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Phylogenetic relatedness and plant traits influenced flowering phenology change patterns in natural habitats in China (2003–2021)

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Abstract

Background Phenology research has provided important insights on the influence of climate change on ecosystems. Investigation of spatial and interspecific difference can help us to better understand the phenology change pattern. In this study, observational data for 190 species collected from 2003 to 2021 at eight ecological stations in China were assessed via linear regression to detect trends in first flowering date (FFD), air temperature, and precipitation. We then examined the relationship between FFD change patterns, air temperature and precipitation through redundancy analysis, calculated the relative importance of phylogenetic relatedness, climate change, site conditions and plant traits in explaining variations in FFD change intensity using boosted regression tree method.

Results We found that (1) FFDs of nearly 40% of the observed species changed significantly ($p < 0.05$), with species showing advanced and delayed FFDs accounting for half. (2) Air temperature increased at most stations, particularly in spring and summer, while precipitation decreased in humid and subhumid temperate zones and increased during most seasons in arid temperate and subtropical zones. (3) Spatial differences were observed in FFD trends. At stations in Northeast, North, and Southwest China, which are regions with increased temperature, the percentage of species with advanced FFD was higher than that of species with delayed FFD, with the mean trend ranging from -2.4 to -6.5 d decade^{-1}. Conversely, at stations distributed in Northwest and South China, which are regions with increased precipitation, the percentage of species with advanced FFD was lower than that of species with delayed FFD, with the mean trend ranging from 1.3 to 7.1 d decade^{-1}. (4) Air temperature and precipitation had a stronger influence on FFD change in the temperate zone than in the subtropical zone. Climate factors with the greatest influence on FFD change patterns varied with the observation site. Interspecific variations in FFD change intensity were mostly explained by phylogenetic relatedness, although plant traits, site conditions, and climate change also had a certain effect.

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Conclusions Our research found that the first flowering phenology of large percent of the observed plants changed significantly from 2003 to 2021, showing spatial and interspecific differences across observation sites. Our research also demonstrated the importance of plant phylogeny on interspecific differences in phenological changes, plant traits such as growth form, plant height, and flowering time influence flowering phenology to a certain extent. These findings will help us to better understand phenological responses to climate change on a national scale, and help us better predict the response of various plants to climate change in the future.

Keywords Phenology, Climate change, Ecosystem, Temperature, Precipitation

Introduction

The flowering period is an important stage in the plant life cycle. Changes in flowering phenology affect plant reproduction and evolution, interspecific competition, symbiosis in plant communities, and overall ecosystem stability [1]. Numerous studies have been conducted on the changes in flowering phenology in the context of climate change. These studies indicated that the first flowering dates (FFDs) of numerous plants have significantly advanced at several sites in America and Europe [2–8]. In contrast, researchers have also found that FFDs have not advanced dramatically, with several species even showing delayed FFDs at the same sites [9–12]. In China, the FFDs of numerous plants have advanced in many regions over the past 30–60 years [13–14]). However, the results have varied, with the FFD of some species not being significantly advanced while that of others showing a delay [15–16]. Therefore, the trends in FFD change not only differ between regions but also between species within a region [17]. Plant traits such as growth form, woodiness, plant height, longevity, and specific leaf area reflect the response and adaptation of plants to environmental changes [18]. They are closely correlated with the phenological response of the plant to climate change [19]. Plants with different functional traits exhibit varied phenological responses to environmental changes [20–21].

In China, Ge et al. (2015) analyzed the differences in phenological change between growth forms using observational data on 104 plant species collected from 145 sites over the period 1960–2011 [14]. However, their study did not include plant traits such as plant height, flowering time, and woodiness when examining the influence of plant traits on phenological change. In addition to plant traits, previous studies have shown that phenology is phylogenetically conserved, with closely related species tending to have similar phenological rhythms [22–24]. Hence, plant species cannot be considered statistically independent but rather are related via phylogeny; therefore, phylogenetic relatedness should be included when examining patterns of phenological change.

Phenological change research relies on long-term observational data. Because of traffic and manpower limitations, many phenological observation sites are located in parks, botanical gardens, or other areas in or near cities. In urban areas, the “heat island effect” can contribute more than 20% to climate warming and has a direct effect on plant phenology [25–28]. This may interfere with our understanding of the changes in plant phenology in the context of global warming. In addition, phenological observation objects often include cultivated plants, such as *Syzygium aromaticum*, *Salix matsudana*, *Ulmus pumila*, *Populus simonii*, and *Fraxinus chinensis* while fewer plants from natural habitats have been selected for observation [29–30]. This is not conducive to understanding phenological changes in natural ecosystems. Therefore, more attention should be paid to the phenological trends of plants in their natural habitats.

In this study, based on the FFD observation data of plants with different growth forms collected from 2003 to 2021 by eight ecological stations affiliated with the Chinese Ecosystem Research Network, we calculated the FFD change intensity (number of days/year) of each species using a linear regression model and then assessed the general trend of FFD change at the country and station scales. Furthermore, we investigated the contributions of phylogenetic relatedness, plant traits, changes in climate, and site conditions to the variations in observed FFD changes using boosted regression tree analysis (BRT) according to the method presented by König et al. (2018) [19]. This study aimed to examine how phylogeny, environmental background, climate change, and plant traits influence spatial and interspecific differences in FFD trends. Specifically, we focused on the following questions: Has flowering phenology changed in plants in natural habitats over the past 20 years (2003–2021)? Have clear spatial and interspecific differences in flowering phenology changes occurred? To what extent do phylogenetic relatedness, plant functional traits, site conditions, and climate change influence spatial and interspecific variations in flowering phenology?

This study aimed to provide scientific support for understanding regional and interspecific differences in phenological changes in large regions. The outcomes of this study will improve our understanding of the mechanisms underlying phenological changes and the influence of climate change on natural ecosystems.

Data and methods

Data sources

Phenology observation data

To monitor changes in China's ecosystem, the Chinese Academy of Sciences established the Chinese Ecosystem Research Network (CERN) in 1998. All CERN ecological stations are located within a typical ecosystem in a specified region. The CERN stations conduct long-term observations of the ecosystem in accordance with unified monitoring protocols and observation indicators. Phenology is an important component of CERN monitoring, and includes multiple phenological periods. Phenological data were collected from eight CERN ecological stations across various ecological zones in China (Fig. 1). These stations include: Changbai Mountain Forest Ecosystem Research Station (CBF) in a humid middle-temperate zone; Beijing Forest Ecological Station (BJF) in a subhumid warm-temperate zone; Shapotou Desert Research and Experiment Station (SPD) in an arid middle-temperate zone; Maoxian Mountain Ecosystem Research Station (MXF) in the northern region of a humid middle-subtropical zone; Huitong Research Station of Forest Ecosystem (HTF) and Ailaoshan Station for Subtropical Forest Ecosystem Studies (ALF) in southern regions of humid middle-subtropical and humid southern-subtropical zones respectively; Dinghu Mountain Research Station of Forest Ecosystem (DHF) and Heshan Mountain Integrated Experimental Station of Hilly Land (HSF) in eastern regions of a humid southern-subtropical zone. At each ecological station, typical species of different growth form (tree, shrub and herbs) were selected to perform the observation, particularly the dominant species in plant community. However, the number of selected species is not uniform for the varied species richness across ecological stations. Table 1 summarizes the altitude, annual mean temperature, annual precipitation, accumulated temperature > 10 ℃, and number of observed species for each station.

