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The ecological implications of intra- and inter-species variation in phenological sensitivity

Yingying Xie[1,2], **Hanna T. Thammavong**[1] and **Daniel S. Park**[1,2]

[1]Department of Biological Sciences, Purdue University, West Lafayette, IN 47906, USA; [2]Purdue Center for Plant Biology, Purdue University, West Lafayette, IN 47906, USA

Authors for correspondence:
Daniel S. Park
Email: danielpark@purdue.edu

Yingying Xie
Email: yingying.xie1@gmail.com

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Summary

- Plant–pollinator mutualisms rely upon the synchrony of interacting taxa. Climate change can disrupt this synchrony as phenological responses to climate vary within and across species. However, intra- and interspecific variation in phenological responses is seldom considered simultaneously, limiting our understanding of climate change impacts on interactions among taxa across their ranges.
- We investigated how variation in phenological sensitivity to climate can alter ecological interactions simultaneously within and among species using natural history collections and citizen science data. We focus on a unique system, comprising a wide-ranged spring ephemeral with varying color morphs (*Claytonia virginica*) and its specialist bee pollinator (*Andrena erigeniae*).
- We found strongly opposing trends in the phenological sensitivities of plants vs their pollinators. Flowering phenology was more sensitive to temperature in warmer regions, whereas bee phenology was more responsive in colder regions. Phenological sensitivity varied across flower color morphs. Temporal synchrony between flowering and pollinator activity was predicted to change heterogeneously across the species' ranges in the future.
- Our work demonstrates the complexity and fragility of ecological interactions in time and the necessity of incorporating variation in phenological responses across multiple axes to understand how such interactions will change in the future.

Introduction

The timing of diverse species' life history events (i.e. phenology) has been dramatically shifting in response to anthropogenic climate change (Thackeray *et al.*, 2008; Boutin & Lane, 2014; Carter *et al.*, 2018; Piao *et al.*, 2019). For instance, highbush blueberry (*Vaccinium corymbosum*) and yellow wood sorrel (*Oxalis europaea*) advanced their flowering time in spring by 21 and 32 d respectively over the last 150 yr in Concord, Massachusetts, USA (Miller-Rushing & Primack, 2008) and butterflies in central California have advanced their first flight by > 3 wk over the last three decades (Forister & Shapiro, 2003). Such phenological shifts can have substantial ecological impacts, as they can influence species fitness and abundance (Willis *et al.*, 2008; Springate & Kover, 2013), facilitate biological invasions (Wolkovich *et al.*, 2013), and alter biophysical processes (Richardson *et al.*, 2013; Estiarte & Peñuelas, 2015).

Climate change-induced phenological shifts can also disrupt species interactions (Edwards & Richardson, 2004; Donnelly *et al.*, 2011; Thackeray *et al.*, 2016) because species can vary greatly in their phenological responses to changes in climate (Morin *et al.*, 2009; Primack *et al.*, 2009; Cole & Sheldon, 2017). Phenological mismatches among mutualistic taxa are likely to cause reduced fecundity or increased mortality of those involved, and may have cascading effects throughout the ecosystem (Kudo & Ida, 2013; Kudo & Cooper, 2019; Visser & Gienapp, 2019). In particular, the disruption of synchrony in plant–pollinator systems could negatively impact plants through pollen limitation (Rafferty & Ives, 2011; Kudo & Ida, 2013), and pollinators through a reduction of floral resources (CaraDonna *et al.*, 2018; Schenk *et al.*, 2018). This can lead to collapses of mutualisms (Warren II & Bradford, 2014), reductions in animal-pollinated crop yields (Bartomeus *et al.*, 2013), and local extinction (Revilla *et al.*, 2015). It has been estimated that climate change-induced phenological shifts may cause a reduction of the floral resources available to 17–50% of all pollinator species, resulting in up to half of the historical pollinator activity period falling at times when no food plants are flowering (Memmott *et al.*, 2007).

Further complicating this issue is the fact that phenological sensitivity to climate varies extensively within species across their ranges (Høye *et al.*, 2013; Fitchett *et al.*, 2014; Park *et al.*, 2019; Song *et al.*, 2020; Love & Mazer, 2021; Pearson *et al.*, 2021). For example, the timing of leaf out, flowering, and fruiting have been found to be more sensitive to temperature in warmer regions across many plant species in temperate ecosystems (Zhang *et al.*, 2015; Park *et al.*, 2019). Thus, with climate change, intraspecific interactions and gene flow can be altered (Fox, 2003; Rivest *et al.*, 2021; Park *et al.*, 2022) and phenological synchrony between interacting

species may shift heterogeneously across the landscape, differing among populations or morphotypes (Park *et al.*, 2022). Knowledge of both intra- and interspecific variation in phenological responses is therefore critical to assessing the ecological impacts of climate change. However, less is known about the phenological responses of insect pollinators such as bees (Bartomeus *et al.*, 2011), and most studies to date examining climate-driven phenological mismatches have not considered the consequences of intraspecific variability (Charmantier *et al.*, 2008). This may be due in part to the general lack of phenological observation experiments that track multiple interacting species simultaneously across wide geographic scales. Indeed, many phenological studies on plant–pollinator interactions are limited to relatively small geographic areas (Forrest & Thomson, 2011; Kudo, 2014; Pyke *et al.*, 2016; Olliff-Yang & Mesler, 2018), and it is possible that the trends observed in such studies may not apply across species' ranges.

Here we investigate how intraspecific variation in phenological sensitivity to climate can alter ecological interactions simultaneously within and among species using over 120 yr of natural history collections and citizen science data. We focus on a unique system, comprising *Claytonia virginica* (Portulacaceae; Virginia spring beauty) and its specialist pollinator *Andrena erigeniae* (Andrenidae; spring beauty miner bee). *Claytonia virginica* is an understory spring ephemeral that has distinct floral color morphs ranging from white to pink, which often occur in sympatry (Frey, 2004). It is not certain how these color morphs are maintained, but pollinator preference and divergent selection by pathogens and herbivores have been suggested to play a role (Frey, 2004). Variation in flowering phenology can also allow different color morphs to coexist (Tarasjev, 1997) and even small differences can potentially lead to divergence and reinforcement among phenotypes through assortative mating (Hopkins, 2013). Comparatively little is known about how the phenology of *C. virginica* and *A. erigeniae* varies across color morphs and populations (Schemske *et al.*, 1978), though some degree of reproductive isolation and phenological differences has been suggested to occur among races of *C. virginica* (Lewis, 1976; Lewis & Suda, 1976; Doyle, 1981, 1983). Most studies of plant–pollinator mismatch focus on generalist pollinators, and analogous studies of specialist species that may be more vulnerable are rare, particularly for oligolectic bee species such as *A. erigeniae* (Bartomeus *et al.*, 2011; Maglianesi *et al.*, 2020).

Along these lines, we test the following hypotheses: flowering phenology varies among white and pink *C. virginica* color morphs, contributing to their maintenance in sympatry; phenological sensitivity to climate varies across the ranges of *C. virginica* and *A. erigeniae* and among color morphs of *C. virginica*; and climate change will result in larger temporal gaps among species and color morphs.

