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Citizen Science across Two Centuries Reveals Phenological Change among Plant Species and Functional Groups in the Northeastern US

Kerissa Battle
Portland State University, kerissabattle@gmail.com

Anna Duhon
Hawthorne Valley Farmscape Ecology Program

Conrad R. Vispo
Hawthorne Valley Farmscape Ecology Program

Theresa M. Crimmins
University of Arizona

Todd Rosenstiel
Portland State University, rosensti@pdx.edu

See next page for additional authors

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Kerissa Battle, Anna Duhon, Conrad R. Vispo, Theresa M. Crimmins, Todd Rosenstiel, Lilas L. Armstrong-Davies, and Catherine de Rivera

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RESEARCH ARTICLE

Citizen science across two centuries reveals phenological change among plant species and functional groups in the Northeastern US

Kerissa Fuccillo Battle[1,2] | Anna Duhon[3] | Conrad R. Vispo[3] | Theresa M. Crimmins[4] | Todd N. Rosenstiel[1] | Lilas L. Armstrong-Davies[2] | Catherine E. de Rivera[1]

[1]Environmental Science and Resources, Portland State University, Portland, Oregon, USA

[2]Community Greenways Collaborative, Inc, Bearsville, New York, USA

[3]Hawthorne Valley Farmscape Ecology Program, Ghent, New York, USA

[4]USA National Phenology Network, School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA

Correspondence
Kerissa Fuccillo Battle
Email: kerissabattle@gmail.com

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Abstract

1. Understanding the breadth and complexity of changes in phenology is limited by the availability of long-term historical data sets with broad geographic range.
2. We compare a recently discovered historical data set of plant phenology observations collected across the state of New York (1826–1872) to contemporary volunteer-contributed observations (2009–2017) to evaluate changes in plant phenology between time periods. These multi-site, multi-taxa phenology data matched with temperature data uniquely extend historical observations back in time prior to the major atmospheric effects of the Industrial Revolution.
3. The majority of the 36 trees, shrubs and forbs that comprised our analysable data set flowered and leafed out earlier in contemporary years than in the early to mid-19th century. This shift is associated with a warming trend in mean January-to-April temperatures, with flowering and leafing advancing on average 3 days/°C earlier. On average, plants flowered 10.5 days earlier and leafed out 19 days earlier in the contemporary period. Urban areas exhibit more advanced phenology than their rural counterparts overall, and insect-pollinated trees show more advanced phenology than wind-pollinated trees and seasonality and growth form explain significant variation in flowering phenology. The greatest rates of temperature sensitivity and change between time periods for flowering are seen in early-season species, particularly trees. Changes in the timing of leaf out are the most advanced for trees and shrubs in urban areas.
4. *Synthesis*. Citizen science observations across two centuries reveal a dramatic, climate-driven shift to earlier leaf out and flowering. The magnitude of advancement varies across settings, species and functional groups, and illustrates how long-term monitoring and citizen science efforts are invaluable for ecological forecasting and discovery.

KEYWORDS
citizen science, climate change impacts, community science, historical data, long-term monitoring, phenological shift, plant phenology, pollination syndrome

1 | INTRODUCTION

A rapidly growing body of studies from around the globe demonstrate clear impacts of changing climate conditions on plant and animal phenology (e.g., Cohen et al., 2018; Menzel et al., 2020; Parmesan & Yohe, 2003; Root et al., 2003). The effect of climate change on the phenology of organisms is of primary ecological concern due to potentially profound ecosystem impacts. The cascading consequences of phenological change include disruptions in interactions among species, ecosystem structure and functioning, and nutrient cycling (Edwards & Richardson, 2004; Rafferty et al., 2015; Thackeray et al., 2016; Visser & Both, 2005). The inherent variability in phenological changes across studies, sites and species makes it difficult to determine which species and interactions deserve priority for further investigation, or to incorporate phenology into ecological forecasts related to impacts on climate change (Peñuelas et al., 2009).

