Journal of
Plant Ecology

Research Article

# Solar radiation shapes the spatial pattern of spring phenology on the Qinghai-Tibetan Plateau

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**Handling Editor:** Yongshuo Fu

**Received:** 15 September 2024, **First Decision:** 18 November 2024, **Accepted:** 22 December 2024, **Online Publication:** 31 December 2024

**Citation:** Meng Fandong, Yan Yanzi, Li Lili, Zhang Lirong, Guo Bixi, Yang Zhiyong, Dorji Tsechoe (2025) Solar radiation shapes the spatial pattern of spring phenology on the Qinghai-Tibetan Plateau. *J Plant Ecol* **18**:rtae114. https://doi.org/10.1093/jpe/rtae114

## Abstract

The spatial pattern of phenology reflects long-term plant adaptation to local environments, yet the drivers of these patterns remain poorly understood. Using satellite data from 2001 to 2018, this study employed the normalized difference vegetation index for vegetation structural greenness and solar-induced chlorophyll fluorescence for vegetation functional photosynthesis to analyze spring phenology on the Qinghai-Tibetan Plateau (hereafter, QTP). A machine learning method, Boosted Regression Trees (BRT), was applied to evaluate the contributions of 19 abiotic and biotic factors to the spring phenology. The results showed that both the spring leaf phenology ($SOS_{NDVI}$) and photosynthesis phenology ($SOS_{CISF}$) exhibited a delayed trend decreasing from east to west across the QTP. BRT analysis demonstrated shortwave radiation or/and elevation as key drivers, with higher radiation or elevation associated with more delayed spring phenology spatially, likely due to the constraints of extreme radiation and elevations on spring phenology. Furthermore, we also noted that plants were acclimated to strong radiation to some extent with increasing elevation, namely declined negative effect of radiation/elevation on spring phenology. This acclimation likely enhances plant fitness in the harsh environments of the QTP. Our study provides novel insights into plant phenology on the QTP and highlights the importance of integrating spatial and temporal analysis to improve the localization of phenology models.

***Keywords:*** spatial pattern, boosted regression trees, strong radiation, acclimation, phenology

## 辐射塑造了青藏高原春季物候的空间格局

摘要：物候的空间格局反映了植物对当地环境的长期适应性，但其驱动因素尚未得到系统解析。本研究利用2001－2018年的归一化植被指数(NDVI)和太阳诱导叶绿素荧光(SIF)数据，分析了青藏高原春季物候的空间特征。采用增强回归树(BRT)方法，量化了19个非生物和生物因子对春季物候空间变化的相对贡献。结果表明，春季绿度物候($SOS_{NDVI}$)和光合物候($SOS_{SIF}$)均呈现由东向西逐渐延迟的趋势。增强回归树分析表明，短波辐射或/和海拔是春季物候的关键驱动因子，较高的辐射或海拔通常与春季物

候的延迟相关，这可能源于强辐射和高海拔对植物春季物候的限制作用。此外，随着海拔升高，植物对强辐射表现出一定的适应性，即辐射和海拔对春季物候的负面影响逐渐减弱。这种适应性可能增强了植物在青藏高原严酷环境下的生存能力。本研究为青藏高原物候动态提供了新的认识，并强调了结合空间与时间维度分析的重要性，以提升物候模型的本地化精度。

关键词:空间格局，增强回归树，强辐射，适应性，物候

## INTRODUCTION

Climate change significantly influences plant phenology, affecting carbon budget and energy flux in different spheres (Richardson *et al.* 2013). For example, advanced spring phenology and delayed autumn phenology prolong the growing season (Wang *et al.* 2014), enhancing carbon assimilating (Park *et al.* 2016; Piao *et al.* 2007). However, earlier spring phenology could also increase evapotranspiration (Richardson *et al.* 2013) potentially causing summer soil drought and reducing carbon sink capacity (Lian *et al.* 2020). Accurate phenology estimation is essential for understanding plant–climate interactions. Although phenology dynamics under warming are well-studied, regional and driver heterogeneities remain significant (Piao *et al.* 2019), highlighting gaps in current understanding.

