



Overlooked climate parameters best predict flowering onset: Assessing phenological models using the elastic net

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Abstract

Determining the manner in which plant species shift their flowering times in response to climatic conditions is essential to understanding and forecasting the impacts of climate change on the world's flora. The limited taxonomic diversity and duration of most phenological datasets, however, have impeded a comprehensive, systematic determination of the best predictors of flowering phenology. Additionally, many studies of the relationship between climate conditions and plant phenology have included only a limited set of climate parameters that are often chosen a priori and may therefore overlook those parameters to which plants are most phenologically sensitive. This study harnesses 894,392 digital herbarium records and 1,959 in situ observations to produce the first assessment of the effects of a large number (25) of climate parameters on the flowering time of a very large number (2,468) of angiosperm taxa throughout North America. In addition, we compare the predictive capacity of phenological models constructed from the collection dates of herbarium specimens vs. repeated in situ observations of individual plants using a regression approach—elastic net regularization—that has not previously been used in phenological modeling, but exhibits several advantages over ordinary least squares and stepwise regression. When herbarium-derived data and in situ phenological observations were used to predict flowering onset, the multivariate models based on each of these data sources had similar predictive capacity ($R^2 = 0.27$). Further, apart from mean maximum temperature (TMAX), the two best predictors of flowering time have not commonly been included in phenological models: the number of frost-free days (NFFD) and the quantity of precipitation as snow (PAS) in the seasons preceding flowering. By vetting these models across an unprecedented number of taxa, this work demonstrates a new approach to phenological modeling.

KEYWORDS

flowering time, herbarium specimen, phenoclimate modeling, phenology

1 | INTRODUCTION

Observations of how individual plants alter the timing of leaf production, flowering, and fruiting in response to local temperature or rainfall provide a way to evaluate the impacts of climate variation on the world's flora. Changes in flowering phenology that have occurred

in response to recent warming have resulted not only in reproductive failure in some taxa (Inouye, 2008; Inouye & McGuire, 1991; Inouye, Saavedra, & Lee-Yang, 2003), but in some cases has produced mismatches between plants and the animals that depend on their flowers as food resources (Huang & Hao, 2018; Reddy et al., 2015; Schenk, Krauss, & Holzschuh, 2017). Thus, identifying the climate parameters that best predict changes in the timing of

flowering, and accurately predicting the changes in flowering phenology that are likely to occur under future climate change, is essential to the prediction and management of the effects of climate change on the reproductive success of angiosperm taxa and on the antagonistic (e.g., herbivores) and mutualistic (e.g., pollinators and seed dispersers) animals that rely on them. Generating robust predictions of the effects of local climatic conditions on plant phenology is therefore a critical first step toward forecasting the effects of climate change on plant populations, species, and communities, as well as on the animals that depend on them.

To date, the intensive work required for repeated *in situ* phenological observation has largely restricted long-term studies of plant phenology and its relation to climate in the United States to either a comparatively small number of species (Leopold & Jones, 1947; Schwartz & Reiter, 2000; Zhao & Schwartz, 2003) or to a narrow geographic range (Abu-Asab, Peterson, Shetler, & Orli, 2001; Cook et al., 2007; Dunnell & Travers, 2011; Miller-Rushing & Primack, 2008). As a result, our ability to generalize from these studies to a wider array of species and climatic conditions remains limited. The design and application of models that can detect the climatic factors that best predict timing of phenological events in native plant species have until recently also been limited by the lack of spatially extensive, long-term climate data (particularly for populations located at some distance from the nearest weather monitoring station), and by the limited number of gridded climatic variables that have been readily available.

As a result, most spatially extensive examinations of the relationship between local climate conditions and plant phenology have depended on comparatively simple climate parameters, many of which are chosen *a priori*. In such cases, the resulting models may fail to include either the specific parameters to which plants are most phenologically sensitive or all of the climate parameters to which plants respond. The recent availability of digital herbarium records, however, in combination with datasets such as those produced by PRISM and ClimateNA, which collectively provide estimates of a wide array of historical climate parameters at local scales throughout much of the globe (Wang, Hamann, Spittlehouse, & Carroll, 2016), offers the opportunity not only to conduct phenological assessments across an unparalleled diversity of taxa and at broad spatial scales, but also to conduct a continental-scale assessment designed to identify those climate parameters that best predict the flowering phenology of each focal species.

Herbarium collections have been used in numerous studies to document the seasonality of a wide array of species (Borchert, Robertson, Schwartz, & Williams-Linera, 2005; Boulter, Kitching, & Howlett, 2006; Sahagun-Godinez, 1996) and to examine regional, climate-based variation in the phenological timing of well-collected species (Lavoie & Lachance, 2006; Matthews & Mazer, 2015; Park, 2016; Willis et al., 2017) at spatial scales that exceed the current spatial and temporal scope of repeated *in situ* phenological observations. Furthermore, the unparalleled taxonomic diversity of herbarium records has been leveraged to examine the collective phenological properties of entire floras (Park, 2014, 2016) that could not be assessed using other kinds of phenological records.

Assessments of phenological change over recent decades (Bertin, Searcy, Hickler, & Motzkin, 2017; Lavoie & Lachance, 2006; Primack, Imbres, Primack, & Miller-Rushing, 2004) or across spatial climate gradients (Bowers, 2007; Hereford, Scmitt, & Ackerly, 2017; Houle, 2007; Miller-Rushing, Primack, Primack, & Mukunda, 2006) have reported similar shifts based on observations of both living plants and herbarium-based phenological records.

While herbarium records are a useful source of phenological information (Jones & Daehler, 2018), few studies have compared the capacity of phenoclimatic models based on herbarium records to predict flowering to those constructed from repeated *in situ* observations of the phenological status of living plants (hereafter referred to as *in situ* observations, in contrast to phenological records derived from herbarium collections). There is good reason to expect that models based on herbarium collections will have lower predictive power than those based on *in situ* observations of individual plants. At the level of individual plants, if the flowering date is estimated by the collection date of an herbarium specimen, it is intrinsically less precise than if it is estimated using repeated observations of individual plants recorded at known intervals. This is because an herbarium specimen may have been collected at any time during its flowering period, so the collection date itself does not provide a precise metric of either the date of flowering onset, its midpoint, or peak flowering. Moreover, the digitally recorded information that is associated with the majority of herbarium records typically documents only whether a given specimen was in flower at the time of collection and therefore cannot distinguish among specimens collected at the onset of flowering, at peak bloom, or at any other stage of flowering. By contrast, *in situ* phenological observations that of an individual extend from before the onset of flowering to after its termination within a single flowering season can be used to estimate the individual's flowering onset and termination dates with a known level of precision (depending on the frequency of observation). These dates, in turn, can be used to estimate the date of the midpoint of flowering of an individual plant.

