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Tracking phenology over 125 years among native flora of the New Jersey Pine Barrens[1]

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Abstract. Climate change has altered the phenological timing of plants across the globe. These changes are especially concerning for plants with small distributions and in unique ecological sites. Here, we examined changes in phenology with respect to temperature and year over a 125-yr span for 12 herbaceous species native to the lowlands of the New Jersey Pine Barrens using herbarium specimens and citizen science observations. Among early summer flowering species, flowering occurred on average 1.42 days/°C earlier in the spring of the corresponding year. Early summer flowering species flowered at an average rate of 0.071 days/yr earlier over the 125-yr study period, whereas no significant change was detected in flowering times of late summer species. Exploration of a set of sister taxa with differing range sizes resulted in no detectable shifts in phenology, which may be explained by evolutionary relatedness or flowering in late summer. The variation in responses to species in the New Jersey Pine Barrens may alter the balance of this ecosystem in the future, as some species respond to changing temperatures, whereas others do not. These results add to a growing body of work suggesting that variations in temperature due to climate change are affecting plant phenology.

Key words: citizen science, climate change, *Eupatorium*, herbarium specimens, species distribution modeling

Climate change is a phenomenon that affects all aspects of the sustainability of plant life, including plant diversity (Thuiller et al. 2005), plant respiration (Ryan 1991), and plant diseases (Garrett *et al.* 2006). Plant phenology is yet another vital component of a plant's life cycle that is greatly affected by climate change as the timing of flowering and fruiting often depends on environmental cues, particularly temperature (Miller-Rushing and Primack 2008; Calinger *et al.* 2013; Davis *et al.* 2015; Pearson 2019).

Variation in flowering times due to changes in mean spring temperature has been detected among plant communities within small regions (Primack *et al.* 2004; Miller-Rushing et al. 2006; Panchen et al. 2012; Park and Schwartz 2014; Davis *et al.* 2015) and at continental scales (Calinger *et al.* 2013; Panchen and Gorrelick, 2016; Munson and Long 2017; Park *et al.* 2019; Pearson 2019). Furthermore, studies focused on select taxa across their native range have revealed shifts to earlier flowering times in warmer years (Robbirt *et al.* 2011; Hart *et al.* 2014; Matthews and Mazer 2015; Rawal *et al.* 2015). Considering the species diversity of any given community, flowering times can span several months, starting with early spring ephemerals extending to early fall bloomers. Categorization of flowering time within a growing season in an ecosystem has led to the supposition that spring and early summer flowering species exhibit more variation in bloom times in response to changes in mean spring annual temperature as compared with late summer or fall flowering species (Calinger *et al.* 2013; Mazer *et al.* 2013; Park and Schwartz 2014; Davis *et al.* 2015; Park *et al.* 2019; Pearson 2019). Such studies have found that spring flowering time has changed 1.8 (Pearson 2019) to 3.5 days/°C (Davis *et al.* 2015) earlier over the past century.

Although plants can exhibit variable responses to our changing climate that may prevent their extinction at local scales, changes in the timing of phenology can also affect interactions between plants and their environment, which are often tied to a plant's reproductive success. This includes the recruitment of animal pollinators and seed dispersers (Calinger *et al.* 2013), timing of water availability within an ecosystem (Munson and

Long 2017), and exposure to herbivores (Meineke *et al*. 2018). Pollination is a key phase in plant phenology and any acceleration in flowering date could cause a temporal mismatch with common pollinators (Memmott *et al*. 2007; Rafferty and Ives 2012). Moreover, climate change may also significantly reduce pollinator populations because of limited food supply from plants (Memmott *et al*. 2007).

These concerns are especially relevant in the New Jersey Pine Barrens, where to date, no studies have examined the effects of changes in climate on phenology. This unique habitat spans seven counties in central New Jersey and is characterized by distinct higher-elevation areas dominated by pines and oaks, as well as lower-elevation areas inhabited by a diverse array of herbaceous species. There are *ca*. 850 vascular plant species growing in the Pine Barrens, of which 580 are native (Boyd 2008). Wildflowers in the community bloom between March and October (Boyd 2001). Previous studies have highlighted that spring flowering species are more variable in their flowering times than later flowering species in our changing climate (Sherry *et al*. 2007; Calinger *et al*. 2013; Mazer *et al*. 2013; Park and Schwartz 2014; Davis *et al*. 2015; Pearson 2019). Given these findings, we would predict that some species, particularly earlier flowering species, will exhibit more variation in flowering times. This suggests that these species are better able to adapt to changes in climate as compared with late summer or fall flowering species. Although all plant species of the Pine Barrens have the potential to be affected by a changing climate, this study focuses on the phenology of a set of herbaceous species representative of the diversity among lowland habitats.

Recent work comparing annual *versus* perennial plants (Fitter and Fitter 2002), C3 *versus* C4 photosynthesis (Munson and Long 2017), invasive *versus* native plants (Calinger *et al*. 2013), and wind and animal pollination syndromes (Fitter and Fitter 2002; Calinger *et al*. 2013) have continued to help decipher key life-history traits connected to phenological responses to climate change. Phenology is also key to determining species distribution limits (Chuine 2010; Chapman *et al*. 2014). Here we have the opportunity to provide a closer look at sister species with overlapping ranges in the clade *Eupatorium*, namely *E. perfoliatum* L. and *E. resinosum* Torr ex DC. *Eupatorium perfoliatum*, the common boneset, is a widespread perennial species that inhabits open wetlands; *E. resinosum*, the Pine Barrens thoroughwort, is a rare perennial species native to the New Jersey Pine Barrens. Compared with *E. perfoliatum*, *E. resinosum* has fewer heads per ramet, higher variation in seedling survivorship, and greater dependence on asexual reproduction (Byers and Meagher 1997). In this study, we not only compare phenology of these species but also examine and compare niche space on the basis of environmental factors as we explore range as an additional life-history trait in studies of phenology and climate change.