Materials and Methods

Study system

Claytonia virginica L. is widely distributed across the eastern to midwestern USA. Its variation in floral color is influenced by the presence of cream-colored quercetin and kaempferol glycosides, along with darker anthocyanins in the petals (Harborne, 1976; Doyle, 1983). Flower color is unaffected by soil characteristics, uncorrelated with other traits, and has been posited to be regulated by a few genes in the findings of several independent experiments (Frey, 2004, 2007). Though other insects may visit *C. virginica* flowers, the predominant pollinator by far is the pollen-specialist bee *A. erigeniae* Robertson (Schemske, 1977; Parker *et al.*, 2018). *Andrena erigeniae* is a solitary ground-nesting oligolege of *C. virginica* in the eastern woodlands (Davis & LaBerge, 1975; LaBerge, 1986). The bee is reliant upon *C. virginica* for successful reproduction, and seed set in *C. virginica* has been shown to be pollinator-limited (Davis & LaBerge, 1975; Schemske, 1977).

Phenological assessment

We obtained both herbarium specimen collection records and citizen science observations of *C. virginica* across its entire native range in North America for a 120-yr period (1895–2021) from the Global Biodiversity Information Facility (GBIF). These records comprised 18 847 research-grade iNaturalist (https://www.inaturalist.org/) observations (1970–2021), and 735 herbarium specimens with digital images collected (1895–2021) (10.15468/dl.r38aa2, 10.15468/dl.7j2xa7). Research-grade iNaturalist records are verifiable observations for which at least two participants confirm taxon identity. They comprise the date of observation, geographic coordinates of the location, and media (e.g. photographs), and do not represent records of captured or planted taxa. iNaturalist data are opportunistically collected by people with varying levels of botanical knowledge, and can thus be more prone to misidentifications and errors. Nonetheless, data from iNaturalist have been used successfully in plant phenological studies (Heberling & Isaac, 2018; Taylor & Guralnick, 2019; Barve *et al.*, 2020), and *C. virginica* is a distinct, well-known, and easily identifiable member of the woodland flora.

Flowers and fruits were manually identified for all iNaturalist digital photos and specimen images at maximum available resolution using ImageAnt (https://gitlab.com/stuckyb/imageant). Such data may not fully be representative of the flowering season, as they tend to be collected during phenological peaks (Davis *et al.*, 2015). Therefore, our downstream results largely represent estimates and predictions of phenological peaks (e.g. peak flowering, peak pollinator activity). Nonetheless, the timing of phenological peaks has been demonstrated to be correlated with the timing of onset; have significant effects on reproductive interactions; and are less sensitive to the spatiotemporal grain of observation and sampling bias than phenological firsts (Schmitt, 1983; Husband & Schemske, 2000; Nuismer & Cunningham, 2005; Davis *et al.*, 2015; Park *et al.*, 2021). In addition, floral color was also identified for each iNaturalist digital photo. Flowers were classified as pink if petals had any visible trace of pink coloring, and classified as white if petals did not display any nonwhite colors or patterning (Fig. 1a). A total of 5619 images were identified as having white flowers; 13 228 images had pink flowers; and 2362 images showed flowers with both colors at the same

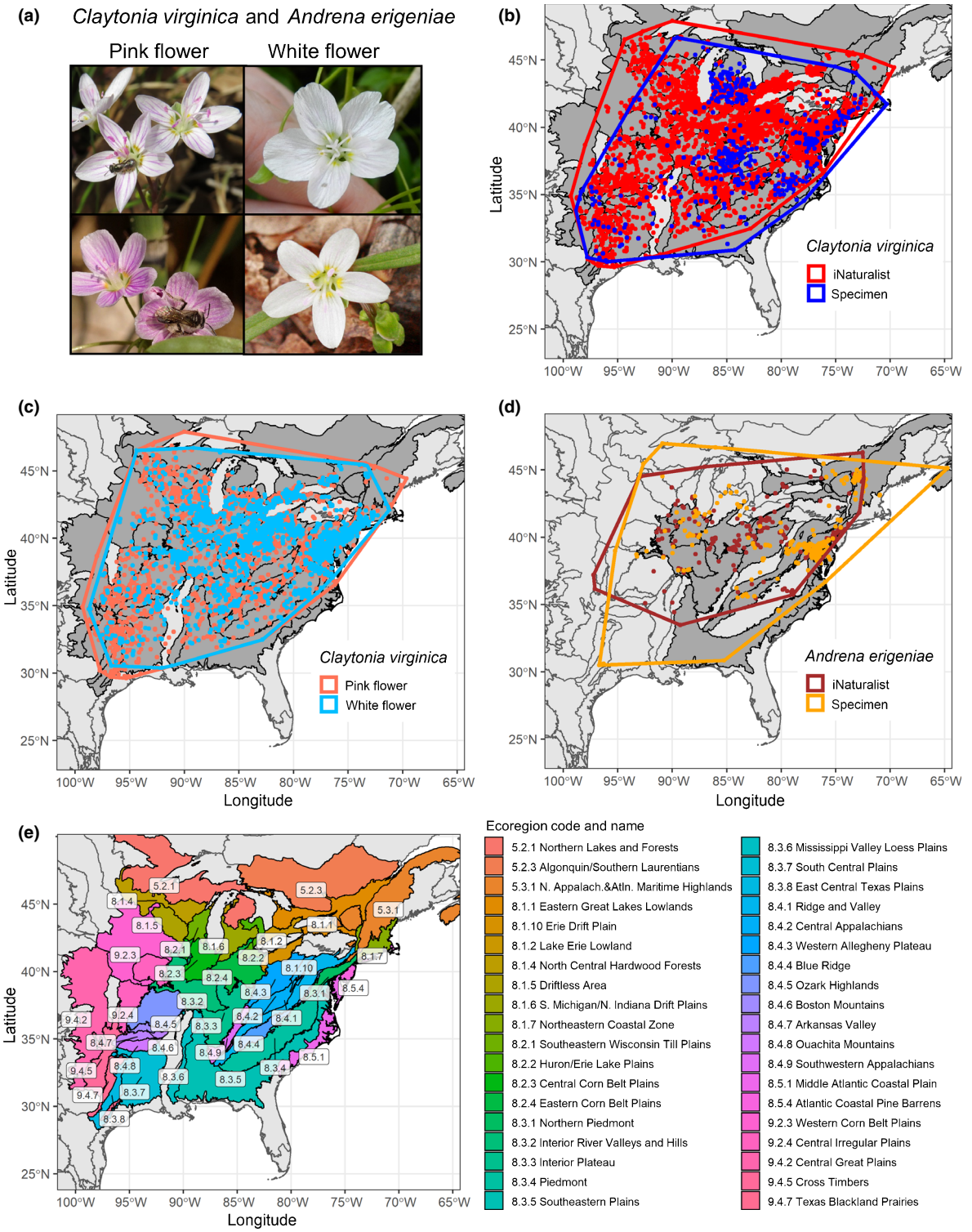

Fig. 1 Examples of digital photos and geographic distributions of Virginia spring beauty and the spring beauty miner bee. (a) Examples of pink and white flowers of *Claytonia virginica* with *Andrena erigeniae* from iNaturalist photos. Photos were cropped to size. Photo credits: Lee Elliott (top left), Scott King (bottom left), Matthew O'Donnell (top right), and Vail Ryan (bottom right). The top two photos are licensed under http://creativecommons.org/licenses/by-nc-sa/4.0/, and the lower two are licensed under http://creativecommons.org/licenses/by-nc/4.0/. The colored polygons in (b), (c), and (d) are convex hulls encompassing occurrence records of each type, representing the geographic ranges of species/color. (b) iNaturalist and specimen data for *C. virginica*. (c) The two color morphs of *C. virginica* identified from iNaturalist observations. (d) iNaturalist and specimen data of *A. erigeniae* in the USA. Maps are divided into Level III ecoregions, and the dark gray areas in (b), (c), and (d) are ecoregions with at least 20 observations. (e) Map of the 38 Level III ecoregions used in this study with their numerical codes and names.

location. Though more elaborate schemes have been suggested (Frey, 2007), it is difficult to subdivide intermediate colors accurately with photographs taken across a variety of conditions, devices, perspectives, and degrees of skill. We did not assess floral color from herbarium specimen images as the original colors had faded with age and desiccation.