Phenological variation arises from short-term plastic responses and long-term adaptive constraints (Franks *et al.* 2014; Hancock *et al.* 2011; Merila and Hendry 2014; Walker *et al.* 2019). Site-level and temporal trend of phenology is mainly determined by sensitivity to climate change (Wolkovich *et al.* 2012). However, spatial pattern of phenology is affected by these combined effects. For example, inter-annual phenological variations are mainly dominated by temperature in the east and precipitation in the west on the Qinghai-Tibetan Plateau (QTP) (Shen *et al.* 2015a, 2015b). Quantifying these relative importance improves phenology model predictability. Traditional latitude or altitude gradients, such as the “Hopkins law” (Hopkins 1920), often fail on the QTP due to its unique topography and climate, as confirmed by site-level studies (Gao *et al.* 2019; Wang *et al.* 2014). Yet, the spatial pattern and attributions have not been fully studied at the regional scale (Shen *et al.* 2022).

The QTP, known as the Earth’s “Third Pole”, is the regulator of climate change in the Northern Hemisphere (Yao *et al.* 2019). Its average altitude is above 4000 m ranging from 1000 m to 8000 m. The long-term harsh environments and changeable terrain may accelerate the evolutionary rates due to a shorter life cycle of grassland (Frei *et al.* 2014; Vitasse *et al.* 2009). Heat requirements of leaf unfolding date also show significant phylogenetic constraints (Yang *et al.* 2021). Moreover, climate change frequently fluctuates in the spatial and temporal scales (for example, warming and cooling spells, day and night temperature changes and background climate) (Meng *et al.* 2016, 2019; Yang *et al.* 2024). Beyond climate, plant traits such as specific leaf area and growth form further affect phenology (Franks *et al.* 2014; Frei *et al.* 2014; Vitasse *et al.* 2013). For example, phenology of plants with high specific leaf area is more conservative (König *et al.* 2018), and perennial plants are more conservative than annual plants. In general, the complexity and diversity of the topography, environmental factors and plant trait changes shape its particularity (Cong *et al.* 2017a, 2017b; Ke *et al.* 2024; Shen *et al.* 2014, 2015a; Yang *et al.* 2021, 2024). This demonstrates that models that only consider single or several factors (such as temperature and moisture) may not fully capture the spatial heterogeneities of phenology (Zhu *et al.* 2016).

To address these challenges, we analyzed the main driving factors of the spatial pattern of plant phenology on the QTP using a satellite-observed dataset (normalized difference vegetation index [NDVI] and solar-induced chlorophyll fluorescence [SIF]). NDVI represents vegetation greenness and structure (Zhu *et al.* 2016), while SIF reflects photosynthetic activity (Baker 2008). Combining these indices provides insights into both structural and functional aspects of vegetation phenology. Using boosted regression tree (BRT) analysis to analyze the main driving factors of spatial patterns of spring phenology on the Qinghai-Tibetan Plateau, integrating altitude environmental, and biological factors. BRT is a machine learning method extended from traditional classification and regression trees (König *et al.* 2018). It can automatically deal with interactive variables due to its insensitive to outliers and multi-collinear variables. Therefore, it has the advantage to analyze a large number of complex predictors (Lian *et al.* 2018).

## MATERIALS AND METHODS

### Datasets

#### *Satellite-observed vegetation index*

The NDVI data, derived from the MOD13C1_C6 product, represent vegetation greenness and ecosystem structure, with a spatial resolution of 0.05 and a temporal resolution of 16-d generating from https://lpdaac.usgs.gov/products/mod13c1v006/. The long-term continuous solar-induced chlorophyll fluorescence (CSIF) data, a machine learning product based on OCO2 SIF and MCD43C1_C6 reflectance datasets, reflects photosynthetic activity and ecosystem function. The dataset has a 0.05 spatial- and 4-d temporal-resolutions (Zhang *et al.* 2018). We choose the time span from 2001 to 2018.

#### *Meteorological datasets*

We adopted the China Meteorological Forcing Dataset generated from http://data.tpdc.ac.cn/en/data/8028b944-daaa-4511-8769-965612652c49/, which includes temperature, precipitation and radiation, with a 0.1 spatial- and 3-h temporal-resolutions. The maximum and minimum temperature, precipitation and radiation were rescaled to a 0.05 spatial resolution using nearest-neighbor interpolation and aggregated to daily temporal resolution. We choose the time span from 2001 to 2018.

#### *Digital elevation model (DEM)*

The Shuttle Radar Topographic Mission has a 30-m spatial resolution, we also resampled the DEM data to a 0.05 spatial resolution to match the spatial resolution of vegetation index. The dataset was generated from https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1-arc?qt-science_center_objects=0#qt-science_center_objects.