Detecting changes in phenology depends on accessing and analyzing a historical record of flowering times. Herbarium specimens are an excellent record of plant history spanning hundreds of years from which phenology and locality data can be extracted and used to detect changes in phenology over the past century (Primack *et al*. 2004; Miller-Rushing *et al*. 2006; Robbirt *et al*. 2011; Davis *et al*. 2015). With large-scale efforts to digitize museum collections over the past decade, these data are all the more accessible (Soltis 2017). Today, there are almost 50 million digitized specimens in the Integrated Digitized Biocollections portal (iDigBio 2021), further enabling studies of changes to plants in recent history. Though declines in recent collections have been noted (Hart *et al*. 2014), verified observations from citizen science initiatives such as iNaturalist or BudBurst can also provide valuable data points to identify flowering times across the globe.

To study phenology changes and generate species distribution models for herbaceous members of the New Jersey Pine Barrens, we used natural history collections and citizen science observations dating back to the years 1801 for locality data and 1895 for phenology data. Taxa selected for this study included both early and late summer blooming species, which allowed for an investigation of the effects of mean spring temperature and year on flowering time, as reflected in similar studies in different regions (Sherry *et al*. 2007; Davis *et al*. 2015; Pearson 2019).

Materials and Methods. Pine Barrens Ecosystem. The Pine Barrens are ecologically defined by nutrient-poor, sandy, acidic soils concentrated with quartz and silica, but deficient in calcium, magnesium, and potash (Boyd 2008). A variety of microclimates as well as a dependence on

Table 1. Descriptive information for the 12 focal species occurring in the lowland habitat of the New Jersey Pine Barrens. For each species, the family, common name, general flowering season (bloom time), and microenvironment are provided. Also, whether a species range extends beyond New Jersey (outside NJ) in addition to the New Jersey Department of Environmental Protection (NJDEP) status and the number of herbarium specimens and observations (No. records) consulted in the analyses are indicated.

Species	Family	Common name	Bloom time	Pine Barrens microenvironment	Outside NJ	NJDEP status	No. records[a]
Asclepias rubra L.	Apocynaceae	Red milkweed	ES	WCS/OB	Yes	Imperiled	92
Eupatorium perfoliatum L.	Asteraceae	Common boneset	LS	WCS/OB	Yes	Least concern	201
Eupatorium resinosum Torr ex DC.	Asteraceae	Pine Barren thoroughwort	LS	WCS/OB	No	Imperiled	172
Iris prismatica Pursh	Iridaceae	Slender blue flag	ES	HSF & SMFP	Yes	Least concern	133
Narthecium americanum Ker Gawl	Nartheciaceae	Bog asphodel	ES	SMFP	No	Imperiled	103
Oclemena nemoralis (Aiton) Greene	Asteraceae	Bog aster	LS	WCS/OB	Yes	Least concern	198
Rhexia mariana L.	Melastomataceae	Maryland meadow beauty	LS	HSF	Yes	Imperiled	113
Rhexia virginica L.	Melastomataceae	Meadow beauty	LS	WCS/OB	Yes	Least concern	244
Sabatia difformis (L.) Druce	Gentianaceae	Lance-leaved sabatia	LS	WCS/OB & HSF & SMFP	Yes	Least concern	354
Sarracenia purpurea L.	Sarraceniaceae	Purple pitcher plant	ES	WCS/OB & HSF & SMFP	Yes	Least concern	58
Schwalbea americana L.	Orobanchaceae	American chaffseed	ES	SMFP	No	Critically imperiled	75
Trientalis borealis Raf.	Primulaceae	Starflower	ES	WCS/OB	Yes	Least concern	126

ES = early summer blooming species, LS = late summer blooming species, WCS/OB = white cedar swamps/open bogs, HSF = hardwood swamp forests/along wooded streams, SMFP = savannas/meadows/floodplains.

[a] Records implies both herbarium specimens and observations.

frequent wildfires to open the canopy and add minerals to the soil are unique ecological traits that distinguish the Pine Barrens from other types of nearby habitat in the region. The Pine Barrens are home to 150 rare and endangered plant species (Pinelands Preservation Alliance 2020) with limited range sizes that may be especially vulnerable to climate change (Thomas et al. 2004). This ecosystem is already fragile because of encroachment of human development, past exploitation of its resources, and the suppression of wildfires (Boyd 2008), meaning climate change represents yet another risk to the area.

Two distinct environments comprise the New Jersey Pine Barrens—higher- and lower-elevation areas. The higher-elevation areas, or uplands, are dominated by the iconic pitch pine (*Pinus rigida* Mill.), shortleaf pine (*Pinus echinata* Mill.), and several species of oak (*Quercus* spp.). Here, the understory consists of stands of mountain laurel (*Kalmia latifolia* L.), black huckleberry (*Gaylussacia baccata* (Wangenh.) K.Koch), blueberry (*Vaccinium corymbosum* L.), and other shrub species of the Ericaceae (Boyd 2008). Although pitch pine extends into the lower-elevation areas, the lowlands are quite distinct from the uplands in having increased access to water (both standing and in aquifers) as well as increased access to sunlight due to gaps in the tree canopy. Having the water table close to the surface soil in the lowlands creates several unique microenvironments such as swamps, bogs, savannahs, and floodplains that support the growth of hundreds of herbaceous plant species, making it much more speciose as compared with the uplands. This study focuses on phenological responses of lowland herbaceous species.

