Detecting temporal changes in the temperature sensitivity of spring phenology with global warming: Application of machine learning in phenological model

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ABSTRACT

Phenological models can effectively infer historically missing phenological data, so as to investigate the long-term relationship between plants and climate change. Large numbers of ecophysiological and statistical models have been developed in the past few decades, but these models have been unable to make accurate predictions based on external data. Machine learning (ML) methods have an advantage over traditional statistical methods for natural science studies. However, only a few phenological models have been coupled with ML methods. In this study, using long-term leaf unfolding date (LUD) observations collected in Harbin, China, we adopted three popular ML algorithms for predicting plant LUD and compared the performances of 10 phenological models. We detected the temperature sensitivity (ST) of the LUD at the species level for the periods 1962–1987 and 1988–2016 (before and after the recent, sudden warming) and temporal changes in ST with a 15-year moving window for each period. The results show that the gradient boosting decision tree (GBDT) model performs obviously better than the other models for external validation data, while avoiding model overfitting. Most species showed an increase in ST during the 1988–2016 period, and the temporal changes in ST significantly decreased during both periods. The temporal changes in ST from the phenological data predicted by the GBDT model is significantly higher than that of other models, which indicates that the traditional phenological models may underestimate the response of LUD to climate warming. We found a prevalent decline in the magnitude of ST with increasing preseason temperature variance at the species level. Our research suggests that machine learning algorithms should be more widely used in future phenological model research, and temporal changes in ST should be investigated in order to broaden our understanding of plants' ability to adapt to future climate change.

1. Introduction

Air temperatures in the Northern Hemisphere have risen rapidly in the past few decades, and plant phenology has arrived earlier in years with warmer temperatures (Mulder et al., 2017). Plant phenology has proven to be a sensitive biological indicator for climate change (Menzel and Fabian, 1999; Menzel et al., 2006; Wang et al., 2015). Climate-induced changes in leaf unfolding date (LUD was defined as the date when an individual plant of a given species unfolded the first young leaves) can significantly influence the structure and function of eco-systems by advancing the onset of the growing season (Menzel et al., 2006; Fu et al., 2015b), enhancing spring carbon uptake (Desai, 2015; Piao et al., 2017), increasing annual forest productivity (Keenan et al., 2014), changing species' abundance and distribution (Sparks and Carey, 1995; Chuine, 2010; Saikkonen et al., 2012), and affecting plant–animal interactions (Hunter, 1992; Memmott et al., 2007; Moreira et al., 2017). Changes in the phenology of LUD can also result in biophysical feedbacks with the climate (Peñuelas et al., 2009; Richardson et al., 2013). It is therefore crucial to understand the effects climate has on plant growth. However, the underlying physiological mechanisms regulating bud development, nevertheless, remain unclear, making it difficult to develop widely applicable predictions of LUD (Hanninen and Kramer, 2007; Fu et al., 2014a; Laube et al., 2014b; Piao et al., 2015). Although there are many factors that can lead to pheno-logical fluctuations, such as photoperiod (Way and Montgomery, 2015), humidity (Laube et al., 2014b), precipitation (Li and Zhou, 2012; Fu et al., 2014a), soil moisture and temperature (Ishioka et al., 2013; De Barba et al., 2016), nutrient availability (Jochner et al., 2013), and light
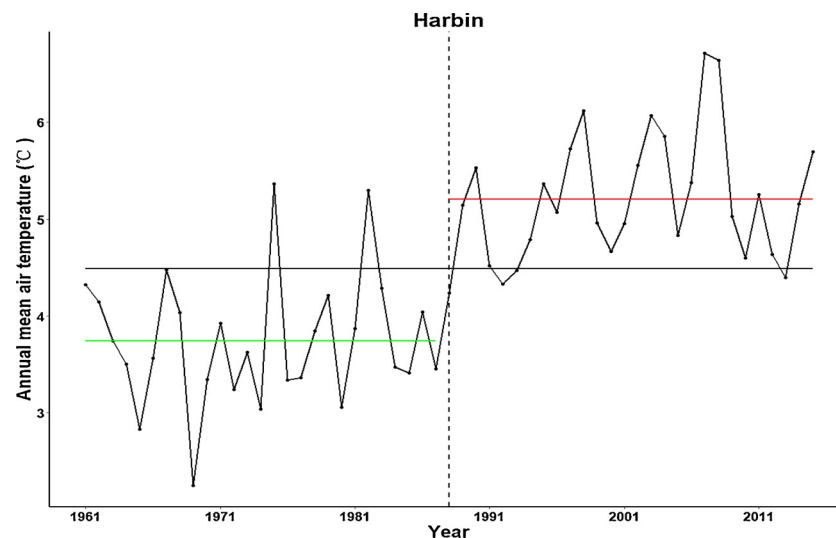
Fig. 1. Changepoint analysis of the annual mean air temperature for Harbin.

regime (Linkosalo and Lechowicz, 2006), air temperature is the main factor that controls the rate of plant development as it affects essential biochemical processes and plays a determining role in the appearance of phenological stages and the length of the phenophases (Chuine et al., 2010; Fu et al., 2016), while all other factors are presumed to capture some of the remaining, unexplained variance.

Long-term phenological observations on multiple plant species are necessary to be able to accurately determine the interactions between temperature and spring plant phenology. However, phenological observations vary between phenological networks and among stations within networks because these observations are often collected by volunteers and can thus result in discontinuous, incomplete data series (Du et al., 2017). Moreover, different individuals may apply different standards to their observations (Dose and Menzel, 2004). When phenological observations are missing, the phenological responses that species have due to climate change cannot be compared, and may even be overestimated or underestimated. Accurate plant phenological models are vital tools for predicting the missing year data and can therefore reflect the real extent of phenological responses to climate change. In order to accurately predict plant LUD and illustrate the mechanisms of temperature responses, since the early 1970s, many temperature-based models have been proposed. The applications of phenological models range from reconstruction and quality assessment of phenological time-series, to spatial extrapolation of observations, and even to species-specific predictions of phenology, and thus to species' performance in future climate conditions.

These models can be divided into two categories: ecophysiological and statistical. The statistical models predominantly use classical statistical methods like simple linear regression, and rarely incorporate other curve fitting methods (e.g., logarithmic and quadratic) (Mulder et al., 2017). These methods, however, have the major disadvantage of being only partially complete and requiring longer records, because trend detection at a single site strongly depends on the number of years included in the linear regression. Ecophysiological models are able to reflect the nonlinear responses of phenology to temperature. However, with an increasing number of factors, model complexity increases dramatically and parameterization becomes increasingly difficult. Comparing the accuracy of leaf unfolding predictions depends on different ecophysiological hypotheses for different species; there is no consensus, let alone any one hypothesis that seems significantly better than the others (Chuine et al., 1998; Andreini et al., 2014; Basler, 2016). Species-specific ecophysiological models derived from greenhouse experiments are limited in the scope of their application. Such temperature manipulations are short-lived and put stress on saplings or

dormant twigs, and therefore cannot adequately reflect lag effects or buds' adaptability to temperature, and further, may elicit phenological responses that do not accurately reflect the responses of mature trees in natural conditions (Wolkovich et al., 2012; Vitasse, 2013). For these reasons, ecophysiological models are particularly difficult to fit, test and compare. The methodological difficulties involved, as well as the diversity of existing hypotheses, have greatly impeded the improvement of phenological models (Chuine, 2000).

Several comparative studies have already shown that machine learning (ML) algorithms can outperform traditional statistical approaches in a wide variety of problems in earth science and ecology (Bond-Lamberty et al., 2013; Thessen, 2016; Cai and Ge, 2017; Hoffman et al., 2017; Yao et al., 2018). ML has an advantage over the traditional statistical methods for understanding and predicting the complex interactions between biotic and abiotic systems in the natural sciences, such as ecology and earth science. The power of ML approach over traditional methods is mostly related with ensemble approach and non-linear techniques that might be applied within ML. Meanwhile, ML is an algorithm that can automatically analyze the rules from the data and use it to predict the unknown data. Thus, a wider adoption of machine learning methods in ecology and earth science has the potential to greatly accelerate the pace and quality of the science. Despite these advantages and its potential uses, ML algorithms have few applications in the field of plant phenology research (Czernecki et al., 2018; Capinha, 2019), and there is big room for further improvement. The spring phenology of plants in temperate regions strongly responds to spring temperatures. Climate warming has already substantially altered phenology, but future trends are uncertain. Temperature sensitivity (ST) is the phenological advance statistically associated with a 1 °C warmer mean temperature during the "preseason", which is defined as the most temperature-sensitive period preceding the phenological event (Fu et al., 2015b; Güsewell et al., 2017). Recent analyses of phenological records have revealed a decline in the temperature sensitivity of leaf unfolding, but the underlying mechanisms remain unclear. The fifth IPCC Report concluded that globally averaged land surface air temperature has risen since the late 19th century and that this warming has been particularly marked since the 1970s (Stocker et al., 2013), plant phenology is perhaps the simplest and most frequently used bio-indicator to track climate changes (Dose and Menzel, 2004). While the climate of Northeast China has been deeply affected by the abrupt climate change that took place in the late 1980s (Jia and Guo, 2011), a similar signal was detected in 1988, in Harbin (Fig. 1). In addition, current studies rarely explore temporal changes in ST because of the relatively short time series of ground observations available. As a

result, phenological ST and temporal changes in ST before and after the climatic change of 1988 should be analyzed to broaden our understanding of the adaptability of plants to future climate change.