Previous examinations of bias in herbarium collections have found that temporal gaps in collection often occur during periods of inclement weather; that collection effort is often concentrated at locations that are easily accessible; and that herbarium holdings often under-sample threatened or endangered taxa while preferentially sampling certain clades (most notably graminoids, Daru et al., 2017). While *in situ* phenological observations may exhibit similar biases, the repeated nature of *in situ* observations allows those cases where gaps in observation occur (potentially leading to biased estimates of flowering time) to be identified and removed, which is not possible for herbarium specimens. Nevertheless, estimates of mean flowering time in Boston based on the collection dates of herbarium specimens were found to provide accurate estimates of mean flowering time; to exhibit variation in flowering date similar to *in situ* observations; and to remain accurate among taxa with both short and long flowering durations (Primack et al., 2004).

The current study was designed to construct phenological models using a regression approach—elastic net regularization—that has

several advantages over ordinary least squares regression and stepwise regression analysis, both of which have been used extensively to identify climatic parameters that influence the flowering dates (FDs) of species represented by either herbarium-derived data or observations of living plants. In particular, elastic net regularization is capable of incorporating multiple collinear explanatory factors (De Mol, De Vito, & Rosasco, 2009; Raschka, 2017). This is highly advantageous in the development of robust phenoclimate models, as potentially important climate parameters are often highly collinear (Rawal, Kasel, Keatley, & Nitschke, 2015). To our knowledge, this is the first study to apply elastic net regularization to develop phenological models that predict the FD of any species.

Here, we harnessed the power of 894,392 digital herbarium records and 1,959 in situ observations to construct species-specific models of flowering phenology for each of 2,468 angiosperm taxa using 25 distinct climate parameters. For seven additional species, we constructed phenological models using both herbarium-based data and repeated in situ phenological observations. With this unprecedented number of species-specific phenological models, we aimed to (a) determine the predictive ability of these species-specific phenological models at a continental scale; (b) compare the predictive capacity of phenological models derived from herbarium records of flowering dates vs. repeated in situ observations of flowering; and (c) determine which climate parameters best predict flowering phenology, while conducting model selection from a more extensive array of climatic parameters (25 distinct climate parameters) than has previously been used. By developing and vetting these phenoclimatic models across an unparalleled number of taxa throughout North America using elastic net regularization, a powerful under-utilized method, our goal is to provide a foundation and launching point for a new approach to phenological modeling.

2 | MATERIALS AND METHODS

2.1 | Phenological data

Herbarium-based estimates of FDs were obtained from 894,392 specimen records of angiosperm species drawn from the digital archives of 72 herbaria throughout North America (see acknowledgements and supporting information for complete listing) collected between 1901 and 2015. From these records, specimens that were not explicitly recorded as being in flower were eliminated, as were those that did not include either the precise GPS coordinates from which the sample was collected or the precise date of collection. Duplicate specimens (i.e., specimens of a given species collected on the same date and from the same location) were also excluded from analysis.

In situ estimates of FD among living plants were derived from flowering onset phenometric data collected from 2009 to 2015, as provided by the USA National Phenology Network's database (<https://data.usanpn.org/observations/>), and defined as the midpoint between the estimated dates of flowering onset and termination by a given individual in a given year. In order to ensure the accuracy of these in situ estimates of flowering time, we included only those

individual plant records for which no more than 10 days had elapsed between a date on which the plant had been recorded not to have flowered yet and the date on which it was first observed to have started flowering, and for which no more than 10 days had elapsed between a date on which the plant was last observed in flower for a given year and the date on which it was first observed to no longer be in flower. In other words, data from the USA-NPN included only those individual plants for which the estimated flowering onset date was no more than 10 days after a date on which the plant was observed *not* to be in flower, and for which the last date on which an individual was observed in flower was no more than 10 days prior to a date on which the plant was observed *not* to be in flower. As a result of this filtering, the date of the midpoint of flowering is accurate within a maximum of 5 days.

2.2 | Data preparation and standardization

Herbarium specimens were collected across many decades and by many collectors who sometimes documented collections using differing taxonomic nomenclature, so we standardized the taxonomic nomenclature using the Taxonomic Name Resolution Service iPlant Collaborative, Version 4.0 (Boyle et al., 2013, Accessed: April 4, 2017; <http://tnrs.iplantcollaborative.org>). Specimen identification was updated using taxonomic information from The Plant List, the International Legume Database and Information Service, the Global Compositae Checklist, and Tropicos.org. Specimens that could not be identified unambiguously to the species level were eliminated.

In order to include only those species with a sufficient number of observations for the development of accurate phenological models, we excluded species represented by fewer than 100 herbarium samples. 2,468 taxa met these criteria, comprising 2,171 distinct species as well as 117 taxa with subspecific epithets and 180 horticultural varieties across 119 plant families, representing a total of 563,501 herbarium specimens distributed across North America (Supporting Information Figure S1). These taxa represent a combination of woody and herbaceous taxa, including both annual and perennial species. We further identified seven of these angiosperm species that were also represented in the USA-NPN database by at least 100 in situ estimates of FD; this dataset comprised a total of 1,959 individual FD estimates. These seven species, which consisted of three tree species (*Cornus florida*, *Quercus agrifolia*, and *Quercus rubra*) and four perennial shrubs (*Baccharis pilularis*, *Eriogonum fasciculatum*, *Larrea tridentata*, and *Symphoricarpos albus*) distributed throughout North America (Figure 1), were analyzed separately in order to compare the explanatory power of statistical models based on herbarium records to the explanatory power of independently constructed models based on repeated in situ phenological observations.