Species Selection. A total of 12 herbaceous plant species from the lowlands of the New Jersey Pine Barrens was selected, representing 10 genera and nine families (Table 1). In selecting focal taxa for this study, aquatic species, grasses (Poaceae), sedges (Cyperaceae), or species such as orchids, which were represented by too few (< 50) digitized herbarium specimens, were not considered. Another criterion applied to species selection

was confident assessment of phenological stage from digitized herbarium specimens. Applying these criteria resulted in sampling only species that flowered in early and late summer, but not in spring. In total, our sampling reflects the full breadth of microenvironments found in the lowlands (Table 1), with species that occur in white cedar swamps/open bogs, hardwood swamp forests/along wooded streams, and savannas/meadows/flood plains.

To explore range size in conjunction with changes in phenology, we focused on sister species with drastically different distributions from our 12 focal species, namely *E. perfoliatum* (common boneset) and *E. resinosum* (pine barren thoroughwort; McKain et al. 2010). Both species occupy open wetlands, but the range of *E. perfoliatum* spans the eastern half of North America, whereas *E. resinosum* is represented by a few remaining populations in the Pine Barrens of New Jersey and possibly North Carolina (Byers and Meagher 1997). The entirety of the range of *E. resinosum* is contained within the range of *E. perfoliatum* (Byers and Meagher 1997).

HERBARIUM DATA COLLECTION. A total of 1,869 herbarium records of the 12 focal species were obtained from regional herbaria. Digitized collections from over 40 individual herbaria were accessed from the Mid-Atlantic Herbaria Consortium as well as additional specimens from the C.V. Starr Virtual Herbarium at The New York Botanical Garden Steere Herbarium. Specimens were examined in person at the Chrysler Herbarium of Rutgers University and the Harvard University Herbaria. Only collections from New Jersey were studied despite some species with ranges extending beyond state borders (Table 1). An additional 53 records for the Pine Barrens (Burlington, Camden, Ocean, Gloucester, Atlantic, Cumberland, and Cape May counties) were obtained from iNaturalist (2020) and filtered to include only the earliest flowering record for each year (data available for years 2003 to 2019), as well as verified through comparison with herbarium specimens when observations were not classified as research grade or definitively identified by the community and experts on iNaturalist. First flowering was determined from assessment of multiple specimens or observations, particularly for collection years spanning 1900–2000. However, some years were represented by a single flowering specimen during this span. Ultimately,

this set of specimens represented all 21 counties in New Jersey with collection years ranging from 1801 to 2019.

For each specimen, the date of collection, reproductive condition, and locality information were recorded. Reproductive condition, scored as flowering or not flowering, was added for each specimen on the basis of visual analysis. Specimens were scored as flowering by the presence of full petals and stamens exhibiting signs of dehiscence (e.g., presence of pollen grains). Everything else was scored as not flowering (flowers only in bud, fruiting, sterile). Using R statistical software (R Core Team 2020) version 3.5.0, data were filtered to remove records that did not have county or state information, and then spelling and formatting errors were corrected through comparison with a correct list of state/county pairs (U.S. Census Bureau 2016).

PHENOLOGY IN THE NEW JERSEY PINE BARRENS. To track changes in phenology, we analyzed how each species' earliest flowering date correlated to year and mean spring temperature of the corresponding year it was collected. To extract the earliest flowering date and year for each species from the herbarium specimens, data were filtered, which involved several steps completed in R. As only *E. resinosum*, *Narthecium americanum* Ker Gawl, and *Schwalbea americana* L. have distributions restricted to the Pine Barrens of New Jersey (Table 1), the remaining data were filtered to only include specimens with localities within the seven counties encompassing the New Jersey Pine Barrens (Burlington, Camden, Ocean, Gloucester, Atlantic, Cumberland, and Cape May). The date of collection of each specimen was converted to day of year from year–month–day entries by creating a time series from the data with the R core stats function ts. Specimens without complete collection dates were removed. Then, the data were filtered to only include specimens that were flowering. This resulted in a data set of 819 records. Specimens with flowering dates 30 days before or after the average flowering date for a given species were considered outliers and resulted in removal of 31 records from the analysis. The earliest flowering date for each year represented in specimens for each species was determined from these filtered sets of data and used in downstream analyses. Available climate data ranged from 1895 to 2019, and therefore occurrence records before this period were excluded from further analyses.

Before focusing on mean spring temperature, the mean annual temperature of each year was calculated in R. Mean annual temperature was compared with year, was visualized in a plot, and a linear regression was used to verify an overall increase in temperature due to climate change over the time span of the study. To identify mean spring temperature (defined as the mean temperature of February through May) for all years of the study, average monthly temperature data from 1895 through 2019 were obtained from the Rutgers University Climate Lab (Rutgers University 2019) for the southern half of the state of New Jersey. These data were combined with flowering data for each corresponding year. The data were visualized in R and a linear regression was performed between mean spring temperature and year to verify its increase during the period of our study.