#### *Leaf traits datasets*

All the leaf traits were generated from TRY database (https://www.try-db.org/TryWeb/Data.php#60). We extracted leaf nitrogen content per leaf dry mass (LNC, mg/g), leaf phosphorus content per leaf dry mass (LPC, mg/g) and leaf area per leaf dry mass (SLA, $mm^2/mg$) from a global plant feature map with a spatial resolution of 1 km.

#### *Vegetation types*

The map of different vegetation types with 1:1 000 000 was downloaded from https://www.geodata.cn/main/face_science_detail?typeName=face_science&guid=269869575217290.

#### *Daily photoperiod:*

The photoperiod in each pixel is calculated by latitude and day of year (eqn 1).

$$DL = 2 \times \frac{\cos^{-1} \times \left(-\tan(\mathrm{Lat}) \times \tan\left(23.45 \times \sin\left(360 \times \frac{283+\mathrm{Doy}}{365}\right)\right)\right)}{15} \quad (1)$$

where Lat is the pixel-level latitude in degrees and Doy is the day of the year of the spring onset date.

#### *Phenological extraction*

To minimize the impact of outliers or spikes, we applied the Savitzky-Golay filter to smooth the original dataset (Chen *et al.* 2004). The average value of data outside the thermal growing season was used as the baseline. Subsequently, we adopted six-order polynomial function to smooth the NDVI and CSIF datasets, it is a widely used method for phenology extraction (Piao *et al.* 2006). Previous study also validated it as a better choice than other methods on the Qinghai-Tibetan Plateau (Meng *et al.* 2021). After smoothing process, we calculated the maximum change rate of NDVI and CSIF at the start of the growing season ($SOS_{NDVI}$ and $SOS_{CSIF}$, eqns 2 and 3) (see Meng *et al.* 2021 for more details).

$$\mathrm{NDVI}(x) = a_0 + a_1x + a_2x^2 + \ldots + a_6x^6 \quad (2)$$

$$\mathrm{NDVI}_{\mathrm{ratio}}(x) = \frac{\mathrm{NDVI}(x+1) - \mathrm{NDVI}(x)}{\mathrm{NDVI}(x)} \quad (3)$$

where $x$ is the day of the year, $\mathrm{NDVI}(x)$ is the fitted NDVI value at time $x$ and $a_{0-6}$ are the parameters of the function.

### Data analysis

Firstly, we excluded the cultivated pixels that were mainly affected by human activity such as irrigation and harvest based on a vegetation type map, which could not reflect the effect of climate change on plant phenology. Meanwhile, we also excluded the subtropical and sparse regions (multi-year average NDVI is <0.1).

Secondly, we calculated the optimal preseason environments. The preseason was defined as the period before the multi-year average date of SOS with the highest absolute partial correlation coefficient between SOS and each environmental factor (Fu *et al.* 2019). Specifically, taking the multi-year average date of SOS as the end day of the preseason, then moving forward in a step of 10 days as the start day, the interval between the start and end day is the preseason length. The preseason environmental factors were used to execute the partial correlation analysis for each possible preseason, and preseason with the maximum absolute partial correlation coefficient was the optimal preseason among all possible preseasons. Meanwhile, we extracted the eventual environmental factors in the optimal preseason.

Thirdly, we then calculated the chilling days (CDD) and growing degree days (GDD). The 0 °C was the base temperature for CDD and GDD, CDD was the summation days less than the base temperature from the previous year of 1st November and GDD was the accumulation of temperatures above the base temperature from 1st January.

Fourthly, we performed BRT analysis based on all abiotic and biotic factors to disentangle the attributions of spatial pattern of spring phenology using the *gbm* package in R (Supplementary Table S1). It combines regression trees with boosting to iteratively refine predictions and effectively capturing non-linear relationships and interactions among variables. The BRT model could deal well with outliers and collinearity of variables and it can contribute to analyze a large set of complex predictors (Elith *et al.* 2008; Friedman 2001). The model parameters, including learning rate, tree complexity and bagging fraction, were set as 0.01, 5 and 0.5, respectively. Variable importance was ranked by contribution to model improvement (i.e. prediction accuracy), while partial dependence plots illustrating the marginal effects of predictors could be calculated from the function of plot.gbm.