For trees and shrubs, three to five individual plants of each target species were selected for permanent observation, and the FFD was defined as the day on which a branch with multiple buds had at least one fully opened flower. For herbs and grasses, three to five permanent quadrats (1 m×1 m) were selected to perform phenological observations for each target species, and the FFD was defined as the day on which 10% of the observed plants had one or more flowers fully opened for the first time. Phenological observations were performed manually daily from the beginning to end of the growing season. During the flowering period, observations were made in both the morning and afternoon to ensure that flowering events were not omitted. For more detailed description of phenological observation methods see Wu et al. (2019) "Protocols for standard biological observation and measurement in terrestrial ecosystem [31]."

FFD data from 2003 to 2021 for 190 plant species were used in this study. Among these species, 66 were trees, 59 were shrubs, 54 were herbs, and 11 were grasses

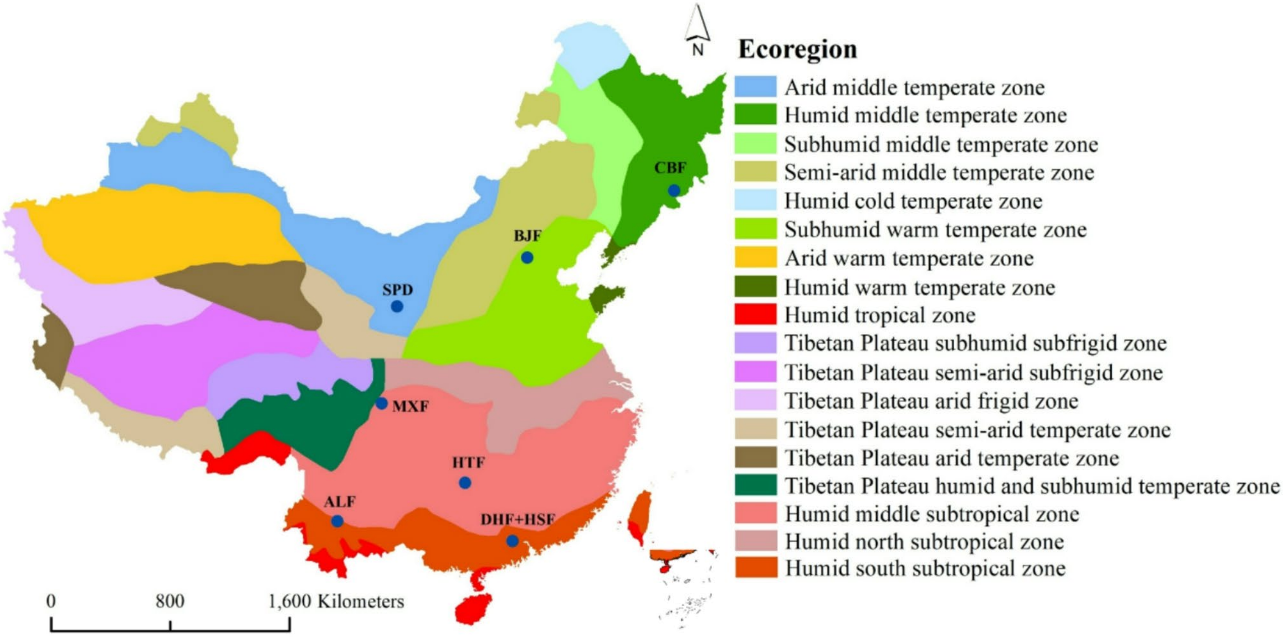

Fig. 1 Locations of the eight ecological stations of the Chinese Ecosystem Research Network (CBF, Changbai Mountain Forest Ecosystem Research Station; BJF, Beijing Forest Ecological Station; SPD, Shapotou Desert Research and Experiment Station; MXF, Maoxian Mountain Ecosystem Research Station; HTF, Huitong Research Station of Forest Ecosystem; ALF, Ailaoshan Station for Subtropical Forest Ecosystem Studies; DHF, Dinghu Mountain Research Station of Forest Ecosystem; HSF, Heshan Mountain Integrated Experimental Station of Hilly Land)

Table 1 Environmental factors and number of observed species at each ecological station

Ecological zone	Station name	Station code	Altitude (m)	Annual mean temperature (℃)	Annual precipitation(mm)	> 10 ℃ accumulated temperature	Number of observed species
Humid middle temperate zone	Changbai Mountain Forest Ecosystem Research Station	CBF	2000	3.5	850	2300	36
Subhumid middle temperate zone	Beijing Forest Ecological Station	BJF	1250	5.6	650	2157	36
Arid middle temperate zone	Shapotou Desert Research and Experiment Station	SPD	1350	9.6	186	3000	20
North region of humid middle subtropical zone	Maoxian Mountain Ecosystem Research Station	MXF	1840–1890	8.6	919	2690	11
South region of humid middle subtropical zone	Huitong Research Station of Forest Ecosystem	HTF	400–550	16.5	1300	5100	70
West region of humid south subtropical zone	Ailaoshan Station for Subtropical Forest Ecosystem Studies	ALF	2400–2600	11	1931	3420	13
East region of humid south subtropical zone	Dinghu Mountain Research Station of Forest Ecosystem,	DHF	230–350	21	1996	7495	8
	Heshan Mountain Integrated Experimental Station of Hilly Land	HSF	30–70	21.7	1761	7597	3

(with 10 annual plants). The FFD data are presented in Supplementary Table S1. As there are missing values in the ground phenological observation data, therefore, for a specified species, if the values of first flowering date missed in more than 20% of the observation years, the phenological sequence of this species was excluded from the dataset. We also made linear regression analysis between first flowering date and the year (details were presented in Sect. 2.2.1), and interpolated the missed values according to the fitted linear regression function. The interpolated dataset was used to make the Redundancy analysis in the following data analysis procedure.

Temperature and precipitation data

A weather station was installed at each ecological station within 1 km of the phenological observation site to collect air temperature and precipitation data. Air temperature data were recorded using an air temperature sensor (Vaisala series) at the automatic weather station, and precipitation data were collected through manual observations of the precipitation collection system. The air temperature and precipitation data are presented in the Supplementary Table S2.