To examine the relationship between phenology, climate, and year, a series of linear mixed-effects models was used. These models were used to test for overall relationships between earliest flowering date and year as well as earliest flowering date and mean spring temperature. Linear mixed-effects models were conducted using the nlme package (Pinheiro *et al*. 2018) using the lme function in R (R Core Team 2020) as outlined in Davis *et al*. (2015). Species were treated as a random effect in the model, as this test did not examine each species in isolation, but rather the set of species as a whole. Two linear mixed-effects models analyzing each relationship described above were conducted for three sets of species. The first was completed with the complete set of 12 focal species, the second with the set of 6 early summer flowering species (late May–early July; Table 1), and the third with the set of 6 late summer flowering species (early July–late September; Table 1), as defined by Boyd (2001).

SPECIES DISTRIBUTION MODELING AND PHENOLOGY IN *EUPATORIUM*. To provide a clear picture of the distributions of *E. perfoliatum* and *E. resinosum* within New Jersey, species distribution models (SDMs) were generated for each species. All available 19 climate predictors from the World-Clim version 2.0 database (Fick and Hijmans 2017) were downloaded at a 0.5-min resolution over the geographic area of New Jersey. A collinearity analysis was conducted to remove variables contributing similar predictions to improve the model. This analysis was applied using the core stats functions in R to the 19 climatic variables and predictor variables of $r > 0.7$ were removed to leave only the most informative variables (Dormann *et al*. 2013). Nine variables were highly correlated with one another and removed, leaving 10 variables for use in SDMs. The 10 selected variables included annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, and precipitation of driest quarter.

As most herbarium records examined were not georeferenced, the collection location of each specimen was approximated by the New Jersey municipality centroid in which it was collected. Data for municipality centroids were generated using a shapefile of New Jersey municipalities (U.S. Census Bureau 2016) and the rgeos package (Bivand and Rundel 2018) in R. To account for the fact that presence locations were extrapolated from herbarium specimens rather than precise global positioning system coordinates, climatic variables were averaged over the entire municipality using the rgeos and raster (Hijmans 2017) packages for both species ranges (Park and Davis 2017). Using the 10 climate variables and municipality centroids extracted for each species, two present-day SDMs were created using the maximum-entropy method MAXENT (Phillips *et al*. 2006) as implemented in the R package dismo (Hijmans *et al*. 2017). SDMs were fit with 80% of the data used for training and 20% used for testing the model. Ten replicates were completed, and model fit was evaluated on the basis of the area under the receiver operating characteristic curve (AUC) using AUC values (Spriggs et al. 2019). The border of the Pinelands National Reserve of New Jersey was then added to each SDM (NJGIN Open Data 2020).

To compare the climate space of *E. perfoliatum* and *E. resinosum*, a principal component analysis (PCA) was conducted to provide a visual analysis of the correlation between the environmental variables of both species. The PCA incorporated all 19 available WorldClim climatic values across the ranges of *E. perfoliatum* and *E. resinosum* on the basis of herbarium locality data by municipality and using the pcaMethods package (Stacklies et al. 2007) in R (R Core Team 2020).

Statistical assessment of the differentiation of the niche spaces occupied by *E. perfoliatum* and *E. resinosum* was performed with an identity test

using the ENMTools package in R with 100 pseudoreplicates (Warren et al. 2017). Schoener's D values, which are the output of an identity test and measure the probability of finding the right environmental conditions for the species in any one pixel, range from 0 (niches do not overlap) to 1 (niches are identical). Two sets of D empirical values were analyzed, representing overlap in geographic space (D) and the other representing overlap in environmental space (D env.). These values were then compared with those created by the pseudoreplicates of randomly partitioned data sets from a pool of both species. The results of this test either support or refute the null hypothesis that the geographic space and environmental space occupied by the two species are identical.

To explore the effect of mean spring temperature and year on flowering time for each species of *Eupatorium*, a linear regression analysis (lm function) was completed using a subset of the main data set as prepared for phenological analysis described above in the R core stats package (R Core Team 2020).

Results. Effects of Year and Temperature on Phenology. A significant increase in mean annual temperature since 1895 was observed ($P < 0.01$), as well as a significant increase in mean spring temperature ($P < 0.01$). Our analysis of the effects of year (Fig. 1) and mean spring temperature (Fig. 2) on earliest flowering date shows differences across the 12 focal species. Although some species did not show a strong relationship, others showed that earlier flowering date corresponded to warmer mean spring temperatures and later years (e.g., *E. perfoliatum*, *N. americanum*; Figs. 1, 2); other species flowered later in the season with increased temperatures and later years (e.g, *Oclemena nemoralis* (Aiton) Greene, *Rhexia virginica* L.; Figs. 1, 2).

Analyses of variance of the linear mixed-effect model using a random effect of all 12 species showed no significant relationship between earliest flowering date and year ($P > 0.05$; Fig. 1), nor a significant relationship between earliest flowering date and mean spring temperature ($P > 0.05$; Fig. 2). For the six early summer flowering species, a significant negative relationship was found between year and flowering time ($P < 0.05$), as well as between mean spring temperature and flowering time ($P < 0.05$). Early summer flowering species were estimated to flower 1.42 days/°C increase in

mean spring temperature earlier and 0.071 days/yr earlier during the entire 125-yr period of our study. For the six late summer flowering species no significant relationship between earliest flowering date and year ($P > 0.05$; Fig. 1) nor between earliest flowering date and mean spring temperature ($P > 0.05$; Fig. 2) was revealed.