## RESULTS AND DISCUSSION

### The attribution analysis of spatial pattern of spring phenology

Consistent with previous studies (Shen *et al.* 2015b), we observed a delayed trend in SOS from east to west using both NDVI and CSIF data sets (Fig. 1a and b). SOS spanned from April to June for NDVI and May to July for CSIF across the entire QTP (Fig. 1a and b). This heterogeneous spatial pattern of spring phenology shapes the unique QTP landscape, benefiting tourism and ecological functions (Gao *et al.* 2019). While temperature and moisture are recognized as the key drivers of SOS spatial pattern (Shen *et al.* 2015b), considering only several factors will limit our understanding of phenological dynamics, as multiple factors interactively affect SOS (Piao *et al.* 2019).

Using the BRT model, we analyzed the effects of 19 abiotic and biotic factors on the spatial pattern of SOS. Among the three major categories of factors, environmental factors were the dominant factors of two spatial patterns of SOS (95% for NDVI and 77% for CSIF), followed by biogeographic factors (4% and 21%), with biological factors having minimal influence (<1% and 2%, Supplementary Table S2). Among individual factors, shortwave radiation and altitude emerged as the primary drivers of $\mathrm{SOS_{NDVI}}$ (52.3%) and $\mathrm{SOS_{CSIF}}$ (49.5% and 20.8%) (Fig. 1c).

The BRT model performed well in predicting SOS based on 19 predictors ($R^2 = 0.95$ for $\mathrm{SOS_{NDVI}}$ and $R^2 = 0.92$ for $\mathrm{SOS_{CSIF}}$, Supplementary Fig. S1). Both shortwave radiation and elevation negatively correlated with SOS (Fig. 2), indicating delayed SOS with increasing radiation and elevation. These factors co-varied from east to west, driving the observed phenological delay (Fig. 1a and b). High radiation on the QTP, second only to the Sahara Desert (Norsang *et al.* 2011; Wang and Qiu 2009), inhibits plant development, with increasing altitude exacerbating further aggravated the adverse effect (Fig. 3).

Radiation affects SOS through two primary mechanisms. On one hand, light is a signal of morphogenesis (or $\mathrm{SOS_{NDVI}}$), inducing budburst, leaf development, flowering and leaf coloration (Brelsford *et al.* 2019). Although the phenology model seldom considers the light effect for grassland (Liu *et al.* 2017), >50% of all observed species are sensitive to light in the Alps (Keller and Korner 2003). Therefore, the light effect incorporated into the phenology models could improve the performance on alpine regions. Photomorphogenesis can regulate the beginning and end of the growth phase through inducing hormone secretion such as gibberellin (GA) and abscisic acid (ABA) (Brelsford *et al.* 2019). When the radiation becomes stronger, the hormone secretion may be restricted. Additionally, intense light could inhibit nutrients absorption and allocation, further delaying leaf-out (Fu and Shen 2017).

On the other hand, excess radiation may exceed the light saturation point, causing photo-inhibition and reducing the photosynthetic rate (Cui *et*

