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New Phytologist

Incorporating plant phenological responses into species distribution models reduces estimates of future species loss and turnover

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Received: *20 November 2023*
Accepted: *4 March 2024*

New Phytologist (2024) **242:** 2338–2352
doi: 10.1111/nph.19698

Key words: biodiversity, climate change, macroecology, phenology, species distribution models, species loss, species turnover, trait evolution.

Summary

- Anthropogenetic climate change has caused range shifts among many species. Species distribution models (SDMs) are used to predict how species ranges may change in the future. However, most SDMs rarely consider how climate-sensitive traits, such as phenology, which affect individuals' demography and fitness, may influence species' ranges.
- Using > 120 000 herbarium specimens representing 360 plant species distributed across the eastern United States, we developed a novel 'phenology-informed' SDM that integrates phenological responses to changing climates. We compared the ranges of each species forecast by the phenology-informed SDM with those from conventional SDMs. We further validated the modeling approach using hindcasting.
- When examining the range changes of all species, our phenology-informed SDMs forecast less species loss and turnover under climate change than conventional SDMs. These results suggest that dynamic phenological responses of species may help them adjust their ecological niches and persist in their habitats as the climate changes.
- Plant phenology can modulate species' responses to climate change, mitigating its negative effects on species persistence. Further application of our framework will contribute to a generalized understanding of how traits affect species distributions along environmental gradients and facilitate the use of trait-based SDMs across spatial and taxonomic scales.

Introduction

The geographic distribution of species is strongly influenced by climate (Parker, 1963; Whittaker, 1975; Kelly & Goulden, 2008). As global anthropogenic change intensifies, a better understanding of the abiotic and biotic factors that shape species distributions at large geographic, temporal, and taxonomic scales is urgently needed to forecast species' future range shifts and their associated consequences for regional and global biodiversity patterns. Species distribution models (SDMs) are the primary tool used to make these forecasts. Species distribution models apply associations between the known occurrences of individual species and co-incident environmental variables, such as temperature and precipitation, to model current species distributions and forecast future ones (Thomas *et al.*, 2004; Daru & Rock, 2023; Mi *et al.*, 2023).

Despite their widespread use and ease of application, 'conventional' SDMs are based solely on abiotic (especially climatic) factors (i.e. the 'fundamental' niche, *sensu* Hutchinson, 1957). Conventional SDMs thus ignore important functional traits and biotic interactions that also may modulate species persistence and fitness through a variety of mechanisms (Rosenzweig, 1987; Westoby & Wright, 2006; Benito Garzón *et al.*, 2019). Although some studies have incorporated biotic traits into SDMs (Pollock *et al.*, 2012; Bosch-Belmar *et al.*, 2021), such 'trait-based' SDMs still have not been adopted widely. Moreover, most existing trait-based SDMs require additional process-based approaches that explicitly model physiology (Higgins *et al.*, 2012), climate-dependent phenology (Chuine & Beaubien, 2001; Morin *et al.*, 2009), or demography (Treurnicht *et al.*, 2016). They also usually require detailed mechanistic information linking trait variation and fitness, precluding analysis of less-studied taxa for which such information may not be available, and consequently, limiting the generality of inferences regarding predicted and forecasted species distribution patterns across space, time, and taxa (Chuine & Beaubien, 2001; Evans *et al.*, 2016). Recently developed hierarchical trait-based SDMs that directly integrate functional traits do not require the complex parameterization necessary for earlier process-based models and hold tremendous promise for forecasting more general responses across broad spatial and taxonomic scales (Pollock *et al.*, 2012; Vesk *et al.*, 2021). However, to our knowledge, hierarchical trait-based SDMs implemented to date are limited in two ways. First, they normally use a single trait value for each species and ignore intraspecific differences, which represents an important component of trait variation. Second, they have not accommodated the potential for intraspecific changes in the expression of these traits resulting from spatial and temporal shifts in abiotic conditions, such as those predicted to occur as the climate continues to change.

In general, intraspecific variations can be generated through many mechanisms including phenotypic plasticity and local adaptation (Violle *et al.*, 2012). Plasticity traits can respond rapidly to environmental changes and are the result of when one genotype expresses different phenotypes across environmental gradients (Nicotra *et al.*, 2010). Local adaptation is the result of selection where genetically distinct populations of a species are adapted to specific environmental conditions (Savolainen *et al.*, 2013). Plasticity and adaptation are critical in shaping geographic variation in functional traits across the species range (Savolainen *et al.*, 2013; Valladares *et al.*, 2014). To improve the generality of trait-based SDMs and accommodate climate-driven changes in trait expression, we developed a new trait-based SDM that directly incorporates both intraspecific variation in traits and their dynamic response to climate change. Specifically, our method simultaneously models historical data linking traits, climate, and species distributions to forecast where and when climatically suitable areas will exist for focal species (Fig. 1). We tested the utility of our model using a key component of life-history: phenology – the timing of recurrent life-history events such as leaf-out and senescence, budding, flowering, and fruiting. The timing of any of phenological events may respond to climate and ongoing climate change, determine the exposure of reproductive structures to potentially stressful abiotic conditions, influence the ability of a species to capture resources, and affect its interactions with other species (Elzinga *et al.*, 2007; Meineke *et al.*, 2021).

Survival and reproduction often depend on the timing of life-cycle events (Forrest & Miller-Rushing, 2010). Consequently, flowering/fruiting time is often subject to natural selection, especially in temperate regions (Munguia-Rosas *et al.*, 2011), and may have a strong effect on individual fitness in wild populations (O'Neil & Schmitt, 1997). Moreover, phenological shifts resulting from climatic change could be the primary factor limiting species' distributions in some ecosystems (Chuine, 2010; Hereford *et al.*, 2017). Phenology also can exhibit substantial intraspecific variability as a function of climatic variation across a species range (Park *et al.*, 2019; Love & Mazer, 2021). Such intraspecific variability remains unexplored for most species but may confer resilience and increase individuals' fitness under changing climates (Richardson *et al.*, 2017; Benito Garzón *et al.*, 2019).

Our overarching goal was to create a trait-based framework for a SDM and use it to integrate phenological responses into forecasts of plant species range shifts in response to ongoing climatic changes (Fig. 1). We applied our new phenologically informed trait-based SDM to a dataset of > 120 000 herbarium specimens that includes nearly 400 000 phenological observations (i.e. of buds, flowers, and fruits) from 360 plant species growing in the eastern United States (i.e. from Maine to Florida and westward to West Virginia and Georgia). We then used this trait-based SDM to predict changes in species ranges and regional biodiversity as a function of future climate change scenarios.

Specifically, we: modeled relationships between climate and phenology to estimate the phenological responses of individual species to varying climatic factors; validated the modeling approach using hindcasting; forecast the range of each species under current and future environmental conditions; and compared the results of our phenologically informed trait-based SDM with those generated by conventional SDMs. The results illustrate whether and how phenology shapes species' distributions along environmental gradients, and how phenology may modulate species' responses to ongoing and future climate change. Importantly, although the analyses in this paper focused on phenology, our SDM can incorporate any fitness-related functional traits that covary with abiotic factors across space, time, and taxa.

Materials and Methods

Species selection and phenological data collection

We used specimens from two of the most comprehensive digitized regional floras in the world: the Consortium of Northeastern Herbaria (CNH, https://neherbaria.org/portal/) and the Southeast Regional Network of Expertise and Collections (SERNEC, https://sernecportal.org/portal/). We selected species and specimens for analysis when: there were at least 50 unique collections of the species across space and time in the eastern United States; the specimens included both an exact collection date and at least county-level location information; and the specimens had easily identifiable and quantifiable buds, flowers, and fruits. Applying these criteria yielded 124 847 total herbarium specimens representing 360 species that we used in our models and analyses. These species vary in life history, growth form, and native status (i.e. native or not to the eastern United States; see details in Supporting Information Table S1). Information on species' growth form and native status was derived from the United States Department of Agriculture PLANTS Database (https://plants.isda.gov/).