Eupatorium Distribution and Phenology. SDMs generated from herbarium locality data showed distinct distributions for *E. perfoliatum* and *E. resinosum* (Fig. 3). The SDM for *E. perfoliatum* (Fig. 3a) showed suitable climate space throughout the entire state of New Jersey, whereas the SDM for *E. resinosum* (Fig. 3b) was much more concentrated in southern New Jersey in the Pine Barrens and surrounding areas. Each SDM was assessed for fit by the analysis of the AUC, and regardless of the data used in SDMs, the models fit well (AUC $\geq$ 0.80). Visualizing climate space through a PCA showed that *E. resinosum* occupied a subset of the climate space of *E. perfoliatum* (Fig. 4), with PC1 and PC2 accounting for 51.72% and 15.83% of the variation in climate space, respectively. Analysis of individual variables that make up the PCA show that *E. perfoliatum's* climate space is more strongly associated with winter minimum temperatures as compared with *E. resinosum*.

An identity test between the modern ranges of *E. perfoliatum* and *E. resinosum* in New Jersey rejected the null hypothesis that the geographic area covered by both species was identical (D; $P < 0.01$) and also rejected the null hypothesis that the environmental spaces of the two species were identical (D env.; $P < 0.01$). The empirical Schoener's D values of 0.444 (D) and 0.52 (D env.) provided by the identity were significantly lower than those created by the pseudoreplicates of randomly partitioned data sets from a pool of both species ($P < 0.01$).

Parametric linear regressions for *E. perfoliatum's* and *E. resinosum's* change in flowering time in response to year or mean spring temperature resulted in no significant relationship with earliest flowering date in either species ($P > 0.05$).

Discussion. Global Effects of Climate on Phenology in the Pine Barrens. Here we provide the first analysis of the effects of mean spring temperature and year on the phenology of native species to the Pine Barrens of New Jersey over the past century. We did not find evidence to suggest
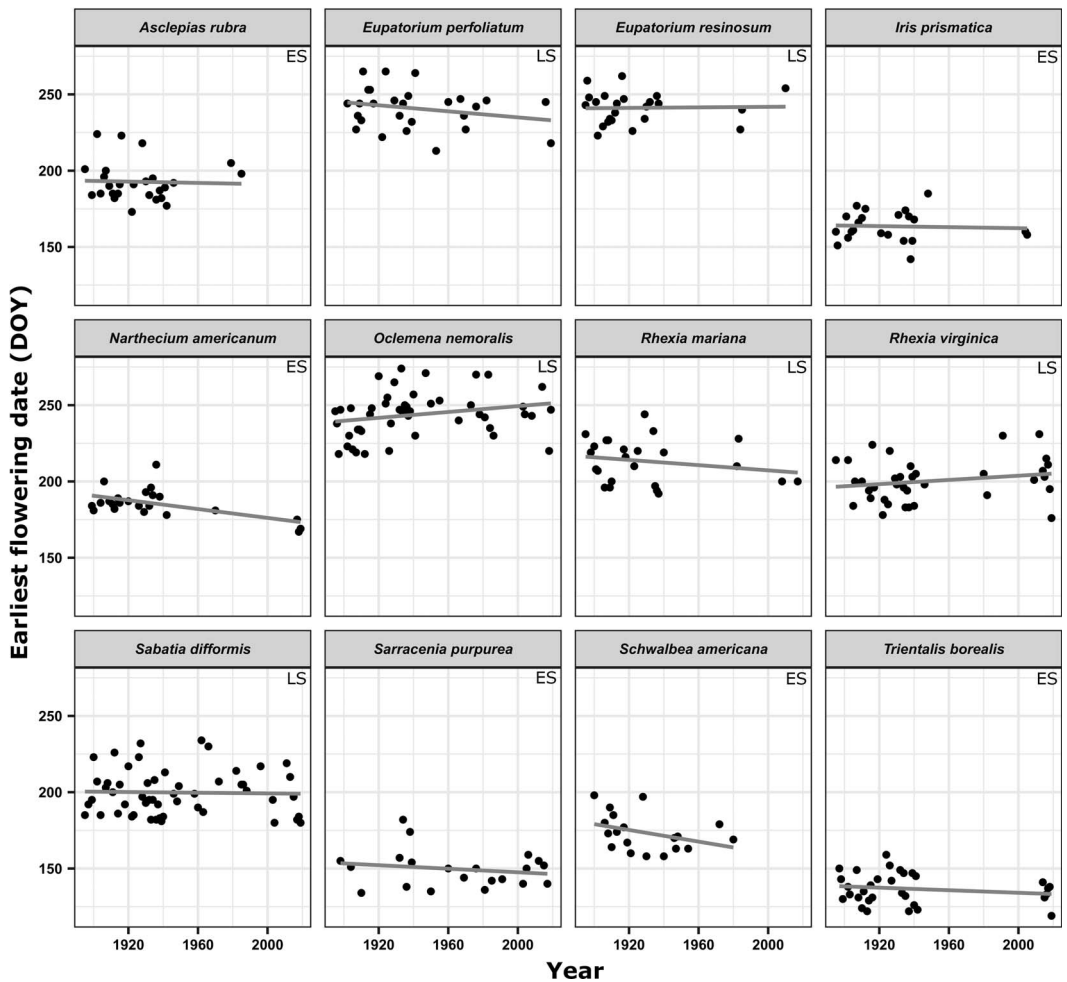
Fig. 1.   Effect of year on earliest flowering time for 12 lowland herbaceous species of the New Jersey Pine Barrens for the years 1895 through 2019. Earliest flowering date is reported as day of year (DOY) in which 150 is late May and 250 is late September. Black dots represent herbarium specimen data or citizen science observations and a line of best fit is indicated in gray. Each graph is labeled with the species name and designated as either an early summer (ES) or late summer (LS) flowering species. Total number of observations range from $n = 19$ (*Schwalbea american*a) to $n = 53$ (*Sabatia difformis*).