The aims of this study are to: 1) apply three popular ML algorithms (random forest, neural network and gradient boosting decision tree) to predict LUD; 2) compare the performance of three types of ML models, five ecophysiological models and two simple linear models; 3) investigate the temperature sensitivity (ST) of leaf unfolding at the species level for forty woody species for two periods (1962–1987 and 1988–2016) during which Harbin's climate was substantially warmer; 4) investigate temporal changes in ST during each period with a 15-year moving window, and relate them to variations in other physiological and environment factors.

To study these questions, historical phenological observation LUD data and meteorological data from 1962 to 2016 were used to fit temperature-based phenological models, model performance were evaluated by *RMSE* on external validation data. We selected the model with best performance to infer missing LUD data. Combining the historical observation data with the inferred missing data, we compared the ST of LUD data before and after abrupt climate change, detected the temporal changes of ST and the possible causes of this phenomenon.

2. Materials and methods

2.1. Data source

The phenological observations were obtained from the Forest Botanical Garden of Heilongjiang Province (Harbin, China; 45.7 °N, 126.6 °E). Over the course of our study period (1962–2016), the annual mean temperature was 4.3 °C and increased by 0.45 °C per decade. The average monthly highest and lowest temperatures for all study years were 23.0 °C in July and −18.4 °C in January, respectively.

According to the observation criteria of the Chinese Phenological Observation Network, 2115 LUD observations have been recorded for 200 woody species (89 genera, 39 families) and have been monitored since 1963 in the Forest Botanical Garden. Unfortunately, data collection for the site has not been continuous. Observations ceased from 1966 to 1972 and from 1989 to 2002: observations were interrupted due to the lack of financial support. Therefore, data for this study cover the periods 1963–1966, 1973–1989, and 2003–2016. In addition, there are some data points missing from specific years for certain species. Time series for species with more than 18 years of data (40 species, belonging to 19 families, Table 1) were available for the quantitative assessment of temporal changes in temperature sensitivity (Menzel et al., 2006; Wang et al., 2014). The daily mean air temperature data from 1962 to 2016 at this site were obtained from the Harbin Meteorological station (about 7 km away from our phenological observation site, the Forest Botanical Garden of Heilongjiang Province).

2.2. Data analysis

2.2.1. Ecophysiological models

Temperature-based ecophysiological models mainly include: spring warming model (SW) (Cannell and Smith, 1983; Hunter and Lechowicz, 1992), alternating (AL) (Murray et al., 1989; Kramer, 1994), sequential (SE) (Hänninen, 1990; Kramer, 1994), parallel (PA) (Landsberg, 1974), unified (UN) (Chuine, 2000), deepening rest (DR) (Kobayashi and Fuchigami, 1983) and four phase (FP) (Vegis, 1964; Hänninen, 1990) models. Model with high number of parameters did not significantly improve its performance (Chuine, 2000), in addition, due to the limitation of sample size, only five temperature-based ecophysiological models with less than 10 parameters (SW, AL, SE, PA and UN) were studied to simulate LUD in this paper. These models assumed that the temperature influence on bud development until a critical developmental threshold for leaf unfolding is reached. Their respective equations are summarized in Table 2. The model parameters were adjusted

Table 1
Summary of 40 species at the Forest Botanical Garden of Harbin, Northeast China. 'LUD' is Julian day of the leaf unfolding date.

Species	Family	Growth habit	Origin	LUD	Years
Acer ginnala	Aceraceae	Tree	Native	126 ± 8.7	21
Acer negundo	Aceraceae	Tree	Nonnative	121 ± 7.0	19
Albizia kalkora	Leguminosae	Tree	Native	137 ± 6.0	23
Amygdalus triloba	Rosaceae	Shrub	Native	130 ± 7.4	25
Armeniaca sibirica	Rosaceae	Tree	Native	132 ± 6.9	25
Betula platyphylla var. mandshurica	Betulaceae	Tree	Native	126 ± 6.3	20
Caragana arborescens	Leguminosae	Shrub	Native	128 ± 7.2	25
Catalpa ovata	Bignoniaceae	Tree	Nonnative	144 ± 7.1	21
Euonymus maackii	Celastraceae	Tree	Native	118 ± 7.9	20
Flueggea suffruticosa	Euphorbiaceae	Shrub	Native	139 ± 7.6	19
Forsythia mandschurica	Oleaceae	Shrub	Nonnative	125 ± 8.6	24
Fraxinus mandschurica	Oleaceae	Tree	Native	136 ± 6.1	24
Hemiptelea davidii	Ulmaceae	Tree	Nonnative	126 ± 8.8	25
Juglans mandshurica	Juglandaceae	Tree	Native	132 ± 7.4	28
Larix olgensis	Pinaceae	Tree	Native	119 ± 7.5	23
Lonicera maackii	Caprifoliaceae	Shrub	Native	121 ± 6.1	26
Lonicera tatarinowii	Caprifoliaceae	Shrub	Nonnative	120 ± 4.7	20
Malus baccata	Rosaceae	Tree	Native	118 ± 6.5	20
Morus alba	Moraceae	Tree	Native	140 ± 6.5	26
Phellodendron amurense	Rutaceae	Tree	Native	134 ± 6.4	24
Philadelphus schrenkii	Saxifragaceae	Shrub	Native	121 ± 7.2	23
Picea koraiensis	Pinaceae	Tree	Native	133 ± 6.6	23
Pyrus ussuriensis	Rosaceae	Tree	Native	125 ± 7.8	23
Quercus mongolica	Fagaceae	Tree	Native	127 ± 9.1	26
Rhododendron dauricum	Ericaceae	Shrub	Native	122 ± 7.5	19
Ribes odoratum	Saxifragaceae	Shrub	Nonnative	120 ± 5.4	19
Sambucus williamsii	Caprifoliaceae	Shrub	Native	114 ± 6.5	25
Sorbaria sorbifolia	Rosaceae	Shrub	Native	109 ± 8.9	26
Sorbus pohuashanensis	Rosaceae	Tree	Native	122 ± 6.4	25
Spiraea trichocarpa	Rosaceae	Shrub	Nonnative	126 ± 7.5	20
Syringa oblata	Oleaceae	Shrub	Nonnative	125 ± 6.9	28
Syringa oblata var. alba	Oleaceae	Shrub	Nonnative	124 ± 6.3	23
Syringa reticulata	Oleaceae	Tree	Native	115 ± 7.5	24
Tilia amurensis	Tiliaceae	Tree	Native	128 ± 7.3	19
Ulmus davidiana	Ulmaceae	Tree	Nonnative	126 ± 7.0	21
Ulmus pumila	Ulmaceae	Tree	Native	125 ± 6.7	27
Viburnum burejaeticum	Caprifoliaceae	Shrub	Native	117 ± 7.4	23
Viburnum opulus	Caprifoliaceae	Shrub	Native	121 ± 7.1	24
Weigela florida	Caprifoliaceae	Shrub	Nonnative	127 ± 7.1	21
Xanthoceras sorbifolium	Sapindaceae	Shrub	Nonnative	137 ± 7.0	20

by minimizing the root mean square error (*RMSE*) between observed and model predicted LUD (Chuine et al., 1998; Fu et al., 2015b):

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(d_i(x) - d_i(obs))^2}{n}}$$

where $d_i(x)$ is the model fitted value of the observation i, $d_i(obs)$ is the observed value and n is the number of observations. According to the methods of Chuine et al. (Chuine et al., 1998), we calibrated the models using Generalized Simulated Annealing (GenSA). "GenSA" (Hufkens et al., 2018) available for the R programming language (R Core Team 2019) was selected to calculate the optimum parameters of each model.

2.2.2. Simple linear regression models

The two simple linear regression models were unique in their

Table 2
Equations for the five ecophysiological models in this study.