Site conditions

Site condition-related variables were included in the analysis to test whether site conditions had an obvious influence on spatial differences in the FFD change. Variables of site conditions include altitude, annual mean temperature, annual precipitation, and accumulated temperature (> 10 ℃). The altitudes of the observation sites were measured using a handheld GPS. The annual mean temperature, annual precipitation, and accumulated temperature were the mean values calculated based on the meteorological observation data obtained over the last 20 years. The site condition data are presented in the Supplementary Table S3.

Plant traits

As proposed by König et al. (2016), plant traits known to be biologically relevant and potentially relevant for phenological reactions should be selected to make the analysis. Plant traits such as growth form, woodiness, annual/perennial, plant height, leaf distribution along the stem, leaf fresh area per leaf dry mass, leaf dry mass per leaf saturated mass, flowering time and pollination type were included in the research of König et al. (2016). In our research, limited by the data availability, plant traits of growth form (trees, shrubs, herbs, and grasses), woodiness(woody/non-woody), annual/perennial, plant height, and flowering time were included in the analysis to understand the interspecific differences in phenological responses to climatic changes. Growth form, woodiness, and annual/perennial data for each observed species were acquired from the Flora of China (online version, https://www.iplant.cn/frps). The plant height of observed species was measured at the flowering stage. For herb, grass and short shrubs, steel tape was used to measure the plant height. For trees and tall shrubs, measuring rod or laser ranger was used to measure the plant height. The flowering time was obtained from long-term phenological observation data. The plant traits data are presented in the Supplementary Table S4.

Data analysis

Analysis of FFD trends

The original FFD data were recorded in the year-month-day format. For the convenience of data statistics, we

Table 2 Summary of phenological trends

	Number of phenological sequences	Proportion (%)
Flowering phenophases		
Neg_{all}	102	51.8
Neg_{sig}	39	19.8
Pos_{all}	95	48.2
Pos_{sig}	37	18.8
Tr_{mean}(Mean ± SD, days decade^{-1})	197	-0.22 ± 13.6

converted the original date-type data into time sequence data of the FFD, expressed as the days of year (DOY) from January 1 to the day when the first flowering event happened. We analyzed the trend of FFD for each single species using a linear regression, with "year" as the independent variable and DOY as the dependent variable [2, 32]. A negative slope ($slope < 0$) of the linear regression indicated an advance of FFD, whereas a positive slope ($slope > 0$) indicated a delay of FFD. The linear regression analysis was carried out using the "lm" function in the statistical program R version R 3.1.1 [33].

Negative time sequences ($slope < 0$) with a p-value lower than 0.05 were defined as "advanced," positive time sequences ($slope > 0$) with a p-value lower than 0.05 were defined as the "delayed," and both "advanced" and "delayed" were defined as "changed." The p-values, together with the slope values of the linear regression are listed in Table S5. Based on Table S5, we calculated the proportion of species with positive, significantly positive, negative, and significantly negative trends as well as the mean trend of all species (Table 2). Then, we plotted the frequency distribution of phenological trends of the first flowering date (Fig. 2).

At each ecological station, we calculated the percentage of species with changed, advanced, and delayed FFD (Fig. 3) and the mean trend of FFD for all target species at each ecological station (Fig. 4). Slopes of linear regression equation of DOY with "year" were multiplied by 10 as the trend of FFD in each ten years. The slope was defined as the FFD change intensity.

The relationships among FFD change intensity, plant traits, and site conditions were examined in this study. We used ANOVA to test the differences in FFD change intensity between growth forms and woodiness/non-woodiness. The results are presented in Fig. 5. Linear regression was performed to test the relationships between FFD change intensity and plant height and flowering time and between FFD intensity and site condition variables (altitude, annual mean temperature, annual precipitation, > 10 ℃ accumulated temperature). The results are presented in Table S6.

Analysis on the trends of temperature and precipitation change

We analyzed the trends of monthly mean air temperature and total precipitation in spring (March – May), summer (June – August), autumn (September – November) and winter (Prior December – February) using a linear regression with "year" as the independent variable. The R^2 and p-values of the linear regressions are presented in Fig. S1 and Fig. S2. Slopes were used to represent the trends of seasonal temperature and precipitation changes and were included in the following BRT analysis. Beside the linear regression analysis, we used generalized additive model (GAM) to fit the trends of air temperature and precipitation at each ecological station. Twenty-eight GAM models were fitted respectively for variables of air temperature and precipitation. Parameters of fitted GAM models were presented in Table S7. Among these parameters, edf (effective degree of freedom) reflect the degree of nonlinearity. If the edf is higher than 1, this indicates

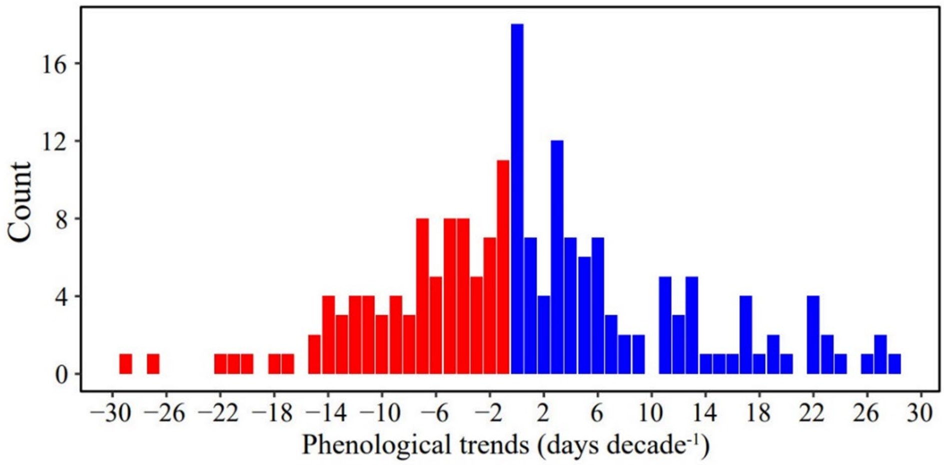

Fig. 2 Frequency distribution of phenological trends of first flowering date (FFD). Data include 197 data points on 190 species from eight sites across China. Negative values indicate advancing trends, whereas positive values indicate delaying trends