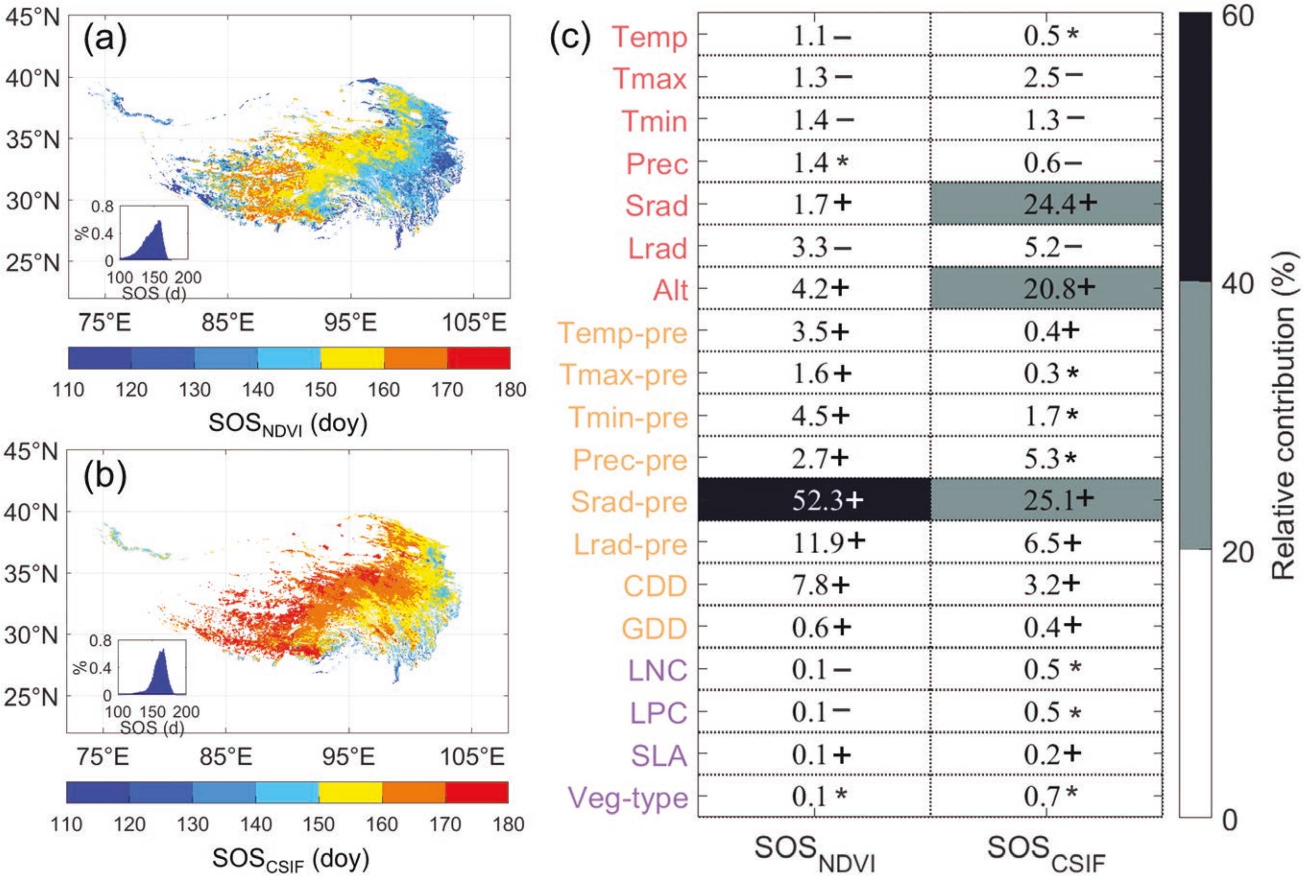

**Figure 1:** Spatial patterns of SOS on the QTP from 2001 to 2018 and their attributions. (a) Spatial pattern of $SOS_{NDVI}$; (b) spatial pattern of $SOS_{CSIF}$ and (c) the attribution analysis of spatial pattern of SOS based on BRT analysis. The inset is the frequency distribution. More details about the different factors are shown in the Supplementary Table S1 and S2. The numbers in the different partitions are the relative contributions of each factor for SOS. Here, we only consider the factors that contribute >15% as the dominant factor. + indicates the increase of variable with more SOS delays, – indicates the increase of variable with more SOS advances and * indicates diverse changes.

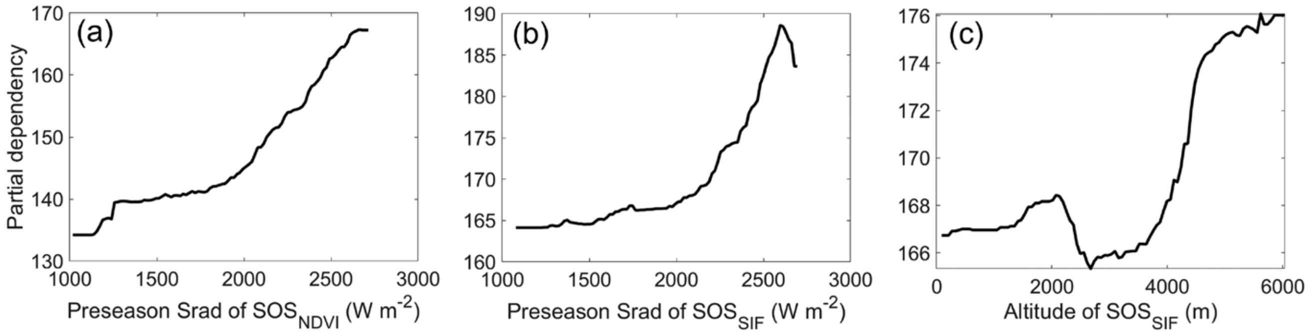

**Figure 2:** The partial dependency between phenological events and dominant factors. (a) The partial dependency between $SOS_{NDVI}$ and preseason shortwave radiation; (b) the partial dependency between $SOS_{CSIF}$ and preseason shortwave radiation and (c) the partial dependency between $SOS_{CSIF}$ and elevation.

