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Trade-off between spring phenological sensitivities to temperature and precipitation across species and space in alpine grasslands over the Qinghai–Tibetan Plateau

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Summary

- Elucidating climatic drivers of spring phenology in alpine grasslands is critical. However, current statistical estimates of spring phenological sensitivities to temperature and precipitation (β_T and β_P) might be biased and their variability across sites and species are not fully explained.
- We benchmarked species-level β_T and β_P statistically inferred from historical records with observations from a field manipulative experiment. We then analyzed landscape scale β_T and β_P estimated from the best statistical approach in the benchmark analysis across 57 alpine grassland sites in the Qinghai–Tibetan Plateau.
- Compared with manipulative experiment results, process-agnostic regression-based approaches underestimate β_T by 2.36–3.87 d °C^{-1} (54–88%) while process-based phenology model fitting predicts comparable β_T and β_P. Process-based estimates of β_T and β_P are negatively correlated across species ($R = -0.94$, $P < 0.01$) and across sites ($R = -0.45$, $P < 0.01$). β_T is positively correlated with mean annual temperature, and β_P is negatively correlated with elevation at the regional scale.
- Using process-based model fitting can better estimate spring phenological sensitivities to climate. The trade-off between β_T and β_P contributes to species-level and site-level variabilities in phenological sensitivities in alpine grasslands, which needs to be incorporated in predicting future phenological changes.

Introduction

Phenology shift plays a critical role in how ecosystem responds to climate change and has far-reaching consequences for ecosystem functioning, such as growing season length, vegetation productivity, ecosystem carbon sink, land surface albedo, and species interactions (Richardson *et al.*, 2013; Chen *et al.*, 2016; Buermann *et al.*, 2018; Wang *et al.*, 2020). Phenology in alpine grasslands (elevation > 3000 m) is particularly sensitive to climate change because temperature is a main limiting factor in the biome, and climate warming is generally amplified in higher altitudes (Pepin *et al.*, 2015). Spring phenological onset has significantly advanced in alpine grasslands across continents since the early 1980s suggested by both field observations (Badeck *et al.*, 2004; Cleland *et al.*, 2006; Zheng *et al.*, 2016; Ji *et al.*, 2021) and remote sensing data (Ren *et al.*, 2020; Bellini *et al.*, 2022; Shen *et al.*, 2022). These phenological shifts are likely driven by responses to both temperature and precipitation changes (Badeck *et al.*, 2004; Shen *et al.*, 2022; Wang *et al.*, 2022) as well as the resultant changes in snow cover (Chen *et al.*, 2015; Xie *et al.*, 2020). Quantifying spring phenological sensitivities to climate change, particularly β_T and β_P which are defined as changes in spring onset dates per unit changes in temperature and precipitation, respectively, in alpine grasslands are thus essential for predicting future ecosystem changes in this biome (Möhl *et al.*, 2022). However, the current estimates of phenological sensitivities in alpine grasslands might be biased and our ecological understanding of the diverse and heterogeneous phenological responses to temperature and precipitation remains limited, which can further feed into uncertainties of

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Earth System Model (ESM) predictions (Chuine & Régnière, 2017).

First, there are large discrepancies between phenological sensitivities statistically estimated from phenological records and manipulative experiments. For example, at the species level, the apparent β_T estimated from *in situ* phenological observations (Zheng *et al.*, 2016; Yang *et al.*, 2021) was 12–62% lower than β_T estimated from field experiments (Suonan *et al.*, 2017, 2019; Chen *et al.*, 2020) in alpine grasslands at the Qinghai–Tibetan Plateau (QTP). At the landscape level, β_T derived from remote sensing observations (Shen *et al.*, 2015; Chen *et al.*, 2023) is also 43–88% lower compared to warming experiments (Chen *et al.*, 2020). Similarly, the β_P derived from remote sensing observations (Shen *et al.*, 2015) is shown to be weaker than that observed in community (Zheng *et al.*, 2016) or through manipulative experiments (Suonan *et al.*, 2019; Ma *et al.*, 2023). These discrepancies suggest current statistical analysis of spring phenology based on temporal phenological variability might have underestimated phenological sensitivities to temperature and precipitation. The underestimation of β_T and β_P likely result from the usage of process-agnostic methods such as the apparent sensitivity approach (Shen *et al.*, 2015). Apparent sensitivity is known to be heavily influenced by the choice of preseason length and suffer from statistical artifacts because the method simplifies phenological responses to a linear response to average preseason climates (Keenan *et al.*, 2020; Wolkovich *et al.*, 2021). Partial least square regression (PLSR) can help to provide more detailed climatic signals to which plants actually respond by integrating hundreds of climatic predictors (Luedeling & Gassner, 2012; Li *et al.*, 2019; Wenden *et al.*, 2020), potentially providing more accurate and robust estimates of β_T and β_P than apparent sensitivities. Furthermore, process-based model inversion might avoid such statistical artifacts at both the species (Chen *et al.*, 2015; Fu *et al.*, 2015; Basler, 2016) and landscape levels (Hufkens *et al.*, 2018) because those models explicitly represent nonlinear phenological responses to different environmental cues. However, evaluation of process-based and PLSR phenological sensitivity estimates against manipulative experiments has not been reported in alpine grasslands.

Second, although spring phenological sensitivities are known to vary across environmental gradients and species, ecological drivers of such heterogeneity are not fully understood in alpine grasslands (Wang *et al.*, 2014; Shen *et al.*, 2015; Sun *et al.*, 2021). In QTP that encompasses large areas of alpine grassland, spatial analyses suggested satellite-derived spring phenology was more sensitive to temperature in regions where mean annual precipitation (MAP) is higher (Shen *et al.*, 2015). Sensitivity of spring phenology to precipitation in the ecosystem was also found to be stronger in drier regions (Shen *et al.*, 2011, 2015). In addition, *in situ* leaf emergence observations across global tundra ecosystems, which are strongly limited by temperature like alpine grasslands, revealed that spring phenological sensitivities were stronger at colder sites (Prevéy *et al.*, 2017). While some of the spatial patterns, for example, greater β_T in colder regions, can arise from nonlinear plant physiological responses to climatic cues (Chuine & Régnière, 2017; Keenan *et al.*, 2020), species adaptation might be a key ecological driver of the spatial heterogeneity (Shen *et al.*, 2022). Such species adaptation is expected to result in a negative correlation between β_T and β_P across space because species that are more responsive to temperature should better tolerate increased drought risk associated with higher temperature and thus are less sensitive to water supply. Furthermore, the covariance between β_T and β_P might also exist at the species level because species diversity in spring phenological sensitivities of alpine grasslands likely arise from distinctive strategies of plant temperature tolerance and water use (Cleland *et al.*, 2006; Chen *et al.*, 2020). Yet, variations of β_T and β_P across species and environmental gradients are rarely analyzed together and whether and how β_T and β_P are correlated remains unknown. As a consequence, the diversity and heterogeneity in phenological sensitivities are seldom considered in process-based phenology models, which is recognized as a major source of uncertainty and bias in modern trait-based modeling frameworks (Fisher & Koven, 2020; Xu & Trugman, 2021).