Phenological data extraction

Crowdsourcers hired through Amazon's Mechanical Turk service (MTurk; https://www.mturk.com/) counted the number of each type of structure (i.e. buds, flowers, and fruits) present on each specimen using the CrowdCurio platform (Willis *et al.*, 2008). Each specimen was scored independently by at least three crowdsourcers. We estimated the reliability of each crowdsourcer and their data following Park *et al.* (2019). Specifically, each 10-image set scored by one person included nine unique images and one duplicate image randomly selected from the other nine. The nine images plus the duplicate image were

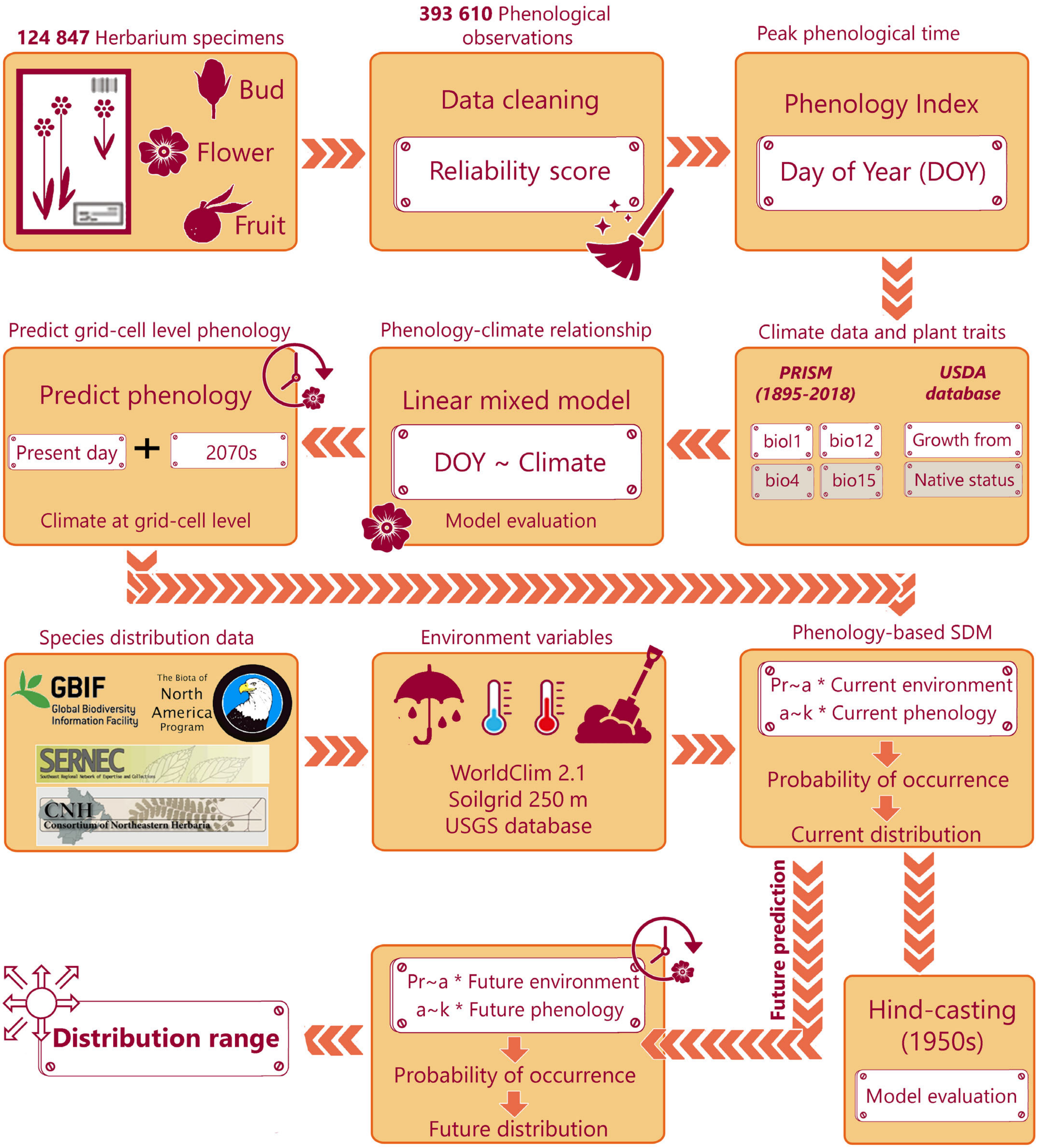

Fig. 1 Phenology-informed species distribution model (SDM) workflow. Predicted phenology (peak budding, flowering, and fruiting time (Day of Year, DOY)), ascertained from > 120 000 herbarium specimens and *c.* 400 000 phenological observations under both current and future climates, was estimated for each species in each grid cell based on species-specific phenology–climate relationships. We then built phenology-informed SDMs to test whether phenology mediates responses of individual plants to environmental gradients, and forecast species distributions and regional diversity under future climate scenarios. To validate model reliability, we hindcasted our model using historical data to project species distributions before 1950 and compared them with actual species distributions recorded before 1950.

presented to each crowdsourcer in a random order. We then calculated a reliability score for each crowdsourcer based on the data for each 10-image set. The absolute differences between the two duplicate specimens in counts of buds, flowers, or fruits, were separately divided by the total counts for each phenological state, and then subtracted from 1 (Eqn 1):

$$\text{Reliability} = 1 - \left(\frac{|\text{count1} - \text{count2}|}{|\text{count1} + \text{count2}|} \right) \qquad \text{Eqn 1}$$

The reliability score ranged from 0 (unreliable) to 1 (reliable). Specimen observations scored by crowdsourcers with a reliability score of zero were excluded from the analysis (Park *et al*., 2019). If an individual received a reliability score of zero for any phenological phase, the reliability scores for that individual's counts of the other phenological states were also set to zero (and similarly excluded from the analyses). Our final dataset included a total of 393 610 phenological observations spanning 124 yr (1895–2018).

We calculated the median number of buds, flowers, and fruits from the multiple phenological observations for each specimen. We then estimated the day of year (DOY) of 'peak' budding, flowering, and fruiting if their buds, open flowers, or fruits separately represented ≥ 50% of the total number of reproductive structures (Park *et al*., 2019). Two species each were excluded from the 'peak budding' category (*Primula mistassinica* and *Sarracenia rubra*) and the 'peak fruiting' category (*Calopogon barbatus* and *Narcissus poeticus*) because there were no specimens of these species at these developmental stages. Of the original 124 847 herbarium specimens, 29 094 specimens were scored as being at peak budding (representing 358 species), 55 767 specimens at peak flowering (representing 360 species), and 37 071 specimens at peak fruiting (representing 358 species).

Species distribution data

County-level species' distribution data were obtained from the Biota of North America Program's (BONAP; http://www.bonap.org/) North American Plant Atlas (NAPA; Kartesz, 2015; accessed November 2022). These data are available as binary occurrences (i.e. presence/absence) for 3067 counties in the United States, excluding Alaska and Hawai'i. We supplemented the species' distribution records from BONAP using additional data from the GBIF database (https://www.gbif.org) and all available specimen records in the CNH and SERNEC database. Most (≈70%) of these additional data points (i.e. GBIF + NH + SERNEC) represented specimens collected between 1960 and 2000. We then transformed county-level distribution maps into equal-area grid cells with a resolution of 40 × 40-km (see details in Methods S1).