*al.* 2003; Fan *et al.* 2011). Strong radiation also increases leaf temperature, boosting ecosystem respiration (Grace 1987). UV-B accompanying strong radiation further damages photosynthetic organs (Lütz and Engel 2007), limiting plant physiological activity, because 90% of UV-B can penetrate thin clouds to reach the surface (https://www.who.int/uv/publications/en/UVIGuide.pdf). These combined effects, therefore, delay photosynthetic phenology at higher altitudes.

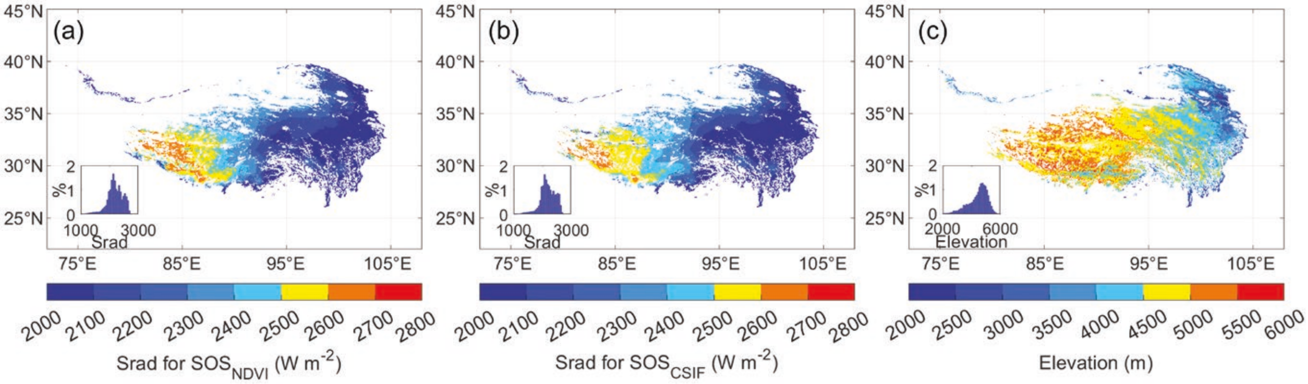

**Figure 3:** Spatial patterns of dominant factors. (a) Spatial pattern of preseason shortwave radiation for SOS$_{NDVI}$; (b) spatial pattern of preseason shortwave radiation for SOS$_{CSIF}$ and (c) spatial pattern of elevation. The inset is the frequency distribution.

## Acclimation of spatial pattern of SOS to radiation and elevation

Plants may maintain their fitness through long-term adaptation to local environments, which might have shaped the current spatial relationships between SOS (start of the growing season) and radiation/elevation. Our study found that shortwave radiation exhibited an increasing trend from east to west and with rising elevation (Fig. 3). Across different climatic spaces, both SOSNDVI (SOS based on NDVI) and SOSCSIF (SOS based on chlorophyll fluorescence) showed delayed trends with increasing elevation and radiation, indicating that plant adaptation to various elevation and radiation conditions significantly influences current phenological spatial patterns.

To disentangle the high collinearity between elevation and radiation, we analyzed the relationship between phenological changes and radiation while controlling for elevation, and compared phenological sensitivity to radiation across different elevations. The results revealed that increased radiation generally delayed SOS, but the effect varied across elevation gradients. Below 5500 m, radiation sensitivity decreased with elevation, suggesting that high-elevation plants have higher adaptability to radiation than low-elevation plants. This adaptability likely stems from long-term evolutionary adjustments to maintain fitness (Franks 2011; Franks *et al.* 2014). However, above 5500 m, radiation sensitivity increased significantly, potentially indicating the threshold of plant adaptability under these conditions.

Moreover, with increased radiation, the phenological trend with elevation shifted from delay to advance (Fig. 4). This further suggests that high-elevation plants exhibit stronger adaptability, greater tolerance and higher responsiveness under the same radiation conditions. Previous transplant experiments along elevation gradients also showed that under identical climatic conditions, plants from higher elevations (e.g. 3800 m) have earlier spring onset than those from lower elevations (e.g. 3200 m) (Wang *et al.* 2014). Overall, stronger radiation generally delays SOS, but high-elevation plants, due to long-term adaptation to high radiation, have a smaller radiation sensitivity. However, above 5500 m, the delaying effect of radiation increases again, potentially reflecting a critical threshold of adaptability. Direct empirical observations further verified the robustness of our finding at species level, showing that plants adaptation to higher elevations have a higher reflectance and absorptance to radiation (Ke *et al.* 2024).