2.3 | Azimuthal date corrections

The collection date of each herbarium specimen was converted into a day of year (DOY) value from 1 (January 1) to 366 (December 31 on a leap year). However, DOY values exhibit an artificial discontinuity

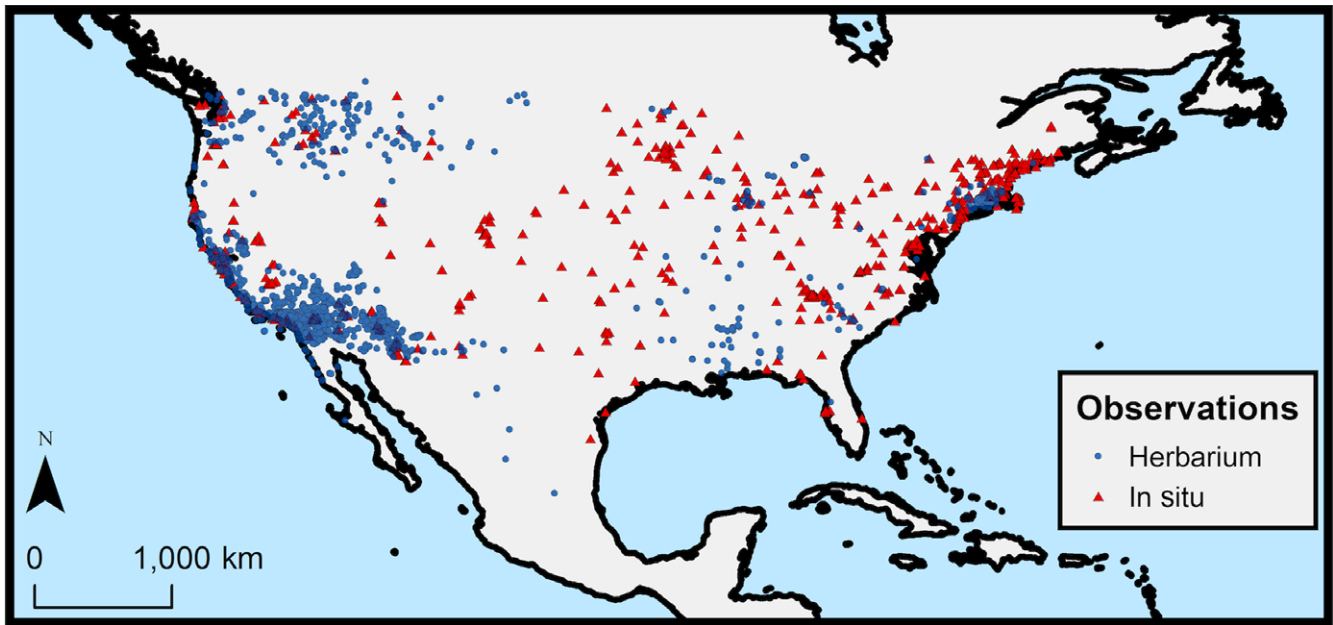


FIGURE 1 Distribution of herbarium specimens and repeated in situ observations of *Baccharis pilularis*, *Cornus florida*, *Eriogonum fasciculatum*, *Larrea tridentata*, *Quercus agrifolia*, *Quercus rubra*, and *Symphoricarpos albus* throughout North America

between December 31 (DOY 365 or 366) of 1 year and January 1 (DOY 1) of the next. This discontinuity makes it problematic to treat DOY as a continuous variable when considering species in which individuals flower both before and after January 1 in different locations or years. In order to eliminate this discontinuity, we converted DOY into a circular variable (Batschelet, 1981; Jammalamadakka & Sengupta, 2001) by rescaling the DOY into an azimuth (A), using Equation 1a, or Equation 1b in the case of leap years.

$$A = \text{DOY} * 360/365 \quad (1)$$

$$A = \text{DOY} * 360/366 \quad (2)$$

The coordinates of the endpoint of a vector with azimuth (A) and length 1, beginning at the origin point (0,0), were then calculated using the formula [$x = \cos(A)$ and $y = \sin(A)$]. The mean position of these coordinates was then calculated across all specimens of each species. The mean azimuth (or angular direction) from the origin point (0,0) to this mean position was then calculated for each species and rescaled into a DOY value representing the mean FD of each species across all climatic regions and all available years. Angular deviations of each specimen's azimuth from its respective species' mean azimuth were then calculated, with the direction of angular rotation being enforced as the direction of rotation that required the smallest angular change. The angular difference of each specimen from its species-wide mean was rescaled into a measure of departure in DOY (ΔDOY), with the direction of the difference (i.e., toward earlier or later DOY) being determined by the direction of angular rotation. The adjusted DOY (hereafter referred to simply as DOY) of collection for each specimen was then computed by adding its ΔDOY to its species-wide mean flowering DOY.

Among specimens for which the resulting collection date was prior to January 1 (DOY < 1) but the mean DOY was after January 1, the respective year of collection was converted to year + 1 in order to place it in the same year as the flowering season to which it was closest (i.e., a specimen of a species with an overall mean FD of January 15 that was collected on December 23, 2007, would be converted to DOY = -23, year 2008). Similarly, in cases where a specimen was collected after December 31 (DOY < 365, or 366 in leap years) but the mean DOY for the species was prior to December 31, the respective year of collection was converted to year - 1 (i.e., a specimen of a species with an overall mean FD of December 10 that was collected on January 5, 2006, would be converted to DOY = 370, year 2005).

2.4 | Climate data

Climate parameters included in this study consisted of a variety of annual and seasonal climate metrics across multiple periods of reference. Seasonal data in this study consisted of mean conditions during the autumn of the previous year (from October 1 to December 31), and from the winter (January 1 – March 31), spring (April 1 – June 30), summer (July 1 – September 30), and autumn (October 1 – December 31) of the year in which flowering occurred. In order to ensure that phenological behavior was modeled using only conditions prior to flowering for each species, we also calculated the mean FD for each species across all years and collection locations, and excluded from the phenoclimate models those climate variables representing all seasons that fell after the mean FD for that species.