Environmental data

Climatic data of specimen localities We extracted average monthly temperature and precipitation data (1895–2018) at a 4-km resolution from Prism (product AN81m, http://prism.oregonstate.edu/) to characterize the climate of the locality where and when each specimen was collected. Following Park *et al.* (2022), we used the climatic data for the county centroid if precise coordinate data were not available for historical specimen records. Previous studies found that within-county climatic variation had little effect on estimates of phenological response in the eastern United States (Park & Davis, 2017). Based on the extracted monthly temperature and precipitation data, we estimated annual mean temperature (abbreviation in Worldclim: bio1), temperature seasonality (bio4), annual precipitation (bio12), and precipitation seasonality (bio15) for each locality–year combination and assigned these values to corresponding specimens. These climatic variables have been shown to be strongly associated with plant budding, flowering, and fruiting times (Park *et al*., 2019; Li *et al*., 2021). Although these variables are calculated over periods over which ephemeral species might not be present, spatiotemporal variation in mean annual climatic conditions tends to be correlated with variation of narrower seasons within a year ($r > 0.7$). Therefore, these variables may capture climatic variation relevant to all species.

Environmental data used for modeling species' distributions 'Recent' (1970–2000) and future (2061–2080; henceforth referred to as '2070s') climatic data at 2.5-arc-minute (*c.* 5-km) resolutions were obtained from WorldClim (https://www.worldclim.org/, v.2.1; all 19 climatic variables: bio1–bio19; Table S2). Elevation data with a 30-arc-seconds spatial resolution (*c.* 1-km) were obtained from the US Geological Survey. We also included five soil variables – sand content, clay content, silt content, bulk density, and coarse fragments – because previous studies have demonstrated that soil structure may improve the fit of SDMs (Figueiredo *et al*., 2018). We calculated the mean values of each of these soil variables at two soil depths (0–5 and 5–15 cm) using soil data from the SoilGrids250m database (https://www.soilgrids.org/) and assumed that these values would be constant through time. We did not include soil chemical variables that may be highly temporally variable. The values for climate, soil, and elevation data assigned to each 40 × 40-km grid cell were the means of all data points within it.

Future climatic projections were derived from the general circulation models (GCMs) used by the Coupled Model Intercomparison Project Phase 6 (Eyring *et al*., 2016; CMIP6) for four Shared Socio-economic Pathways (SSPs). We used the most extreme, SSP5-8.5 projections, which have similar 2100 radiative forcing levels as its predecessor (i.e. Representative Concentration Pathway: RCP 8.5). To account for potential uncertainties in projections induced by different GCMs, we forecast future species distributions using six different GCMs: ACCESS-CM2, CMCC-ESM2, GISS-E2-1-G, HadGEM3, INM-CM4-8, and MIROC6.

Statistical modeling

Relationships between climate and phenology We first applied linear mixed models (LMMs) to all herbarium specimens pooled across the 360 species to identify species-specific relationships between plant phenology and climatic variables. Separate but identically structured models were built for peak budding, flowering, and fruiting. For each full model, we used the DOY for the phenological state recorded for each specimen as the response variable. Predictor variables in the full model included: the year of specimen collection, four bioclimatic variables (annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality; all centered and scaled), two species-level plant traits (growth form and native status), and their two-way interactions (bioclimatic variables × Growth form; bioclimatic variables × Native status) as fixed terms. The full model also included the species and sampling locations as random effects for the intercept, and species as a random effect for the slope for each of the environmental variables. The eight interaction terms between native status or growth form and climate indicated whether the effect on phenology of each of the four climatic variables depended on growth form or native status. We did not find obvious nonlinear relationships between DOY and any climatic variables in the preliminary analysis for most species, so we did not include quadratic terms in our models.

All models were fitted using the 'lmer' function in the LMERTEST package (Kuznetsova *et al.*, 2017; v.3.1-2) of the R software system (v.4.2.1). The significance of the predictor variables' effects in mixed effects models was evaluated using the *z* distribution to obtain *P*-values from the Wald *t*-values provided by the model output (Luke, 2017). We also checked residuals of all models to ensure that all assumptions were met and used Moran's *I* to confirm that there was no evidence of spatial autocorrelation. No models showed significant spatial autocorrelation ($P > 0.05$). To predict the peak budding, flowering, and fruiting date of each current and future species grid-cell combination, we used the 'predict' function in the base STATS package (v.4.0.0) with fits of the models previously described and the estimated values of recent and future bio1, bio4, bio12, and bio15 of each grid cell. We further checked our model with phylogenetic LMM to examine whether our results were affected by phylogenetic relationship among species (see Methods S2 for details in construction of phylogenetic tree and Methods S3 for phylogenetic linear model; Tables S3–S6). We found no substantial differences in the results between the LMMs described above and those that accounted for phylogenetic relationships.

Constructing phenology-informed SDMs We quantified how peak budding, flowering, and fruiting dates (DOY) separately influenced the effects of environmental change on the species' probability of occurrence. All Worldclim bioclimatic variables may affect plant distributions, and these variables are often highly correlated. To avoid model overfitting, we first divided the 19 WorldClim environmental variables and the five soil variables into four groups (Table S2): mean temperature (bio1, bio5, bio6, bio8, bio9, bio10, and bio11); mean precipitation (bio12, bio13, bio14, bio16, bio17, bio18, and bio19); climatic fluctuation (bio2, bio3, bio4, bio7, and bio15); and soil variables. Principal component analysis (PCA) was then used to reduce the dimensionality of each group using the 'prcomp' function from the STATS package (v.4.0.0). In the subsequent analyses, we used either one or two principal component scores (PCs) as predictor variables in our models (see Methods S4; Fig. S1). Elevation was also included as a predictor variable. Our final phenology-informed SDMs kept elevation, the aforementioned seven PCs (i.e. one PC for temperature, and two PCs for each of other environmental group) and the predicted grid-cell level phenology, all of which were weakly or moderately correlated ($|r| < 0.7$; Table S7).

We used generalized linear mixed models (GLMMs) as the framework for our phenology-informed SDM (Pollock *et al.*, 2012). We fitted GLMMs using restricted maximum likelihood (REML) with the R package LMER4 (Nakagawa & Schielzeth, 2013; v.1.1-27). We fitted a random intercept, random slope binomial model with a logit link function to species × grid cell presence/absence data (Eqns 2–5).

$$\Pr\left(Y_{ij}=1\right)=\operatorname{logit}^{-1}\left(a_{[i]}+S_{k[i]}\times \text{Environment}_{jk}\right) \qquad \text{Eqn 2}$$

In this base model, the logit probability that species *i* occurs at the *j*th of 1, 2, 3, …, 1158 grid cells is equal to an intercept term plus the product of a matrix of eight environmental variables (7 PCs and elevation; Environment_{jk}) and a vector of eight coefficients ($S_{k[i]}$). Here, *k* represents environmental variables. The parameters $a_{[i]}$ and $S_{k[i]}$ differed among species:

$$a_{[i]} \sim \text{Normal}\,(\mu,\sigma) \qquad \text{Eqn 3}$$

The submodel for $a_{[i]}$ includes the parameter μ, which represents the average probability of occurrence (on a logit scale) among species within a hypothetical grid cell, and the parameter σ, which is the degree to which a given species departs from average probability of occurrence. The parameter $S_{k[i]}$ indicates the response of a given species to the relevant environmental variables.

$$S_{k[i]}=B_{k[i]}+C_k\times \text{Phenology}_{[i]} \qquad \text{Eqn 4}$$

In the submodel for $S_{k[i]}$, its estimate is calculated as the intercept $B_{k[i]}$ plus the coefficient matrix C_k and matrix of trait values $\text{Phenology}_{[i]}$. $\text{Phenology}_{[i]}$ is measured as the day of year (DOY). The intercept $B_{k[i]}$ is modeled as:

$$B_{k[i]} \sim \text{Normal}\left(U_{[k]},\tau_{[k]}\right) \qquad \text{Eqn 5}$$

where $U_{[k]}$ indicates the average response of species to environmental variables and $\tau_{[k]}$ reflects the degree to which each species departs from the among-species average response. C_k describes how plant phenology regulates the probability of occurrence of an individual species in a certain environment (i.e. DOY × PC[*k*] interaction coefficients). For example, positive values of C_k suggest that a high value of DOY (i.e. later phenology) increases the probability of occurrence of a species under high values of the focal environmental variable. We also added species as a random component for the slope of occurrence vs environment, which allowed us to explore species-specific differences in responses to environmental variables. We also constructed conventional SDMs without phenological information (i.e. only Eqns 2, 3) to compare the results of phenology-informed and conventional SDMs. In conventional SDMs, we also included species as a random component.