## Implications and limitations

Unlike previous studies (Liu *et al.* 2016; Zhang *et al.* 2020), this study found radiation as a limiting factor shaping the spatial distribution pattern of plant phenology on the QTP (Fig. 1c). This suggests that the underperformance of phenological models on the QTP (Liu *et al.* 2019) may stem from the unique response mechanisms of vegetation in this region. Incorporating these regional peculiarities into model development could significantly enhance predictive accuracy. In addition, this may also indicate limitations in the classical space-for-time substitution method in ecological studies (Mäkelä 2013; Wolkovich *et al.* 2012).

Firstly, the spatial pattern of phenology reflects long-term adaptation to local environments (Anderson *et al.* 2012; Gugger *et al.* 2015; Wang *et al.* 2014). However, the temporal trend captures

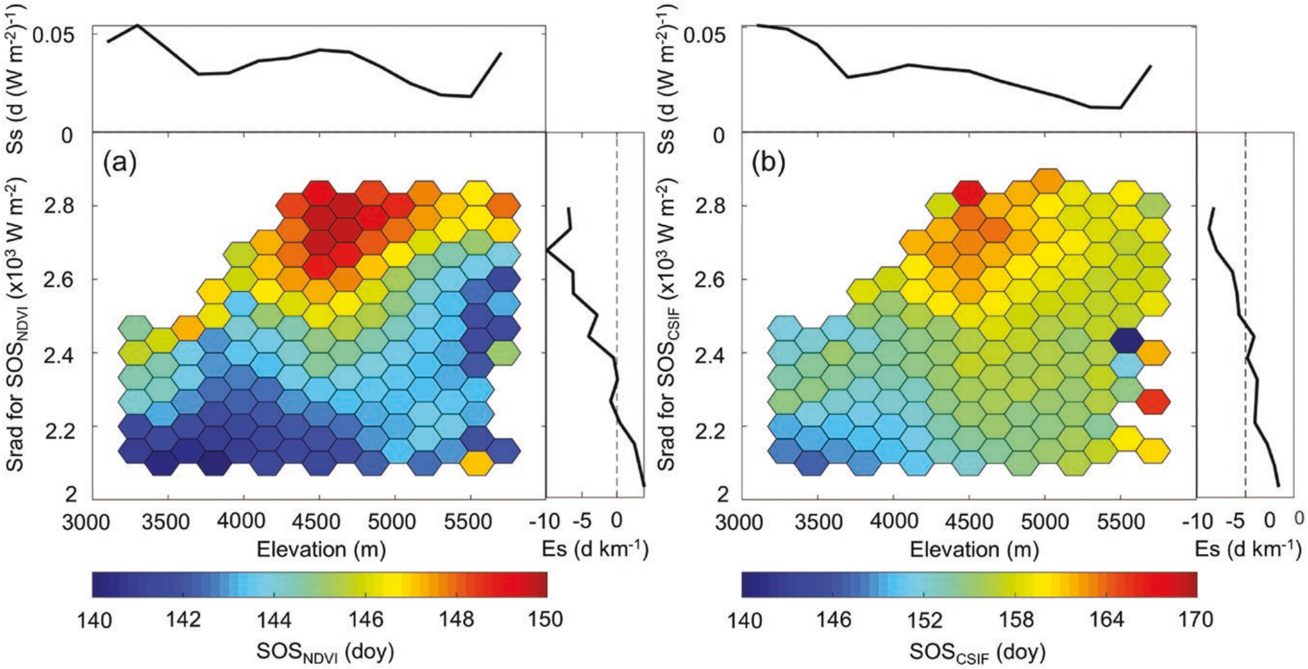

**Figure 4:** Characteristics of SOS between different bins of elevation and preseason shortwave radiation. (a) The mean $SOS_{NDVI}$ at different intervals of elevation (200 m) and radiation (50 W $m^{-2}$); (b) The mean $SOS_{CSIF}$ at different intervals of elevation (200 m) and radiation (50 W $m^{-2}$). The up-inset is the trend of SOS with radiation at the same elevation intervals. The up-inset is the radiation sensitivity (Ss, Supplementary Table S3) of SOS at the same elevation intervals. The right inset is the elevation sensitivity (Es, Supplementary Table S3) of SOS at the same radiation intervals. The pixels of each interval should be >20.

short-term phenotypic plasticity (Nicotra *et al.* 2010; Vitasse *et al.* 2013). Secondly, spatial substitution may not fully replicate temporal processes due to confounding factors such as day length and solar radiation (Jochner *et al.* 2013; Mäkelä 2013). Future applications of space-for-time substitution should consider latitude or elevation gradients to minimize these influences.