Spring warming model (SW) : parameters are t_0, T_b and F^*

$$S_f = \sum_{t_0}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_b \\ x_t - T_b & x_t > T_b \end{cases}$$

Sequential model (SE) : parameters are T_0, T_b, F^* and C^*

$$S_f = \sum_{t_2}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_b \\ \dfrac{28.4}{1 + e^{-0.185(x_t - 18.4)}} & x_t > T_b \end{cases}$$

$$C^* = \sum_{t_1}^{t_2} R_c(x_t)$$

$$R_c(x_t) = \begin{cases} 0 & x_t \leq -3.4 \cup x_t \geq 10.4 \\ \dfrac{x_t + 3.4}{T_0 + 3.4} - 3.4 & -3.4 < x_t \leq T_0 \\ \dfrac{x_t - 10.4}{T_0 + 10.4} & T_0 < x_t \leq 10.4 \end{cases}$$

Parallel model (PA): parameters are T_0, K_m, F^* and C^*

$$S_f = \sum_{t_1}^{y} R_f(x_t) = F^*$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq 0 \\ (K_m + \dfrac{1 - K_m}{C^*} S_c) f(x_t) & x_t > 0 \cap S_c < C^* \\ f(x_t) & x_t > 0 \cap S_c \geq C^* \end{cases}$$

$$f(x_t) = \dfrac{28.4}{1 + e^{-0.185(x_t - 18.4)}}$$

$$S_c = \sum_{t_1}^{y} R_c(x_t)$$

$$R_c(x_t) = \begin{cases} 0 & x_t \leq -3.4 \cup x_t \geq 10.4 \\ \dfrac{x_t + 3.4}{T_0 + 3.4} - 3.4 & -3.4 < x_t \leq T_0 \\ \dfrac{x_t - 10.4}{T_0 + 10.4} & T_0 < x_t \leq 10.4 \end{cases}$$

Alternating model (AL): parameters are T_b, C^*, a and b

$$S_f = \sum_{t_2}^{y} R_f(x_t) = F^* = a \times e^{b \times S_c}$$

$$C^* = \sum_{t_1}^{t_2} R_c(x_t)$$

$$S_c = \sum_{t_1}^{y} R_c(x_t)$$

$$R_c(x_t) = \begin{cases} 0 & x_t > T_b \\ 1 & x_t \leq T_b \end{cases}$$

$$R_f(x_t) = \begin{cases} 0 & x_t \leq T_b \\ x_t - T_b & x_t > T_b \end{cases}$$

Unified model (UN): parameters are t_c, C^*, k, w, a, b, c, d and e

$$S_f = \sum_{t_2}^{y} R_f(x_t) = F^* = w \times e^{k \times C_{tot}} \quad w > 0 \cap k < 0$$

$$S_c = \sum_{t_1}^{t_2} R_c(x_t) = C^*$$

$$C_{tot} = \sum_{t_1}^{t_c} R_c(x_t)$$

$$R_c(x_t) = \dfrac{1}{1 + e^{a(x_t - c)^2 + b(x_t - c)}}$$

$$R_f(x_t) = \dfrac{1}{1 + e^{d(x_t - e)}}$$

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y: leaf unfolding date; x_t: daily mean air temperature (°C); $R_f(x_t)$: forcing rate function; $R_c(x_t)$: chilling rate function; S_f: state of forcing; S_c: state of chilling; K_m: minimum potential of unchilled buds to respond to forcing temperature; C^*: critical value of state of chilling for the transition from rest to quiescence; F^*: critical values of state of forcing for the transition from quiescence to leaf unfolding date; C_{tot}: total state of chilling achieved; t_1: date of onset of rest (fixed to 1 st September); t_2: date of onset of quiescence; t_c: date of total state of chilling reached; T_b: base temperature; T_0: optimal temperature of the rate of chilling; a, b, c, d, e, k and w: constants.

method for selection of independent variables: the relevant month (RM) model selected relevant monthly temperature and the relevant pre-season (RP) model selected relevant preseason (a number of days before the mean LUD) as independent variables. A single month's temperature in the month prior to LUD, average temperature of the preceding two months or average temperature of successive 3-month intervals (beginning in August of the preceding year) were selected as RM independent variables. We selected the best variable for each species based on the highest Pearson correlation coefficient between LUD and air temperature. The optimal preseason for RP was defined as the period (at 15-day intervals) before the mean leaf unfolding date for which the Pearson correlation coefficient between leaf unfolding and

air temperature was highest. The core algorithm for these models was ordinary least squares.

2.2.3. Machine learning models

We chose three widely used machine learning algorithms to predict LUD: random forest (RF), neural networks (NN) and gradient boosting decision tree (GBDT). The "caret" package in R provides an excellent facility to tune machine learning algorithm parameters, grid search method was used for optimizing tuning parameters (Kuhn, 2008). Both 10-fold cross-validation and random resampling were used to limit and reduce overfitting on the training set. In order to ensure the reproducibility of models, setting random seeds were used in the stage of tuning parameters, resampling and model training. These three algorithms use functions from the R packages "randomForest", "nnet" and "gbm", respectively (Breiman, 2001; Friedman, 2002; Venables and Ripley, 2002; Lantz, 2013; Ghatak, 2017).

The process of bud development before leaf unfolding should be divided into three phases: 1) morphogenesis and development to dormancy, 2) dormancy, 3) subsequent growth to full bloom (Landsberg, 1974; Singh et al., 2017). Leaf bud morphogenesis commences in later spring to early summer. A forcing experiment showed that the forcing conditions for the seedlings from 30 July to 10 September had advanced the LUD and that the longer the heating period, the earlier the leaves unfolded (Ueno et al., 2013). In this study, the single monthly temperatures, beginning in May of preceding year to April of the LUD year, were used as input variables for RF and NN models. In addition to these variables, species were also individually selected as independent features for the GBDT model (Fig. 2).

2.2.4. Model performance comparison

Models should always be validated with independent data that was not used to construct the model itself. In this study, two-thirds of the LUD data was randomly selected as training data for model fitting and parameter estimation, and the remaining third was used as test data for model validation. To avoid the randomness of one-time random selection, the data were randomly sampled 10 times. Using test data as an external validation for each model, the corresponding *RMSE* was used to evaluate the performance of the model. Tukey HSD (Tukey's 'Honest Significant Difference' method) provides an ideal method for comparison between paired groups (Bretz et al., 2011), we used this method to evaluate the model performance within different type of models and within all models.

2.2.5. Temporal changes in temperature sensitivity

The relevant period used to determine leaf unfolding is typically one to three months prior to the phenological event and can differ among species and locations (Menzel et al., 2006), though others have used a different combination of successive month intervals for mean temperature in the preceding 11 months (Du et al., 2017). At the same time, some studies suggest that the optimal preseason is defined as the period (with 15-day steps) before the mean LUD when the correlation coefficient between LUD and air temperature is highest (Fu et al., 2015b; Güsewell et al., 2017). However, others have proposed a fixed length (e.g., 60 days or 90 days) before the mean LUD as the optimal preseason (Fu et al., 2014b). In any case, the length of the optimal preseason has been significantly reduced during the past decades (Güsewell et al., 2017). For each species at the study site, missing data was filled by the predicted data from the better performing phenological models. To investigate the ST of leaf unfolding at the species level from 1962 to 1987 and from 1988 to 2016 (before and after the recent sudden warming) and temporal changes in ST with a 15-year moving window during each period, we found that the optimal length of the preseason ranged between 15 days and 4 months across all forty species and that the beginning of the optimal preseason for all species was at the end of March (the historical mean Julian day temperature at the study site indicated that temperatures did not exceed 0 °C until the end of March)
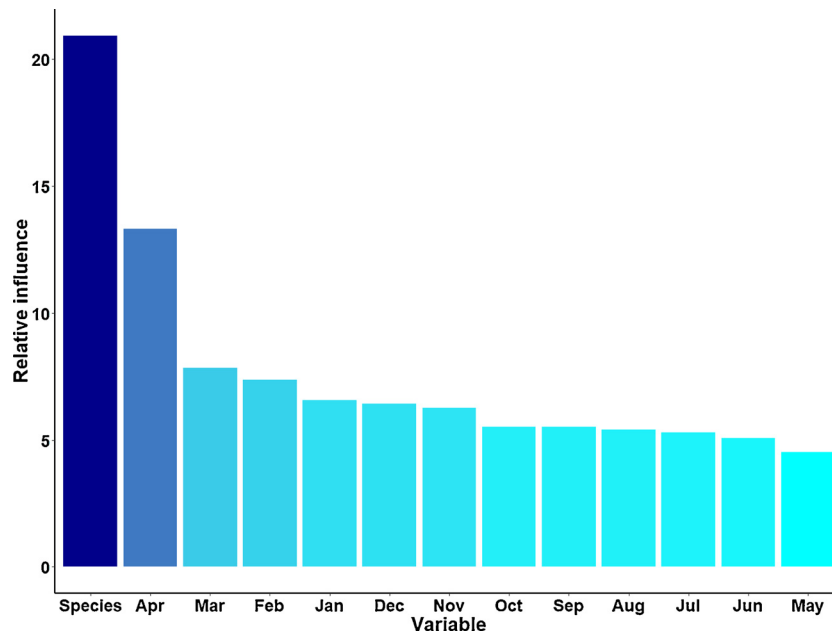
Fig. 2. The relative influence of variables for the gradient boosting decision tree (GBDT) model. Apr, Mar, Feb and Jan: mean temperature of LUD year; Dec, Nov, Oct, Sep, Aug, Jul, Jun and May: mean temperature of preceding LUD year.