To assess model performance, we calculated the conditional R^2 reflecting the total variance explained (Nakagawa & Schielzeth, 2013). We also calculated the area under the curve (AUC) with the pROC package (Robin *et al*., 2011; v.1.16.1). Area under the curve represents the predictive accuracy of the model and ranges from 0.5 to 1 (1 is the highest accuracy). We then converted the probability of occurrence of each species × grid-cell combination into binary maps. We adopted the threshold that maximized the specificity and the sensitivity, using the ROCR package (Sing *et al*., 2005; v.1.0-11). If the probability of a species occurrence in a given grid cell was higher than this threshold (Table S1), then the species was considered to be present in that grid cell.

Model validation through hindcasting To validate the reliability of our model, we created both phenology-informed SDMs and conventional SDMs using the distribution and phenology records collected between 1970 and 2022 for 57of annual herb species, and then hindcast the models using historical climatic data to project species distributions before 1950 (see Methods S5 for details of hindcasting).

Data analyses

We calculated three metrics that reflect potential changes in the areas suitable for species occurrence under future climate change (combining all GCMs): the proportion of the currently occupied range that is forecast to have high suitability in the future (i.e. range persistence; probability of occurrence > threshold); the proportion of the currently occupied range forecast to have low suitability (i.e. range retreat; probability of occurrence ≤ threshold); and the proportion of the currently unoccupied range forecast to have high suitability (i.e. range expansion). Present and future suitable areas were determined, respectively, from the number of grid cells in which a species currently occurs and the number in which it is forecasted to occur in the 2070s. To examine whether phylogenetic relationships explain the degree of predicted range preservation, expansion, or contraction among species, we calculated the proportion of each species' range persistence, range retreat, and range expansion and then tested for phylogenetic signal in these three traits using Blomberg's *K* (Blomberg *et al*., 2003) and Pagel's lambda (Pagel, 1999).

To assess the percentage of local extinctions for a given grid cell, we then examined the geographical patterns in the proportion of species loss based on the species' current and future distributions, which was calculated as the number of species lost (L) divided by the current species richness (S) of each grid cell (L/S). The same procedure was also applied to evaluate the proportion of species gain, which was calculated as the number of species gain (G) divided by the current species richness of each grid cell (G/S). Species gain was assessed under the assumption that species could colonize any new suitable climate space within the eastern United States and that their future distributions will not be limited by dispersal. The proportion of species turnover is then given by $T = (L + G)/(G + S)$. Relationships between the proportion of species gains, losses, and turnover as a function of different degrees of climate change (e.g. changes in mean annual temperature) were further explored to examine the stability of species composition under climate fluctuations. All these analyses were conducted separately for the conventional and phenology-informed SDMs. We then compared the changes in suitable areas and geographical patterns in species gains (losses and turnover) between conventional and phenology-informed SDMs.

To further explore the mechanisms underlying the phenological regulation of species distributions, we explored the relationship between seed size and phenology (see Methods S6).

Results

Plant phenological responses along climatic gradients

Key predictors of DOY of peak budding, flowering, and fruiting time included annual mean temperature, temperature seasonality, precipitation seasonality, and species' growth form (Table S8). The strongest climatic predictors for budding, flowering, and fruiting time were annual mean temperature and temperature seasonality, but their effects differed significantly among species with different growth forms. For example, holding other predictors constant, a 1-standard deviation (SD) increase in temperature (*c*. 5.3°C), would advance the budding time of herbaceous annuals by 8 ± 3.6 d (mean ± one standard error of the mean (SE)), of herbaceous perennials by 10 ± 3.2 d, and of woody plants by 10.0 ± 3.9 d (Fig. S2).

Moreover, plant seed size significantly decreased with mean flowering/fruiting time (flowering: slope = -4.46; $P < 0.001$; fruiting: slope = -2.473; $P = 0.03$).

Parameterizing phenologically informed SDMs

All GLMMs of plant distributions performed well, with an average explained deviance of > 90% (conditional R^2) and AUC of 0.932 (Table 1). Plant reproductive phenology had a strong modulating influence on the occurrence of plants along environmental gradients (i.e. significant interactions between phenology and environmental factors; Table 1), and the impacts of phenology on the responses of species to environmental conditions varied among environmental variables (Fig. 2; Table 1). In general, temperature was the most critical factor affecting phenology-mediated species distributions. Precipitation and altitude were also important factors, and these patterns were basically consistent among different phenophases. A positive value of standardized coefficient estimates associated with these interaction terms suggested that a higher value for DOY increased the probability of occurrence of species under a high value of a certain environmental variable (i.e. later DOY generated either less negative or

Table 1 Summary of phenology-informed species distribution models.

Phenological traits	Budding		Flowering		Fruiting	
	Z	P	Z	P	Z	P
Temperature PC1	−13.525	< **0.001**	−13.076	< **0.001**	−8.324	< **0.001**
Precipitation PC1	12.431	< **0.001**	11.066	< **0.001**	14.171	< **0.001**
Precipitation PC2	8.397	< **0.001**	5.608	< **0.001**	12.567	< **0.001**
Climate Fluctuation PC1	0.478	0.633	0.315	0.753	4.877	< **0.001**
Climate Fluctuation PC2	−2.829	**0.005**	−2.250	**0.024**	0.486	0.627
Soil PC1	−5.392	< **0.001**	−6.171	< **0.001**	−0.187	0.851
Soil PC2	−0.098	0.922	3.243	0.42	−1.885	0.059
Elevation	−7.348	< **0.001**	−9.643	**0.001**	2.092	**0.036**
DOY	4.162	< **0.001**	−1.162	0.245	−0.982	0.326
Temp PC1: DOY	21.981	< **0.001**	21.298	< **0.001**	15.164	< **0.001**
Precip PC1: DOY	−13.111	< **0.001**	−11.564	< **0.001**	−15.235	< **0.001**
Precip PC2: DOY	−12.352	< **0.001**	−9.558	< **0.001**	−16.507	< **0.001**
Clim Fluc PC1: DOY	4.848	< **0.001**	5.483	< **0.001**	−0.167	0.87
Clim Fluc PC2: DOY	2.115	**0.03**	1.175	0.24	−1.617	0.11
Soil PC1: DOY	6.324	< **0.001**	7.582	< **0.001**	0.82	0.41
Soil PC2: DOY	0.751	0.452	−3.210	**0.001**	2.896	**0.004**
Elevation: DOY	9.461	< **0.001**	12.365	< **0.001**	−1.03	0.30
Conditional R^2	0.917		0.912		0.913	
Marginal R^2	0.082		0.079		0.067	
AUC	0.917		0.946		0.946	

The various principal components (PCs) represent different environmental components and DOY refers to the Day of Year for peak budding, flowering, or fruiting time. Positive Z-statistics suggest that a high value for DOY increases the probability of occurrence of species under high values of the certain environmental variable. The ':' symbol in the phenological traits column represents an interaction between variables. Significant effects ($P < 0.05$) are given in bold. The area under the curve (AUC), conditional R^2, and marginal R^2 are calculated to assess model performance.

more positive relationships between probability of occurrence and a given environmental variable).