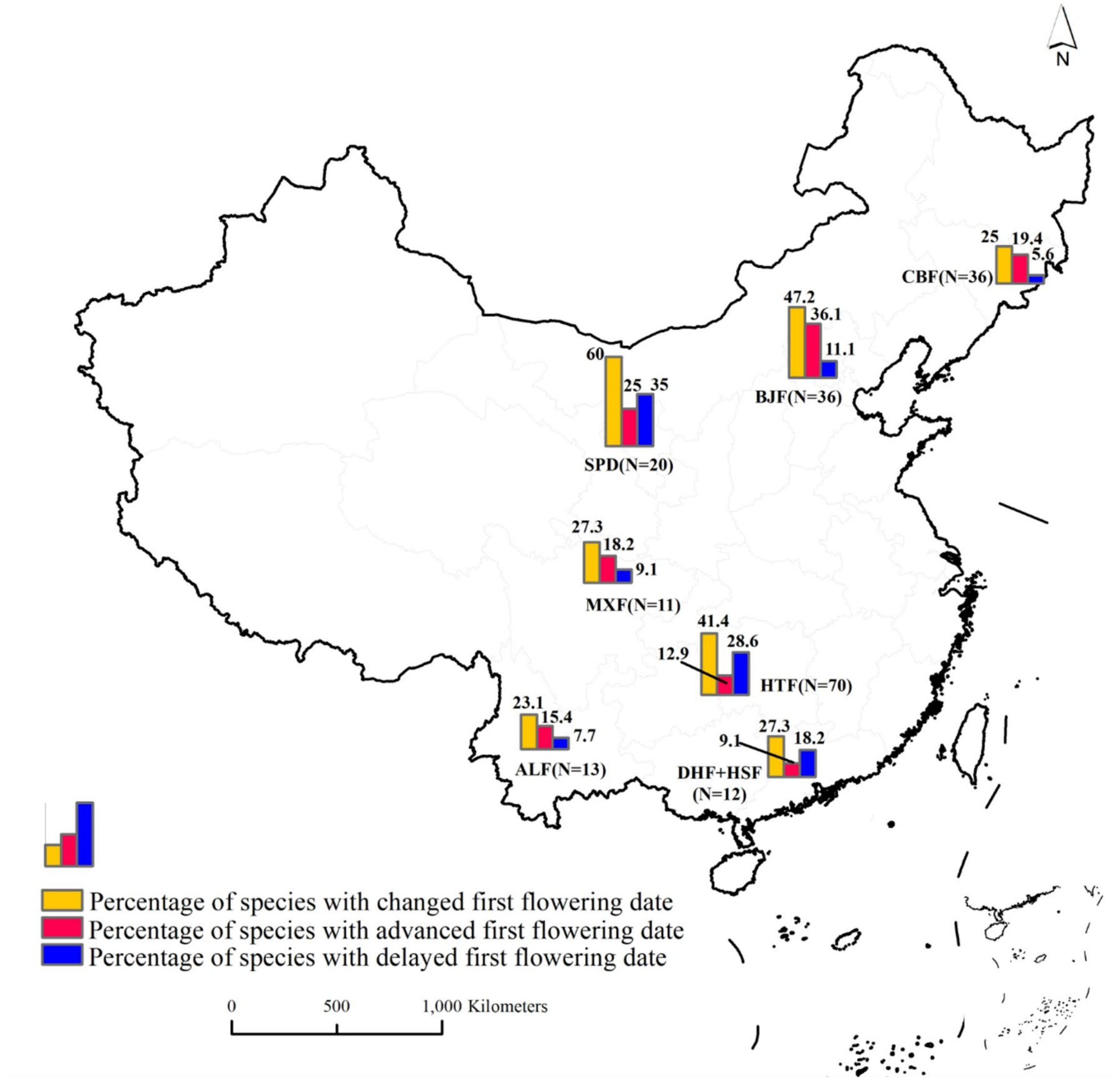

Fig. 3 Percentage of species with changed, advanced, and delayed first flowering date in different ecological stations (CBF, Changbai Mountain Forest Ecosystem Research Station; BJF, Beijing Forest Ecological Station; SPD, Shapotou Desert Research and Experiment Station; MXF, Maoxian Mountain Ecosystem Research Station; HTF, Huitong Research Station of Forest Ecosystem; ALF, Ailaoshan Station for Subtropical Forest Ecosystem Studies; DHF, Dinghu Mountain Research Station of Forest Ecosystem; HSF, Heshan Mountain Integrated Experimental Station of Hilly Land; N indicates the number of phenological sequences.)

the nonlinearity of the trend of air temperature and precipitation. The linear regression analysis was carried out using the "lm" function, and GAM was performed using the "mgcv" package, both analysis were executed in the statistical program R version R 3.1.1 [33].

Redundancy analysis between phenological data matrix and environmental data matrix

Redundancy analysis (RDA) was used to detect the relationships between phenological change trends, air temperature, and precipitation. RDA is a Principal Component Analysis (PCA) of the fitted value matrix of the multivariate multiple linear regression analysis between the response (phenology data matrix, DOY×species) and explanatory variables (air temperature and precipitation data matrix). The aim of RDA is to find a linear combination of a series of explanatory variables that can best explain the variation in the response variables [34]. Through RDA, we obtained the portion of the total variance of the response variable matrix that can be explained by the explanatory variables (portion constrained) (Table 3). We also obtained the phenology-environmental ordination plot and biplot scores for constraining variables (Table S8), which can be used to represent the role of environmental factors in explaining the variance of the response variables, that is, which variable has a greater influence on phenological changes.

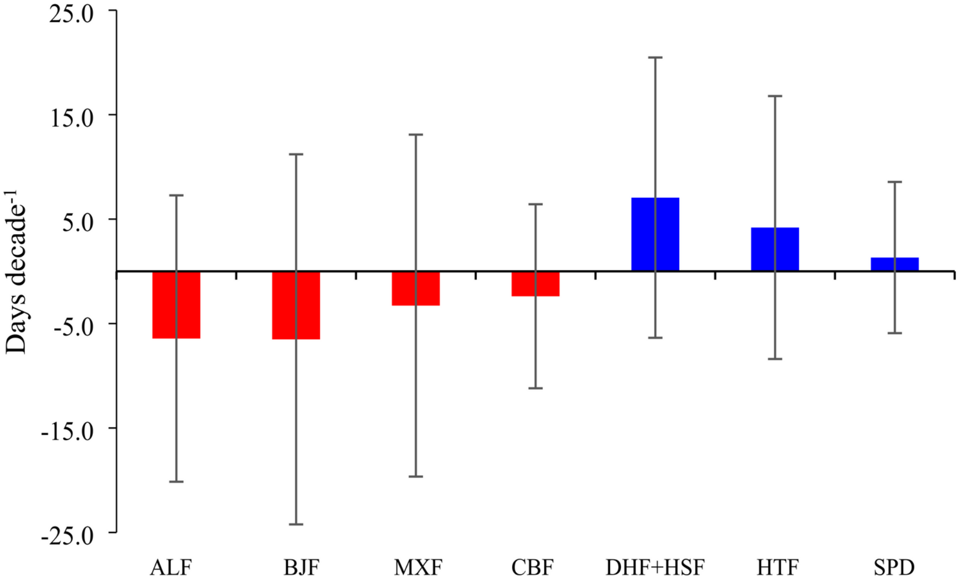

Fig. 4 Mean trends (mean ± SD) in first flowering date across ecological stations (CBF, Changbai Mountain Forest Ecosystem Research Station; BJF, Beijing Forest Ecological Station; SPD, Shapotou Desert Research and Experiment Station; MXF, Maoxian Mountain Ecosystem Research Station; HTF, Huitong Research Station of Forest Ecosystem; ALF, Ailaoshan Station for Subtropical Forest Ecosystem Studies; DHF, Dinghu Mountain Research Station of Forest Ecosystem; HSF, Heshan Mountain Integrated Experimental Station of Hilly Land)