All climate data used in this study were estimated using the ClimateNA v5.21 software package, available at <http://tinyurl.com/>

ClimateNA (Wang et al., 2016), which produces estimates of local monthly, seasonal, and annual climate conditions at 4 km resolution. Climate parameters used to characterize conditions within each season included the number of frost-free days (NFFD) mean daily minimum temperatures (TMIN), mean daily maximum temperatures (TMAX), total precipitation (PPT), and total precipitation as snow (PAS) within each season. In addition, the date on which the frost-free period began (BFFP), the mean temperature of the coldest month (i.e., January or February) in the year of flowering (i.e., the calendar year in which flowering occurred), as well as the date on which the previous year's frost-free period ended (EFPF), the total annual precipitation (TAP) throughout the previous year, and the mean annual temperature (MAT) of the previous year were considered as aspects of annual climate. In locations that typically do not experience freezes, the date on which the previous year's frost-free period ended was considered to be December 31, and the date on which the frost-free period began was considered to be January 1.

2.5 | Modeling reproductive phenology

In order to model the flowering phenology of each species, multiple regression methods have commonly been used to construct predictive models. Stepwise regression, in particular, represents a frequently used framework for constructing phenological models, particularly when the goal is to select which climate parameters to include in such models (Doi & Katano, 2007; Fraga et al., 2016; Gerst, Rossington, & Mazer, 2017; Hart, Salick, & Xu, 2014; Mazer, Gerst, Matthews, & Evenden, 2015; Richardson, Chaney, Shaw, & Still, 2017; Roy & Sparks, 2000; Sparks & Carey, 1995; Sparks, Jeffree, & Jeffree, 2000; Szabó, 2016; Tryjanowski, Kuźniak, & Sparks, 2005). In order to avoid collinearity, however, stepwise regression techniques often eliminate variables that are highly correlated. This may reduce the accuracy of the resulting phenological models and result in distorted perceptions of the importance of the parameters involved if important information is discarded. As many of the climate parameters that were considered in this study are highly correlated (Supporting Information Table S1), we instead use an alternative regression method, elastic net regularization, which is better suited to cases in which explanatory factors are strongly collinear.

2.6 | Elastic net regularization

Elastic net regularization is an increasingly popular method for multiple regression that is often used in place of stepwise linear regression techniques, particularly in cases where the number of explanatory factors is high or where significant collinearity among explanatory factors exists (De Mol et al., 2009; Zou & Zhang, 2009). Instead of selecting variables in a binary fashion, as with forward selection or backward elimination regression techniques, elastic net regularization enforces parsimony through the use of two penalty terms: the sum of the absolute value of all parameter coefficients (L1, Equation 2a) and the sum of all parameter coefficients squared (L2, Equation 2b, Zou & Hastie, 2005).

$$L1 = \sum ||\beta|| \quad (3)$$

$$L2 = \sum ||\beta^2|| \quad (4)$$

The degree to which model complexity is penalized is controlled by a penalty weighting term (α), while the relative weighting of L1 vs. L2 penalties is controlled by a relative weighting term (ρ). The overall model is then identified as the model for which the sum of the SSE (sum of squared errors) and the L1 and L2 penalties, modified by the two weighting terms, is minimized (C; Equation 5).

$$C = SSE + \alpha\rho||L1|| + \alpha(1 - \rho)||L2|| \quad (5)$$

In combination, L1 and L2 penalize model complexity and force the coefficients of unimportant parameters to zero, as does lasso regression (Tibshirani, 2011). The combination of L1 and L2 penalization also provides several advantages over OLS regression, particularly in cases where potential explanatory factors are highly correlated. In OLS-based regression methods, a high degree of collinearity often leads to large increases in the variance of coefficients as well as in their standard errors, making the resulting models unstable and therefore unreliable (Berry & Feldman, 2011). In elastic net regularization, however, the L2 penalty term prevents the model from generating extreme coefficients when confronted with highly collinear parameters. Instead, models constructed using this method typically exhibit a “grouping effect” (Zou & Hastie, 2005), in which the weights of the coefficients are distributed across all of the collinear parameters. As a result, models constructed through elastic net regularization typically remain highly stable when confronted by collinear parameters, while also avoiding the problems associated with variance inflation of parameter coefficients that occurs when conducting OLS-based regressions on datasets with high collinearity (De Mol et al., 2009; Raschkla, 2017). Given that potentially important climate parameters are often highly collinear (Rawal et al., 2015; Supporting Information Table S1), this makes elastic net regularization a better tool for the construction of, and variable selection among, phenoclimatic models.

2.7 | Constructing phenoclimatic models

For each of the 2,468 plant taxa for which sufficient herbarium data were available, phenological models were constructed using the elasticCV class contained within Scikit-Learn 0.814.4 in python in order to predict the FD of each species using local climate data. This method represents an internally cross-validated version of the elastic net regularization methods developed by Zou and Hastie (2005), and selects the optimal balance both between L1 and L2 penalization (ρ) and between the sum of squared standard errors (SSE) and combined L1 and L2 (α) in order to minimize both the standard error and model complexity.

For each species, this method conducted iterative fitting along a regularization path, using 100 values of α and 22 values of ρ (ranging from 0.01 to 0.99) in order to determine the optimal balance between minimizing error vs. model complexity and between L1 and

L2 penalization. The optimal model coefficients were then selected using 25-fold cross-validation. For the seven species for which sufficient in situ data were also available from the USA-NPN database to model FD, the same method was used to develop models using in situ observations. The R^2 values of these models (i.e., their explanatory power) were then compared to those based on the herbarium-based data representing the same seven species.

2.8 | Evaluating the predictive capacity of models derived from herbarium collections and in situ observations

The R^2 value for each model is the mean of the 25 iterations in which it was trained and tested using separate datasets; this value was considered to represent the capacity of each phenological model to predict the timing of FD for a given species under novel conditions that were not included in the training data set. Using the seven species for which sufficient data were available to construct models using both herbarium collections and in situ phenological observations, we then compared the predictive capacity (i.e., the R^2 values) of the models constructed using herbarium records vs. in situ observations using paired sample *t* tests in SPSS.