that flowering time was affected by changes in either year or mean spring temperature overall. However, when our focal species were grouped by general flowering time, early summer flowering (late May to early July) or late summer flowering (late July to September), we detected a significant negative relationship for changes in the flowering of early summer flowering species that correlated with both year and mean spring temperature. As this was not the case for late summer flowering species, these findings add to the growing number of studies that identify greater responses of early as opposed to late flowering species to changes in

spring temperatures (Sherry *et al*. 2007; Calinger *et al*. 2013; Mazer *et al*. 2013; Park and Schwartz 2014; Davis *et al*. 2015; Pearson 2019).

Previous phenology studies have examined the relationship between changes in temperature and flowering time at the individual species level (Walkovsky 1998; Matthews and Mazer 2015), genus level (Hart *et al*. 2014, Rawal *et al*. 2015), community level (Davis *et al*. 2015), regional level (Park and Schwartz 2014; Munson and Long 2017; Pearson 2019), multiregional level (Park *et al*. 2019), and continental level (Zalamea *et al*. 2011). Whether the study area, such as Concord,
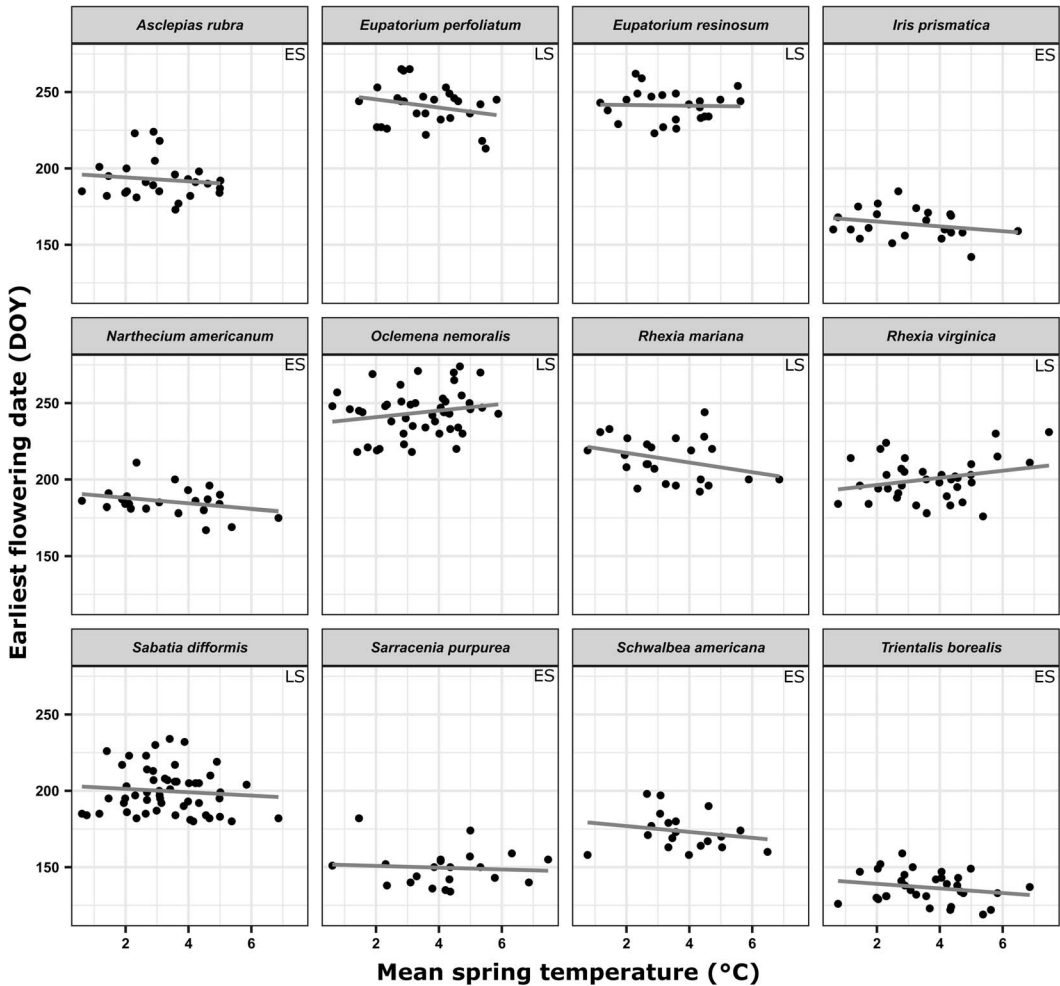
Fig. 2. Effect of mean spring temperature (°C) on earliest flowering time for each of the 12 focal species of this study. Mean spring temperature represents the average of temperatures recorded from February through May of a given year. Earliest flowering date is reported day of year (DOY) in which 150 is late May and 250 is late September. Black dots represent herbarium specimen data or citizen science observations; a line of best fit is indicated in gray. Each graph is labeled with the corresponding species name along with the designation of early summer (ES) or late summer (LS) flowering species. Total number of observations ranged from $n = 19$ (*Schwalbea americana*) to $n = 53$ (*Sabatia difformis*).