We also obtained 9008 records of *A. erigeniae* occurrences across its native range in North America from GBIF (10.15468/dl.h8wfvk), ranging from 1903 to 2021. The *A. erigeniae* occurrence data were largely from iNaturalist and the USGS Native Bee Inventory and Monitoring Lab. In contrast to other animal taxa, long-term standardized monitoring schemes across large spatial scales are lacking for (nondomesticated) bees. The specimen records and iNaturalist photos of *A. erigeniae* we used indicate that the individual was in flight on the collection/observation date, and in aggregate can represent a reliable estimate of the timing and span of foraging activity – it has been argued that such data are more robust to sampling bias than records of earliest activity each year (Bartomeus *et al.*, 2011).

Duplicated data, such as multiple photos of the same incident or observations of the same species/color morph on the same day at the same location were removed. All iNaturalist data for *C. virginica* and most GBIF occurrence data for *A. erigeniae* had recorded geographic coordinates. When specimens did not have coordinates, we assigned the centroid coordinates of the county where they were collected. However, plant and bee specimen data without coordinates were only used to confirm the representativeness and accuracy of iNaturalist data in terms of species' geographic distributions (Fig. 1), and not in downstream phenological analyses. Outliers (i.e. flowering or occurrence records after June), which accounted for < 1% of the total data, were removed to reduce bias. *Claytonia virginica* iNaturalist records with observation dates before 2008, which represent legacy data predating the launch of the platform, were also removed to avoid uncertainties in the associated proximate dates or geographic coordinates ($n = 33$).

Geographic and phenological distributions

Geographic boundaries of iNaturalist and specimen data were identified using the 'convexHull' function from the SPATIALECO R package (Evans, 2021). For both *C. virginica* and *A. erigeniae*, iNaturalist and specimen data showed a high degree of overlap geographically (Fig. 1b,d), suggesting that iNaturalist observations are accurate and representative of the general distributions of the two species. We also confirmed a high degree of range overlap between white and pink color morphs of *C. virginica* as well as with their pollinator (Fig. 1c) (Davis & LaBerge, 1975).

To examine the phenological variation between color morphs of *C. virginica*, we aggregated the iNaturalist observations to 5 × 5 km grids and selected grids with at least three observations for each color morph ($n = 1027$). We then calculated the mean dates of flowering for each color morph in each grid, and compared them between color morphs. *Andrena erigeniae* occurrences were aggregated to the same 5 × 5 km grids. Mean dates of occurrence were calculated for the grids with at least three observations, then compared to the flowering dates of *C. virginica*.

Environmental data

An elevation value for each occurrence was assigned from the USGS Elevation Point Query Service using the R package ELEVATR (Hollister *et al.*, 2021) based on the coordinates. Together with occurrence coordinates, we used these values to extract climatic data including mean annual temperature (MAT), mean annual precipitation (MAP), mean minimum, average, and maximum temperature and total precipitation in winter for each collection site over 121 yr (1901–2021) using the CLIMATENA v.7.3 software package, which downscales gridded climate data to scale-free point locations (Wang *et al.*, 2016). Winter was defined as a 3-month period from December to February, following common practices for phenological studies conducted in the region (Primack *et al.*, 2015; Park *et al.*, 2019, 2022). Winter climate was used in this study because *C. virginica* can emerge as early as January (Risser & Cottam, 1967) and the onset of flowering in *C. virginica* is likely limited by low temperatures early in the year, which also restricts pollinator activity (Schemske, 1977). Following Kharouba & Vellend (2015) and Munson & Long (2017), we calculated the 121-yr long-term mean temperature and precipitation conditions for each collection/observation site, and the 'anomalies' in temperature and precipitation – the deviation between long-term climatic conditions and those of the year of collection/observation for each site. As local precipitation conditions can vary greatly across the geographic range of species, the biological effects of precipitation anomalies of equal magnitude may also vary among sites. Thus, to standardize the precipitation effects across sites, we calculated precipitation anomalies as proportional to the long-term mean values, as suggested by Pearson *et al.* (2021). It has been suggested that the use of climate anomalies allows quantification of inter-annual variation in temperature and precipitation independent of the geographic variation in climate across species ranges (Kharouba & Vellend, 2015; Munson & Long, 2017; Pearson *et al.*, 2021).

Statistical modeling

We applied linear mixed-effect models to examine the phenological sensitivities of *C. virginica* flowering and the occurrence of *A. erigeniae* to climate across their ranges. This approach has been commonly used in previous phenology studies (Donoso *et al.*, 2016; Xie *et al.*, 2018; Park *et al.*, 2019; Augspurger & Zaya, 2020), as the models allow the incorporation of phenological variation across multiple groups and estimation of heterogeneity in phenological responses to abiotic factors in a hierarchical structure (Zuur *et al.*, 2009). Models were fitted for each species separately using the same model structure and explanatory variables. Correlation coefficients among all selected explanatory variables were < 0.5, limiting the effect of multicollinearity and overfitting (Dormann *et al.*, 2013). Fixed components in the models comprised two groups of variables representing the spatial and inter-annual variations in climate.

Initially, two sets of variables were tested to account for the former preliminary models. One set included latitude and elevation, and the other included the long-term average of MAT and MAP. Latitude and elevation in models provided better fits compared to the models which included long-term average MAT and MAP values. The second group of fixed variables included temperature anomalies, proportional precipitation anomalies, and their interaction. Two additional steps of model selection were applied to determine the optimal structure of final fixed components. First, preliminary models were fitted with three different sets of climate variables, as well as latitude and elevation values and random components (see next paragraph) to select the optimal set of climate variables. Three sets of climate anomaly variables were tested; the mean minimum, average, and maximum temperature anomalies and proportional precipitation anomalies in winter, and their interaction. The mean minimum winter temperature anomaly model was selected for both *C. virginica* and *A. erigeniae* based on Akaike information criterion (AIC) values (Supporting Information Table S1). The second step involved further optimizing the structure of the selected models by dropping insignificant fixed variable terms with no significant explanatory effect ($P > 0.05$) and evaluating AIC values of the resulting models (Table S2). We selected the models with the lowest AIC values and simplest structure (i.e. smaller number of variables) as the final (best) model for each species. All explanatory variables were centered and scaled to a mean value of 0 and an SD of 1 to avoid introducing bias during model development with variables on different scales.