2.9 | Relationship of sampling intensity to model complexity and to predictive capacity

In order to determine whether the number of specimens analyzed for each species influenced the complexity or predictive power of the resulting phenological model, we conducted two linear regressions among all species. In each regression, the number of herbarium specimens was the independent variable and the dependent variable was either (a) the number of parameters with nonzero coefficients in each phenological model (which we considered to be an estimate of its complexity) or (b) the predictive capacity (as measured by the cross-validated R^2) of each phenological model.

2.10 | Importance of each type of climate parameter in predicting flowering phenology

For each species represented by herbarium data, the importance of each type of climate parameter (i.e., TMAX, TMIN, NFFD, BFFP,

EFFP, MAT, MCMT, PPT, PAS, or TAP) for predicting FD was estimated based on the R^2 values of parameter-specific phenological models (Table 1). These models were constructed using a series of multiple regressions in which only those variables associated with a given type of climate parameter (e.g., TMAX, etc.) were included as independent variables in a given model; in all cases, the DOY of collection was the dependent variable. In the case of climate parameter types that were measured across multiple reference periods, the value of that of parameter in each time period within which it was measured was included in the model as an independent variable, with the exception of season-specific variables (i.e., values for the selected type of climate parameter within each season, such as TMAX_{winter}, TMAX_{spring}, etc.) that were not retained in the overall model. For example, the assessment of each type of parameter (e.g., TMAX) included up to five distinct variables: the mean value during the autumn of the previous year, and the mean value during the winter, spring, summer, and autumn of the year in which flowering occurred. For each species, the conditions during any season(s) experienced after its mean flowering date were always excluded. Using elastic net regularization, each regression was conducted using 25-fold cross-validation, and the overall predictive power of each model was calculated using the mean R^2 of all iterations.

Prior to testing for significant differences among the 10 distinct types of climate parameters listed above with respect to the mean R^2 values of the models that included them, we first tested for the homogeneity of variances of the R^2 values using Levene's test. As variances in the R^2 values of models constructed using each parameter type were found to be unequal ($F_{9,24670} = 591.013$, $p < 0.01$), the mean R^2 of models constructed using each of the 10 types of climate parameters evaluated in this study were then compared following a nonparametric ANOVA (with type of climate parameter as the independent variable) using Tamhane's T2 tests in SPSS. These parameter-specific models typically exhibited lower explanatory power than the overall models. This reduction in explanatory power is intentional, however, as these models were used to evaluate the relative importance of each type of climate parameter in explaining the observed phenological variation.

In order to evaluate the possibility that some parameters might be retained only rarely in the phenoclimate models, but have high explanatory power when included (such as the potential for precipitation as snow to be highly important for species inhabiting locations

TABLE 1 Types and purposes of regression models tested in this study

Model type	Climate parameters	Purpose	Example
Overall	All	Prediction of FD by all potential climate parameters	BFFP + Tmax _{winter} + Tmax _{spring} + Tmax _{summer} + Tmin _{winter} + Tmin _{spring} + Tmin _{summer} ...
Parameter-specific	All season-specific values of a single type of climate parameter	Determine the predictive power of each climate parameter on FD, independent of season	Tmax _{winter} + Tmax _{spring} + Tmax _{summer}
Reference period-specific	All climate parameters within a given season	Determine the predictive power of season-specific climate parameters on FD, independent of individual climate parameters	Tmax _{winter} + Tmin _{winter} + NFFD _{winter} ...

with high snowfall, but irrelevant in areas with little to no snowfall), we also calculated the number of species in which a given parameter exhibited a partial R^2 of more than 0.5, more than 0.3, more than 0.2, and more than 0.1.

2.11 | Importance of climate conditions during different reference periods

For each species represented by herbarium data, we constructed seven season-specific phenological models using elastic net regularization. Excluding those parameters that were not retained in the overall model, each model potentially included all types of climate parameter within one of the following reference periods: the autumn of the prior year; the winter, spring, summer, or autumn of the year in which flowering occurred; or, for those parameters that are inherently annual rather than seasonal in nature, the year in which flowering occurred or the year prior to flowering (Table 1).

As with previous models, each regression was conducted using 25-fold cross-validation, and the predictive power of each model was estimated as the mean R^2 of all iterations. The homogeneity of variances of the R^2 values among the seven distinct reference periods listed above was tested using Levene's test. As the variances in the R^2 values were unequal among reference periods ($F_{6,14802} = 1217.7$, $p < 0.01$), the mean R^2 values were then compared following a non-parametric ANOVA (with reference period as the independent variable) using Tamhane's T2 tests in SPSS. In order to determine the reference period that exhibited the greatest predictive power for the greatest number of species, we also calculated the number of species in which conditions during each reference period exhibited a partial R^2 of more than 0.5, more than 0.3, more than 0.2, and more than 0.1.

3 | RESULTS AND DISCUSSION

Models of flowering phenology can be produced using digitized herbarium records across a wide array of taxa, as phenological models of FD derived from herbarium data explained an average of 27% of the variance in FD among observations not used in model construction, with models for 1,514 taxa explaining over 20% of observed variance, and models for 494 taxa explaining <10% of observed variance (Figure 2). The predictions of FD based on herbarium specimens were as accurate as those produced based on in situ observations; no significant difference was detected in the mean explanatory power (R^2) of phenoclimatic models constructed using herbarium records vs. in situ observations ($t = -0.765$, $df = 6$, $p = 0.474$, Figure 3, Supporting Information Table S3). Similarly, the complexity of the phenological models constructed using herbarium vs. in situ observations did not differ significantly, as represented by the number of variables selected for model inclusion ($t = -0.525$, $df = 6$, $p = 0.619$). Further, phenological models constructed using herbarium and in situ observations selected or excluded the same climate parameters 79% of the time on average (Supporting Information Table S4). No significant differences in the mean values of the regression coefficients for each climate parameter were detected between the phenoclimatic models