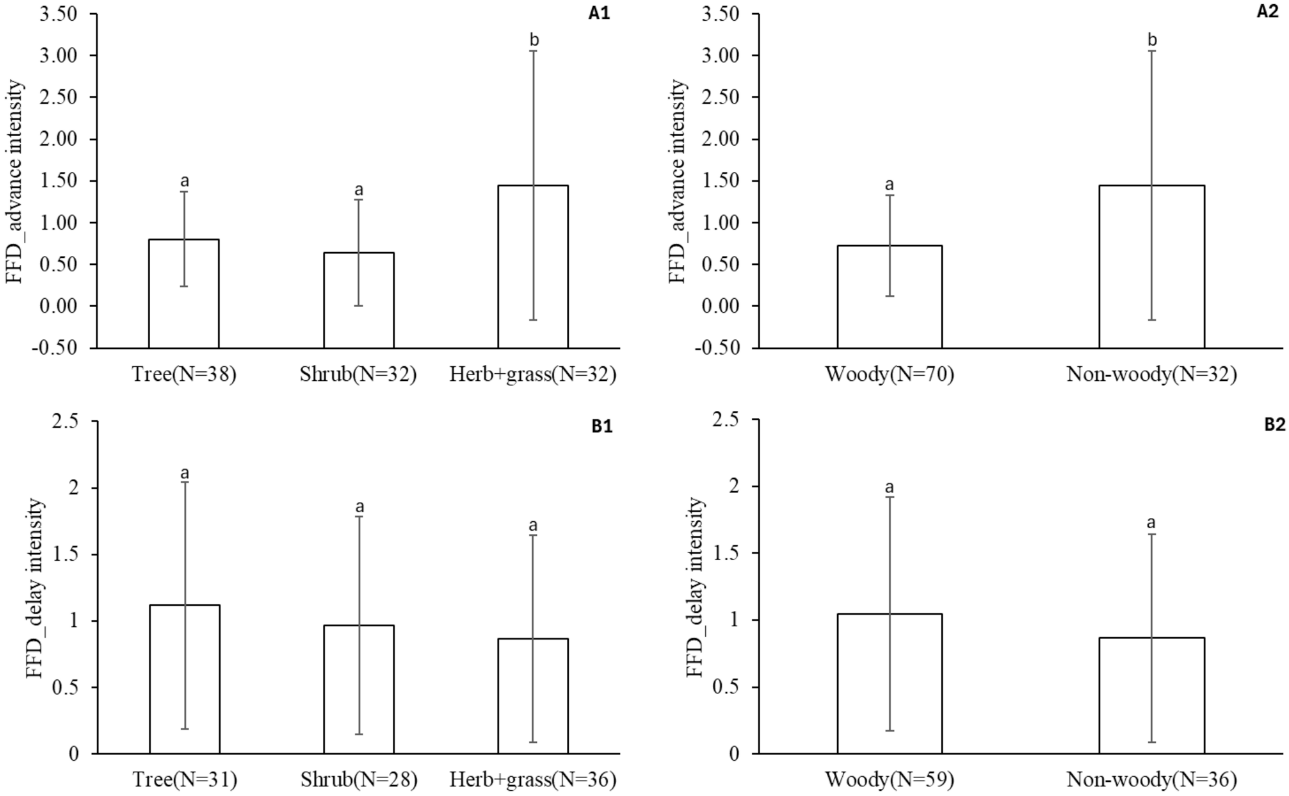

Fig. 5 Differences in FFD change intensity between growth forms. A1 indicates the difference between growth forms in FFD advance intensity, A2 indicates the difference between woody and non-woody plants in FFD advance intensity; B1 indicates the difference between growth forms in FFD delay intensity, B2 indicates the difference between woody and non-woody plants in FFD delay intensity. FFD indicates first flowering date. Different letters (a, b) indicate significant difference between plant trait groups. N indicates the number of phenological sequences in plant traits group

Table 3 Proportion of explained variance in the redundancy analysis between phenological change pattern and temperature and precipitation variables at each observation site

Ecological zone	Site	Proportion of explained variance
Subhumid middle temperate zone	BJF	0.56
Humid middle temperate zone	CBF	0.53
Arid middle temperate zone	SPD	0.71
North region of humid middle subtropical zone	MXF	0.56
South region of humid middle subtropical zone	HTF	0.26
West region of humid south subtropical zone	ALF	0.46
East region of humid south subtropical zone	DHF + HSF	0.49

(CBF, Changbai Mountain Forest Ecosystem Research Station; BJF, Beijing Forest Ecological Station; SPD, Shapotou Desert Research and Experiment Station; MXF, Maoxian Mountain Ecosystem Research Station; HTF, Huitong Research Station of Forest Ecosystem; ALF, Ailaoshan Station for Subtropical Forest Ecosystem Studies; DHF, Dinghu Mountain Research Station of Forest Ecosystem; HSF, Heshan Mountain Integrated Experimental Station of Hilly Land)

More details of the RDA can be found in Numerical Ecology with R (Second Edition) published by Bocard et al. (2018) [34].

Phylogenetic analysis

Because phylogenetic relatedness may exist among the studied species, we applied the following procedure to include phylogenetic information in the subsequent BRT analysis. We first used the R package "plantlist" to calibrate the Latin names of the genera and families of the studied species. Then, we created a phylogenetic tree of the studied species and linked the trait data to the species phylogeny using the function "phylo.maker" from the package V. PHYLOMAKER2 [35]. We adopted the same approach and procedure reported by Sporbert et al. (2022) [24] to account for the phylogeny based on the phylogenetic eigenvector regression by Diniz-Filho et al. (1998) [36]. This procedure was proposed by Pistón et al. (2019) [37] and Bianchini and Morrissey (2020) [38]. We first used the function "vcv.phylo" to compute a pairwise distance matrix (Table S9 is the matrix for species with advanced FFD sequence, and Table S10 is the matrix for species with delayed FFD sequence) from our phylogenetic tree, and then we performed a principal coordinates analysis (PCoA) to extract eigenvectors from this distance matrix using the function "pcoa" from the APE package v.5.8-1 [39]. The phylogenetic relationships among species were well represented by phylogenetic eigenvectors, which can be used to control for phylogenetic autocorrelation when a sufficient number of eigenvectors are included in the analysis [36, 38]. According to the research of Sporbert et al. (2021), the eigenvectors selected into the BRT analysis could explain more than 90% of the variation in the phylogenetic distance matrix. In our BRT models, the covariates for advanced FFD sequences included the first 28 eigenvectors of a total of 99 eigenvectors (Table S11), while those for delayed FFD sequences included the first 31 eigenvectors of a total of 95 eigenvectors (Table S12), both of which explained over 90% of the phylogenetic structure in the distance matrix (see Table S13, Table S14). Besides the phylogenetic relatedness among species, phylogenetic relatedness at genus level was also included in the BRT analysis to explain the inter-specific variation of flowering phenology. The phylogenetic relatedness among genus, represented by phylogenetic vectors, was also achieved using the procedure proposed by Pistón et al. (2019) and Bianchini and Morrissey (2020). The phylogenetic distance matrix at genus level for species with advanced FFD sequence was presented in Table S15, and the phylogenetic distance matrix at genus level for species with delayed FFD sequence was presented in Table S16. The number of selected phylogenetic vectors was also determined according to the proposition of Sporbert et al. (2021). For advanced FFD sequences, the first 63 eigenvectors of a total of 76 eigenvectors (Table S17) were included in the BRT model fitting, and the first 33 eigenvectors of a total of 82 eigenvectors (Table S18) were included in the BRT model fitting. Both of which explained over 90% of the phylogenetic structure in the distance matrix (see Table S19, Table S20).