(Fig. 3). Even so, the correlation coefficient between optimal preseason and fixed preseason (mean temperature in April) showed that the difference was not significant (Fig. 4a). To make the temporal changes in ST comparable in magnitude, we selected April as the fixed preseason. We then calculated the average temperature during the fixed preseason for each year and calculated ST using ordinary least squares linear regression for the remaining research. All statistical analyses were conducted in the programming language R 3.5.3 (R Core Team, 2019).

3. Results

3.1. Model performance

The performance of the five phenological models with optimized parameters (Table 3) was evaluated and compared based on the internally and externally validated *RMSE* of the predicted LUD (Table 4). With the same testing data, the average *RMSE* for the external validation of each type of phenological model is shown in Table 4. The comparison of the two simple linear regression models shows that the
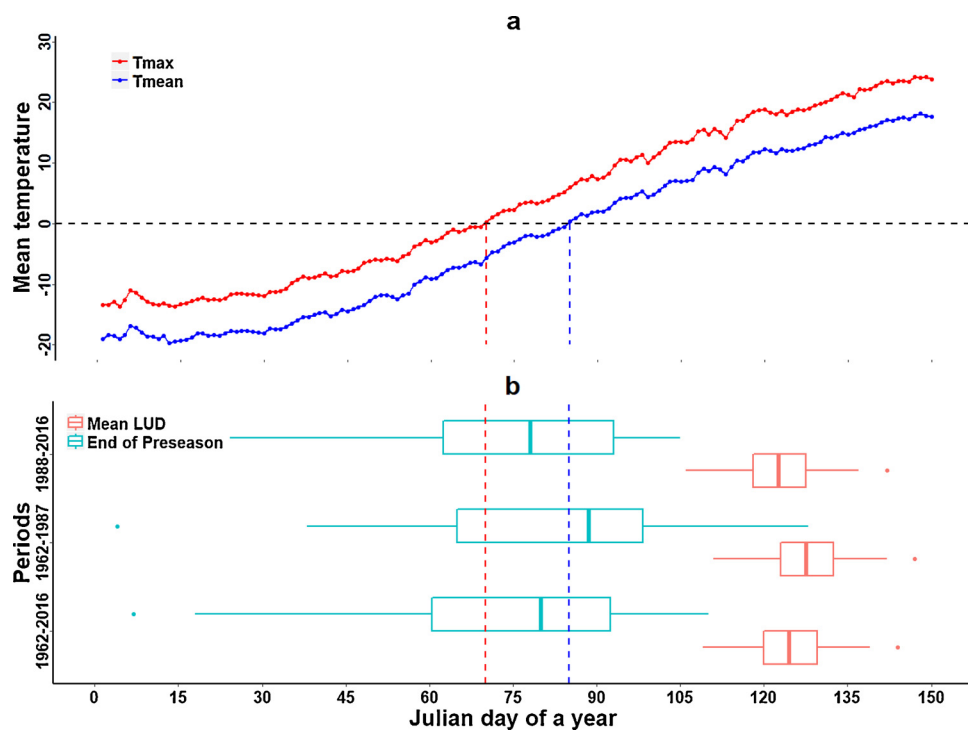
Fig. 3. Average daily mean temperature (Tmean) and average daily max temperature (Tmax) during 1962–2016 (a). Optimal preseason length (from mean LUD to end of preseason) distribution for all species in the study site (b).
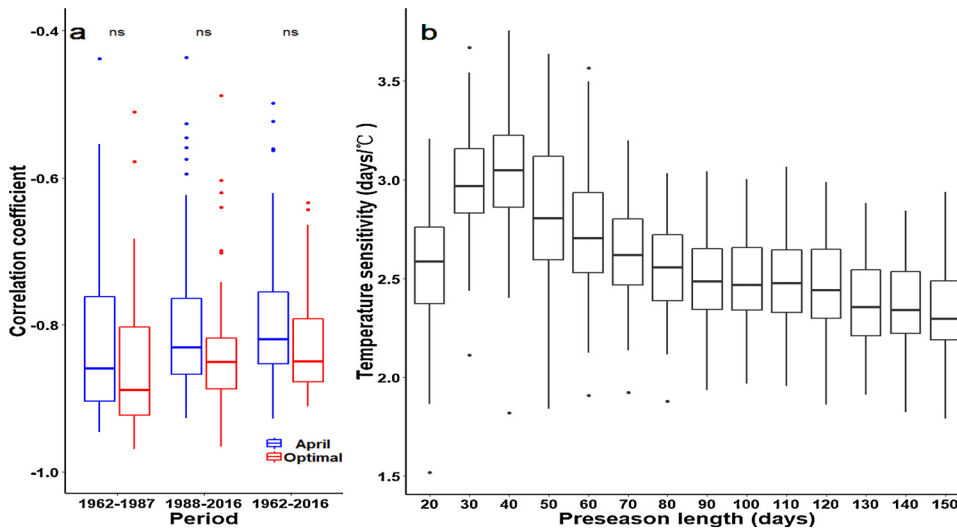
Fig. 4. Comparison of correlation coefficients between LUD and preseason temperature (April: mean April temperature, Optimal: mean temperature of optimal length before mean LUD for which the correlation coefficient between LUD and air temperature was highest) during 1962–1987, 1988–2016 and 1962–2016 (a). Relationships between temperature sensitivity and fixed preseason length for all species during the period 1962–2016 (b).

Table 3

Estimates of the parameters for five ecophysiological models and the range of variation for each parameter. Parameters are defined in Table 2.

Model	Parameter	Range of variation	Mean
Spring warming model	t_0	20~120	75.2
	T_b	0~10	2.3
	F^*	100~1000	216.9
Sequential model	T_0	−3.4~10.4	2.6
	T_b	0~10	3.8
	F^*	0~1000	166.0
	C^*	0~200	17.5
Parallel model	T_0	−3.4~10.4	−0.2
	F^*	0~1000	240.1
	C^*	0~200	48.3
	K_m	0~1	0.16
Alternating model	T_b	−10~10	5.6
	C^*	1~200	63.2
	a	0~600	441.5
	b	−1~0	−0.007
Unified model	t_c	1~200	94.7
	C^*	0~200	109.3
	k	−0.0001~0	−0.00012
	w	0~100	74.0
	a	0~10	1.1
	b	−50~50	3.2
	c	−50~50	10.4
	d	−10~0	−4.9
	e	−30~0	−15.2

Table 4

Average root mean square error (RMSE) ± SD in leaf unfolding dates (LUD) for 40 plant species from internal and external validation predicted by 3 types of phenological models. Ecophysiological models: spring warming (SW), alternating (AL), sequential (SE), parallel (PA) and unified (UN) models; Machine Learning models: random forest (RF), neural networks (NN) and gradient boosting decision tree (GBDT) models; Simple Linear Regression models: relevant preseason (RP) and relevant month (RM) models. T-type and T-all represent the results of multiple comparisons analysis (Tukey HSD) within model types and within all models for external validation RMSE. Letter: there was no significant difference between groups with the same letter; Sig.: difference between internal and external validation RMSE.

Type	Model	External	T-type	T-all	Internal	Sig.
ML models	GBDT	3.5 ± 1.4	a	a	3.3 ± 1.0	ns
	RF	5.4 ± 1.6	b	d	2.5 ± 0.5	***
	NN	9.8 ± 4.3	c	f	0.1 ± 0.1	***
ECO models	SW	4.3 ± 1.5	a	b	3.5 ± 0.8	***
	SE	4.3 ± 1.5	a	b	3.3 ± 0.8	***
	PA	4.5 ± 1.6	ab	bc	3.6 ± 0.9	***
	AL	4.7 ± 1.7	b	bc	4.0 ± 1.0	***
	UN	6.8 ± 2.2	c	e	5.6 ± 1.0	***
SLR models	RP	4.6 ± 1.6	a	bc	3.6 ± 0.9	***
	RM	4.8 ± 2.0	a	c	3.6 ± 0.9	***

average *RMSE* for RP of 4.6 days was smaller than that for RM of 4.8 days (P = 0.04). Of these five ecophysiological models, the average *RMSEs* for SW, SE, PA and AL (4.3, 4.3, 4.5 and 4.7 days, respectively) were significantly smaller than for the UN model (P < 0.01). Of the three machine learning models, the *RMSE* of the GBDT model (3.5 days) was the smallest, followed by that of the RF model (5.4 days), and lastly by the NN model (9.8 days). Overall, the lowest mean *RMSE* was clearly obtained with the GBDT model (Table 4). The *RMSE* values indicate that, for each plant species, the average difference between the best-predicted and the observed LUDs was approximately 3.5 days.