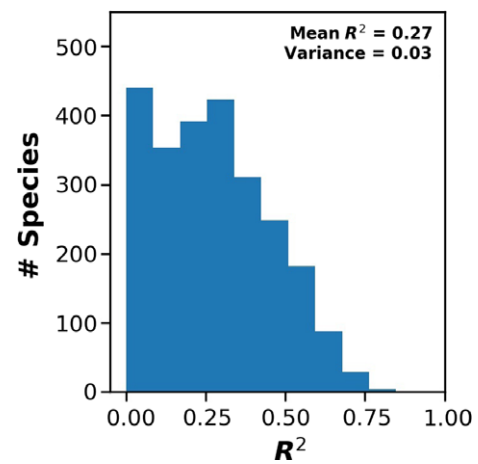


FIGURE 2 Distribution of cross-validated R^2 values of all phenoclimatic models derived from herbarium data using elastic net regularization ($n = 2,468$ taxa, Table S2)

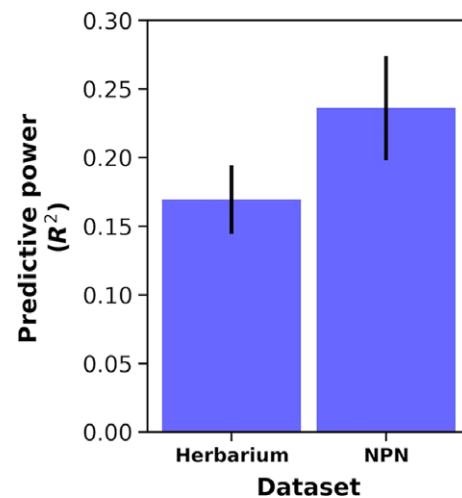


FIGURE 3 Cross-validated R^2 values among phenoclimatic models independently constructed using digital records of herbarium collections and in situ estimates of FD provided by the USA National Phenology Network's database (NPN). Vertical black lines indicate standard errors. Each set of phenoclimatic models evaluated seven distinct taxa

constructed using herbarium-derived vs. repeated in situ phenological observations (Supporting Information Table S5).

The number of observations required to construct such models also appears to be comparatively small, as extremely low correlations were detected between sample size and model accuracy when considering species represented by 100 or more herbarium specimens ($R^2 \leq 0.01$, $df = 2,467$, $p < 0.01$, Figure 4a). Similarly, the relationship between sample size and model complexity was also very low ($R^2 = 0.03$, $df = 2,467$, $p < 0.01$, Figure 4b), indicating that limited specimen availability does not overly restrict the complexity of the resulting models. Herbarium-based phenological models incorporated a mean of 9.38 climate parameters (Figure 5a), and increased model

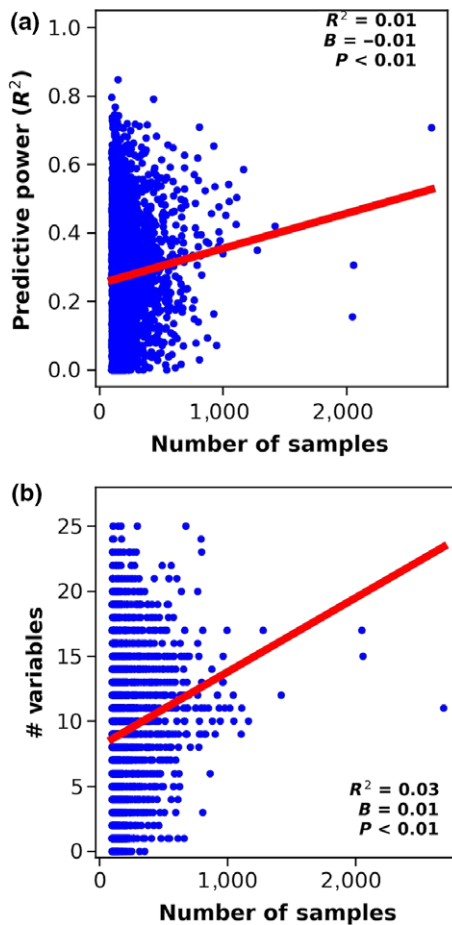


FIGURE 4 Sensitivity of model R^2 and model complexity to sample size, estimated from the linear relationship between the number of digital herbarium records available for each species and (a) the predictive power (represented by cross-validated R^2 values) or (b) the complexity (measured as the number of climate parameters with nonzero coefficients) of the associated phenoclimatic model for that species. Points represent the explanatory power and model complexity of the phenoclimatic models associated with each species. Each species is represented by one model (selected by the elastic net regularization approach). Solid lines represent significant linear relationships. $n = 2,468$ taxa in both analyses

complexity was associated with moderate increases in predictive power ($R^2 = 0.23$, $df = 2,467$, $p < 0.01$; Figure 5b). Variation among species in the mean temperature of collection sites, the breadth of their climate envelope, the mean latitude of the collection sites, or the number of years across which they were observed played a minimal role in determining the predictive power of the resulting phenoclimatic models ($R^2 < 0.03$ in all cases, Supporting Information Table S6).

3.1 | Importance of climate parameters to the prediction of FD

Parameter-specific climatic models differed significantly with respect to their mean explanatory power (Supporting Information Table S7).

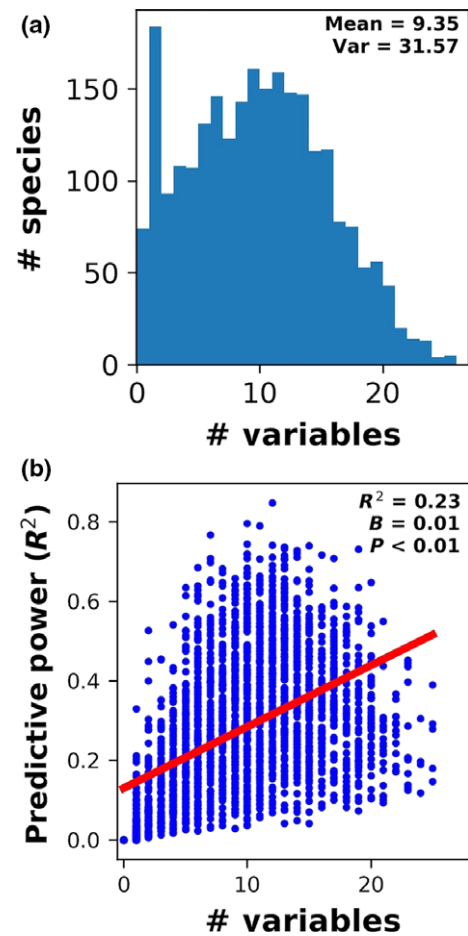


FIGURE 5 Summary of elastic net regularization models across all species and selected models. Frequency distribution of the number of climate parameters with nonzero coefficients among all phenoclimatic models constructed from digital records of herbarium collections (a); relationship between the explanatory power (represented by cross-validated R^2) of phenoclimatic models for each species and the number of climate parameters with nonzero coefficients (b). Each point represents the phenoclimatic model that was developed for a single taxon. The solid line represents the linear relationship between the predictive power of each model and the number of explanatory variables included in it. $n = 2,468$ taxa in both analyses