Analysis of the relative importance of phylogenetic relatedness, plant traits, site conditions, and climate change on variations of FFD change intensity

We used BRT to fit the relationships between FFD change intensity, site conditions, climate change, plant traits, and phylogenetic eigenvectors. The BRT models were fitted using the "gbm" [40] and "dismo" [41] of R library. All calculations were performed using the statistical program R 3.1.1 [33]. We built two BRT models: one for FFD sequences with negative slopes and the other for FFD sequences with positive slopes. As proposed by König et al. (2016) and Sporbert et al. (2021), we set bag fraction as 0.5, and tree complexity as 2 in the procedure of BRT model fitting. Considering the small number of training data points, we selected a smaller value of learning rate (0.001) to fit the BRT according to the recommendation of König et al. (2016). In the procedure of model fitting, following the recommendation of Elith et al. (2008), we conducted a cross-validation procedure (cv. folds = 5) to optimize the number of trees with the chosen learning rate using the gbm.step function. Considering the high number of variables included in the fitting of BRT models, we used a step-wise procedure for model simplification (gbm.simplify) that reduces the number of

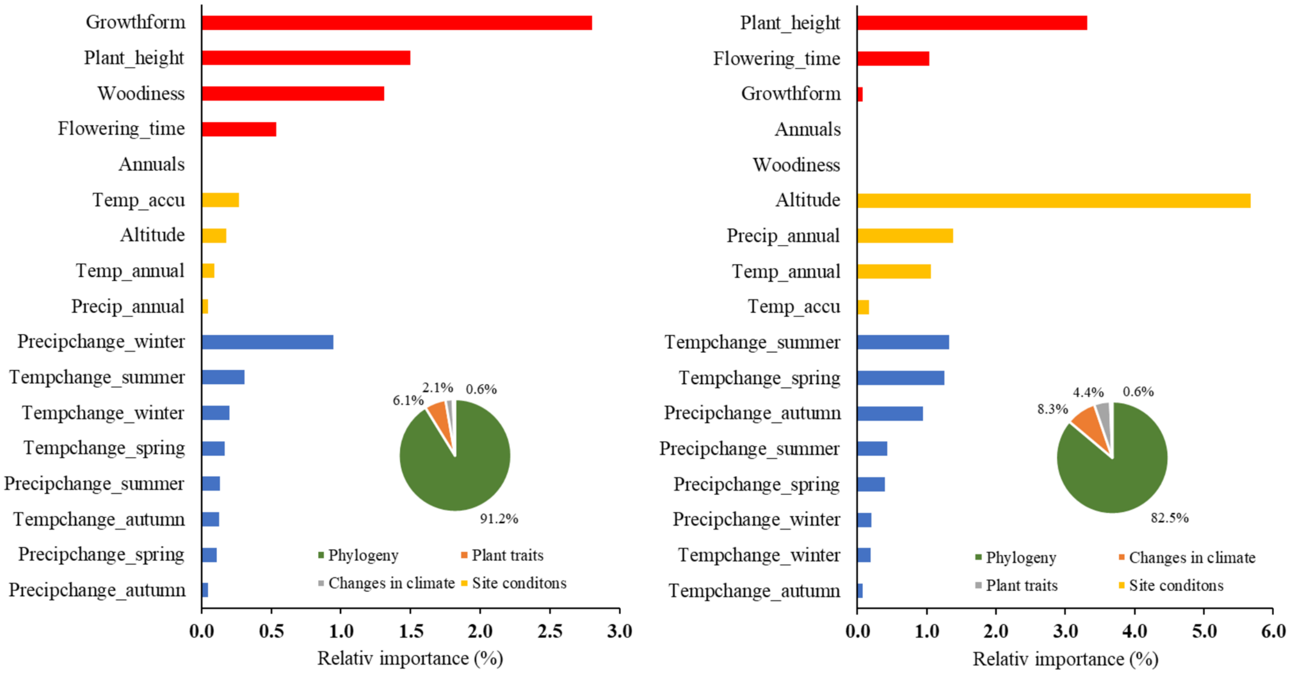

Fig. 6 Relative importance (%) of plant traits, site conditions, climate change, and phylogeny on FFD advance intensity, deduced from boosted regression trees. Models were fitted separately for (**a**) advanced phenological sequences (the chart on the left) [$n = 102$] and (**b**) delayed phenological sequences (the chart on the right) [$n = 95$]. Pie charts represent overall importance of the four variables categories. Temp_accu, accumulated temperature; Temp_annual, annual mean air temperature; Precip_annual, mean annual precipitation; Precipchange_spring, change trend of total precipitation in spring; Precipchange_summer, change trend of total precipitation in summer; Precipchange_autumn, change trend of total precipitation in autumn; Precipchange_winter, change trend of total precipitation in winter; Tempchange_spring, change trend of monthly mean air temperature in spring; Tempchange_summer, change trend of monthly mean air temperature in summer; Tempchange_autumn, change trend of monthly mean air temperature in autumn; Tempchange_winter, monthly mean air temperature in winter

predictor variables without substantial gains in the cross-validation error (cv.folds = 5). For the simplified (most parsimonious) models, the optimal number of trees was estimated again using the gbm.step function. Parameters such as the mean total deviance, mean residual deviance, training data correlation were used to assess the performance of the fitted BRT models (Table S21). The relative importance of site conditions, plant traits, changes in climate, and phylogenetic relatedness for the variation in FFD change intensity was deduced from boosted regression tree models (Fig. 6). For more detailed description of parameters and settings on BRT model see “A working guide to boosted regression trees” by Elith et al. (2008) [42].

Results

General trend of the first flowering phenology

Based on the p-values of the linear regression between the FFD time sequences and year, 39 FFD time sequences showed a significant advanced trend over the past 19 years ($p < 0.05$) while 37 FFD time sequences showed a significant delayed trend ($p < 0.05$), with the mean trend of FFD for all time sequences at -0.22 ± 13.6 d decade^{-1} (Table 2). The FFD trend was less than 15 d decade^{-1} for 80% of these phenological sequences (Fig. 2).