In this study, we aim to improve our quantitative and ecological understanding of phenological sensitivities to temperature and precipitation in alpine grasslands by integrating *in situ* (3 sites) and remote sensing (57 sites) historical phenological records across QTP and a recent manipulative experiment at Haibei Alpine Grassland Ecosystem Research Station. Particularly, we tested three hypotheses related to the key knowledge gaps about spring phenological sensitivities:

H1: *β_T and β_P estimated from process-based model inversion are more consistent with manipulative experiment results compared with process-agnostic methods such as apparent sensitivity and PLSR. We expect process-agnostic methods generate weaker phenological sensitivities, which should not be used for further ecological analyses and model benchmarking.*

H2: *Process-based estimates of β_T and β_P demonstrate a negative correlation across species and sites after controlling for climatic effects, which means species that have high phenological sensitivity to temperature is less sensitive to precipitation.*

H3: *Ignorance of the spatial heterogeneity in β_T and β_P in phenological model parameters can result in significant biases in future spring phenology date predictions. In particular, we expect considering changes of β_T and β_P along climatic gradients can improve accuracy of phenological model predictions.*

Materials and Methods

Phenological responses to manipulative experiments

Phenological responses to warming and precipitation addition experiments at Haibei Alpine Grassland Ecosystem Research Station managed by the Chinese Academy of Sciences (Haibei station, 101°120E, 37°300N, 3200 m asl) were used to constrain the statistical inference selection. Average leaf-out responses of nine common alpine grassland plant species (e.g. *Elymus nutans*, *Kobresia humilis*, *Tibetia himalaica*, *Melilotoides archiducis-nicolai*, *Gentiana*

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lawrencei, *Aster diplostephioides*, *Potentilla saundersiana*, *Gentiana straminea*, *Saussurea superba*) to water addition (50% increase in precipitation) and warming (+2°C) treatments in year 2013 and 2014 were used to estimate the temperature (β_T) and precipitation (β_P) sensitivity of spring phenology. Detailed site and species information and the experimental setup can be found in previous papers (Suonan *et al.*, 2017; Liu *et al.*, 2018).

Historical phenological records across QTP

We collected *in situ* long-term (1990–2011) measurements of green-up dates for common alpine grass species at three sites: Haibei station (Li *et al.*, 2019), Henan station, and Qumalai station (Zhou *et al.*, 2014), which vary in elevation (Supporting Information Fig. S1; Table S1). Outliers in the phenological records were removed according to the 30-d rule (Schaber & Badeck, 2002). Detailed information on species at each station is listed in Table S2. The presence of *Kobresia pygmaea* at different elevation sites provides data for comparing the climatic adaptation of phenology across elevations. The observed daily mean temperature, maximum temperature, minimum temperature, precipitation, and sunshine hours used to predict spring phenology were collected from nearby national surface weather stations during 1990–2017, provided by the China Meteorological Administration as well.

At the landscape level, the land surface phenology from MODIS C61 MCD12Q2 land surface dynamics product was used to analyze spatial patterns of phenological sensitivity at 500-m spatial resolution from 2001 to 2017 (Gray *et al.*, 2019). This product provides full life-history metrics using the time series of the two-band Enhanced Vegetation Index (EVI2) and is reliable to monitor changes in vegetation phenology over time, particularly in response to climate change (Peng *et al.*, 2017; Moon *et al.*, 2021). We used the MCD12Q2 Greenup metric, which is defined as the day of the year when EVI first crossed 15% of its seasonal amplitude (Gray *et al.*, 2019), as spring phenological onset. Specifically, we extracted satellite-derived spring phenology for 57 meteorological stations, where high-quality climate data are available, along an elevational gradient of 2200 m to 4700 m in QTP to study the spatial patterns of phenological sensitivity (Fig. S1). All the stations are located in grassland based on the ESA global land cover map with minimal anthropogenic activities. For each site, we averaged MODIS phenological dates over 3 × 3 pixels centered around the site as an estimate of the landscape-level spring phenological dates.

Process-agnostic methods

Process-agnostic models primarily focus on correlating observed data with climatic variables with little representation of the underlying biological mechanisms. In this study, we used two commonly used statistical models, multiple linear regression and PLSR, to calculate the process-agnostic phenological sensitivity.

Apparent sensitivity In this study, we quantified apparent phenological sensitivity to preseason mean temperature (apparent β_T) and to cumulative precipitation (apparent β_P) as the coefficients of temperature and precipitation variables in the multiple linear regression for historical phenological variations. We did not include light as a variable for calculating temperature and precipitation sensitivity to maintain methodological consistency with other studies (Shen *et al.*, 2015). In addition, we used two common definitions of preseason (Table 1): (1) 1 month before multiyear averaged spring events (Apparent_1M) and (2) from 1 January to multiyear averaged spring events, which spans *c.* 4 months (Apparent_4M). The attempt aimed to illustrate how the length of the preseason influences the apparent β_T and β_P (Güsewell *et al.*, 2017; Keenan *et al.*, 2020) and to align with various studies that often use different preseason definitions.