The random component in the model incorporated variations in phenological timing and phenological sensitivity to climate across different regions within the range of each species and morph. For the *C. virginica* model, we included flower color (white and pink) and the Level III ecoregion of occurrence (see a map and list of ecoregion codes and names in Fig. 1e) as nested random components, as phenological sensitivities to climate may vary across color morphs and geographic ranges. Ecoregion designations followed the United States Environmental Protection Agency Level III delimitations for North America (Omernik & Griffith, 2014). Specifically, the *C. virginica* model included a random intercept term and a random slope term of temperature anomaly for each color morph in each ecoregion. The random intercept allowed the model to incorporate the phenological variation in each group (i.e. specific color morphs in specific ecoregions), while the random slope estimated the phenological sensitivities to temperature anomaly change (i.e. inter-annual variation) for each group. Similarly, the *A. erigeniae* model contained a random intercept term for ecoregion, and a random slope of temperature anomaly for each ecoregion. Our analyses do not account explicitly for spatiotemporal sampling biases – including ecoregion-level random effects as we have done here reduces the possible impacts of such issues but may not eliminate them altogether. We only included ecoregions with at least 20 observations for each species and/or color morphs in model development to reduce potential bias from small sample sizes. Our final dataset comprised 18 183 *C. virginica* flowering observations across 38 ecoregions and 1043 documented *A. erigeniae* occurrences across 13 ecoregions (Fig. 1c,d). Data were analyzed in the R software environment (R Core Team, 2020) using the packages LME4 (Bates *et al.*, 2015) and LMERTEST (Kuznetsova *et al.*, 2017).

Future predictions

To increase our understanding of how climate change-driven phenological shifts will affect the interactions between *C. virginica* and *A. erigeniae* in the future, we used the best models for each species to predict their phenologies across two 20-yr time periods (2041–2060 and 2081–2100) and two shared socioeconomic pathway (SSP) scenarios (SSP2-4.5 and SSP5-8.5). SSP2-4.5 assumes middle of the road development with medium challenges to mitigation and adaptation, which may be the most realistic development trajectory, while SSP5-8.5 represents fossil-fueled development with strong challenges to mitigation and weak challenges to adaptation, as the low-effort baseline (Riahi *et al.*, 2017; Meinshausen *et al.*, 2020). Future predictions under these two scenarios offer a range of reference points for climate impact assessment on species interactions. Future climate projection data from 13 CMIP6 GCM ensembles for two 20-yr time periods under the two SSP scenarios were obtained using CLIMATENA v.7.3 (Wang *et al.*, 2016). To evaluate how phenology will shift in the future, we used the best models fitted above to estimate the current phenology of two species as a baseline using the 30-yr normal (1981–2010) (Laskin *et al.*, 2019; Tao *et al.*, 2021). Differences in phenology between the recent years and future predictions at the ecoregion scale were calculated for two species by subtracting the estimated dates from the predicted dates at each ecoregion. The temporal gap between *C. virginica* flowering dates and *A. erigeniae* occurrence dates was calculated for each color morph under both current climatic conditions (30-yr normal) and future conditions (20-yr predicted normal) under two different socioeconomic pathways across 12 ecoregions with at least 20 observations for both color morphs of *C. virginica* and *A. erigeniae*. The predicted changes in temporal gaps between the current and future periods across 12 ecoregions were calculated by subtracting the modeled estimates. The temporal gaps and the changes in the gaps between the two color morphs of *C. virginica* in the future predictions were also calculated this way.

Results

On average white flowers of *C. virginica* opened 3.1 d earlier than pink flowers across 5 × 5 km grids (Fig. 2a). *Andrena erigeniae* bees were generally observed later than the flowering dates of both color morphs of *C. virginica* in most grids (Fig. 2b). On average, bees were observed 9.3 d later than white flowers, and 5.8 d later than pink flowers.

The best models for each species suggested that the timing of *C. virginica* flowering and *A. erigeniae* occurrence were significantly affected by latitude, elevation, and winter minimum temperature anomaly (Table 1). Phenology for both species was delayed at higher latitudes and elevation, and during colder winters. *Claytonia virginica* flowers were estimated to bloom 1.3 d

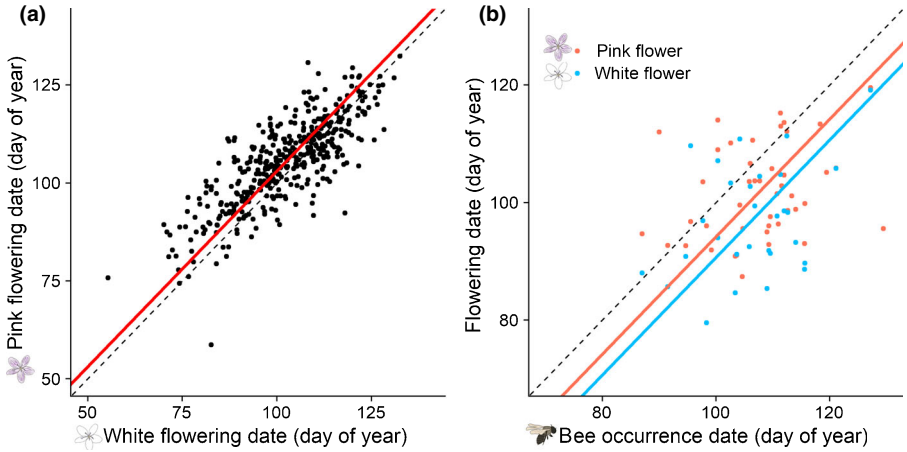

Fig. 2 Comparisons of mean phenologies in 5 × 5 km grids. The black dashed lines represent a 1 : 1 ratio. Colored straight lines are fitted linear lines with a fixed slope = 1. Deviations between colored lines and dashed lines (i.e. the intercept values of colored lines) represent the differences in phenology between the groups on the *x* and *y* axes. (a) Comparison of mean flowering dates between white and pink flowers of *Claytonia virginica*. (b) Comparison between *Andrena erigeniae* mean occurrence date and the mean flowering dates of white and pink flowers of *C. virginica*.

Table 1 Unscaled coefficients of fixed effect variables in the best spring beauty and bee models.

Species	Variable	Coefficient ± SD	*P*-value
Claytonia virginica	Latitude	5.1 ± 0.1	< 0.001
	Elevation	0.02 ± 0.001	< 0.001
	$T_{min(wt)\_anm}$	−1.3 ± 0.2	< 0.001
	$ppt_{(wt)\_anm}$	4.7 ± 0.5	< 0.001
	$T_{min(wt)\_anm} : ppt_{(wt)\_anm}$	−2.4 ± 0.4	< 0.001
Andrena erigeniae	Latitude	4.4 ± 0.5	< 0.001
	Elevation	0.02 ± 0.004	< 0.001
	$T_{min(wt)\_anm}$	−1.8 ± 0.5	0.01

$ppt_{(wt)\_anm}$, proportional precipitation anomaly in winter; $T_{min(wt)\_anm}$, mean winter minimum temperature anomaly.

earlier per degree (°C) increase in mean winter minimum temperature. *Andrena erigeniae* bees were estimated to occur 1.8 d earlier per degree (°C) warming of winter minimum temperature (Table 1). In addition, increased winter precipitation was estimated to delay *C. virginica* flowering time. The effect of winter minimum temperature anomaly on *C. virginica* was also mediated by winter precipitation anomaly – increases in temperature were estimated to advance flowering to a greater degree in wetter conditions (Table 1).