Tr_{mean} is the mean trend of all the time sequences; Neg_{all} and Pos_{all}: proportion of negative and positive trends, respectively; Neg_{sig} and Pos_{sig}: proportion of significant negative and positive trends ($p < 0.05$), respectively.

Spatial differences in the trends of the first flowering phenology

The percentage of species with a changed FFD showed large variations between the ecological stations (Fig. 3). The percentages of species with advanced and delayed FFD also showed large regional differences (Fig. 3).

The percentage of species with an advanced FFD was higher than that of species with a delayed FFD in ALF, BJF, MXF, and CBF (Fig. 3), and the mean trends in FFD were − 6.4, − 6.5, − 3.3, and − 2.4 d decade^{-1}, respectively (Fig. 4). In DHF + HSF, HTF, and SPD, the percentage of species with a delayed FFD was higher than that of species with an advanced FFD (Fig. 3), and the mean trends in FFD were 7.1, 4.2, and 1.3 d decade^{-1}, respectively (Fig. 4).

Differences in the trends of first flowering phenology between plant trait groups

Among species with advanced FFD, the FFD advance intensity was higher in herbaceous plants than in trees and shrubs (Fig. 5), whereas for FFD delay intensity, no significant differences were observed between growth forms (Fig. 5).

Strong positive linear relationships were observed between FFD change intensity (both advance and delay) and plant height for herbs and grass ($p < 0.1$, Table S6), whereas for trees and shrubs, no clear linear relationships were observed between FFD change intensity and plant height (Table S6).

The FFD delay intensity increased significantly with later flowering time ($p < 0.05$) in shrubs, whereas the FFD advance intensity decreased with later flowering time in herbs and grasses ($p < 0.1$). No clear relationships were observed between FFD change intensity and flowering time in trees (Table S6).

Relationship between flowering phenology change, air temperature and precipitation

In the temperate zone, the mean air temperatures at CBF, BJF and SPD increased in most seasons over the period to 2003–2021 (Fig. S1), particularly in spring and summer. In the subtropical zone, the mean air temperatures during most seasons at MXF, ALF, HSF, and DHF also increased over the past 19 years. In contrast, the mean air temperature at HTF showed a slight decreasing trend in most seasons, except spring, over the past 19 years (Fig. S1). From 2003 to 2021, the total precipitation decreased in most seasons in CBF and BJF. However, the total precipitation during each season increased at SPD (Fig. S2). At MXF and HTF, the total precipitation increased in most seasons. At ALF, the total precipitation decreased in most seasons, except winter. At HSF and DHF, the total precipitation decreased in spring and summer but increased in autumn and winter (Fig. S2).

The RDA analysis (Table 3) revealed that air temperature and precipitation have great explanatory power for phenological change patterns. In addition, this power varied greatly at different ecological stations and was greater in temperate zones than subtropical zones. From the biplot scores for the constraining variables (Table S8), the variables with the greatest influence on phenological change patterns varied with the observation site. In the temperate zone, monthly mean air temperatures in spring and winter were the most important variables in CBF and BJF, whereas total precipitation in spring and summer were the most important in SPD. In the humid middle subtropical zone, the monthly mean air temperature in spring and total precipitation in summer were the most influential variables in MXF, total precipitation in summer and autumn were the most important variables in HTF, and monthly mean air temperatures in spring and autumn were the most important variables in ALF and DHF + HSF.

Relative importance of site conditions, climate change, plant traits and phylogenetic relatedness on FFD change intensity

The pie charts in Fig. 6 present the overall contributions of the variables grouped by “plant traits,” “site conditions,” “changes in climate,” and “phylogeny” deduced from the BRT models. “Phylogeny” was the factor with the greatest importance on variations in FFD change intensity in the BRT models for both advanced and delayed FFD sequences. Growthform and plant height are the most important plant traits on variations in FFD change intensity in the BRT models.

Discussion

In this study, the proportion of significant phenological sequences in our study was similar to that of Ge et al. (2015) [14], who found that 43% of spring and summer phenological events changed significantly between 1960 and 2011 based on 1263 phenological observations of 112 species collected across 145 locations in China. However, the observation period in our study was much shorter than that of Ge et al. (2015) [14]. This indicated that obvious phenological changes occurred from 2003 to 2021. Furthermore, the proportion of significantly delayed phenological sequences (18.8%) in our study was much higher than that reported by Ge et al. (2015) (1.2%) [14]. This might be because the numbers of phenological records in temperate zones collected by Ge et al. [14] were much larger than those in the subtropical zone and more species had advanced spring and summer phenological events in temperate zones [43]. This discrepancy may have led to a statistical bias in the proportion of significantly delayed and advanced phenological events. Therefore, to fully understand trends in phenological events at large scale, more attention should be paid to the collection of phenological observation records in subtropical zones.

In RDA analysis, the variance explained by air temperature and precipitation in the temperate zone was higher than that in the subtropical zone. This indicates that air temperature and precipitation have stronger influences on phenology in temperate zones, particularly in regions with increasing temperatures [44]. In humid and subhumid middle temperate zones, the monthly mean air temperature in spring and winter had the most important influence on the phenological change pattern of CBF and BJF. This was consistent with the conclusion proposed by Mo et al. (2011) [45], who stated that temperature has the greatest influence on phenology in temperate and cold regions. SPD is located in an arid middle temperate zone and experiences extreme drought; thus, water is the most important factor controlling plant growth [46]. This explains why precipitation in spring and summer had the most significant influence on the phenological change patterns in SPD. This conclusion is consistent with the research of Crimmins et al. (2010) [47], who considered precipitation to be the most important variable explaining flowering phenology changes in dry regions. The relationships among phenological change patterns and air temperature and precipitation were more complex in the subtropical zone than in the temperate zone. MXF and HTF are located in the humid middle subtropical zone, and due to the influence of monsoon, drought often occurs in late spring and early summer in Southwest China before the monsoon arrives. Thus, precipitation is the most important factor affecting flowering phenology. In tropical and near-tropical regions, temperature and photoperiod vary little throughout the year, plants have high heat requirements, and changes in plant phenology are mainly caused by temperature change [45]. This might explain why the monthly mean air temperature in spring was the factor with the greatest influence on flowering phenological changes in DHF and HSF. Although ALF is located in the southern subtropical zone, temperature is the most important variable controlling phenological changes because of the high altitude.