The difference between the internal and external validation *RMSEs* was highly significant for all the models, except the GBDT model (P = 0.19). Although the internal validation *RMSE* for the NN and RF models was smaller than that of the GBDT model, the external validation data for these two models was much larger than that of GBDT, showing obvious overfitting (Table 4).

Fig. 5 shows that the performance of the 10 phenological models depends on the plant species. According to the *RMSE*, GBDT is the best

model for 73% of the 40 plant species (Fig. 5), while the SW model performs best for an additional five species. For the remaining six species, the best performing phenological models were AL, SE, RM and RP. Statistical analysis of the 40 plant species reveals broadly consistent results across the 10 phenological models for both criteria.

3.2. Temporal changes in temperature sensitivity

The LUD were negatively correlated with the April average temperature, all individual tree-level correlations were negative and these correlations were statistically significant at P < 0.05, with an average linear correlation coefficient of -0.78 ± 0.05 for the 1962–2016 time period (there was no significant difference between colder and warmer periods, which had coefficients of -0.79 ± 0.06 and -0.75 ± 0.07, respectively) (Fig. 6). The timing of LUD was substantially earlier for all species from 1962 to 2016, by an average rate of 2.76 ± 0.24 days°C^{-1} across all species (hereafter, a positive value indicates advancement) (Fig. 6). There was a significant difference in temperature sensitivity during the warmer and colder periods, with an average of 2.18 ± 0.25 days °C^{-1} in 1962–1987 and an average of 2.83 ± 0.41 days °C^{-1} in 1988–2016 (consistent with those of other model fitted data). 82.5% of species (33 of the 40 species) showed an increase in ST
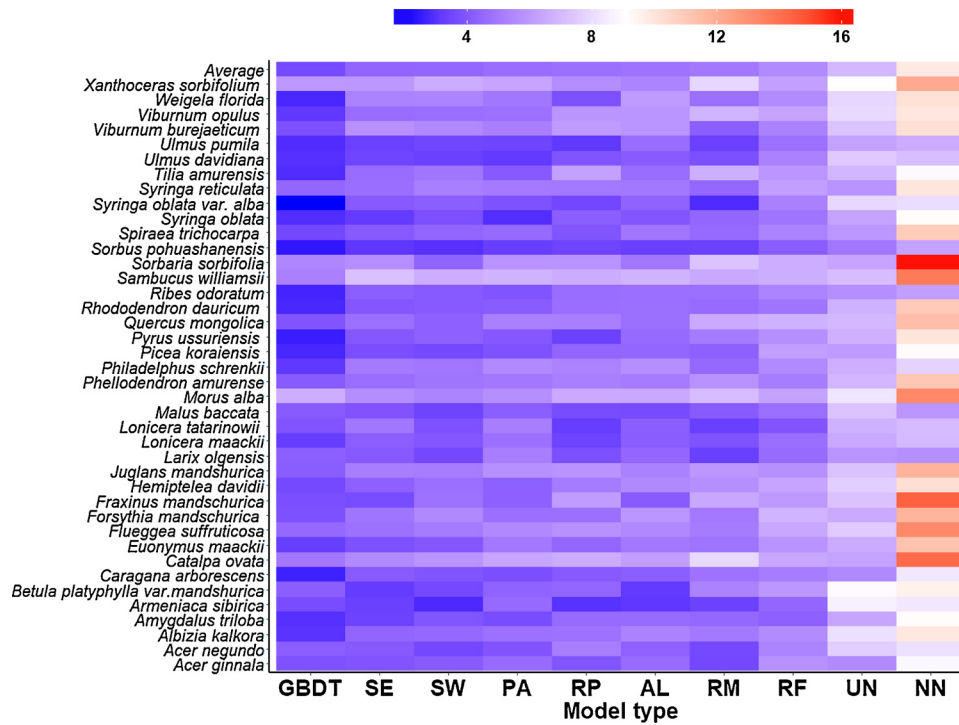
Fig. 5. *RMSE* performance of external validation data from 10 phenological models at the species level. *RMSE* ranges from 2 to 16, the species information is consistent with Table 1 and the first row in the table reports the average *RMSE* of each phenology model.

between the two periods.

We further calculated temporal changes in ST with a 15-year moving window during colder and warmer periods: the surprising result is that temporal changes in ST significantly decreased during both periods. For the colder period (1962–1987), ST significantly decreased by an average of 0.87 days$°C^{-1}$ per decade across all species and by 37.2%, from 2.89 ± 0.34 days$°C^{-1}$ during 1962–1976 to 2.11 ± 0.30

days$°C^{-1,}$ during 1973–1987 (P < 0.001). The majority of the species showed similar decreases in ST (Fig. 7), although the extent of the reduction was species-specific: for example, *Syringa oblata* had the largest decrease in ST (1.26 days$°C^{-1}$). Only *Sorbaria sorbifolia* showed a slight increase in ST (-0.13 days$°C^{-1}$). For the warmer period (1988–2016), ST significantly decreased by an average of 0.95 days$°C^{-1}$ per decade across all species and by 42.4%, from 3.59 ± 0.20 days$°C^{-1}$ during
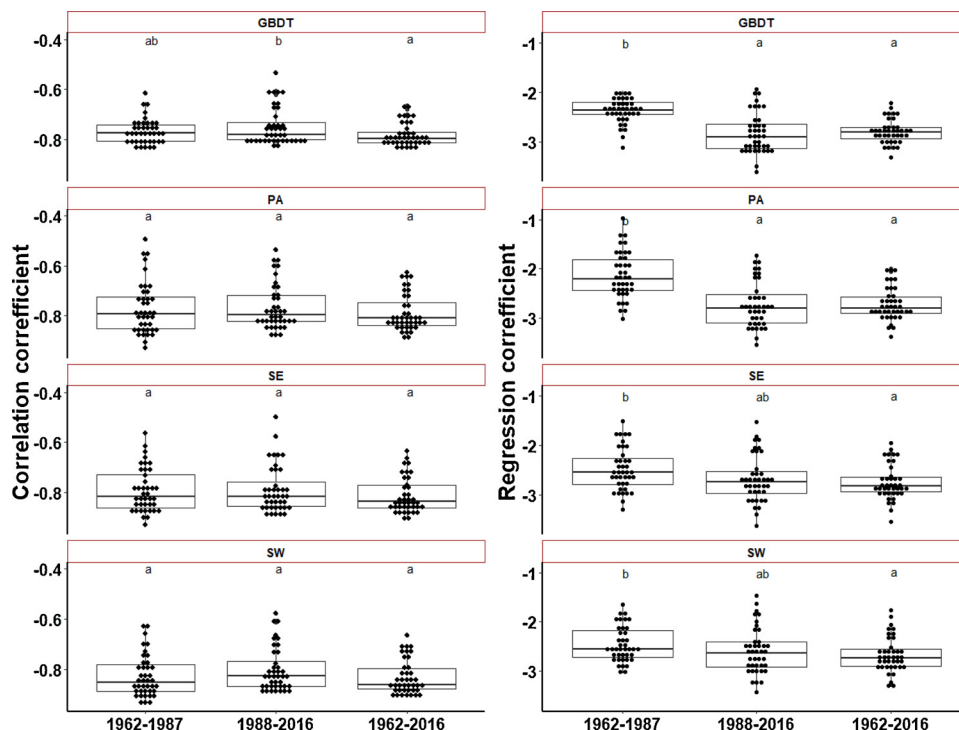