Massachusetts (Davis *et al*. 2015), was similar to ours or encompassed a much larger area such as the Southeastern Coastal Plains of the United States (Pearson 2019), species that flower closer to spring were shown to exhibit greater fluctuation in flowering time in response to mean spring temperature of the corresponding year than those that flower later in the season. In a similar trend to other studies (Miller-Rushing and Primack 2008; Calinger *et al*. 2013; Davis *et al*. 2015; Pearson 2019), we found that for every 1°C increase in mean spring temperature, there was a significant

acceleration in earliest flowering time by 1.42 days in our six species that flower closer to the spring, which is slightly below other estimates of spring flowering species in North America (2.4 days/°C, Calinger *et al*. 2013; 3.5 days/°C, Davis *et al*. 2015; 1.8–2.3 days/°C, Pearson 2019). One difference is that our study did not include species with an earliest flowering date before the end of May, but instead compared early summer with late summer flowering species. This widens the time frame for which species that bloom earlier in the growing season are affected by changing temper-
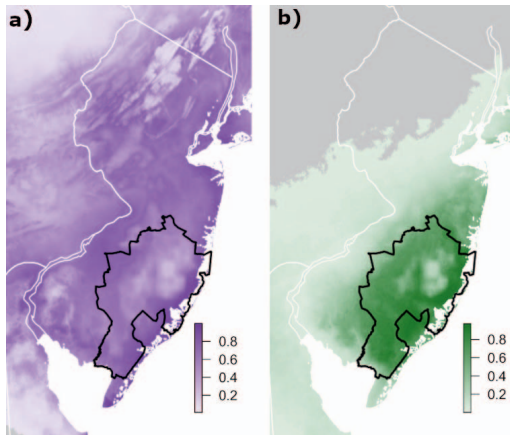
Fig. 3. Modern species distribution models (SDMs) of (A) *Eupatorium perfoliatum* and (B) *Eupatorium resinosum*. Scale bar indicates the range of relative climate suitability for each model, with darker shades representing greater climate suitability and lighter shades representing less climate suitability. Area of the Pinelands National Reserve of New Jersey are outlined in black in each model. This is a logistic output.
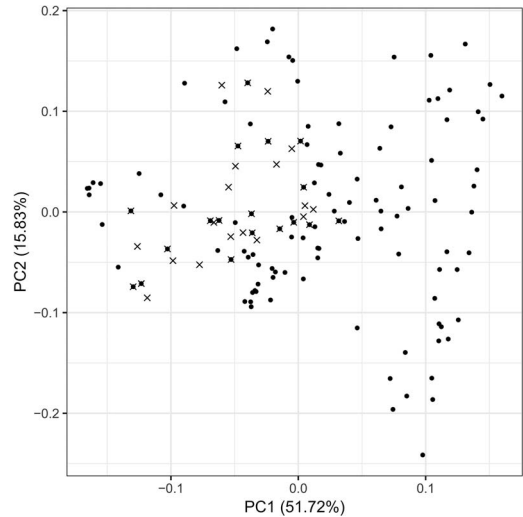

Fig. 4. Principal component (PC) analysis of the climate spaces occupied by *Eupatorium perfoliatum* (dots) and *Eupatorium resinosum* (crosses) on the basis of 19 climatic variables. Percentages of variation captured by PC1 and PC2 are indicated on the *x* and *y* axes, respectively.

atures. As spring blooming species were not included in this study, the phenological response of these species will need to be examined to determine the response to changing temperature and year, but we would predict a similar if not greater response to temperature. Here, we suggest midsummer as the point in the growing season for which there is no longer a significant change in response to changes in mean spring temperature or year for the Pine Barrens community.

A pattern of increase in mean annual temperature over the past century and a significant effect of spring temperature on earliest flowering date of plants in the eastern United States has been well documented over the past decade (Sherry *et al*. 2007; Miller Rushing and Primack 2008; Davis *et al*. 2015; Pearson 2019). However, the relationship between calendar year and earliest flowering date has been less consistent. Miller-Rushing and Primack (2008) found a significant effect of year on earliest flowering date in their study of New England taxa, whereas Davis *et al*. (2015) did not in similar taxa of the same study area. We also saw a significant increase in mean annual temperature and mean spring temperature specifically in the Pine Barrens region since 1895, adding a unique ecological community to the sites in eastern North America for which this pattern has been docu-

mented. Additionally, we revealed an effect of both year and mean spring temperature on early summer flowering species only. This suggests that species flowering closer to spring in the Pine Barrens are exhibiting more variation in flowering times, which may in turn affect their interactions with other changes in the community such as the availability of pollinators or seed dispersers.

Of the 12 species examined in this study, we did not find a consistent response among all species. The early summer flowering species were all found to flower earlier or slightly earlier in the season in response to warmer spring temperatures. Of our focal species, *Sarracenia purpurea* L. and *Iris* have ranges that extend beyond the Pine Barrens and have been included in studies of larger geographic regions that concur with our findings (Park *et al*. 2019). Among the late summer species there was no consistent response to temperature. Whereas some of these species exhibit earlier flowering times as might be expected in warmer years, others appear to react in the opposite way, such as *O. nemorali*s, in which flowering times were delayed with increases in temperatures. Further, two late summer flowering species of *Rhexia* exhibited opposite responses, with *R. mariana* L. flowering earlier with warmer spring temperatures, whereas the flowering time of *R.*

virginica was delayed. Few studies have shown delays in flowering times. A similar response was shown among C4 grasses that push their flowering times later with increasing mean spring temperatures to correspond with oncoming monsoons (Munson and Long 2017). Further inquiry to the unique ecology and microhabitats of the Pine Barrens may reveal why there is a varied response in late summer species, but the lack of a uniform direction of change across this set of species suggests that changes in climate will elicit different responses within this community that may ultimately affect timing of interactions among its members.