Specifically, the probability of occurrence within 40 × 40-km^2 grid cells of individual plants with earlier budding, flowering, and fruiting times decreased much more rapidly with increasing temperature than those with later phenology (Fig. 2). However, the probability of occurrence of individual plants with earlier budding, flowering, and fruiting times increased more rapidly with increasing precipitation than those with later phenology. Individual plants with later budding and flowering time were more likely to occur in areas with high-temperature seasonality than in regions with high precipitation seasonality. Phenology also mediated the effects of soil characteristics on species distributions. The negative relationship between the probability of occurrence and elevation was much stronger for earlier budding and flowering individuals than for those with later phenology. That is, plants with later-flowering (or budding) time have higher probability of occurrence at high elevations than earlier-flowering (budding) plants (Fig. 2; Table 1).

Hindcast validation of the phenology-informed SDM

Both conventional SDMs and phenology-informed SDMs exhibited good hindcasting performance. Specifically, an average of 74.5% and 73.8% of the distribution points of 57 annual herbs before 1950 fell within their predicted past range based on the phenology-informed and conventional SDMs, respectively (Fig. 3), suggesting that both models show relatively high accuracy.

Species distributions under future climate change

Projected range changes There were no obvious phylogenetic signals in the proportional change of suitable areas under the SSP5-8.5 scenario forecasted by both phenology-informed and conventional SDMs (Table S9), so our models did not include a phylogenetic correction. Using the phenology-informed SDMs, we forecast that ≈35% (mean value of all species) of the current occupied ranges of species would have low future suitability (range retreat), and ≈26% of the species would lose at least half of their existing suitable habitats in the future. By contrast, the conventional SDMs forecasted that ≈40% of the current occupied ranges would have low future suitability (Fig. 4a–d,e) and that ≈35% species would lose at least half of their existing habitats. Conventional and phenology-informed SDMs showed similar estimates of the species' current range (paired Wilcoxon test; $P = 0.25$) but significantly different estimates of the species future range ($P < 0.001$). Specifically, the average proportion of current areas forecasted to have high suitability (i.e. range persistence) based on the phenology-informed SDMs was significantly higher than that predicted by the conventional SDMs (Fig. 4a–d, f). By contrast, phenology-informed SDMs forecasted a 20% lower proportion of future occupying regions located outside their current range (i.e. range expansion) than the conventional SDMs (Fig. 4a–d,g; both differences significant at $P < 0.001$).

Geographic trends in regional species diversity At the grid-cell level, we calculated several metrics, including species gains, losses,

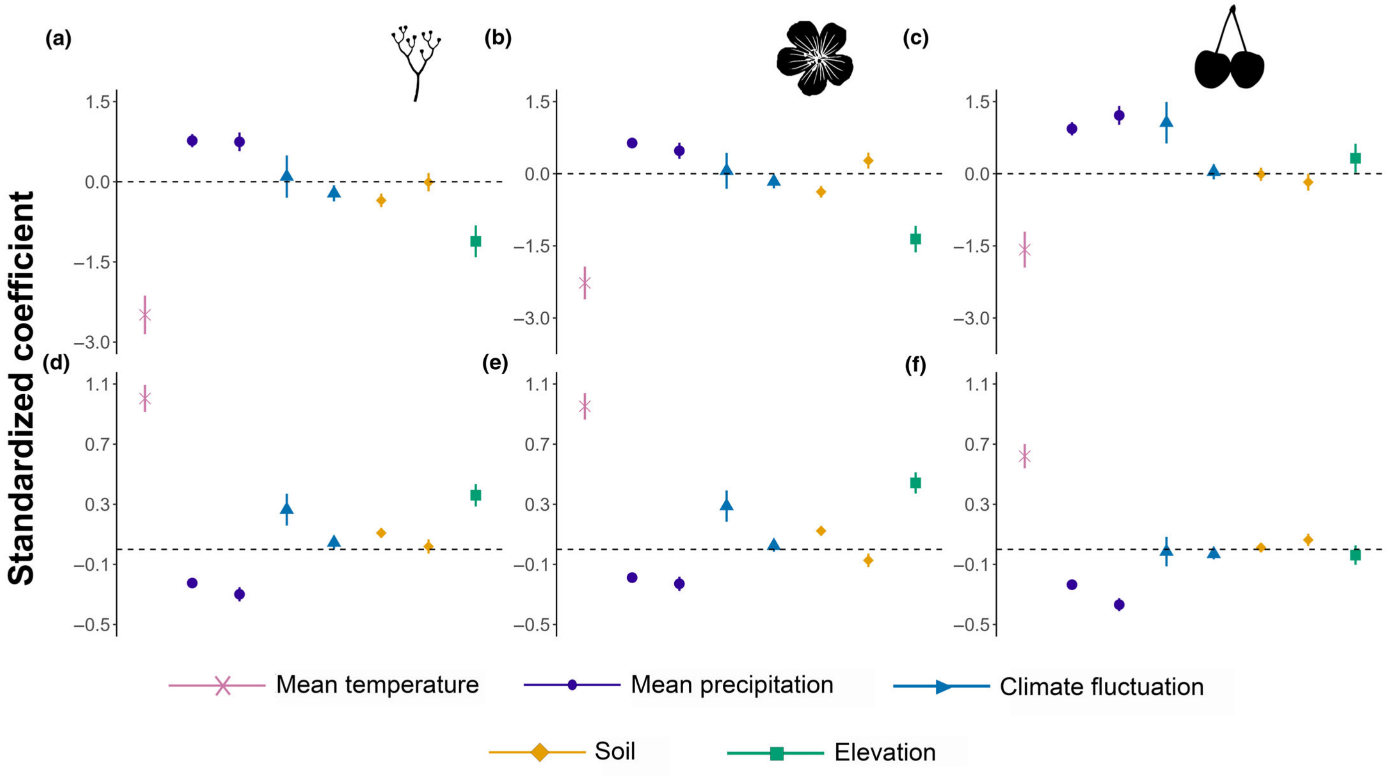

Fig. 2 Contribution of plant phenology to partial responses to environmental variables. Average standardized coefficient estimates among species indicating the main impacts of different environmental factors on species' probability of occurrence (a–c) and how phenology mediates average species response to environmental gradients or, alternatively, how environmental effects on the average probability of occurrence are influenced by phenology (i.e. interaction terms between plant phenology and environmental conditions; d–f). Positive coefficient values for the main effects indicate that probability of occurrence increases for higher values of the environmental variable, whereas negative values indicate the converse. Positive values of the interaction terms indicate that later phenology time (i.e. day of year, DOY) makes the relationship between occurrence and an environmental variable either less negative or more positive, respectively reflecting less severe decreases or higher increases in the probability of occurrence under higher values of the environmental variable. Negative values of the interaction terms indicate the opposite: later DOY leads to stronger decreases or less marked increases in probability of occurrence under higher values of an environmental values. We examined the effects on the probability of occurrence of the interaction between phenology and each of five classes of environmental attributes (mean temperature (one Principal Component, PC), precipitation (two PCs), climate fluctuation (two PCs), soil composition and structure (two PCs), and elevation). Phenology was quantified as the DOY for plant peak budding (a, d), flowering (b, e) and fruiting (c, f). Points and range bars represent among-species average standardized coefficient estimates with 95% confidence intervals (CIs). Standardized coefficient estimates were considered significantly different from one another if their 95% CIs did not overlap zero.

and turnover, which are commonly used in modeling future biodiversity. Spatial patterns in absolute species gains and losses were consistent across GCM scenarios (Figs S3–S5). In general, more gains in species were expected in Florida and the Atlantic coastal plain than in New England and parts of the Appalachian Mountains (Fig. S6). The forecast percentage of species losses exceeded 50% in the southern Coastal Plains, some portions of the Atlantic coastal plain, and the southern extent of the Appalachian Mountains. The combination of high species gains and high species losses in Florida and the Atlantic Coastal Plain was forecast to lead to high turnover rate in these regions (Fig. S6). Conventional and phenology-informed SDMs forecast similar spatial patterns in species gains, losses, and turnover. However, the two models diverge in the magnitude of these indices. Compared with conventional SDMs, phenology-informed SDMs forecast less species gains in Florida, but more species loss and turnover in the southern Coastal Plains, and the Atlantic coastal plain (Fig. 5a–c). We identified significant linear relationships among grid cells between the percentage of absolute species gains (and losses) and the magnitude of change in mean annual temperature. Relative to the conventional SDMs, the phenology-informed SDMs predicted relatively lower species gains when temperature increases were lower than 5°C but higher species gains at higher temperature increases (Fig. 5d). However, phenology-informed SDMs generally predicted stronger negative relationships between species losses (and turnover) and mean annual temperature increases than conventional SDMs (Fig. 5e,f).