Among phenoclimatic models that included only a single type of climate parameter, significant differences were detected in the mean R^2 value of models corresponding to different types of climate parameter ($F = 315.51$, $df_1 = 9$, $df_2 = 24,679$, $p < 0.01$, Supporting Information Table S7). Similarly, models corresponding to different reference periods differed significantly with respect to their mean explanatory power ($F = 848.00$, $df_1 = 5$, $df_2 = 14,807$, $p < 0.01$, Supporting Information Table S8).

Temperature-related parameters were the primary contributors to the predictive capacity of phenoclimatic models. Of these, the most powerful predictors of FD across the 2,468 taxa evaluated in this study were the number of frost-free days (NFFD), the mean maximum temperatures (TMAX), and the quantity of precipitation that fell as snow in the seasons preceding flowering (PAS). NFFD

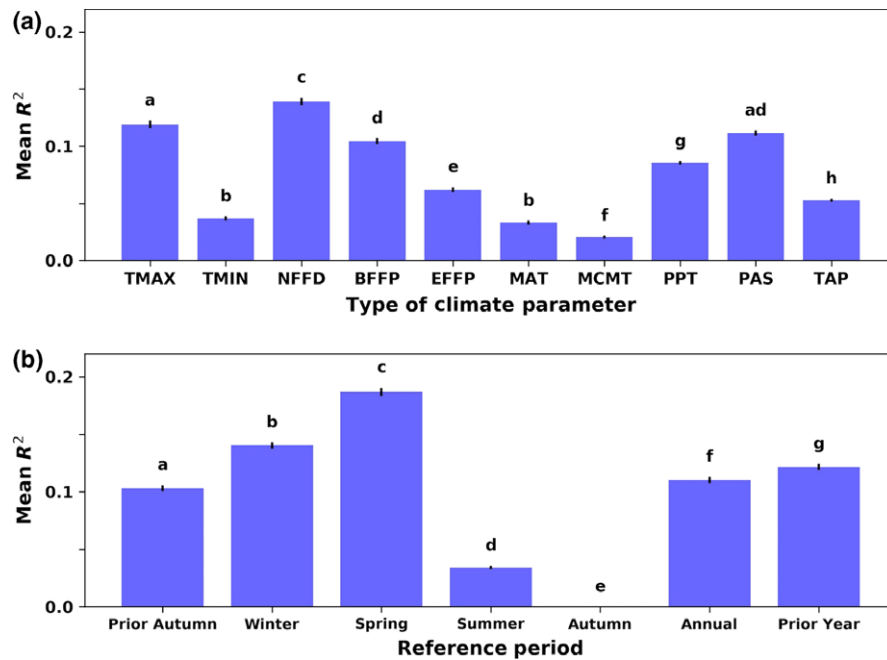


FIGURE 6 Mean predictive power (R^2) associated with each type of climate parameter (a), and with conditions during each reference period (b) in predicting the FD of all taxa included in this analysis and represented by herbarium records ($n = 2,468$ species), as derived from species-specific linear regression analyses conducted using 25-fold cross-validation. Climate parameters consisted of maximum mean seasonal temperature (TMAX), minimum mean seasonal temperature (TMIN), seasonal number of frost-free days (NFFD), date of the beginning of the annual frost-free period (BFFP), date of the end of the annual frost-free period during the prior year (EFPF), mean annual temperature of the prior year (MAT), mean temperature of the coldest month (MCMT), seasonal total precipitation (PPT), seasonal precipitation as snow (PAS), and total annual precipitation of the previous year (TAP). Vertical black lines indicate standard errors of the associated mean. Within each panel, letters that are shared between bars indicate groups that do not differ significantly with respect to their mean R^2 value, based on Tamhane's T_2 tests

TABLE 2 Mean predictive power (R^2) associated with each type of climate parameter and reference period

	Mean predictive power (R^2)	Standard deviation of predictive power
Parameter type		
TMAX	0.12	0.17
TMIN	0.04	0.09
NFFD	0.14	0.16
BFFP	0.10	0.14
EFPF	0.06	0.11
MAT	0.03	0.10
MCMT	0.02	0.06
PPT	0.09	0.08
PAS	0.11	0.12
TAP	0.05	0.07
Reference period		
Prior autumn	0.10	0.13
Winter	0.14	0.14
Spring	0.19	0.18
Summer	0.04	0.08
Autumn	0.01	0.01
Annual	0.17	0.15

explained a mean of 14% of the variance in FD across species (Figure 6a, Table 2). TMAX explained 12% of the variance in FD, and PAS explained 11% of observed variance in FD. By comparison, TMIN, which has commonly been used in phenoclimate models (Bertin, 2015; Mohandass, Zhao, Xia, Campbell, & Li, 2015; Munson & Long, 2017; Munson & Sher, 2015; Rawal et al., 2015; Robbirt, Davy, Hutchings, & Roberts, 2011), exhibited less than a third of the predictive power of NFFD on average (Figures 6a, 7a and Table 2). NFFD and TMAX, which were highly correlated, were likely the best predictors due to the fact that flowering time across many species has been associated with spring warming. PAS, on the other hand, may be a reliable proxy for the date of snow melt, which has been shown to be highly tied to flowering times for some species that occupy habitats with substantial winter snow cover (Inouye & McGuire, 1991).