Partial least square regression Partial least square regression was used to regress phenology variations against interannual variations in multiple daily climatic factors and to predict the phenological sensitivity based on fitted models. We included 30-d accumulated precipitation in PLSR for its biological relevance over raw daily precipitation. In addition, we compared daily mean temperature and growing degree days as predictors in PLSR. Growing degree days were calculated as the amount of daily mean temperature above a base temperature, with 16 base temperatures tested (ranging from −8°C to 8°C with a step of 1°C). The base temperature yielding the best PLSR performance with leave-one-out cross-validation (LOOCV) was selected. However, growing degree days did not improve model accuracy compared to daily mean temperature (Fig. S2). Therefore, we used daily mean temperature as the temperature predictor in PLSR models. Additionally, we incorporated daily sunshine hours as additional variables, allowing for a more direct comparison with process-based models that also consider temperature, precipitation, and light factors. Partial least square regression was performed in R 4.2.2 (R Development Core Team, 2014) using the PLS package (Mevik & Wehrens, 2007).

Process-based model inversion

Unlike process-agnostic methods, which typically rely on linear correlations, process-based modeling more explicitly incorporates the biological processes that drive variability in phenology and can be more readily integrated into ESMs (Chuine & Régnière, 2017). Process-based models usually account for the complex, nonlinear interactions between multiple climatic cues that influence phenology. This is especially important for alpine grassland plant species, which are highly sensitive not only to temperature but also to variations in water availability and light during spring phenology (Shen *et al.*, 2015; Sun *et al.*, 2021).

We considered two process-based spring phenology models that include temperature, precipitation, and light variables and have been used in grassland (Table 1): the grassland pollen release (GPR) model (Garciamozo *et al.*, 2009) and the modified accumulated growing season index (MAGSI) (Jolly *et al.*, 2005; Xin *et al.*, 2015). The GPR model uses a sigmoid function of daily mean temperature to determine the required forcing rate for development, and light and accumulated precipitation trigger the

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Table 1 Overview of the statistical methods for spring phenology included in this study.

Methods	Drivers	Temperature response assumptions	Relationship between different predictors	Comments/references
Process-agnostic				
Apparent_1M	T_{mean}, P	Linear	Additive	Preseason of 1 month
Apparent_4M	T_{mean}, P	Linear	Additive	Preseason of 4 months
Partial least square regression (PLSR)	T_{mean}, P, L	Linear	Additive	Luedeling & Gassner (2012)
Process-based				
Grassland pollen release (GPR) model	T_{mean}, P, L	Sigmoid	Additive	Garciamozo *et al*. (2009)
Modified accumulated growing season index (MAGSI)	T_{min}, P, L	Linear	Multiplicative	Xin *et al*. (2015)
Variable responses additive model (Additive)	T_{mean}, P, L	Linear	Additive	Wang *et al*. (2022)
Variable responses multiplicative model (Multiplicative)	T_{mean}, P, L	Sigmoid	Multiplicative	

The models are implemented with drivers: daily mean temperature (T_{mean}), minimum temperature (T_{min}), cumulative precipitation (P), and sunshine hours (L).

start of forcing accumulation under certain conditions (Garciamozo *et al*., 2009). In MAGSI, standardized climatic variables multiplied to represent the climatic forcing, with daily 30-d leading accumulated precipitation representing water availability (Xin *et al*., 2015). We also designed two additional models assuming additive or multiplicative relationships between temperature, precipitation, and light. The additive model was adapted from Wang *et al*. (2022) and assumes the total climatic forcing is equal to the summation of forcing from individual climatic variables. In the multiplicative model, climate variables have a sigmoid responsive curve, and total climatic forcing is equal to the multiplication of each individual climatic variable. Detailed descriptions and structures for all four models can be found in Notes S1.

In all process-based models, it is assumed that green-up occurs when the accumulated forcing reaches a critical value after the start of the accumulation period (Basler, 2016). While snow cover is frequently cited as a controlling factor for alpine phenology (Chen *et al*., 2015; Xie *et al*., 2020), it was not included as a separate variable in our analysis because precipitation data include both snowfall and rainfall and cumulative precipitation used in our model can capture the phenological impacts of snow cover due to its delayed effects on soil moisture. Meanwhile, we quantified site-level snow cover duration (SCD) derived from daily snow cover products (Qiu *et al*., 2016) given high-quality, *in situ* data for spatiotemporal variations in snow cover is lacking in our study region. We utilized the data to assess whether our results show systematic prediction biases along the spatial gradient of average SCD. In addition, we did not include models accounting for endodormancy release here for the alpine grass species because there was no reported evidence for limitation of fulfilment of chilling requirements on spring phenology from both *in situ* and remote sensing observations in QTP (Cong *et al*., 2017; Jiang *et al*., 2021a). Therefore, we assumed no chilling requirements for alpine grass phenology and compared spring phenology models with only ecodormancy release.

Optimization of model parameters was performed using the GenSA algorithm and this model inversion technique combines both the Boltzmann machine and faster Cauchy machine-simulated annealing approaches for fast optimizations (Tsallis & Stariolo, 1996; Xiang *et al*., 2013; Hufkens *et al*., 2018). First, to assess the predictive performance of the models, each model was evaluated using LOOCV per individual species or per station. For each parameter, the upper and lower limit was defined within a wide, but biologically reasonable range (Table S3). The cost function chosen in this study is the root mean square error (RMSE) between modeled data and observed data. Model inversions were performed in R 4.2.2 (R Development Core Team, 2014) using the *optimize_parameters* function in package PHENOR (Hufkens *et al*., 2018).

Phenological sensitivity calculations

We estimated the corresponding β_T and β_P by changes in model-predicted spring phenology dates when input climatic variables are manipulated. At the species level, in order to make the statistical sensitivities comparable to the phenological sensitivity based on field experiments, we perturbed the input temperature and precipitation variables the same way as the warming (+2°C) and wetting (50% addition) experiments at Haibei station (Suonan *et al*., 2019) and then evaluated the changes in predicted spring phenology in fitted PLSR and process-based models. The estimated β_T and β_P were reported by the changed d per °C increase in temperature and per 10 mm increase in precipitation, respectively. Finally, we tested hypothesis H1 on the consistency of phenological sensitivity estimation across methods by comparing the β_T and β_P from different methods with observed sensitivity from field experiments. At the landscape level, we estimated β_T and β_P using the same methodology and extended analysis across 57 stations with phenological records derived from remote sensing data. By comparing sites for which we had both *in situ* and satellite-derived data, we evaluated the

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methodological robustness across different ecological scales. This also allowed us to assess the consistency of phenological sensitivity estimates when scaled up spatially. We used Tukey's Honestly Significant Difference (HSD) test hypothesis H1 on the consistency between phenological sensitivities from statistical models and manipulative experiments.

