been unequivocally implicated as a major cue for spring onset of growth and flowering (De Beurs and Henebry, 2005; Vitasse *et al.*, 2009; Chen *et al.*, 2014). Likewise, our results provided evidence for minimum temperature triggering of phenological development in AM plants. In a recent study of alpine vegetation in the Tibetan Plateau, the strong control by preseason T_{min} on vegetation green-up date was also indicated by Shen *et al.* (2016), who found that the increase in T_{min} significantly advanced green-up date (by 4 days $°C^{-1}$) and enhanced greenness in summer. The observed sensitivity of phenology to T_{min} was expected to be closely linked with the risk of frost damage in spring (Inouye, 2008; Augspurger, 2013). Fu *et al.* (2003) pointed out that the number of days when frost occurred in the QLMs was roughly the same as that when T_{min} reached a specific criterion (e.g., $\leq 2.0°C$). Frost has been shown to cause severe damage to sensitive growing tissues of mountain plants (Inouye, 2008; Polgar and Primack, 2011; He *et al.*, 2015), especially in evergreen woody species whose flushing shoots often have low resistance to frost (Langvall *et al.*, 2001). To minimize the danger of freezing injury at low temperatures, plants may slow or postpone phenological processes, and thus retard spring green-up and the onset of new growth (Richardson *et al.*, 2013). In addition, minimum temperature also affects the course of soil thawing, altering the conditions for nutrient absorption and water availability, which, in turn, influence the start of vegetation activity in spring (Shen *et al.*, 2016). Therefore, higher T_{min} helps in removing the constraints of dormancy release in AM plants, and thus advance the SOS. In this study, the dependence of forest phenology on T_{min} was greater than in other ecosystems, given that 50.2% of variance in the predicted SOS was explained by T_{min} (Table S2c). This result indicated that forests in AMs were the most sensitive of biomes to variations in minimum temperature.

Further, we also found that preseason precipitation explained a substantial portion of the variability in predicted SOS, indicating an important role of precipitation in driving shifts in phenology. Compared to the well-known control of temperature in triggering SOS, the potential impact of preseason precipitation was often ignored (Chen *et al.*, 2014; Forkel *et al.*, 2015). Generally, variation of preseason precipitation is not as obvious on the interannual timescale as in space range. Hence, correlations between phenology and precipitation that are normally obtained with temporal analysis conducted at regionally aggregated levels, often failure to elucidate the real impacts of precipitation on the SOS (Shen *et al.*, 2015). In this study, we used the mixed models to incorporate the analyses of both temporal and spatial responses. The results indicated a spatial variation in SOS over the climatic precipitation gradient. For example, SOS was delayed in areas with less precipitation, from DOY 146 at an average precipitation of 500 mm, to DOY 155 at 100 mm (Figure S6). Moreover, the importance of precipitation for AM plants can be reflected in their geographic distributions. Forests and shrubs typically grow on shaded (north-facing) or semi-shaded (east-facing) slopes where sunshine intensity and duration is limited, while only some herbs vegetate on sunny slopes where soil moisture is often suboptimal due to intense evapotranspiration (Jin *et al.*, 2009; Du *et al.*, 2014). Water availability is thus an important determinant of plant growth and development responses to climate change (He *et al.*, 2012). Precipitation during the preseason period largely determined water availability in spring, and therefore affected SOS. This may constitute a potential mechanism that could account for the ranking of the contribution of precipitation to the total variability in predicted SOS (Tables 1 and S2a-c). Across the biomes examined, the shrubland ecosystem was found to be the most sensitive to preseason precipitation. Low water retention in shrubs after rainfall resulted in water stress, because the growing environment of shrubs was characterized by steep inclines with thin soil and high soil porosity (He *et al.*, 2018). Lack of shrub adaptability to such water deficits may contribute to the peak hydroclimatic sensitivity.

5 | CONCLUSIONS

An accurate understanding of the response of vegetation phenology to climate on regional scales is critical to the evaluation of the biochemical cycles (i.e., carbon, water, energy, and nutrient) under recent environmental changes. By taking into account the effects of potential climatic factors, this study was the first to quantify climate forcing in spring phenology objectively for major ecosystems in AMs in China. Although the climatic regulation on SOS varied greatly over vegetation types, our results indicate a strong dependence of spring phenology on T_{min} and precipitation. Moreover, our results imply that a reduction in chilling units does not necessarily lead to phenological delays, suggesting that the winter climatic conditions under the current state of warming can still meet the chilling requirement, and that the

AM plants may have a relatively low chilling requirement. If the conclusions obtained from this study are transferable to other mountains in arid or semi-arid regions of the earth, vegetation is anticipated to respond strongly to future fluctuations in both preseason T_{min} and precipitation, given their restrictive effects on plant phenology. Regional climate projections have indicated a trend toward warmer and wetter conditions throughout the AMs in China (Shi *et al.*, 2007). The concomitant increases in T_{min} and precipitation seem to be a positive sign of an extension in the length of the active growing season as a result of advances in green-up dates. However, extreme climate events associated with T_{min} and precipitation, such as droughts and heat waves, need to receive more attention, because influences of these extreme changes may exceed the ability of species to adapt to new conditions through phenotypic plasticity and result in a decrease in fitness (Siegmund *et al.*, 2016). Further studies are thus needed to investigate how extremes specifically impact the timing of spring phenological phases.

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SUPPORTING INFORMATION

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