Overall, our study identifies phenological changes tied to the effects of climate change on unique and speciose ecosystems such as the lowlands of the New Jersey Pine Barrens. By sampling across the many microenvironments that encompass the lowlands, we begin to understand how unique areas of biodiversity may be responding to climate change. This work is important for the conservation of the New Jersey Pine Barrens; we found that species that flower closer to spring are in fact more flexible in their flowering time than late summer flowering species. If this trend continues as climate change continues to progress, this could lead to temporal mismatches in pollination for both historically later flowering species or earlier flowering species, depending on how pollinators shift timing of their own life cycles (Rafferty and Ives 2012). More important, additional species, particularly those flowering in spring and occurring in the uplands, should be examined to fully understand the effects of changing temperature on this community. Further, factors such as precipitation, frost days per year, or the effects of prescribed and nonprescribed burns that are important to the ecology of this community may also be key to describing, interpreting, and predicting changes in plant phenology in the Pine Barrens.

Life-History Traits and Phenology. Our focused study of two sister species of *Eupatorium* did not reveal any significant change in earliest flowering time over the last 125 yr despite a fluctuating and largely warming climate. These findings follow Willis *et al.* (2008) and Mazer *et al.* (2013), which revealed similar phenological responses among closely related plants (e.g., taxonomic signal) with regard to changes in temperature. Furthermore, the late summer flow-

ering of *E. perfoliatum* and *E. resinosum* may also explain this outcome, as these findings concur with a growing number of studies that fail to reveal a significant change in flowering time of late summer blooming plants in conjunction with fluctuations in mean spring temperature (Calinger *et al.* 2013; Mazer *et al.* 2013; Park and Schwartz 2014; Davis *et al.* 2015; Park *et al.* 2019; Pearson 2019).

Although we detected no change in phenology, our exploration of species distribution models for *Eupatorium* emphasizes the importance of studying additional life-history traits connected to phenology as our climate continues to change. A growing number of studies have analyzed phenology and climate change alongside additional plant life-history traits such as life span (e.g., perennial *versus* annual; Fitter and Fitter 2002), mode of photosynthesis (Munson and Long 2017), pollination syndrome (Fitter and Fitter 2002; Calinger *et al.* 2013), and invasive *versus* native species (Calinger *et al.* 2013). As the northern and southern limits of a range are limited by a plant's phenology (Chuine 2010; Chapman *et al.* 2014), species distribution may also play a role in understanding and predicting broader community-level changes due to climate change. Of the two species of *Eupatorium* studied here, the distribution of *E. resinosum* occurs within the broader distribution of *E. perfoliatum* in New Jersey, but the climate spaces occupied by these species are significantly different from one another. This is reinforced by our PCA, which found that *E. perfoliatum's* climate space is more strongly associated with winter minimum temperatures as compared with *E. resinosum*. We might predict that these key climate factors will continue to shape the overall distribution of species such as *E. resinosum*. To further investigate the relationship between phenology and range that creates these range distinctions in *Eupatorium*, distribution models that utilize phenological data as well as locality data spanning the entire range of the species could provide more holistic insight to future changes in range size due to climate change (Chuine 2010; Chapman *et al.* 2014). However, this will require detailed study of the life cycle of *Eupatorium* and an abundance of locality data.

Power of Herbarium Specimens in Climate-Change Studies. Our study has shown that plants in the New Jersey Pine Barrens are indeed reacting to a changing climate. Herbarium specimens

represent a rare historical record of plant diversity that provides multitudes of opportunities to examine the effects of climate change on plant biology as here exemplified by a study of earliest flowering times. Recent efforts to digitize museum collections large and small have increased accessibility to these specimens, thereby increasing opportunities to incorporate these data into studies of large and small scales. With reference to our focal species in New Jersey, herbarium specimens were available dating back nearly 200 yr for generating SDMs and 125 yr for studying phenology. We were able to use these data because of the careful notes on locality, flowering status, and date of collection recorded by collectors, thus providing irreplicable data in the study of phenology and climate change. As contemporary collections, particularly of rare plants, are replaced with digital formats of documenting events such as flowering times, we can also look to an increase in utilizing data from citizen science efforts to augment studies of phenology as demonstrated here.

Conclusions. The New Jersey Pine Barrens represent a unique environment in which many threatened and endangered plants occur. In studying 12 herbaceous species that flower in early and late summer, we provide the first evidence for the Pine Barrens that early summer flowering species are flowering earlier now than they were 125 yr ago, and that this change in flowering time is significantly related to the mean spring temperature of the corresponding year, mirroring similar studies of the eastern United States. In a focused examination of sister species with differing distributions, we detected no difference in flowering time, which adds to a growing number of studies that predict similar phenological responses on the basis of evolutionary relatedness and a lack of phenology response in late flowering species. Overall, this study is the first step in showing that changes in spring temperature due to climate change could be affecting species unique to the Pine Barrens, supporting further work incorporating a greater proportion of the flora of this unique ecosystem. Additionally, we advocate for continued incorporation of life-history traits such as distribution to better understand community-level changes associated with shifts in phenology. Finally, as not all species had similar responses to changes in temperature and year, changes of the timing of life events of plants in this community will likely affect the balance of the many ecological interactions occurring among members of the Pine Barrens.

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