Evaluating spatial variability in phenological sensitivity

We utilized the model that generated the most consistent β_T and β_P with manipulative experiments to estimate spatial variations in spring phenological sensitivities across QTP. We examined the relationship between phenological sensitivity and site-specific environmental factors, including mean annual temperature (MAT), MAP, and elevation, as well as the correlation between β_T and β_P across 57 study sites using multiple linear regression to test hypothesis H2.

To address hypothesis H3, which concerns the impact of spatial variability in β_T and β_P on phenological predictions, we simulated phenological responses to 2°C warming and 50% precipitation addition using the most reliable model. Three spatial parameterization scenarios were compared: (1) the 'spatially identical' (SI) parameterization assumes uniform phenological sensitivity across all sites. The sensitivity was estimated by optimizing phenology model using remote sensing data from all 57 stations. (2) The '-climate-adapted' (CA) parameterization establishes PLSR models to relate site-specific parameters with bioclimatic variables, including six variables (Bio1-min temperature of coldest month, Bio2-mean temperature of driest quarter, Bio3-mean temperature of coldest quarter, Bio4-precipitation of wettest month, Bio5-precipitation of wettest quarter, and Bio6-precipitation of warmest quarter). Using PLSR models, we derived bioclimatic-based parameters for the 57 stations, reflecting local climatic adaptations. (3) The 'site-specific' parameterization (SS) optimizes the parameters of the process-based model to obtain site-specific optimal parameters. Through the comparison, we assessed how incorporating local climatic adaptations improves the accuracy of phenological predictions in a changing climate.

Results

Comparison of phenological sensitivities inferred from different methods

For species at Haibei station, the observed temperature sensitivity in the warming experiment was -4.07 ± 0.88 d °C^{-1} and β_T inferred from *in situ* historical phenological variations had a large range, depending on the method used (Fig. 1a). β_T from additive and multiplicative models were most comparable to the manipulative experiment (-4.41 ± 0.48 d °C^{-1} and -4.39 ± 1.51 d °C^{-1}, respectively), whereas GPR model reported more negative β_T (-5.18 ± 0.40 d °C^{-1}) and MAGSI model reported less negative β_T (-2.10 ± 0.44 d °C^{-1}) compared to manipulative experiments. By contrast, process-agnostic methods generally underestimated the temperature sensitivity and reported less negative β_T. Particularly, PLSR-inferred β_T (-0.47 ± 0.29 d °C^{-1}) was significantly smaller than the observed β_T in field experiments although PLSR had comparable LOOCV RMSE with other process-based models (Fig. S2a). Inferred β_P were broadly consistent across different statistical models except for the GPR model (no sensitivity to precipitation additions). β_P estimated from Multiplicative (-1.44 ± 0.47 d 10 mm^{-1}), Additive (-0.90 ± 0.37 d 10 mm^{-1}), and PLSR (-1.49 ± 0.92 d 10 mm^{-1}) closely matched the observation from precipitation addition experiments (-1.33 d 10 mm^{-1}) (Fig. 1b). Overall, process-agnostic methods reported comparable β_P but less negative β_T compared with most process-based model inversion methods. This methodology difference was also found in the other two sites with field observations (Fig. S3).

We additionally compared sensitivities derived from MODIS green-up data at the field observation sites. The additive model based on MODIS green-up dates at Haibei station produced temperature (-3.41 d °C^{-1}) and precipitation (-2.23 d 10 mm^{-1}) sensitivities comparable to observed in the warming and precipitation addition experiments (Fig. 1a), while multiplicative and MAGSI models overestimated the response of green-up to precipitation additions (Fig. 1b). Consistent with species-level results, we also found that process-agnostic β_T was significantly smaller than model inversion β_T using MODIS green-up data over 57 meteorological stations (Fig. 1c), although their LOOCV RMSE was not so different (Fig. S2). Specifically, the averaged β_T was -4.40 d °C^{-1} in process-based models, whereas they were -0.16 d °C^{-1} in PLSR, -0.44 d °C^{-1} in Apparent_1M, and -0.89 d °C^{-1} in Apparent_4M. By contrast, β_P was more comparable among methods and across scales, while there were greater species and spatial variability in PLSR and apparent sensitivity than in process-based models (Fig. 1b,d).

Spatial variability of phenological sensitivity

Spatial variations of phenological sensitivity were analyzed based on the additive model because it reproduced the historical phenological variability (Fig. S2) and generated the most comparable results to field experiments across scales (Fig. 1). Spatially averaged β_T and β_P were -3.99 ± 2.02 d °C^{-1} and -1.43 ± 1.20 d 10 mm^{-1}. The spatial variations in β_T were positively correlated ($P < 0.01$) with MAT of stations but was not correlated with MAP or elevation. The spatial changes of β_P were negatively correlated ($P < 0.05$) with elevation through partial correlation analysis but had no correlation with MAT or MAP (Fig. 2). In addition, spatial variations of β_T and β_P were significantly negatively correlated in both field observations of 10 species ($R = -0.94$, $P < 0.001$) and remote sensing records across 57 stations ($R = -0.45$, $P < 0.001$) (Fig. 3).