Though both color morphs of *C. virginica* advanced their flowering in response to warmer winters across their ranges, their phenological sensitivities to winter temperature anomalies varied among colors and ecoregions (Fig. 3a,b; Table S3). The phenological sensitivity of white flowers ranged from −0.2 to $-2.7\ d\ °C^{-1}$ while that of pink flowers ranged from 0.1 to $-2.8\ d\ °C^{-1}$ across co-occurring ecoregions. White flowers showed higher degrees of phenological sensitivity to temperature than pink flowers in 12 ecoregions, especially at the more southern latitudes. The difference was $0.1–0.8\ d\ °C^{-1}$. Pink morphs were estimated to be more sensitive to winter temperature anomalies in 10 ecoregions by $0.1–1.6\ d\ °C^{-1}$.

Andrena erigeniae also displayed varying degrees of phenological sensitivity to winter temperature change throughout its range (Fig. 3c; Table S3). The range of phenological sensitivities was −0.6 to $-3.3\ d\ °C^{-1}$ across ecoregions. Higher degrees of sensitivity ($< -3\ d\ °C^{-1}$) were found in the Northern Appalachian and Atlantic Maritime Highlands (ecoregion code 5.3.1, see Fig. 1) and the Eastern Great Lakes Lowlands (8.1.1). Lower degrees of sensitivity ($> -1\ d\ °C^{-1}$) were found in the Southeastern Plains (8.3.5) and the Interior River Valleys and Hills (8.3.2).

To gain insight into the potential drivers of these spatial patterns, we examined the relationships between ecoregion climate (i.e. long-term average mean winter minimum temperature) and the phenological sensitivities of *C. virginica* and *A. erigeniae* (Fig. 4). Phenological sensitivity was significantly correlated to temperature in all cases. However, the phenological sensitivities of *C. virginica* and *A. erigeniae* showed opposing relationships with temperature (*C. virginica* white: $r = -0.44$, $P = 0.04$; *C. virginica* pink: $r = -0.53$, $P < 0.001$; *A. erigeniae*: $r = 0.76$, $P = 0.003$). While the flowering times of both white and pink color morphs of *C. virginica* were more sensitive to winter temperature in warmer ecoregions, *A. erigeniae* occurrence times were more sensitive in colder ecoregions. Due to these opposing trends, *C. virginica* phenology tended to be more sensitive to temperature than *A. erigeniae* phenology in warmer ecoregions (e.g. Southeastern Plains (8.3.5)), while *A. erigeniae* phenology was more sensitive than *C. virginica* to temperature in colder areas (e.g. Northern Appalachian and Atlantic Maritime Highlands (5.3.1); Fig. 4).

Advances in *C. virginica* and *A. erigeniae* phenology were predicted across two 20-yr future time periods and two climate change scenarios (Figs S1, S2, S3). This was largely driven by higher winter minimum temperatures in future climate projections. Along these lines, the greatest degree of phenological advancement was predicted for 2081–2100 under the highest warming scenario (SSP5-8.5; Fig. 5). However, due to different phenological sensitivities to winter warming, the occurrence of *A. erigeniae* and the flowering dates of both *C. virginica* color morphs were predicted to change in different ways among ecoregions (Fig. S3). The largest degrees of phenological advancement were predicted for white flowers of *C. virginica* in the Northeastern Coastal Zone (12 d), and for pink flowers of *C. virginica* in the Lake Erie Lowland (14 d) (Fig. 5a,b). By contrast, *A. erigeniae* phenology was predicted to advance to greater degrees in the

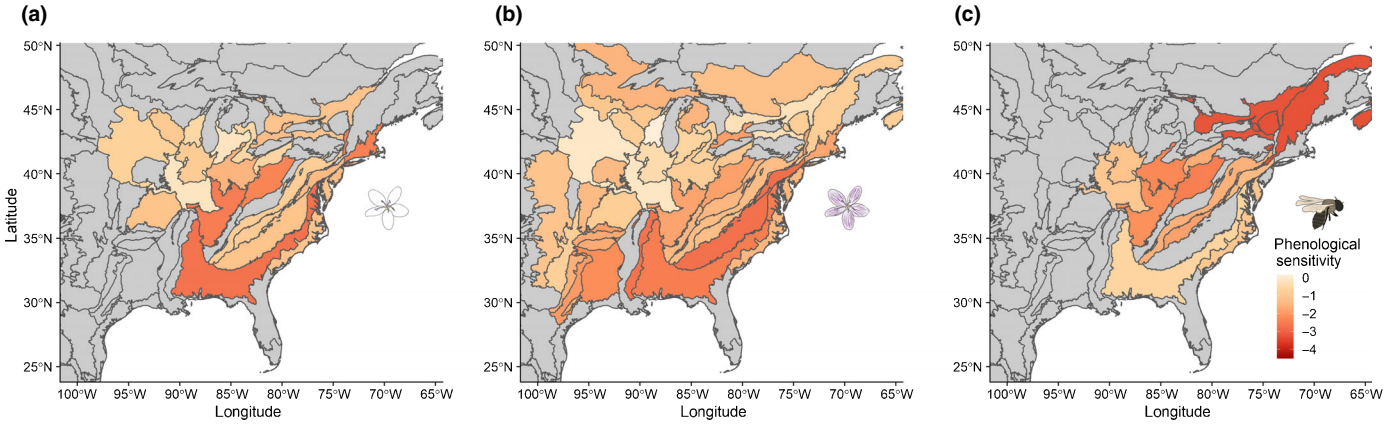

Fig. 3 Choropleth maps of phenological sensitivities to winter minimum temperature anomalies at each ecoregion. Unit is d °C^{-1}. (a) Flowering of white *Claytonia virginica* flowers across 22 ecoregions; (b) flowering of pink *C. virginica* flowers across 38 ecoregions; and (c) occurrence of *Andrena erigeniae* across 13 ecoregions.

northern parts of its range, including the Eastern Great Lakes and Hudson Lowlands (8.1.1) and the Northern Appalachian and Atlantic Maritime Highlands (25 d; Fig. 5c). These heterogeneous responses to climate change resulted in varying degrees of expected change in the temporal gaps among taxa (Figs 6, S4). Increased temporal gaps of 1–8 d between *C. virginica* flowering date and *A. erigeniae* occurrence were predicted for both 20-yr time periods and two climate change scenarios in the Southeastern Plains (8.3.5) and Northern Piedmont (8.3.1; pink flowers only), while the temporal gaps were predicted to become shorter by 0.5–17 d in all 10 of the other ecoregions (Figs 6, S4). However, this was predicted to lead to *A. erigeniae* occurring earlier than *C. virginica* flowering in three ecoregions: the Eastern Great Lakes and Hudson Lowlands (8.1.1), Erie Drift Plain (8.1.10), and Eastern Corn Belt Plains (8.2.4). This was particularly evident in the 2081–2100 time period, due to the faster advancement of bee occurrence driven by a stronger response to warming than that of Virginia spring beauties. *Andrena erigeniae* occurrence was expected to remain later than *C. virginica* flowering in the other nine ecoregions. By contrast, while the predicted temporal gaps of flowering time between color morphs of *C. virginica* varied among ecoregions, consistent trends across scenarios and time periods were observed (Fig. S5). Among the 22 ecoregions where both color morphs have been observed, increased temporal gaps were predicted in 11 ecoregions by 0.4–6 d, while the temporal gaps were predicted to become shorter in 10 ecoregions by 0.2–7 d, and no changes were predicted in one ecoregion (Interior River Valleys and Hills, 8.3.2) (Fig. S5).