Flowering phenology is phylogenetically conserved, closely related species tending to flower or leaf out at similar times [22–24]. In our research, phylogenetic relatedness had the most important influence on FFD change intensity compared with plant traits, site conditions, and climate change trends. This indicated the change trend of flowering phenology is phylogenetically conserved, closely phylogenetic related species show similar phenological response to climate change. One possible mechanism for the conservation of flowering phenology change might be that related species generally have similar morphological traits, such as flower size, shape, aroma and nectar content, which determine the success of pollination [48], so closely phylogenetic related species tend to have similar phenological response to climate change and blossom at the same time to attract pollinators [49]. Another possible mechanism might be that closely phylogenetic related species have the almost same genetic basis, possess similar evolutionary direction, and easier to generate approximate phenological response to climate change [50]. This finding highlights the importance of phylogenetic relatedness, which not only influences the timing of phenological events but also the intensity of phenological changes. Phylogenetic relatedness should be considered as an important factor in the analysis of phenological patterns. However, our conclusion differs from that of König et al. (2018) [19], who concluded that phylogeny was not important for changes in phenology. This difference might be related to the distinct geographical scale and constructed phylogenetic tree between our study and that of König et al. (2018) [19]. In the research of König et al. (2018), the phenological observation data was collected at a larger geographical scale (Europe and North America) compared with that of our research, geographical isolation and divergent evolution may lead to more distant phylogenetic relatedness among species. In the research of König et al. (2018), the phylogenetic information was extracted from the Daphne phylogenetic tree [51], which is based on a backbone family phylogeny of the Angiosperm Phylogeny Group III. Whereas in our research, the phylogenetic tree was constructed based on the combination of GBOTB for seed plants [52] and the clade in Zanne et al.'s (2014) [53] phylogeny for pteridophytes. This may lead to the difference of the relative importance of phylogenetic information in explaining the interspecific difference of flowering phenology change trend between our research and that of König et al. (2018).

Plant height is closely related to the competitive ability of an ecosystem [54]. To enhance their competitive ability, small grasses and herbs may show stronger phenological responses to environmental changes than larger plants [19]. Previous studies have demonstrated that plant height is positively correlated with the onset of flowering [22, 24, 55–56]. In this study, we found that plant height and FFD change intensity exhibited different relationships between growth forms. Plant height and FFD change intensity were positively correlated for herbaceous plants but did not show a clear relationship for trees and shrubs. In general, shorter species may respond faster to environmental changes [57], and they are more likely to flower earlier than taller ones in herbaceous plants [55]. Plant height or size should be included in the analysis of interspecific differences in phenological response to climate change because this trait greatly influences species interactions, survival, and reproduction [58].

Growth form has an important influence on interspecific variation in phenological changes [14, 19]. In our research, FFD advance intensity varied significantly with the growth form, with herbaceous plants having a significantly higher FFD advance intensity than trees and shrubs. This finding is consistent with that of Ge et al. (2015) [14] but inconsistent with that of König et al. (2018) [19]. This discrepancy might be related with the bias in the number of observed species with different growth form in the phenological observation dataset, and the diverse trends of climate change at local scale. In addition, we found that the FFD delay intensity was not significantly different between the growth forms. The exact reason for this deserves further investigation.

The intensity of FFD advances in early flowering plants is usually higher than that in late-flowering plants [59, 60]. König et al. (2018) also found that early flowering grasses showed more intense advances than late-flowering ones [19]. In this study, we also found a clear negative relationship between FFD advance intensity and flowering time for herbaceous plants, which is consistent with the conclusions of Dunne et al. (2003) [59] and König et al. (2018) [19]. For shrubs, a significant positive relationship was detected between FFD delay intensity and flowering time. We speculate that the increased temperature and precipitation in late spring and early summer may produce unsuitable environments for blossoming, thus strengthening the intensity of the FFD delay.

Regarding longevity (annual/perennial), Fitter and Fitter (2002) [61] found that annual plants were more likely to flower earlier than congeneric perennials as temperature increased. In our study, the relative importance of longevity was very low in the BRT analysis, which may have been due to the limited number of observed annual plants.

In this study, site conditions and changes in climate contributed to the variation in FFD change intensity; however, the relative importance of site conditions and climate change was much lower than that reported by König et al. (2018) [19]. An interesting finding in our research is that site conditions have a more important influence on FFD delay intensity than on FFD advance intensity. The linear regression analysis also revealed stronger correlations between the FFD delay intensity and site conditions than between the FFD advance intensity and site conditions. Furthermore, the intensity of FFD delay decreased with the increase of altitude for trees and shrubs, whereas for herbs and grass, the intensity of FFD delay increased with the increase of altitude. We speculated that the harsh environmental conditions at high altitudes lead to a short growth season, which does not allow trees and shrubs to delay the flowering event; otherwise, they would not be able to complete their life cycle. In contrast, herbs grow fast, are more plastic in terms of the timing of their internal physiological and chemical dynamics, and may respond faster to environmental changes [57]. Therefore, herbs may be more likely to show a stronger FFD delay intensity than trees and shrubs.

In general, phylogenetic relatedness and differences in biological and ecological characteristics among species lead to variation in flowering phenology in response to climate change. Furthermore, environmental factors such as climate, soil, and topography have distinct effects on plant growth in different ecological zones. All these factors lead to interspecific and regional differences in phenological responses to climate change [62].

At last, we should be aware that in this study, very limited phenological observation data from the Northwest and Southwest China (particularly the Tibetan Plateau) was included in the analysis, and the number of species observed at different ecological stations varied considerably, which may bring uncertainty to this research.

Conclusion

Our research found that the first flowering phenology of nearly 40% of the observed plants changed significantly from 2003 to 2021, FFD showed spatial and interspecific differences, and flowering phenology trends varied across observation sites. Our research also demonstrates the importance of plant phylogeny on interspecific differences in phenological changes. In addition to phylogenetic relatedness, plant traits such as growth form, plant height, and flowering time influence flowering phenology to a certain extent. These findings will help us to better understand phenological responses to climate change on a national scale. The conclusion about the relative importance of phylogenetic relatedness and plant traits on interspecific differences in phenological change will help us better predict the response of various plants to climate change in the future. Phylogenetic relatedness, plant traits, trends in climate change, and site conditions should all be considered as important factors when analyzing the mechanisms and predicting the patterns of plant phenology change. Our research also found that the phenological change patterns in the subtropical zone were more complex than those in the temperate zone. Thus, to fully understand phenological patterns in China, additional phenological observations should be performed in subtropical zones.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06572-0.

Supplementary Material 1
Supplementary Material 2
Supplementary Material 3
Supplementary Material 4
Supplementary Material 5
Supplementary Material 6
Supplementary Material 7
Supplementary Material 8
Supplementary Material 9
Supplementary Material 10
Supplementary Material 11
Supplementary Material 12
Supplementary Material 13
Supplementary Material 14

Supplementary Material 15

Supplementary Material 16

Supplementary Material 17

Supplementary Material 18

Supplementary Material 19

Supplementary Material 20

Supplementary Material 21

Supplementary Material 22

Supplementary Material 23

Supplementary Material 24

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Author contributions
Chuangye Song made the formal analysis, methodology, writing original draft, review and editing.Lin Zhang reviewed and edited the manuscript. Yuan Jia made the figures of this manuscript.Dongxiu Wu presented the conceptualization, reviewed the manuscript and edited the text.

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Data availability
Data is provided as supplementary information files.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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