Fig. 6. The correlation and regression coefficients between leaf unfolding dates and April average temperatures during three periods. The letters above represent the results of ANOVA analysis within the three periods for various models.
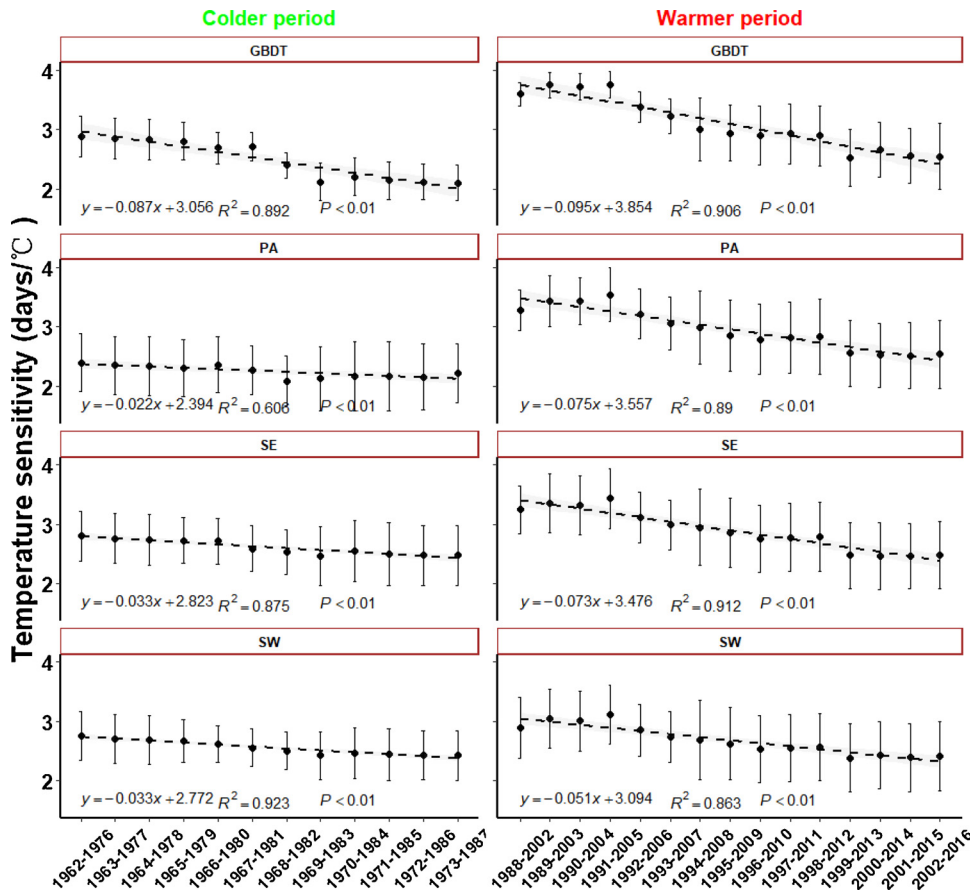
Fig. 7. Temporal change in ST (LUD response to April temperature) for individual species and combined totals for all species with a 15-year moving window during the periods 1962–1987 and 1988–2016 (before and after the recent sudden warming). The black point indicates the average across all species and the dotted line indicates the linear regression.

Fig. 8. Temporal change in ST (LUD response to optimal preseason temperature) for individual species and for combined totals for all species with a 15-year moving window during the period 1962–1987 and 1988–2016 (before and after the recent sudden warming). The black point indicates the average across all species and the dotted line indicates the linear regression.
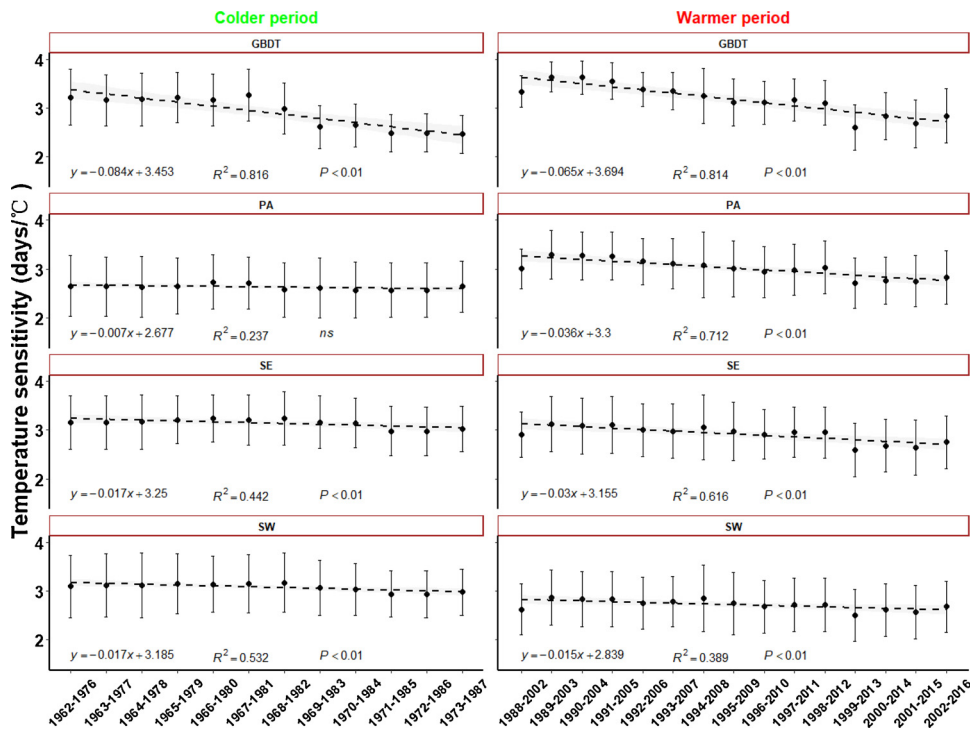
[1988]–2002 to 2.55 ± 0.55 days°C^{-1}, [during 2002]–2016 (P < 0.001). Of the 40 species, only *Quercus mongolica* showed a slight increase (-0.15 days°C^{-1}) in ST. The largest decrease in ST was observed in *Xanthoceras sorbifolium* (2.50 days°C^{-1}). During both warmer and colder periods, later-spring species showed a larger decrease in ST. The temporal

change in ST, calculated when the phenological data are fitted to the GBDT model, is significantly higher than those of the other phenological models. To further test the temporal change in ST during the warmer and colder periods, we applied the three better-performing phenological models (SW, SE and PA model) to fit the missing data. All
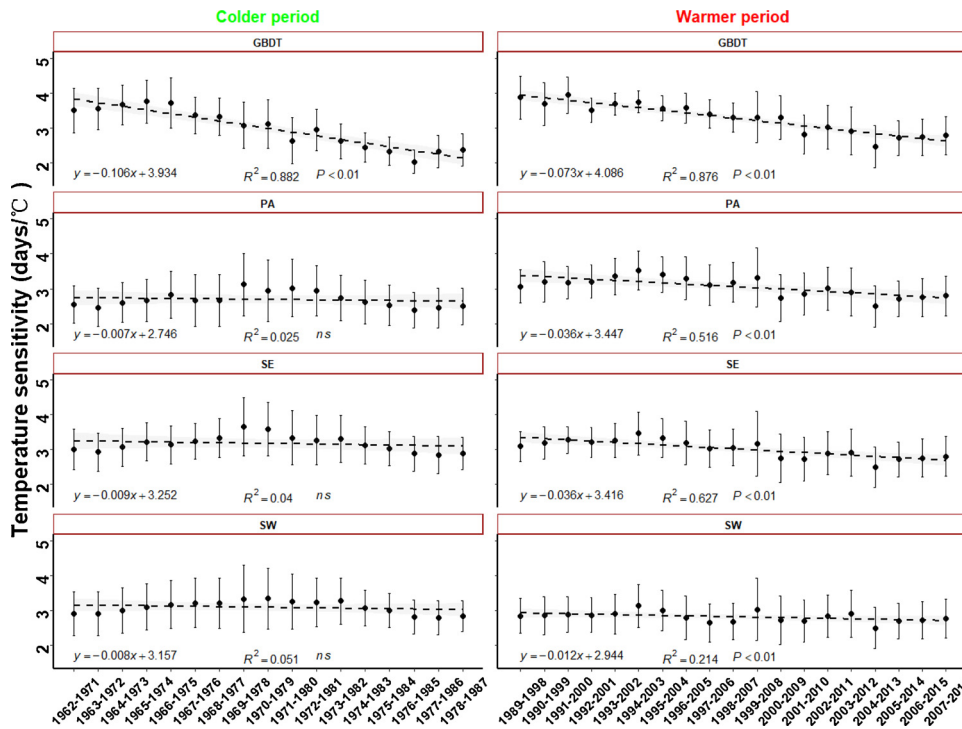
Fig. 9. Temporal change in ST (LUD response to April temperature) for individual species and for combined totals for all species with a 10-year moving window during the period 1962–1987 and 1989–2016 (before and after the recent sudden warming). The black point indicates the average across all species and the dotted line indicates the linear regression.

three models captured the declining ST, irrespective of species (Fig. 7). The modeled relative reductions in ST during the two periods, 1962–1987 and 1988–2016, were, however, smaller than the GBDT model fitted decline. During the colder period, simulated ST was reduced by 13.5%, 13.1% and 7.9% for the SW, SE and PA models, respectively, whereas the GBDT model ST was reduced by 37.2%. However, during the warmer period, simulated ST was reduced by 21.5%, 31.1% and 28.1% for the SW, SE and PA models, respectively, whereas the GBDT model ST was reduced by 42.4%. Similar results were also obtained when using an optimal preseason length as revelant preseason (Fig. 8). We also calculated ST using 10-year intervals (instead of 15-year intervals) and found that the results were consistent (Fig. 9). These results suggest a remarkable reduction in the response of LUD to the ongoing climate warming in all studied tree species in Harbin.