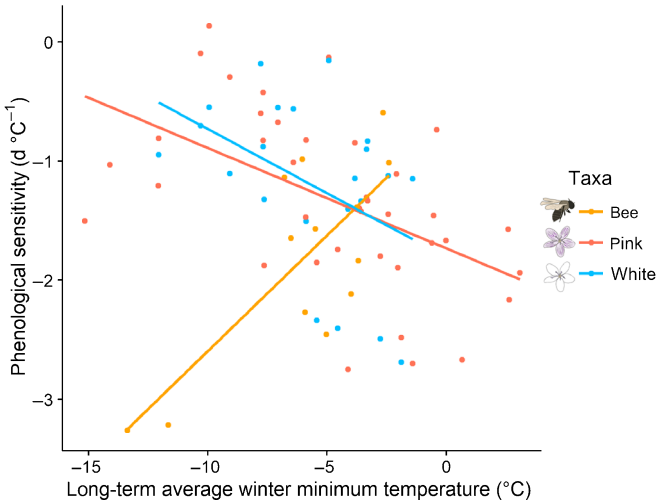

Fig. 4 The relationship between phenological sensitivity and long-term 121-yr average mean winter minimum temperature (1901–2021) across sites in Level III ecoregions for two color morphs of *Claytonia virginica* and *Andrena erigeniae*. The colored lines are fitted linear regression lines.

Discussion

Ecological synchrony of interacting taxa can be disrupted by varying responses to climate change (Thackeray *et al.*, 2016; König *et al.*, 2018; Park *et al.*, 2022). Of particular concern are mutualistic interactions between plants and their pollinators. Plants form the basis of all terrestrial ecosystems, and nearly 90% of the world's flowering plant species are pollinated by animals to at least some degree (Ollerton *et al.*, 2011). We used natural history collections and citizen science data to assess variation in phenological responses to climate within and across species in a near obligate plant–pollinator relationship. We demonstrated that phenological sensitivity to winter temperature varies between *C. virginica* color morphs and *A. erigeniae* across their ranges. This intra and inter-specific variation in phenological sensitivity, and its contrasting distribution across climatic gradients among the two species, was predicted to result in complex patterns of shifting in their temporal synchrony with climate change.

Flowering phenology varies across geographic ranges and color morphs

Flowering dates among *C. virginica* color morphs largely overlapped, but on average white flowers were observed earlier than pink flowers by *c.* 3 d (Fig. 2a). As a result, the flowering times of pink *C. virginica* tended to be more synchronous with *A. erigeniae* phenology compared to white morphs. This may explain the bees'

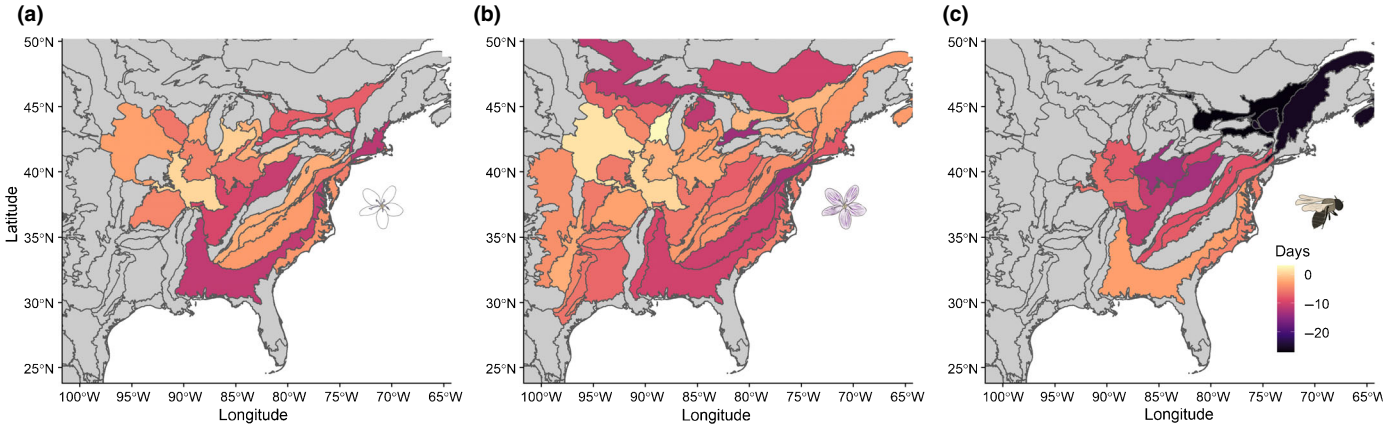

Fig. 5 Maps of changes in phenology at the ecoregion scale between future predictions for a 20-yr time period (2081–2100) with the shared socioeconomic pathway (SSP) scenarios (SSP5-8.5) and model-estimated dates for a recent 30-yr time period (1981–2010). (a) Mean flowering dates of white flowers of *Claytonia virginica*; (b) mean flowering dates of pink flowers of *C. virginica*; and (c) mean occurrence dates of *Andrena erigeniae*. Negative values indicate earlier dates and positive values indicate later dates compared to present day estimates.

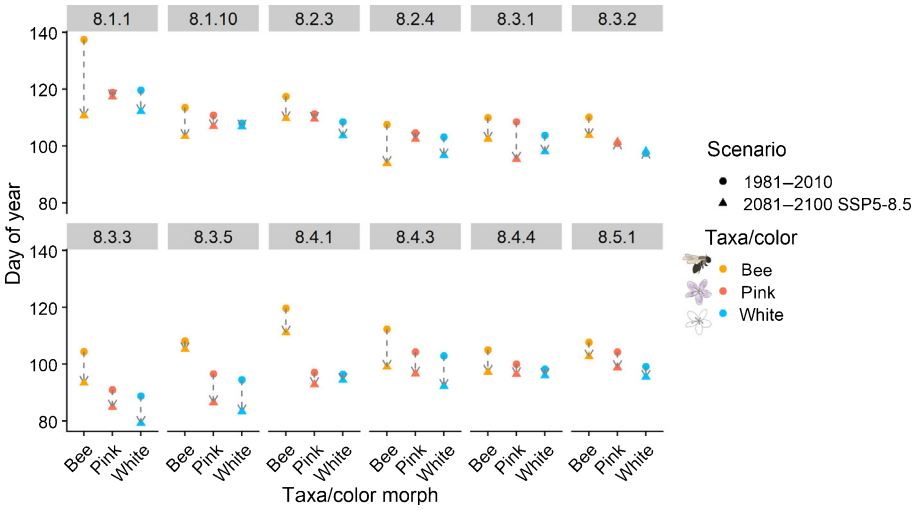

Fig. 6 Predicted shifts of *Claytonia virginica* mean flowering dates (white flowers, blue; pink flowers, coral) and *Andrena erigeniae* mean occurrence dates (orange) between recent (1981–2010) and future (2081–2100) climate conditions (SSP5-8.5) across 12 ecoregions. Circles represent estimates under current average climatic conditions and triangles represent estimates under future conditions. The direction and magnitude of the predicted phenological shifts are represented by dotted arrows. Each panel represents one Level III ecoregion. The twelve listed ecoregions are: Eastern Great Lakes and Hudson Lowlands (8.1.1), Erie Drift Plain (8.1.10), Central Corn Belt Plains (8.2.3), Eastern Corn Belt Plains (8.2.4), Northern Piedmont (8.3.1), Interior River Valleys and Hills (8.3.2), Interior Plateau (8.3.3), Southeastern Plains (8.3.5), Ridge and Valley (8.4.1), Western Allegheny Plateau (8.4.3), Blue Ridge (8.4.4), and Middle Atlantic Coastal Plain (8.5.1).