Discussion

Species distribution models are widely used to assess the potential consequences of climate change for species' distributions (Urban, 2015). However, these models have been criticized for omitting critical biological components, including intraspecific phenotypic variation in functional traits, which may have important consequences for species fitness (Fordham *et al*., 2018) or for

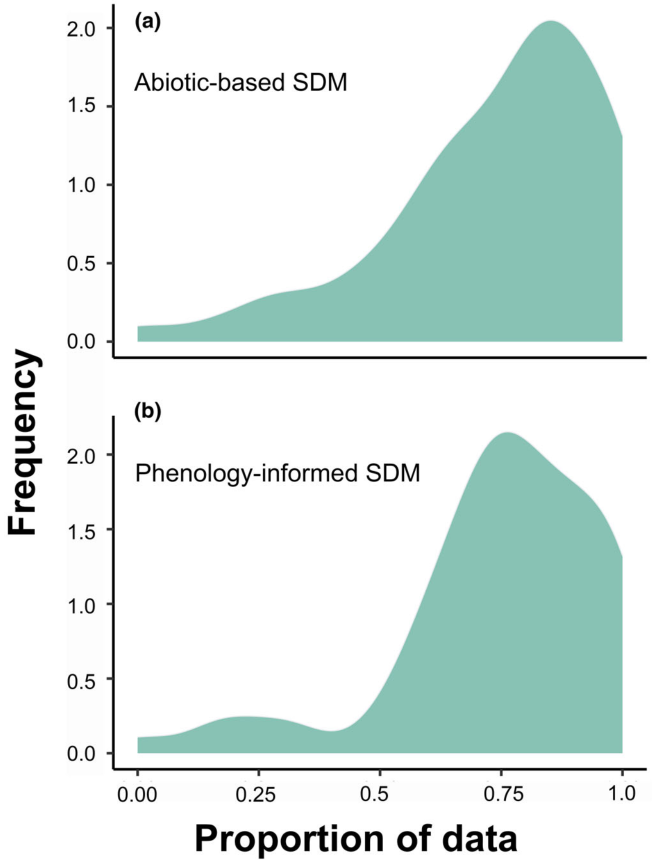

Fig. 3 Hindcasting distributions of annual herbs before 1950. Density plot showed the proportions of actual species distribution points that fell within the predicted ranges before 1950 by conventional abiotic-based species distribution models (SDMs) (a) and phenology-informed SDMs (b), respectively.

the ability of a population to persist at a given location. The modeling approach presented here enables the incorporation of key functional trait data to explore how intraspecific variation in fitness-related traits (mediated by climate) affects forecasts of species geographic distributions in the face of climate change. Specifically, we examined how reproductive phenology – a critical life-history trait that often mediates fitness – influences the effects of environmental change on plant species distributions. In general, both conventional and phenology-informed SDMs forecast a long-term decline in species' ranges in the eastern United States. However, our model inferences differed in one key and important way: Our phenology-informed SDM inferred from decades of herbarium specimens suggested a more optimistic forecast for species distributions than did the conventional SDMs.

Our approach differs from existing process-based models that integrate the impacts of climate-mediated phenology on demography and fitness to estimate species distributions (Chuine & Beaubien, 2001; Morin *et al.*, 2009). Despite the many advantages of process-based models in making more accurate predictions under novel environments, they often require detailed mechanistic knowledge of the processes linking phenology (or other traits) and fitness within a system. However, the experimental data required to develop such mechanistic models are not available for most species (Pollock *et al.*, 2012; Vesk *et al.*, 2021). By contrast, our method incorporates the effects of phenology into occurrence–environment relationship statistically and thus does not require such knowledge, enabling scaling range shift assessments to include hundreds or thousands of species by using existing taxonomically and geographically extensive resources (e.g. herbarium specimens).

Phenology mediates the effects of climate on species' distributions

We identified substantial variation in the predicted peak budding, flowering, and fruiting time among individual species based on phenology (DOY)–climate relationships. Our estimates of phenological responses to climate parallel those reported previously for the eastern United States that demonstrated broad and variable phenological responses within and among species (Park *et al.*, 2019). By accounting for phenology–climate relationships in our SDMs, we demonstrate that phenology can modulate the effects of climate on plant occurrence across broad environmental gradients (Fig. 2; Table 1). This suggests that phenological variation accounts for substantial variability in the ability of individual plants to withstand climate change.

The probability of occurrence of individual plants that reproduced relatively early in the growing season decreased more with temperature and increased more with precipitation than plants that flowered relatively late in the growing season (Fig. 2; Table 1). This suggests that plants with late phenology may survive better under future environmental change. Previous studies demonstrate that phenotypic plasticity plays a prominent role in the long-term climate-mediated acceleration of plant phenology (Ramirez-Parada *et al.*, 2024). However, earlier-flowering individuals also tend to have a strong genetic component, which is critical for adaptive responses to climate change (Anderson *et al.*, 2012). Adaptation may be necessary for long-term *in situ* persistence under climate change (Sgrò *et al.*, 2011). Our results, using actual distribution data, show an opposite pattern and we highlight the need for studies on future species occurrence to link real fitness data to estimate extinction risks.

Different life-history stages are biologically linked and the timing of these phases can have direct bearing on reproductive allocation per offspring. For example, in temperate climates, large-seeded species often flower earlier than small-seeded species, presumably because the former require more time to develop and ripen their seeds (Mazer, 1989; Bolmgren & Cowan, 2008). Large seeds subsequently produce larger seedlings, some of which are more drought resistant during the late summer and early fall (Metz *et al.*, 2010). Our results show a negative relationship between plant seed size and mean flowering/fruiting time, which also support such a hypothesis. By contrast, late-flowering species often allocate more resources to maternal growth. However, later-flowering plants often are exposed to risks associated with early frosts during seed maturation (Molau, 1993). From this perspective, late-flowering plants may be more favored under warming scenarios in which the growing season is extended