Projected phenological changes under different spatial parameterizations

The optimized parameters of the additive model for three spatial parameterizations are presented in Table 2. As expected, LOOCV RMSE was lowest for the most complex SS model (6.80 d) and increased to 12.74 d for the CA model and 15.11 d

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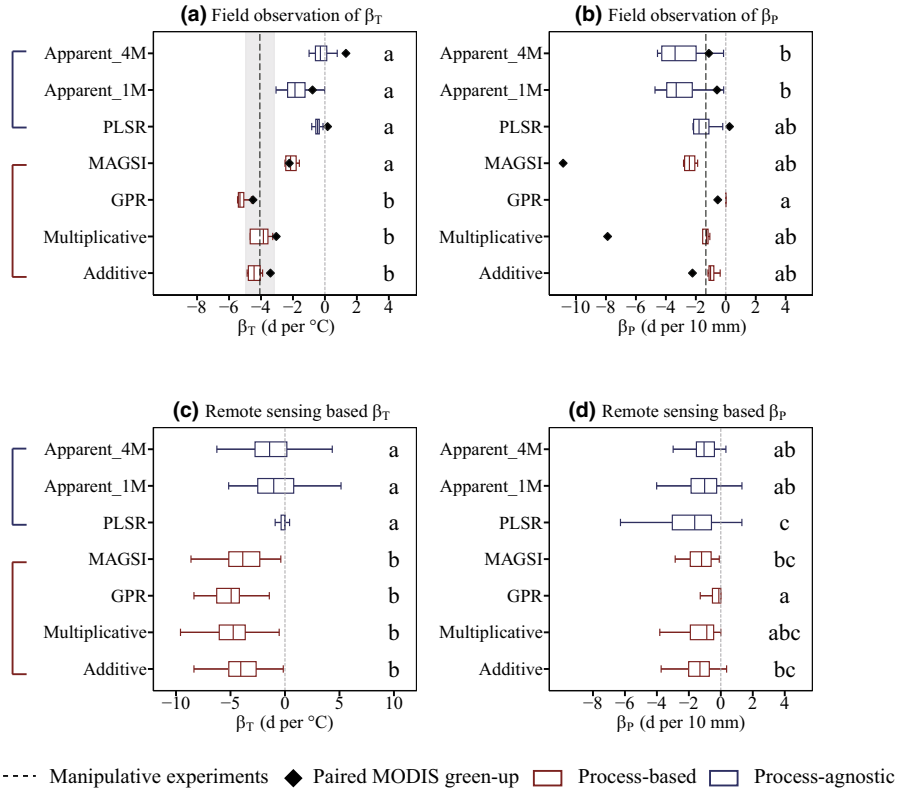


Fig. 1 Phenological sensitivity comparison among different methods using both field and satellite observations. Temperature and precipitation sensitivity of spring phenology was inferred from four mechanistic models (variable responses additive model, Additive; and variable responses multiplicative model, Multiplicative; grassland pollen release model, GPR; modified accumulated growing season index, MAGSI), partial least square regression (PLSR) and apparent sensitivity using 1- and 4-month preseason (Apparent_1M and Apparent_4M). (a) Temperature and (b) precipitation sensitivity of alpine grassland plant species at the Haibei site were compared against the warming and precipitation addition experiment (the black dashed line indicates the observed phenological sensitivity, and the shaded area indicates variability). The bold line in each box refers to the median values, and the black symbol indicates phenological sensitivity of the paired MODIS green-up of the Haibei site. (c) Temperature and (d) precipitation sensitivity of MODIS green-up dates of 57 meteorological sites over the Qinghai–Tibetan Plateau. Tukey's honestly significant difference (HSD) test was applied to show the statistically significant difference between different methods. Different letters indicate significant differences among methods at 0.05 level.

for the SI model. Comparing the SI and CA models, the SI model underestimated the changes in the timing of spring onset by 4.01 d under 2°C warming in the preseason (Fig. 4a), whereas overestimated the changes under 50% precipitation addition by 3.09 d (Fig. 4b). By contrast, the spatially averaged difference of prediction between CA and SS models were 0.25–0.63 d, which is much smaller than the difference between CA and SI, whereas there was a wide distribution of projection differences across sites.

Discussion

Underestimation of β_T in process-agnostic methods

Estimating β_T is challenging because interactions of several phenology-moderating processes, such as warming, winter chilling (Yu *et al.*, 2010; Luedeling & Gassner, 2012), preseason drought (Ji *et al.*, 2021; Zeng *et al.*, 2021), and photoperiod (Basler & Körner, 2012; Zohner & Renner, 2015), complicate the identification of temperature responses. These processes can introduce nonlinearities and intricate interactions that could not be captured by process-agnostic methods (Kovaleski, 2024). Process-based models, as expected in Hypothesis H1, predicted β_T more accurately compared to process-agnostic methods, aligning well with the manipulative experiment results (Fig. 1) even though these methods could all fit historical phenological variability well. However, the apparent sensitivity and PLSR tended to underestimate temperature sensitivities by 54 to 88% compared to field experiments and process-based models. Moreover, when using satellite-derived phenological observations, process-agnostic methods showed even greater underestimations of up to 95% in β_T compared to process-based models.

Process-agnostic methods tend to underestimate temperature sensitivity because they rely on linearity assumptions, while phenological processes are inherently nonlinear. For instance, the apparent β_T simplifies complex phenology cues by using a single temperature metric over a preseason, which can mask true climatic effects due to lower interannual variability in aggregated temperature (Wolkovich *et al.*, 2012; Güsewell *et al.*, 2017; Keenan *et al.*, 2020). Although PLSR is designed to account for complex interactions and daily climatic variability, it also underestimates β_T compared to other methods and field experiments