4. Discussion

4.1. Model selection

Previous studies have shown that the mean prediction of error (*RMSE*) is the most efficient criterion for comparing different phenological models (Chuine et al., 1998; Andreini et al., 2014). For ecophysiological models, no single model accurately predicts LUD dates for every species, a point that has been illustrated by many previous studies and that indicates that all different possible models must be tested for each species (Chuine et al., 1998). The UN model performed the worst: this result is consistent with the conclusion that the UN model did not explain significantly more variance than the null model (the model with the mean of the observations as a single parameter) for specific species, and this is due to the high number of parameters fitted compared with the number of data used to fit them (Chuine, 2000). The *RMSE* of the tested ecophysiological models was approximately 4–5 days, similar to that of previous studies using 36 models to predict the leaf-out dates for six temperate tree species across central Europe (Basler, 2016). Our research shows that GBDT model is obviously better than RF and SLR models, which is consistent with the research conclusion of Czernecki et al., 2018. Considering only models with coupled meteorological data, the *RMSE* of our model is significantly smaller than that of theirs, which

may be because the phenology adopted by their fitting model is only 8 years at most (compared with our nearly 30 years), and the sample size affects the performance of the model (Czernecki et al., 2018). The performance of the simple linear regression models also reveals no obvious advantages, in that not only temperature sensitivity has decreased over the past decades, but the optimal preseason has also changed (Wang et al., 2014; Fu et al., 2015b; Güsewell et al., 2017). In comparing the accuracy of the 10 temperature-based models, our results show that the GBDT model is the most accurate phenological model. The overfitting of NN model is obvious, which may be because we choose the relatively simple fitting method of single-hidden-layer neural network. This algorithm performs quite well on the training data set, but has poor generalization ability and is prone to overfitting. On the other hand, neural networks usually require more data (thousands or even millions of mark samples are enough) than traditional machine learning algorithms. Furthermore, our results show that machine learning (ML) methods have several advantages over traditional statistical methods, for understanding and predicting the complex interactions between phenology and climate change: ML methods do not impose unrealistic assumptions (such as linearity), are capable of inferring missing phenology data, and can reduce long-term expert annotation burden. Thus, a wider adoption of machine learning methods in phenology studies has the potential to greatly improve our understanding of the mechanisms underlying the temperature response. Several comparative studies have already shown that ML techniques can outperform traditional statistical approaches in a wide variety of problems in earth science and ecology (Thessen, 2016). Machine learning phenological models can address issues related to nonlinear and discontinuous phenomena. In addition, the introduction of more nonlinearities into model simulations further reduces uncertainties and bias (Zhao et al., 2013).

The GBDT model *RMSE* from the external validation in Harbin ranged from 1.88 to 6.49 days. This indicates that the externally predicted LUD data were close to the observed values; however, there is still a gap between the predicted data and the actual observations. This may be because, for some plant species, individuals in different regions may develop different adaptions in response to local temperature (Caffarra and Donnelly, 2011) and because daytime warming was

assumed to be more effective at advancing bud break than night-time warming (Rossi and Isabel, 2017). Several factors that influence phenological onset dates have recently been identified in addition to temperature effects on the timing of long-term phenological events: photoperiod, in particular, is another major factor that has been determined to affect phenology (Way and Montgomery, 2015). Different plant species generally rely on different strategies to optimize use of the resources needed for growth (e.g., heat, water, and nutrients) and to protect against damages from unfavorable conditions (e.g., frost and drought) (Misson et al., 2011; CaraDonna and Bain, 2016; Singh et al., 2017; Liu et al., 2018). A multidecadal increase in phenological events was reported to be most strongly associated with rising atmospheric CO_2 concentrations (Pau et al., 2017). Several experiments with cuttings have investigated the influence of air humidity on the spring phenology of tree species. Their results led to the development of a new framework that relates winter chilling to tissue desiccation, and spring development to tissue rehydration processes. They concluded that temperature-related air humidity might be the main trigger of the spring development of trees (Laube et al., 2014b). In addition, intrinsic factors or characteristics (e.g., genome, hormones, wood anatomy, age, and evolution within a plant community) are also the result of plant phenology at the species-specific level, which is associated with biotic potential, photosynthetic activity, absorption of nutrients, constructive metabolism, etc. (Zhao et al., 2013; Panchen et al., 2014; Bowen et al., 2016).

Observational data for fitting models vary between phenological networks and among stations within networks because these observations are often collected by volunteers and thus the resulting data may not be as accurate as expected. Volunteers collect traditional phenological data by working with pencil and paper, filling in and sending observational sheets to their national weather service. Such data collection has been challenged by a number of unknown and complex factors, which together caused a dramatic drop of phenological observations in recent decades. A possible vision for future phenological data collection could include implementing the citizen science approach through internationally coordinated programmes in each country, following a common standard (Scheifinger and Templ, 2016). Leader buds, and buds on large, mature trees, usually burst 1–2 weeks later than the laterals on young trees (Cannell and Smith, 1983). Moreover, different individuals may apply different standards to their observations (Dose and Menzel, 2004). The process of analyzing field observational data collected from nonnatural locations, such as botanical gardens, arboretums, parks or city green belts, should also include the urban heat island effect. Standardized and coordinated phenology data across a network of sites can be used to quantify the direction and magnitude of the relationships between phenology and environmental factors, as well as the degree to which these relationships vary among sites, species, phenophases, and through time (Elmendorf et al., 2016). There are also uncertainties related to the climate that may not be associated with local air temperature for each observation type (humidity, shading, slope, elevation) (Fu et al., 2015b). Mountain plant communities show lags in response to climate change (Alexander et al., 2018). Improved methods in phenological observational data collection and experimental data analysis (e.g., synthetic analytical techniques offered by remote sensing or geographic information systems) could be used to analyze the time series and spatial variation of phenological data (Zhao et al., 2013; Czernecki et al., 2018). Biological processes (e.g., pests, insects, and competition) also play an important role in the individual development of plant species. Many other local factors, including shading, soil conditions, nutrient concentrations, and pathogens, also interact with other key drivers, which could act together to determine a plant's physiological responses and phenology (Zhao et al., 2013).

Remote sensing satellite data are also commonly used to study phenology (Polgar et al., 2014; Buitenwerf et al., 2015; Fu et al., 2015a; Yu et al., 2017), the application of coupled meteorological data

phenology prediction model combined with remote sensing products can greatly increase the performance of the model and improve the RMSE accuracy of the model from 0.6 days to 4.6 days (Czernecki et al., 2018). Although satellite-derived phenology data still cannot capture the differences in phenology among plant species, remote sensing can be an effective way to test the accuracy of phenological models. Tree-ring growth data, based on well-validated, process-based, Vaganov–Shashkin-oscilloscope model simulations, can also provide a unique record of plant phenology (Puchałka et al., 2017; Yang et al., 2017). Herbarium specimens represent a potential new source of information to determine whether the variation in leaf-out times observed in recent decades is comparable to those for longer time frames over past centuries (Everill et al., 2014; Zohner and Renner, 2014). On the other hand, phenological models are essential for investigating plant phenology responses to climate change through herbarium specimens. This data source can also be used to test the performance of phenological models. Research on the mechanisms influencing phenology should be promoted to improve the development of phenological models and to provide better data for future studies on the interactions between phenology and the natural environment.

4.2. Determinants of temporal changes in temperature sensitivity

Earlier spring LUDs have been reported and can be attributed to climate warming in most Northern Hemisphere regions over recent decades. Climate warming is projected to further increase, but due to the imperfect understanding of the mechanisms of plant phenological responses to climate change, it is very difficult to accurately predict the future evolution of plant phenology. However, the magnitude, and even the direction of the apparent ST of the phenology of spring leaf unfolding remains controversial. ST has been found to vary within species and populations, across altitudes and regions (Wang et al., 2014), and may also change over time. In many places, temperatures have risen sharply since the 1990s, indicating that these regions are entering a warmer period. An improved understanding of the temporal and spatial scale variations in phenological responses to spring temperatures is thus valuable.

Our results undoubtedly support the idea that LUD is negatively correlated with increased climate warming and are consistent with other studies. Long-term phenological records indicate that temperature sensitivity can vary in space and time (Fitter and Fitter, 2002; Menzel et al., 2006; Cooke et al., 2012; Fu et al., 2014b, b; Güsewell et al., 2017). The magnitude of ST at the study site fluctuated greatly with the length of the preseason (Fig. 4b), and this result is consistent with a Swiss study that ascribed changes in the temperature sensitivity of spring phenology to recent climate warming and shifts in the preseason (Güsewell et al., 2017). Therefore, when comparing ST between species, locations, or time periods, it is best to choose a unified fixed preseason. Compared with the colder period (1962–1987), the warmer period (1988–2016) showed a 0.65 days$°C^{-1}$ increase in ST. This result may explain why plant phenology has attracted widespread attention in recent decades as a sensitive indicator of environmental change. However, similar research in Switzerland showed that most early-spring and mid-spring events declined in temperature sensitivity between the two periods, while the late-spring events did not change or even increased in temperature sensitivity (Güsewell et al., 2017).