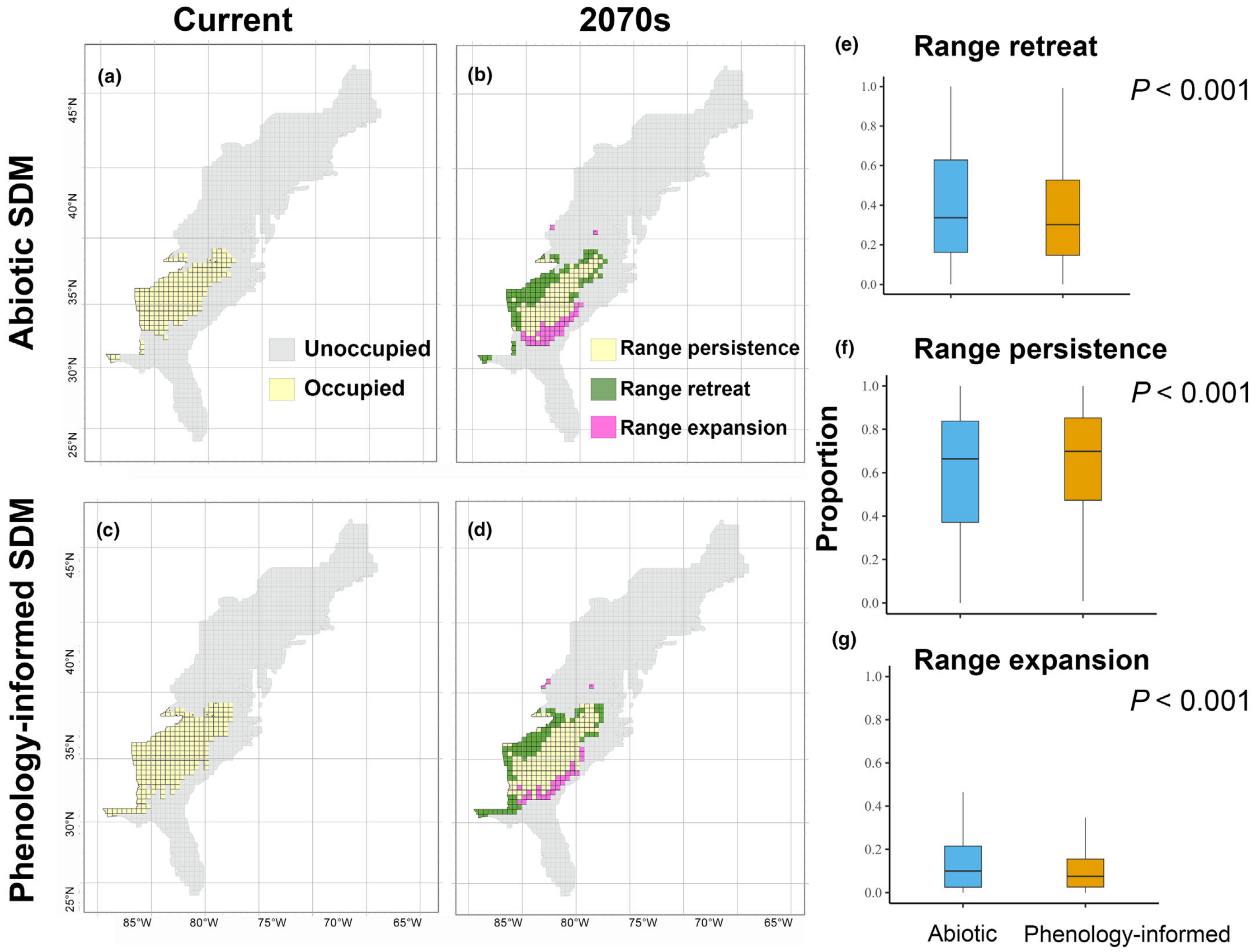

Fig. 4 Changes in species ranges forecasted by conventional abiotic-based species distribution models (SDMs) and phenology-informed SDMs. Maps illustrate the current (a, c) and future (b, d) distributions of *Trillium catesbaei* as an examplar. Yellow areas represent regions currently occupied by *T. catesbaei* that are projected to remain suitable in the future (i.e. range persistence); green areas represent regions currently occupied by *T. catesbaei* that are projected to have low suitability in the future (i.e. range retreat); pink areas represent regions currently unoccupied by *T. catesbaei* that are projected to have high suitability in the future (i.e. range expansion). Box plots illustrate the proportion of species' ranges that persist (d), contract (e), or expand (f) across all 360 species forecasted by conventional abiotic-based SDMs (blue) vs phenology-informed SDMs (orange). The central box in each boxplot shows the median and the interquartile range. The differences between the two models were evaluated by a paired Wilcoxon test. The significant level was set at $P < 0.05$.

(Molau *et al.*, 2005). In support of these hypotheses, we identified higher probabilities of occurrence of late-flowering plants than those of early-flowering plants at higher elevations. Higher elevations tend to be colder and have shorter growing seasons than lower elevations. Plants growing at higher elevations usually have lower seed production, which could be offset by vegetative growth during longer seasonal vegetative periods to ensure the persistence of populations (Pangtey *et al.*, 1990).

Phenology-informed SDMs forecast less severe habitat loss of species in response to climate change

Climate change is contributing to widespread range contractions and local extirpations of species (Thomas *et al.*, 2006; Cahill *et al.*, 2013). Boonman *et al.* (2024) projected that over half of global tree species are at potential extinction risk under global changes. Both phenology-informed and conventional SDMs forecast that > 50% of the species we sampled will experience range loss under future climate change scenarios. However, our results differed between these models in important ways.

First, although the species range loss was forecast to increase in the future (and to similar extents) by both phenology-informed and conventional SDMs, the magnitude of changes in the sampled species' geographic ranges differed significantly between the two types of SDMs. The conventional SDMs forecast that, on average, across species, 60% of the currently occupied ranges of species would have high suitability in the future, whereas the phenology-informed SDMs predicted that an average of 65% of

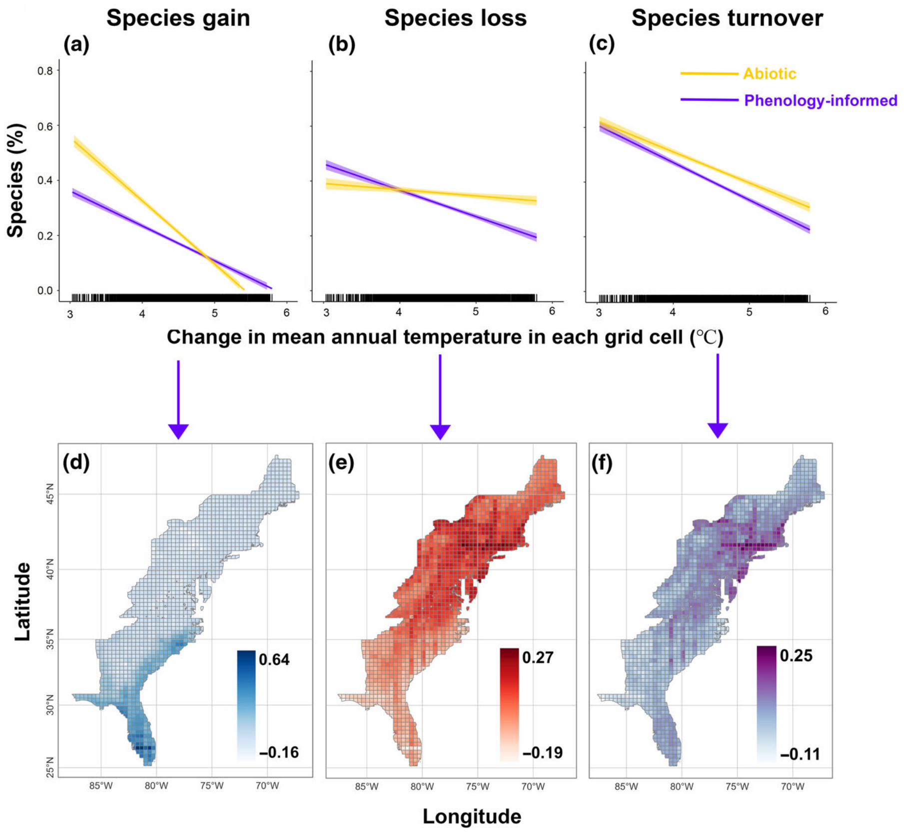

Fig. 5 Changes in species composition within each grid cell under future climate change. (a–c) Relationships between the proportion of species gains, losses, and turnover and changes in mean annual temperature within each individual grid cell. These relationships were separately explored using conventional abiotic-based species distribution models (SDMs) and phenology-informed SDMs. Here, phenology was quantified as the day of year for peak flowering and mean annual temperature in each grid cell was calculated as the average across all six general circulation models under the SSP5-8.5 climate scenario in the 2070s. (d–f) Geographical patterns in the differences in the proportion of species gains, losses, and turnover between the conventional abiotic-based SDMs and phenology-informed SDMs.

the currently occupied ranges would persist (Fig. 4). These findings provide evidence that the geographic range of a species is modulated not only by climate but also by variation in functionally relevant biological traits that allow populations to survive within their local environments (Hargreaves & Eckert, 2014). As a fitness-related trait, plant reproductive phenology exhibits high intraspecific variation across species' ranges (Park *et al.*, 2019; Love & Mazer, 2021). Thus, the fundamental assumption of conventional SDMs – homogeneous responses to climate variations across their range – is unrealistic. Species distribution models that do not include information on traits and their dynamic interactions with the environment and with other traits may result in incorrectly estimating a species' climatic niche, which may, in turn, lead to incorrect forecasts of species loss.