slight preference for pink flowers reported by Frey (2004). Though populations of *C. virginica* may flower across a few weeks, the protandrous flowers are only staminate for 1 d, and the pistillate stage lasts 1–8 d (Schemske, 1977). Thus, even such seemingly small degrees of temporal separation can have ecological significance, and contribute to assortative mating and the maintenance of color morphs. For instance, a difference in flowering of 1 wk between cytotypes of the insect-pollinated *Chamerion angustifolium* can reduce inter-cytotype mating opportunities from 49%, as expected under random mating, to 2% (Husband & Schemske, 2000). Different cytotypes of *C. virginica* may occupy slightly different temporal niches (Lewis, 1976). However, no phenological differences were observed between diploids and polyploids in a previous controlled greenhouse study (Doyle, 1981), and no potential relations between cytotypes and floral color or pollinator visitation are known. Diploids and polyploids do not vary in morphology (with the possible exception of leaf width), and pollinators are commonly observed traveling between diploid and polyploid individuals (Doyle, 1981, 1983). Further, polyploidy in *C. virginica* has been suggested to be a later phenomenon superimposed upon distinct evolutionary lineages post divergence (Doyle, 1983). Nonetheless, further studies are needed to assess the role of cytotype differences in phenological behavior, such as common garden experiments (Segraves & Anneberg, 2016; Rezende *et al.*, 2020).

In addition to differences in flowering time, we found evidence of differing phenological sensitivity to temperature among color morphs across *C. virginica*'s range. Both color morphs were more

phenologically responsive to temperature in warmer regions than in colder ones. Similar patterns have been observed for other insect-pollinated species across the eastern USA (Park *et al.*, 2019). This may be due to the colder and less predictable winter and spring climates of the northeastern USA. Sensitive phenological tracking of temperatures early in the year can pose large risks to reproductive success, because warm periods are often followed by chilling in this area (Zohner & Renner, 2014; Park *et al.*, 2019). By contrast, temperatures are higher, and the advent and progression of seasons are less variable, in the southern range of *C. virginica*, and thus a sensitive phenological response poses less of a risk. The flowering dates of white morphs were more sensitive to changes in winter temperature than those of pink morphs in > 50% of co-occurring ecoregions. Interestingly, the phenological sensitivities of the color morphs were more similar in colder regions, suggesting less room for variable responses in shorter growing seasons. It has been suggested that the phenological sensitivity to interannual variation is largely driven by plastic responses to short-term local conditions (Mazer *et al.*, 2021), and plants in the northeastern USA may have a more limited capacity to adjust their phenology in response to changes in temperature.

Plants and pollinators display opposing patterns of phenological sensitivity

Our data suggest that on average, *A. erigeniae* are in flight 6–9 d later than *C. virginica* flowering, which may coincide with peak abundance of floral resources. Though the opportunistic nature of our data may affect this result, this difference is relatively consistent across the species' ranges, suggesting that this finding is likely accurate. The thermal threshold for bee flight may be higher than that for *C. virginica* flowering (Schemske, 1977), and it has been observed that pollinator emergence does not precisely align with *C. virginica* flowering (Schemske *et al.*, 1978).

It has been suggested that the phenological responsiveness of bees may lag behind that of the flowers they pollinate (Stemkovski *et al.*, 2020). It has also been reported in previous studies that bees may shift their phenology more rapidly than their host plants in response to climate change (Parmesan, 2007; Olliff-Yang & Mesler, 2018). Our study suggests that these conflicting results may not be mutually exclusive. We demonstrate that the phenology of flowering tends to be more sensitive to interannual variations in temperature than that of bees in warmer areas, while bee phenology is more sensitive than flowering phenology in colder areas. This might be attributed to the different life histories of the two species. *Claytonia virginica*, an herbaceous perennial, does not have any chilling requirements for emergence (Risser & Cottam, 1967), but winter temperatures likely affect the speed of its vegetative growth and eventual flowering. In addition, temperature may provide an independent cue to initiate flowering after buds are fully developed (Schemske, 1977; Schemske *et al.*, 1978; Kinmonth-Schultz *et al.*, 2019). Thus, changes in temperature act upon multiple physiological and developmental processes in *C. virginica*, which may also be affected by photoperiod and rainfall (Schemske *et al.*, 1978; Forrest & Miller-Rushing, 2010). *Claytonia virginica* phenology in northern regions may be constrained by shorter day lengths and less rainfall, limiting its response to changes in temperature. Indeed, we found that increases in temperature advanced *C. virginica* flowering time to a greater degree under wetter conditions. By contrast, *A. erigeniae* overwinter as adults underground (Davis & LaBerge, 1975), and are thus likely less affected by abiotic factors other than temperature as a cue for their emergence (Bartomeus *et al.*, 2011; Forrest, 2016). Our results suggest that the phenologies of interacting plants and pollinators may respond to the same environmental cues to different degrees; react to different environmental cues; and differ in their phenological sensitivity to these cues across their ranges.

We found opposing trends of phenological sensitivity variation for *C. virginica* and *A. erigeniae*. In contrast to *C. virginica* flowering, which is more responsive to changes in temperature in warmer regions, *A. erigeniae* occurrence is more sensitive in colder regions. Similar patterns were observed in the flowering time of arctic plants (Prevéy *et al.*, 2017), but to our knowledge, not in insects, though a recent study suggested that butterfly species may be less phenologically sensitive to temperature in cooler areas across a local elevational gradient (Gutiérrez & Wilson, 2021), and another found that a bee species shifted phenology at different rates and directions across latitudes with its host plant species over the last century (Weaver & Mallinger, 2022). Our data do not allow us to ascertain why the phenological sensitivity of *A. erigeniae* shows opposing trends to that of the host plant. However, we may hypothesize that shorter growing seasons in colder areas exert pressure for the bee to initiate flight as soon as conditions become favorable. In contrast to the perennial *C. virginica*, *A. erigeniae* is a univoltine vernal bee with a short lifespan. It must complete reproduction in the short window of time between *C. virginica* flowering and canopy closure, as mating occurs on *C. virginica* plants and oviposition occurs on *C. virginica* pollen balls (Davis & LaBerge, 1975). The bee is further constrained by thermal thresholds for flight and foraging and the short period of time for which *C. virginica* flowers are open each day (Davis & LaBerge, 1975). Finally, shifts in *C. virginica* flowering times can lead to varying levels of reproductive output, suggesting that their pollinators are not tracking climatic changes to the same degree (Schemske, 1977). It will be critical to evaluate whether these opposing patterns of phenological sensitivity between *C. virginica* and *A. erigeniae* are indicative of more general trends across the landscape, as bees are the main animal pollinator in most ecosystems (Gauld & LaSalle, 1993).