Consistent with earlier studies (Fu et al., 2015b), the temporal change in ST showed a remarkable decline over the last three decades, but the surprising result is that ST also significantly decreased during the colder period (1962–1987). The temporal change in ST from the fitted phenological data is significantly higher according to the GBDT model than for any of the other phenological models (PA, SE and SW), which indicates that the traditional phenological models may underestimate the response of LUD to global warming. Our results indicate that, with continued climate warming, early-spring, phenologically driven increases in carbon uptake may decelerate in cold temperate

forests. Extreme climatic events have dramatically increased in recent decades, especially warm winters and springs (Rahmstorf and Coumou, 2011), so the decrease in the time scale of ST may be beneficial to the survival of plants in harsh environments (i.e., it could reduce the risk of spring frost damage by preventing premature leaf unfolding). There are several mechanisms that may explain what causes temperature sensitivity to decline. One possible explanation is decreased winter chilling (Harrington et al., 2010; Fu et al., 2015b), since the amount of heat requirement by temperate and boreal trees is negatively correlated with winter chilling (the accumulation of cold temperatures during the dormancy period) (Laube et al., 2014a): as the accumulated chilling progressively declines, the heat requirement increases and slows down the advance of leaf unfolding. The net effect of reduced chilling can thus be reduced ST (Fu et al., 2015b), and this effect may be further exacerbated by the nonlinearity of the negative correlation between the heat requirement and chilling. The temporal change in ST could therefore partially result from decreased winter chilling. However, winter chilling (chilling accumulation was calculated as the number of chilling days, when daily temperatures are lower than $-5\,°C$ from 1 November to the average date of leaf unfolding) significantly decreased during 1962–1987, while chilling days slightly increased from 1988 to 2016 (Fig. 10). When we further analyzed temperatures below $0\,°C$ as the base temperatures for chilling days, the temporal changes (with a 15-year moving window) in chilling days significantly increased during 1962–1987. This suggests that decreasing winter chilling is not an obvious cause for the apparent temporal decline in the temperature sensitivity of leaf unfolding.

Previous studies have indicated that reduced frost damage in temperate and boreal biomes is an important external factor shaping plant phenological traits (Jonathan et al., 2010). The daily temperature fluctuation and the number of frost-free days in a given period also seem to determine phenophases (Eppich et al., 2009). However, the influence of local spring temperature variance was considered to be the main cause of the significant decrease in phenological sensitivity at the species level (Wang et al., 2014; Fu et al., 2015b; Mulder et al., 2017). Plants may indeed adopt relatively conservative strategies (or higher phenological plasticity) for spring leaf unfolding in places with higher temperature fluctuations, in order to avoid spring frost damage, for example (Vitasse et al., 2014; Wang et al., 2014). Spring phenological sensitivity in plants can be shaped via genotypic plasticity, and by this mechanism plants can decrease the risk of frost damage to their actively growing parts (Zhang et al., 2015; Howe et al., 2016). Our results show that the variance in preseason temperatures significantly increased during both the colder and warmer periods, and ST tends to be lower for periods with larger local spring temperature variance (or higher spring SD) (Fig. 10). The temporal decline in ST could therefore partly result from an increase in the preseason temperature variance. This probably reflects spring phenology adaptations to local climate conditions (Menzel et al., 2006; Wang et al., 2014) and suggests that increased variance in preseason temperature is, at least in part, driving the temporal decline in ST.

Other protective or adaptive mechanisms, such as lag effects, hormone actions, photoperiod, or adaptation mechanisms, may also be the cause of the temporal decline in ST. Leaf bud primordia morphogenesis commences in late spring to early summer (Landsberg, 1974; Fitter et al., 1995). Warmer temperatures may induce some leaf primordia to mature in late fall, either by accelerating development or by delaying bud set (premature maturation), and this may actually represent an advance in spring phenology (Mulder et al., 2017). Photoperiod will become an increasingly important factor for constraining the timing of spring phenology when warmer weather conditions are accelerating development (earlier bud burst) toward genetic photoperiod thresholds, and some late successional species are unlikely to continue tracking the actual (warmer) temperatures as they currently do (Caffarra et al., 2011; Basler and Koerner, 2012). There are also uncertainties related to climate factors that may not be associated with local air temperature. Furthermore, other factors, such as heredity or pests, plant and animal phenological adaptations and interactions, and ecological disturbances (e.g., forest fires and insect outbreaks) may also affect the temporal change in phenological ST. These factors may collectively contribute to the magnitude of the phenological response to climate change; however, they have, thus far, seldom been considered. Clearly, further studies are needed to support these inferences and their roles in determining phenology. Broadening the research scope may result in a breakthrough in future studies on plant phenological responses to climate change. Phenological datasets that are limited to local
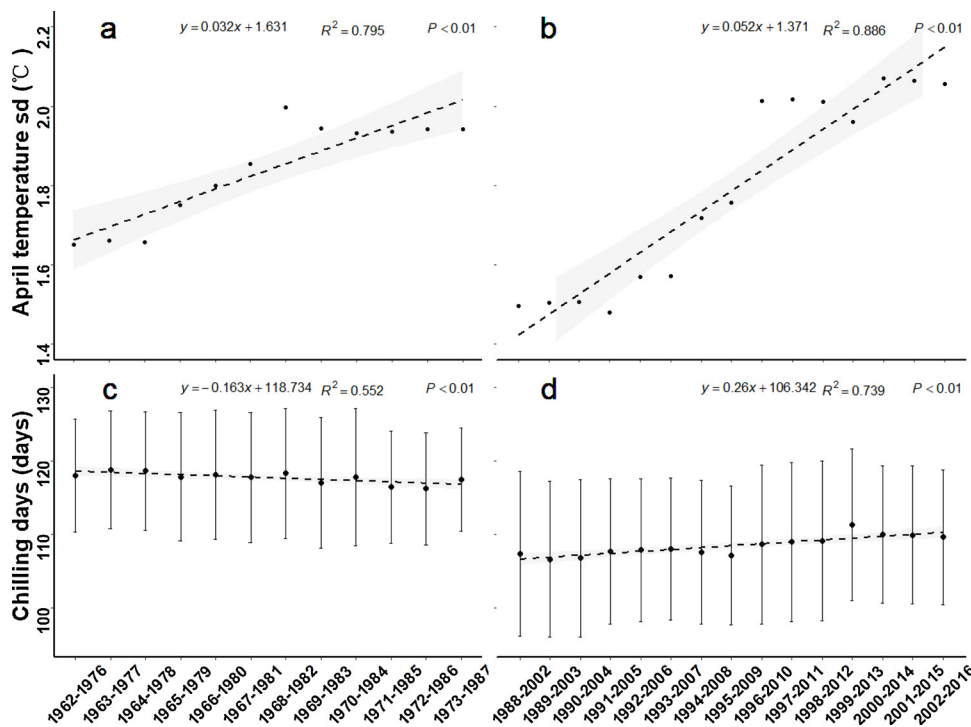
Fig. 10. Changes in April temperature variation and chilling days with a 15-year moving window during 1962–1987 (a, c) and 1988–2016 (b, d). April temperature sd (the standard deviation of mean April temperature). The chilling accumulation was calculated as chilling days when daily temperatures were below $-5\,°C$ from 1 October to 1 April. The dotted line indicates the linear regression and the gray polygon represents the 95% confidence interval.

observations and/or a few species may miss some important features of the relationships between temperature and plant phenology (Cooke et al., 2012).

5. Conclusion

Plant phenological models are effective methods to both predict the timing of phenological phases in the future and infer historical missing data for woody plant. Our research shows that machine learning algorithms are applicable to phenological model studies, and models using ML algorithms can improve model performance on externally validation data sets. The historical observation data combined with the inferred data from the model showed that the temperature sensitivity of plant phenology in Harbin showed a decreasing trend in the 15-year movement interval before and after climate mutation. This may mean that plant phenology has shown adaptability to climate change. In this study, only several relatively simple ML algorithms were applied to phenological model, and compared with the temperature-based models in phenology prediction performance, there should be more sophisticated statistical algorithms coupling more environmental factors (biological and abiotic) models to predict phenological phases, so as to promote the development of phenological research. With the rapid increase of global temperature, it is necessary to study the temporal and spatial scale of phenology response to climate change on a larger scale to reveal the interaction and internal relationship between plant phenology and climate change.

Authors' contributions

ZQZ, YHZ and WJD conceived the ideas and designed methodology; HYJ, WJD and TL analyzed the data; WJD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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