When winter-, spring-, and summer-flowering species were examined separately, three patterns emerged. First, the relative importance of each type of climatic parameter and season was largely similar among spring and summer-flowering species. For these species, Tmax and NFFD are the variables that most strongly affect flowering date. Second, the models applied to spring-flowering species exhibited higher predictive power than those applied to summer-flowering species (Supporting Information Figure S2 and S3). Third, winter-flowering species exhibited more similar R^2 values

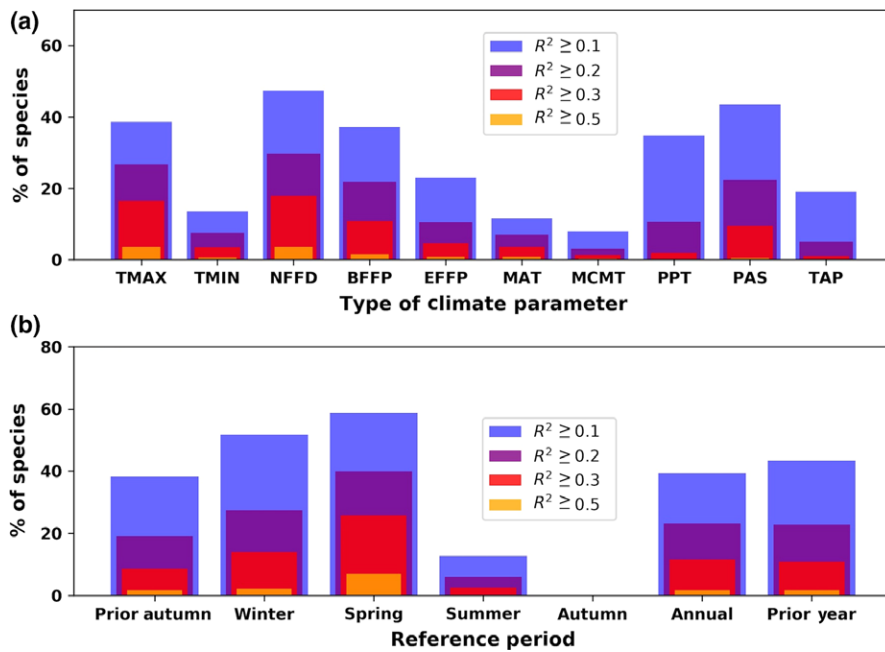


FIGURE 7 Percentage of the 2,468 plant taxa among which the predictive power (R^2) of each species' parameter-specific (a) or reference period-specific (b) model exceeded 0.1, 0.2, 0.3, or 0.5 for each type of climate parameter. Climate parameters consisted of mean maximum seasonal temperature (TMAX), minimum mean seasonal temperature (TMIN), seasonal number of frost-free days (NFFD), date of the beginning of the annual frost-free period (BFFP), date of the end of the annual frost-free period during the prior year (EFFP), mean annual temperature of the prior year (MAT), mean temperature of the coldest month (MCMT), seasonal total precipitation (PPT), seasonal precipitation as snow (PAS), and total annual precipitation of the previous year (TAP)

across all climate parameters and seasons than the spring- and summer-flowering species (Supporting Information Figure S2 and S3).

Interestingly, a survey of phenological studies published over the past 3 years (representing 35 individual studies, Supporting Information Table S9) found no cases in which the number of frost-free days was included in the construction of phenological models, indicating that this parameter has largely been overlooked. Similarly, this survey detected no papers that included PAS in the phenological models. Snow melt dates, which likely represent a similar aspect of climate, have been used in previous examinations of phenology in alpine (Wipf, Stoeckli, & Bebi, 2009), subalpine or montane (Dunne, Harte, & Taylor, 2003; Forrest, Inouye, & Thompson, 2010; Inouye, 2008; Inouye & McGuire, 1991; Price & Waser, 1998), and arctic environments (Bjorkman, Elmendorf, Beamish, Vellend, & Henry, 2015; Cooper, Dullinger, & Semenchuk, 2011; Mortensen, Schmidt, Høye, Damgaard, & Forchhammer, 2016; Wheeler, Høye, Schmidt, Svenning, & Forchhammer, 2015). This study, however, indicates that PAS should be considered in phenological models of taxa that occupy a much wider range of climate regimes. Increases in NFFD and TMAX were typically associated with advances in flowering, while increases in PAS were associated with delays in flowering (Supporting Information Table S10).

3.2 | Importance of reference period to the prediction of FD

When considered across all species, climate conditions during spring exhibited higher mean explanatory power than conditions during any other season, explaining a mean of 18.8% of the observed variance in FD (Figure 6a). Annual climate conditions explained a mean of 17% of the variance in FD, while conditions during the preceding winter explained only 14% of the variance on average, and conditions during the prior autumn explained a mean of 10% of the

variance. Thus, it appears that annual or winter conditions are weaker predictors of FD than conditions during spring (Figures 6b and 7b). Climate conditions during spring were also found to exhibit higher explanatory power than any other reference period among both spring- and summer-flowering species. Among winter-flowering species, however, climate conditions during the prior year were found to exhibit the highest explanatory power (Supporting Information Figure S3).

4 | CONCLUSIONS

Collectively, this study demonstrates that herbarium datasets can be used to produce powerful models for the prediction of flowering date across a vast array of species and that the sample size required to develop phenological models is easily achieved. Further, this study demonstrates that elastic net regression is a powerful tool for the design of phenoclimatic models, and that some of the most important climate parameters for the prediction of phenological variation, such as the number of frost-free days, the quantity of snowfall, and the date of the beginning of the frost-free period, are in fact climate parameters that have largely been overlooked in the construction of phenoclimatic models. This study also demonstrates a scalable method for modeling phenoclimatic variation across a large number of species and represents a powerful new approach for assessing the relationship between recent climatic conditions and flowering phenology. Future work will leverage these methods to evaluate whether systematic differences exist in the phenological responses of angiosperm taxa that exhibit different growth forms, to evaluate the degree of phylogenetic conservatism in the phenological responsiveness of angiosperm taxa, to measure the degree to which the timing of phenological events has changed over time, and to evaluate the degree to which future climate changes are likely to disrupt or enhance synchronies among historically coflowering taxa.

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SUPPORTING INFORMATION

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