Climate change will result in heterogeneous patterns of phenological mismatch

While some studies have shown that plants and their pollinators seem to be maintaining synchrony despite changes in climate (Bartomeus *et al.*, 2011, 2013; Iler *et al.*, 2013), others suggest increasing asynchrony (McKinney *et al.*, 2012; Kudo & Ida, 2013; Olliff-Yang & Mesler, 2018). Our results suggest that the temporal gaps between *C. virginica* flowering and *A. erigeniae* activity will increase in southeastern regions, potentially leading

to phenological mismatches in the future. By contrast, in most other areas, increased temporal convergence among color morphs of *C. virginica* and its pollinator were predicted with continued climate change, driven by the faster advancement of *A. erigeniae* phenology than *C. virginica* flowering time. However, this trend is concerning because it may eventually result in *A. erigeniae* emerging when floral resources are not sufficient. Indeed, our results suggest that *A. erigeniae* occurrence may overtake *C. virginica* flowering in several ecoregions in the following decades. Thus, phenological mismatches can occur even with increased temporal convergence.

The impacts of such mismatches may manifest in different ways across species and their ranges. For instance, pink morphs of *C. virginica* may be less impacted by climate change-induced phenological shifts than their white counterparts, as their sensitivity to warming is closer to that of *A. erigeniae* in many areas. In the northern areas, *C. virginica* is near-exclusively pollinated by *A. erigeniae*, but it can also be pollinated by bee flies (Bombyliidae) in the south (Parker *et al.*, 2018), which may be able to keep pace with advances in flowering. However, *A. erigeniae* females only collect pollen from *C. virginica* (Parker *et al.*, 2016). Given the short life span and univoltine nature of *A. erigeniae* and its obligate reliance upon *C. virginica*, the negative impacts of phenological mismatch may be more immediate and severe for the bees. Finally, the time and resources available for successful *C. virginica* (and *A. erigeniae*) reproduction may decrease due to faster advances of canopy closure – it has been shown that the leaf-out of overstory trees can be more responsive to increased spring temperature than understory wildflower phenology in the northeastern USA (Heberling *et al.*, 2019). Our predictions of how the synchrony of these taxa will change in the future should be tempered with the fact that they largely apply to phenological peaks. Other components of phenology, such as flowering duration, may respond differently to changes in climate (CaraDonna *et al.*, 2014; Iler *et al.*, 2021), and thus require further investigations.

Our work demonstrates the utility of crowd-collected observations and natural history collections for studies of phenology and ecological interactions. However, our findings could be affected by biases, gaps, and uncertainties in natural history collections and citizen science data (Daru *et al.*, 2018). As our species are represented by a large number of records, well documented across space and time, and demonstrate a high degree of congruence among collection-based, observation-based, and expert knowledge-based inferences of their ranges, the effects of such issues may be minimal. Nonetheless, our results should be interpreted with caution, and further integration across multiple phenological data sources may help address some of these gaps and biases (Park *et al.*, 2021). It is also possible that different patterns of phenological sensitivity across species ranges may depend on how climatic and/or geographical regions are delimited, though testing an alternative regionalization scheme (i.e. plant hardiness zone) yielded similar results (Fig. S6), suggesting that the patterns we observe here are robust to spatial binning choices. Still, it should be noted that our assessments of phenological sensitivity patterns across different environments are limited by the relatively small number of spatial bins with sufficient sampling, particularly for *A. erigeniae*. We expect that the rapid increase in specimen digitization and citizen science efforts will enable more informative assessments in the future (Hedrick *et al.*, 2020; Feng *et al.*, 2022). In addition, other behavioral and physiological responses to climate change can also substantially affect species interactions (Harris *et al.*, 2018).

Finally, our future predictions rely on the assumption that phenological responses will continue to follow current relationships. However, these relationships may not scale linearly with increasingly large shifts in climate, changes in species' distributions and abundance (Hegland *et al.*, 2009; Fu *et al.*, 2015; Güsewell *et al.*, 2017), and changes in other environmental factors affecting phenology (Halsch *et al.*, 2021). Further, we do not know whether these phenological responses are plastic or adaptive in nature; nor do we know their limits. Other biotic factors, such as the activity of herbivores and parasites, may additionally influence the phenology of these species (Davis & LaBerge, 1975; Frey, 2004), as can anthropogenic factors such as urbanization (Neil & Wu, 2006; Li *et al.*, 2019). Though iNaturalist observations and natural history collections may be biased towards urban areas (Daru *et al.*, 2018; Di Cecco *et al.*, 2021; Mesaglio *et al.*, 2021), $<11\%$ of *C. virginica* observations in this study were categorized to be in urban areas by the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type product (Friedl *et al.*, 2010). While our predictions represent the most informed estimates of how climate change will affect the temporal (a)synchrony of *C. virginica* color morphs and *A. erigeniae* based on current knowledge, integrating additional information on the physiology and genetics of these species and others they may interact with will be crucial to elucidating the ecological and evolutionary mechanisms underlying this relationship.

Harnessing the power of citizen science and natural history collections, we demonstrated that phenological sensitivity can vary between color morphs of the same species, across species' ranges, and between interacting species. Plant–pollinator systems are susceptible to differing degrees of temporal mismatch across their interacting ranges because pollinators and plants can differ in their phenological responses to warming within and among species. Our study thus demonstrates the complexity and fragility of ecological interactions in time and the necessity of incorporating variation in phenological responses across multiple axes when predicting how ecological interactions will change in the future. We also note the potential of these data for helping develop machine learning approaches to upscale the generation of phenological data from digital products (Davis *et al.*, 2020; Hedrick *et al.*, 2020). Such efforts will be critical to enhancing our ability to forecast future changes in communities and ecosystems across space and time in an era of increasing global change.

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Author contributions

DSP conceived the initial idea. DSP gathered GBIF data and digital images. HTT scored the phenology for the digital images and designed the species icons in graphs. YX analyzed data and prepared the figures. YX wrote the initial draft, DSP made extensive edits, additions, and revisions, and all authors contributed to further revisions.

ORCID

Daniel S. Park https://orcid.org/0000-0003-2783-530X
Yingying Xie https://orcid.org/0000-0002-7759-6178

Data availability

Occurrence data used in the study are publicly available through GBIF (https://www.gbif.org/). The R code used in this study is available on GitHub (https://github.com/phylosaurus/phenology-Claytonia).

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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 Maps of model estimated phenology across Level III ecoregions under 30-yr climate normals (1981–2010).

Fig. S2 Choropleth maps of *Claytonia virginica* mean flowering dates and *Andrena erigeniae* mean occurrence dates across Level III ecoregions from future predictions.

Fig. S3 Choropleth maps depicting future changes in *Claytonia virginica* mean flowering dates and *Andrena erigeniae* mean occurrence dates at the ecoregion scale.

Fig. S4 Estimated present (1981–2010) and future (2041–2060 and 2081–2100) mean flowering dates of *Claytonia virginica* color morphs and mean occurrence dates of *Andrena erigeniae* under two climate change scenarios (SSP2-4.5 and SSP5-8.5) across 12 ecoregions.

Fig. S5 Predicted change in temporal gaps between mean flowering dates of *Claytonia virginica* color morphs.

Fig. S6 The relationships between phenological sensitivities and long-term average winter minimum temperature (1901–2021) across sites in plant hardiness zones for two color morphs of *Claytonia virginica* and *Andrena erigeniae*.

Table S1 Akaike information criterion (AIC) values and difference in AIC values among linear mixed effect models in the first round of model selection for two species.

Table S2 Akaike information criterion values and degrees of freedom of linear mixed effect models in the second round of model selection for two species.

Table S3 Standard deviation of random intercepts and random slopes of climate variable in the best linear mixed effect models for two species.

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