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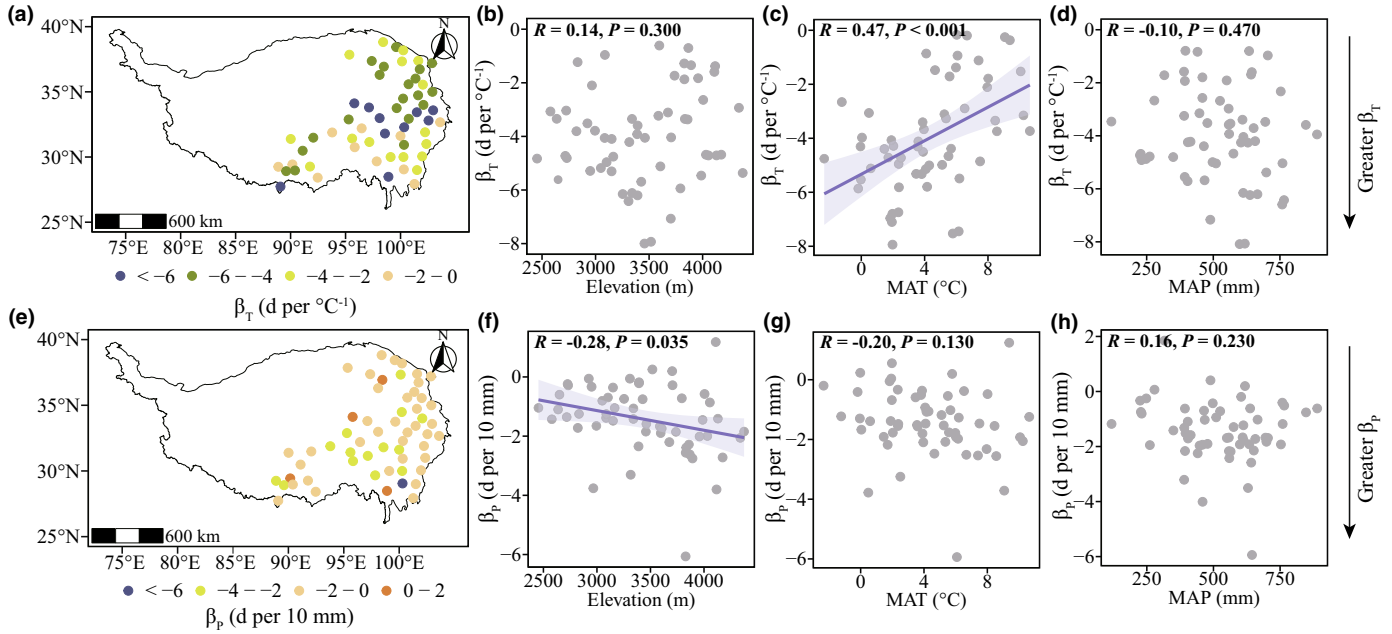


Fig. 2 Spatial patterns of (a) temperature sensitivity (β_T) and (e) precipitation sensitivity (β_P) inferred from additive models. Spatial variability of temperature sensitivity and its partial correlations to (b) elevation, (c) mean annual temperature (MAT) and (d) mean annual precipitation (MAP) and precipitation sensitivity and its partial correlations to (f) elevation, (g) MAT and (h) MAP. The shading area indicates the 95% confidence interval of the linear regression line.

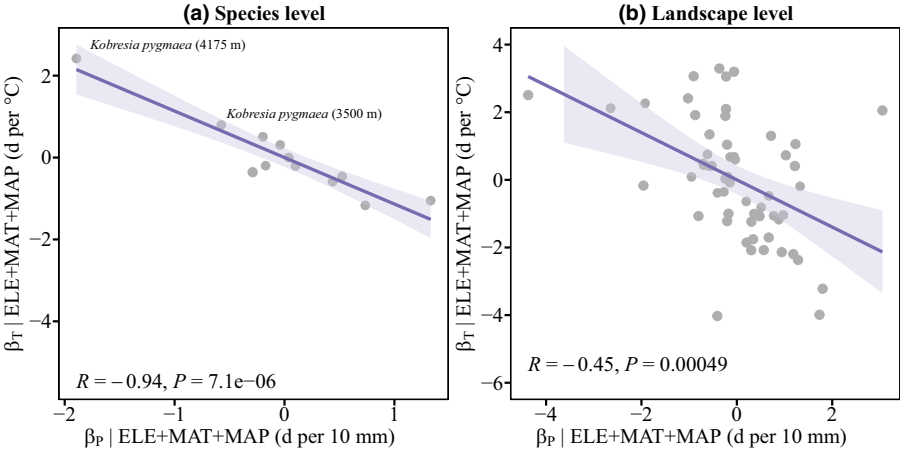


Fig. 3 Negative correlation between the additive model inferred temperature sensitivity (β_T) and precipitation sensitivity (β_P) after controlling the effects of elevation (ELE), mean annual temperature (MAT) and mean annual precipitation (MAP) from (a) field observations of three sites and (b) remote sensing records of 57 sites across the Qinghai–Tibetan Plateau. The shading area indicates the 95% confidence interval of the linear regression line.

(Fig. 1). This is likely due to PLSR's sensitivity to the covariance structure of input predictors, which may not accurately reflect mechanistic responses to daily temperature variations, leading to unrealistic temperature response coefficients. For example, when comparing PLSR predictions for two warming scenarios with the same preseason temperature increase but different day-to-day variability, the model predicted a phenological shift of −19.56 d in a year with significant temperature variance and only −0.46 d with uniform warming (Fig. S4). This suggests that PLSR may not effectively predict phenological responses to future warming scenarios.

By contrast, process-based models effectively capture nonlinear responses to climatic variables and complex interactions between temperature and other factors. Our findings indicate that the additive model, which incorporates the combined effects of temperature, precipitation, and light and aligns with recent meta-analyses of environmental drivers for phenology (Zhou *et al.*, 2023), matches observed β_T and β_P in field experiments (Fig. 1) and shows high predictive accuracy in remote sensing at the landscape scale (Fig. S2). The estimated averaged β_T over the QTP is more negative than reported apparent β_T (ranging from −3.30 to −0.66 d per °C) (Shen *et al.*, 2015; Chen *et al.*, 2023), but consistent with meta-analysis estimates (*c.* −4 d per °C) (Shen *et al.*, 2022). The scalability suggests that the additive model can reliably estimate phenological sensitivities across varying landscapes, highlighting the advantage of process-based methods for alpine grasslands and potentially other ecosystems. Our results also demonstrate that process-based modeling might

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Table 2 Optimized parameters of the additive model for three spatial parameterizations.