As the climate continues to change, populations are expected to persist *in situ* via local adaptation and phenotypic plasticity, track climate through migration, or become locally extinct (Brito-Morales *et al.*, 2018). The first two biological mechanisms are important for the persistence of species by expanding the climatic tolerance of species beyond their present realized niches. Species that can maintain their climatic niche by acclimating their phenology to changing climates may not need to migrate to survive and reproduce (Amano *et al.*, 2014). Therefore, climate-induced phenological responses may alter expectations of species' distributions under future climatic conditions, a prediction consistent with our phenology-informed SDMs, which generally predict a smaller reduction in species' ranges with climate change compared to forecasts generated by abiotic SDMs.

However, we cannot explicitly distinguish between plasticity and local adaptation because our model measures statistical associations that can be generated by both of processes. Unambiguously differentiating local adaptation from plasticity requires common-garden experiments (Benito Garzón *et al.*, 2019), and methods to estimate the contributions of these processes observationally involve statistical frameworks that are not easily integrated with our methods (Ramirez-Parada *et al.*, 2024). Our aim is to explore how the observed values of critical functional traits affect forecasts of species distributions under climate change. As such, we do not rely on partitioning the degree to which phenology–climate relationships are the result of plasticity or adaptation.

Phenology-informed SDMs predict less species turnover in response to climate change

We found significant geographic differences in species gains, losses, and turnover. Florida and the Atlantic Coastal Plain were forecast to have a higher proportion of species losses than the other regions included in this study. We hypothesize that this pattern may be driven by two factors: a narrower range of phenological responses to temperature among southern populations and a thermal tolerance maximum reached by these populations under projected climate change. Although the absolute amount of warming is lower at low latitudes, many species with narrow ranges are endemic to the southeastern United States and the southern Appalachian Mountains. These species frequently exhibit more narrow climatic tolerances, which are likely to promote high rates of species loss under future climate change (Wiens, 2016). These species may also be nearer to their thermal maxima, which may be exceeded in the southeastern United States in future non-analog climatic conditions (Williams & Jackson, 2007). We additionally found a significant positive relationship between the mean amount of warming predicted across the range of species and the proportion of range that persists (Fig. S7), which supported our results of high species loss in southern regions with a relatively low magnitude of warming compared to northern regions.

We identified strong negative relationships between the percentage of species gains, losses, and turnover and the expected amount of warming for individual grid cells. Qualitative patterns were similar for both phenology-informed and conventional SDMs. However, phenology-informed SDMs generally forecasted a lower proportion of species losses and turnover (i.e. persistent regional species composition) in response to warming. We hypothesize that both phenotypic plasticity and adaptive components of plant phenology contribute to the persistence of populations as the climate changes and tend to increase opportunities for species migration to the extent that they contribute to species niche breadth (Ackerly, 2003; Valladares *et al*., 2014).

We also suggest that similar conclusions could be drawn from our model framework if it were used with other fitness-related traits, although the relative importance of plasticity and local adaptation differs among functional traits (Benito Garzón *et al*., 2019). Phenotypic plasticity is considered favorable for the persistent of populations under rapid climatic change, but it can delay evolutionary adaption to new environments in the long term (Wund, 2012; Oostra *et al*., 2018). However, both phenotypic plasticity and local adaptation can allow populations to persist under climatic change. Since our hindcasting analysis showed high prediction accuracy of both phenology-informed and conventional SDMs, we suggest that previous studies using only climatic variables in SDMs may have overestimated the impacts of climate change on species turnover.

In summary, the trait-based framework used in our phenology-informed SDMs readily accounts for the interaction between phenology and environments, considering both intraspecific variability in phenology and dynamic phenological response under different climatic space. Both conventional and phenology-informed SDMs project species range loss across hundreds of plant species in the eastern United States under future climatic change scenarios. However, phenology-informed SDMs forecast significantly less drastic species' range loss and turnover within communities. Our results suggest that trait (co)variation can significantly influence species distributions across geographical gradients and subsequent diversity patterns under new climates. We conclude that future research and conservation efforts should look beyond conventional SDMs and embrace and integrate biological phenomena that contribute to species-specific acclimation and adaptive responses to climate change. Such work also may reveal climatic tolerances beyond those predicted by conventional SDMs. Finally, whereas our study uses phenology as an exemplar trait with which to build taxonomically and geographically broad SDMs, our methodological framework could be further developed to explore how other climate-sensitive traits may mediate future range shifts. Obvious traits to explore include flowering duration, photosynthesis rate, water use efficiency, and resource allocation to roots. Further application of other fitness-related functional traits to our framework will contribute to a general mechanistic understanding of how trait affect species distributions along different environmental gradients, with implications for understanding species response under future climate change.

Acknowledgements

This work was supported by the following grant from the US National Science Foundation: DEB2105903, DEB1754584, EF1208835, DEB2101884, DEB1802209, DEB2105932, MSB2105907, MSB2301322, and MRA2105903. SR was additionally supported by USDA-NIFA-AFRI: ME022425.

Competing interests

None declared.

Author contributions

CCD and AME proposed the initial idea for the study with subsequent development by SP; SP, CCD and AME designed the study; SP, CCD and AME collected the data; SP analyzed the data under the supervision of THR-P, SJM, AME, SR and IP; SP drafted the first version of the manuscript, and all authors contributed significantly to subsequent revisions.

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Data availability

All data and codes used for analyses are publicly available on Github (https://github.com/Shijia818/Phenology-informed-SDM) and archived at the Dryad Digital Repository (doi: 10.5061/dryad.573n5tbdg).

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Supporting Information

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

Fig. S1 Principal component analysis ordination diagram.

Fig. S2 Responses of the peak budding, flowering, and fruiting time for individuals with different growth forms and native statuses to climatic variables.

Fig. S3 Geographical patterns in the proportion of species gains under different general circulation models.

Fig. S4 Geographical patterns in the proportion of species losses under different general circulation models.

Fig. S5 Geographical patterns in the proportion of species turnover under different general circulation models.

Fig. S6 Geographical patterns in the proportion of species gains, losses, and turnover between current and 2070 estimated by abiotic species distribution models (SDMs) and phenology-informed SDMs, respectively.

Fig. S7 Relationships between the mean degree of warming across the range of species and the proportion of species current range that will persist in 2070.

Methods S1 Species distribution data.

Methods S2 Phylogenomic data.

Methods S3 Phylogenetic linear model.

Methods S4 Principal component analysis.

Methods S5 Model validation through hindcasting.

Methods S6 Relationship between seed size and phenology.

Table S1 Taxonomic, life span, growth form, origin information, and threshold used for calculating species distributions.

Table S2 Environmental variables used in conducting principal component analyses.

Table S3 Phylogenetic signals of the mean peak budding, flowering, and fruiting time and the responses of peak budding, flowering, and fruiting time to environmental variables.

Table S4 Summary of phylogenetic linear mixed models for plant peak budding time.

Table S5 Summary of phylogenetic linear mixed models for plant peak flowering time.

Table S6 Summary of phylogenetic linear mixed models for plant peak fruiting time.

Table S7 Pearson's correlation coefficients among variables used in constructing phenology-informed species distribution models.

Table S8 Summary of linear mixed models for plant budding, flowering, and fruiting.

Table S9 Results of tests for phylogenetic signal on predicted changes in species' habitat suitability.