In addition, we found that the constraint effect of radiation on vegetation growth decreased with elevation initially but intensified beyond 5500 m. This may limit species migration to higher altitudes under climate warming, impacting local species diversity (Pauchard *et al.* 2016). High-elevation zones (>5500 m), predominantly in the western plateau (Supplementary Fig. S2), may serve as ecological barriers, preventing invasive species encroachment and preserving native biodiversity.

There are several caveats that may affect the generalization of our study. Firstly, variability in species responses to radiation may create uncertainties at the community level. For example, the different responses of species to radiation may cancel each other out in the community (Fu and Shen 2017; Hock *et al.* 2019), further affecting the regional trends. Although limited ground studies have demonstrated the negative effects of radiation or UV-B on plant growth and physiology (Fu and Shen 2017; Ke *et al.* 2024; Wang *et al.* 2008; Ziska *et al.* 1992), studies are still needed relating to largely spatial scale and multiple species in the future. Secondly, the short-term (only 18 years used in our study) satellite data limit extrapolation to long-term trends. Thirdly, other factors, such as atmospheric pressure or $CO_2$ concentration, may interact with radiation and elevation to influence phenology (Reyes-Fox *et al.* 2014; Wang *et al.* 2017). In addition, we only focused on the spring phenology, but the plant life history included a series of phenological events, such as spring onset, summer peak growth date and senescence, these different phenological events also have complex relationships (Li *et al.* 2016).

## CONCLUSIONS

Unlike most previous studies that focus on temporal changes in phenology driven by climate change, we found that the spatial pattern of static spring phenology on the QTP was mainly driven by shortwave radiation. Using two satellite indices and a machine learning approach, we observed that strong radiation inhibits plant growth, consistent with the strong radiation in this region (Norsang *et al.* 2011; Wang and Qiu 2009). However, plant phenology showed acclimation to increasing radiation with elevation, suggesting that plants improve their fitness through plasticity and adaptation in alpine environments, enabling survival in harsh environments.

Our findings provide insights for localizing phenology models and improving the application of space-for-time substitution. However, limitations relating to complex topography, diverse vegetation types and limited observations at species level constrain a comprehensive understanding of phenological responses. Future research should prioritize long-term ground-based observations of multi-species and -phenological events, to disentangle the spatiotemporal dynamics of phenological changes on the QTP. This will aid in refining phenological prediction and informing grassland management strategies.

### Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: All factors used in BRT analysis.

Table S2: Variations of phenophases and different factors.

Table S3: The solar radiation sensitivity (SS)/elevation sensitivity (ES) of SOS at the same elevation intervals/the same radiation intervals.

Figure S1: Relationships between observations and predictive variables based on BRT analysis. (a) $SOS_{NDVI}$; (b) $SOS_{CSIF}$.

Figure S2: Elevations more than 5500 m on the TP.

### Authors' Contributions

Fandong Meng (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft, Writing—review & editing), Yanzi Yan (Writing—review & editing), Lili Li (Writing—review & editing), Bixi Guo (Writing—review & editing), Lirong Zhang (Writing—review & editing), Zhiyong Yang (Writing—review & editing), and Tsechoe Dorji (Conceptualization, Data curation, Funding acquisition, Writing—original draft, Writing—review & editing)

### Funding

Joint Key Research Fund under a cooperative agreement between the National Natural Science Foundation of China and Tibet Autonomous Region (U20A2005); Strategic Priority Research Program (A) of the Chinese Academy of Sciences (XDA26050501).

### Acknowledgements

F.M. and T.D. conceived the idea and designed the analytical approach. F.M. conducted the statistical analysis, and elaborated the figures. F.M. and T.D. wrote the first draft of the manuscript. All authors contributed to revisions of the manuscript.

*Conflict of interest statement*. The authors declare that they have no conflict of interest.

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