Parameterization	T_b (°C)	k_T	k_P	k_L	F_{crit}
Spatially identical (SI)	−7.99	0.33	12.29	11.09	1127.41
Climate-adapted (CA)	−9.35 to 0.47	0.01 to 1.15	−0.96 to 11.51	0.13 to 11.31	226.90 to 1218.28
Site-specific (SS)	−7.98 to 7.75	0.009 to 1.00	−2.02 to 14.99	0.06 to 14.77	109.21 to 1688.67

Additive model structure. AIP, multiyear average intensity of precipitation; F_{crit}, the critical forcing value needed to trigger green-up; k_T, k_P and k_L, a coefficient that modulates the temperature, precipitation, and light response; T_b, the critical temperature threshold above which temperature contributes to forcing:

$$R_T = k_T * (T_i - T_b), R_P = k_P * \frac{P_i}{AIP}, AIP = \text{mean}\left(\frac{\sum_{t_o}^{t_{green}} P_i}{\sum_{t_o}^{t_{green}} P_{frequent}}\right), R_L = k_L * \frac{L_i}{24}$$

$$F_{crit} = \sum_{t=t_{start}}^{t_{green}} \max(R_T + R_P + R_L, 0)$$

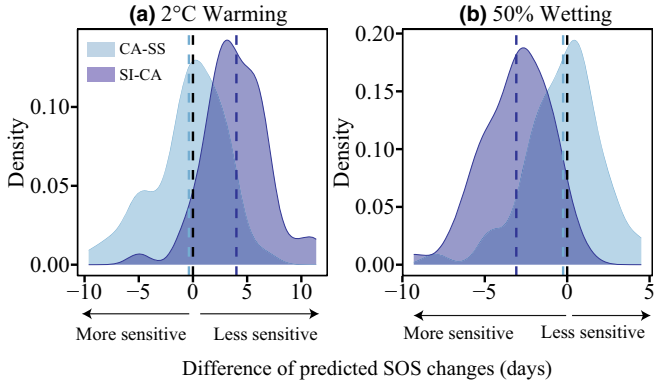


Fig. 4 Difference of the projected start of the growing season (SOS) change in response to (a) 2°C warming and (b) 50% precipitation addition in the preseason (January to April) using the additive model between spatial parameterizations (CA, climate-adapted; SI, spatially identical; SS, site-specific). Since spring phenology dates generally advance under warmer and wetter conditions, positive differences in predicted SOS changes represent lower phenological sensitivity to climate change of the first model in the pairwise comparison.

help to reconcile the mismatch in plant phenological responses inferred from long-term natural variability in phenology compared with field manipulative experiment (Wolkovich *et al.*, 2012). Finally, because our analysis was based on a 2-yr manipulative experiment at one site, there remains a need for longer-term experiments for additional sites across global alpine grasslands to further test the generality of our findings.

Ecological trade-off between β_T and β_P after controlling for environmental effects

We found that spatial variation in β_T was significantly and positively correlated with MAT ($P < 0.001$) (Fig. 2). This indicates that spring onset was more sensitive to nongrowing season temperature changes in colder areas, consistent with previous spatial analyses of apparent β_T estimations in QTP and northern tundra ecosystems (Shen *et al.*, 2015; Prevéy *et al.*, 2017). By contrast, spatial change in β_P was not associated with MAT or MAP but had a weak yet significant negative correlation ($P = 0.035$) with elevation (Fig. 2). This is also in line with evidence of a stronger limiting effect of snow cover on spring phenology at higher elevations in alpine ecosystems (Cornelius *et al.*, 2013; Chen *et al.*, 2015; Ren *et al.*, 2018; Xie *et al.*, 2020). Soils at higher elevations are typically shallower with lower water-holding capacity, making alpine plants at higher elevations more sensitive to precipitation variability. More experiments are needed to confirm the effect of altered precipitation on the spring events at high elevations. Although β_P did not change with MAP, the most negative β_P was observed at the driest site with the lowest MAP (*c.* 50 mm). In this extreme dry condition, plants prioritize water utilization, resulting in greater sensitivity of start of the growing season (SOS) to precipitation (Shen *et al.*, 2015).

As expected in Hypothesis H2, we observed a significant negative correlation between β_T and β_P across species ($R = -0.94$, $P < 0.01$) and across sites ($R = -0.45$, $P < 0.01$) after controlling for climate effects (Fig. 3). This indicates that vegetation with stronger sensitivity to temperature generally has weaker sensitivity to precipitation, and vice versa. At the species level, the negative correlation between β_T and β_P (Fig. 3a) implies a trade-off between temperature limitation and precipitation limitation for spring phenological onset. One possible ecophysiological explanation lies in the joint control of plant water status of temperature and precipitation (Konings *et al.*, 2017). Plants that can take advantage of high temperatures, that is, high β_T, must be able to tolerate enhanced water demand under increased temperature, which means lower sensitivity to moisture. In turn, species that are very sensitive to water supply, that is, high β_P, are likely unable to grow rapidly when atmospheric water demand is too high. Shifts between precipitation and temperature limitation can also occur within species due to local adaptation (Ramirez-Parada *et al.*, 2024). For example, *Kobresia pygmaea*, a common species in QTP, prioritizes precipitation over temperature for leaf growth at high elevations compared to lower elevations (Miehe *et al.*, 2019) and removed soil water stress allowed for an advance in flowering phenology of this shallow-rooted and early-flowering

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species (Jiang *et al.*, 2021b). Our analysis also reports more negative β_P and less negative β_T for *Kobresia pygmaea* as elevation increases from field observations (Fig. 3a). At the landscape level, satellite data reflect phenological variations of dominant species in the community (Melaas *et al.*, 2016; Klosterman *et al.*, 2018; Park *et al.*, 2021), as confirmed by similar cross-site differences in phenological sensitivities to climate inferred from satellite observations and species-level ground observations (Fig. S5). Spatial changes in landscape-level β_T and β_P can result from both local adaptation and turnover of community composition across the temperature gradient (Fig. 2c).

A potential caveat of the interpretation is that the relationship might arise from statistical artifacts because the additive model used to infer sensitivities has an inherent trade-off between the effects of temperature and precipitation (Table 2). However, the same negative relationship was found in species-level responses to temperature and precipitation alterations from manipulative experiments. For example, spring phenology of legumes had greater sensitivity to temperature than grass, sedges and forbs but is nonsensitive to precipitation changes (Suonan *et al.*, 2019). Therefore, we believe that the trade-off between β_T and β_P is ecologically meaningful. However, observational studies are insufficient to robustly estimate cues due to the challenges in disentangling these interdependent interactions among climatic influences. Conducting and synthesizing manipulative experiments across multiple sites with different phenological sensitivities are necessary to directly manipulate and observe the effects of phenological cues and their interactions (Wolkovich *et al.*, 2022).

Another uncertainty may arise from the absence of snow effect in the additive model, as the effect of snow on phenology is often indirect and snow cover protects vegetation from dry and severe cold conditions and simultaneously supplies moisture (Inouye, 2008; Ide & Oguma, 2013; Desai *et al.*, 2016). Our model used a 30-d moving window to account for the temporal lags in soil moisture response after snow melting. Our results showed that the model-simulated SOS aligned well with observed SOS values and that the model prediction residuals against observations did not exhibit correlation with SCD (Fig. S6a). In addition, no significant changes were found in the β_T or β_P when expanding the moving windows to 60 and 90 d (Fig. S6b). Therefore, we conclude that snow cover does not significantly disrupt the inferred sensitivity patterns in our study.

Implications of spatial variations of phenological sensitivity under climate change

Earth System Models often adopt the same parameterization for phenology of the same plant functional type or within a given biome (Dahlin *et al.*, 2015; Chen *et al.*, 2016). This approach does not account for potential variations in phenological sensitivities among different plant communities that have adapted to local climate conditions (Tan *et al.*, 2024). Cao *et al.* (2018) explored local phenological adaptations for historical data on the Tibetan Plateau but did not assess their impact on future phenology predictions. Our study reveals that overlooking spatial variations in phenological sensitivity, as shown in SI models, can lead to substantial inaccuracies in predictions (Fig. 4). In addition, SI models underestimated phenological advancement under warming while overestimating phenological advancement under wetting, suggesting that SI parameters cannot accurately capture the complex interactions between climate variables and plant phenology over a large spatial scale. This result reveals limitations of phenological model based on constant sensitivity to climate change that fails to capture climatic adaptation and trade-off between temperature and precipitation sensitivity (Fig. 3).

The negative correlation between temperature and precipitation sensitivity in spring phenology has often been overlooked in models, despite the consistent trend of earlier spring phenology predicted by various temperature-based models (Asse *et al.*, 2020; Mo *et al.*, 2024). In our study, although SS models, including the interactive effects of temperature and precipitation, exhibited the lowest predictive error, they are challenging to implement in ESMs and may suffer from overfitting due to limited data records at each site. The CA model can be a more practical option and it provides improved predictions by correcting systematic differences between SI models and SS models at a regional scale (Fig. 4).

In the future, the significant regional heterogeneity in warming and precipitation over QTP (Zhang *et al.*, 2022) suggests that current projections of spring phenology advancement by 8.8-d over the Tibetan Plateau (Shen *et al.*, 2022) may underestimate the actual phenological changes. Greater phenological advancement due to climate adaptation and the cumulative influence of precipitation on phenology can affect various ecological aspects, including vegetation growth (Keenan & Richardson, 2015; Zeng *et al.*, 2021), surface albedo and biosphere-to-atmosphere fluxes (Li *et al.*, 2023), and carbon balance (Richardson *et al.*, 2009). Our results indicate that the projections of phenological advances under warmer conditions might exceed initial estimates if spatial variations in phenological sensitivity are not considered. This underscores the need for models that incorporate these spatial variations to reduce uncertainty in predicting ecosystem responses and climate feedback.

Conclusion

Our study presents a comprehensive assessment of phenological sensitivities to temperature and precipitation over alpine grasslands. We found significant inconsistencies in phenological sensitivity estimates among statistical methods. Compared with process-agnostic models such as PLSR and apparent sensitivity method, process-based model inversion predicted phenological responses more consistent with experimental warming and precipitation manipulation. Additionally, the process-based model, which assumes an additive effect of temperature, precipitation, and light, generates similar phenological sensitivities using both *in situ* species-level observations and remote sensing landscape-level observations, suggesting the model is ecologically scalable. By contrast, PLSR and apparent methods tended to underestimate temperature sensitivity at both species and landscape levels. While our focus was on spring phenology in alpine species, these

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findings highlight potential biases in projections using process-agnostic approaches for other events, such as plants flowering, and leaf fall in other temperature-limited ecosystems.

Our study identified spatial variations in phenological sensitivity, revealing higher temperature sensitivity in colder areas and higher precipitation sensitivity at higher elevations. We also observed a significant negative correlation between temperature sensitivity and precipitation sensitivity across species and space in alpine grassland. Further investigation on the generality of the correlation in other ecosystems and its biological foundation are needed in the future.

Our results also recommend explicit consideration of phenological adaptation to the local environment and the interactive effects of temperature and precipitation on phenology in order to accurately predict ecosystem responses to rapid climate shifts in QTP and other alpine ecosystems. Our analyses provide novel and more accurate parameterization for phenological modeling for alpine grassland ecosystems that can be directly assimilated into ESMs, which can improve our understanding of phenological effects on land surface processes in alpine grasslands.

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Competing interests

None declared.

Author contributions

XTL, WG and XTX designed the research. HW and J-SH provided the manipulative experiments data. XTL and XTX designed the process-based models. XTL, WG and HH performed model simulation and data analysis. XTL, XTX, AC, DHW, YXM and YQW led the writing. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

Climate data are acquired from https://data.cma.cn/data/detail/dataCode/A.0012.0001.S011.html. Snow cover data are acquired from http://www.sciencedb.cn/dataSet/handle/55 (doi: 10.11922/sciencedb.55). Phenology data are acquired from Haibei station (Li *et al.*, 2019), Henan station, and Qumalai station (Zhou *et al.*, 2014). Optimized parameters of the additive model for three spatial parameterizations across 57 stations are archived and accessible at doi: 10.6084/m9.figshare.25794111.v1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Distribution of the phenological and weather stations in the Qinghai–Tibetan Plateau used in this study.

Fig. S2 Leave-one-out cross-validation for process-based and process-agnostic models.

Fig. S3 Phenological sensitivity inferred from three field sites.

Fig. S4 Illustration of temperature effects on spring phenology through partial least square regression.

Fig. S5 Comparison of phenological sensitivity between species scale and landscape scale across the three field sites.

Fig. S6 Influence of the snow cover duration on the remote sensing-based phenology assessments.

Notes S1 Brief introduction of the mechanistic models.

Table S1 The climate of the observation sites.

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Table S2 Summary of dominant species at the observation sites.

Table S3 Parameters range in mechanistic models.

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