Long-term, repeated observations offer the greatest insight into the direction and magnitude of change in species' phenology; some of our best records of change originate from long-term observation records (e.g., Cook et al., 2008; Miller-Rushing & Primack, 2008; Primack et al., 2009). Records encompassing multiple species enable an understanding of varying rates of change among members of an ecological community. Phenology records collected across multiple sites enable examination of species response to varying local conditions. Phenology records that are long-term in duration, that are comprised of multiple species and that encompass observations from multiple sites are exceptionally rare in the United States; yet, these types of records, when found and integrated properly, offer extraordinary potential for addressing questions relating to the ecological effects of climate-driven shifts.

Here, we present an analysis of newly uncovered historical phenology records across the state of New York from the 19th century and compare them with a contemporary phenology data set with similar taxonomic and geographic dimensionality collected with comparable protocols by citizen scientist observers in the 21st century. This combined phenology data set, encompassing 36 plant species with sufficient data, and a geographic scope of the state of New York (778 km^2), enables us to explore long-term changes in plant phenology in the northeastern United States. The historical data set arises from the oldest known example of an organized network of institutions collecting paired phenology and weather data at over 90 locations through participatory science methods in the United States—a network established throughout New York State with data collection spanning 1826–1872. We combine selections from this historical data set with observations from a contemporary network of institutions and individuals collecting data in a comparable way across New York State from 2009 to 2017. The modern data are primarily derived from the New York Phenology Project, a regional affiliate of the USA National Phenology Network. These two data sets share dozens of species in common and were sampled regularly and frequently across the state of New York. To our knowledge, no other North American data set provides a multi-decade, multi-site, standardized collection of phenological data from the early industrial period.

This historical initiative, explicitly designed to collect phenological data and concurrent, standardized meteorological information for an entire region, was unprecedented for North America at the time. Prior to this analysis, most attempts to study multispecies reactions to climate change using historical records have relied either on single-site, single-observer efforts (e.g., Thoreau's records at Concord as summarized by Miller-Rushing & Primack, 2008) or compilations of observations from diverse individuals working independently (Büntgen et al., 2022). The historical data set is especially suited for pairing with modern data because it has the geographic extent that permits association with modern regional records, and yet was conducted under the auspices of a centralized, standardizing project and persisted long enough to create a robust baseline. These strengths, combined with the diversity of species observed, allow us to not only detect broad phenological changes but also, as summarized in the predictions below, to more rigorously explore the influences of urbanization and of ecological traits such as growth form, pollination syndrome and the relative seasonality of leafing and flowering. By exploring these factors within a single data set, our work can give a more complete picture of the overlapping factors determining the ecological impacts of climate change on a regional flora.

We capitalize on the taxonomic and geographic breadth of this novel data set to test the following six predictions shaped by findings of previous studies. First, we predict that most plants in our study will show an advancement in phenology over the period of record, varying in degree of magnitude across species (Prediction 1). Around the globe, phenology in numerous plant species has advanced in recent decades (Menzel et al., 2020; Parmesan & Yohe, 2003; Root et al., 2003). Second, we predict these changes in phenology to be associated with increasing temperatures, again varying across species (Prediction 2). Several recent studies from the northeastern U.S. (Ellwood et al., 2013; Miller-Rushing & Primack, 2008; Primack et al., 2004; Schwartz, 1998) demonstrated strong associations between late winter and early spring temperatures and flower and leaf phenology and a clear advancement in these events in recent decades with increased winter and spring temperatures.

Several studies have also documented larger shifts in phenology among species that are active earlier in the spring season than those active later in the season (CaraDonna et al., 2014; Fitter & Fitter, 2002; Miller-Rushing & Primack, 2008; Panchen et al., 2014;

Wolkovich et al., 2014). Species leafing out or flowering earlier in the season are subject to different conditions than species with later-season phenology, including access to light before canopy closure. Because the data we are analysing originate from similar ecoregions, our third prediction is that early spring species will show a greater advancement in the timing of their activity than species undergoing phenological transitions later in the season (Prediction 3). The taxonomic richness in our data set allows us to investigate whether these patterns will hold in observations spanning nearly 200 years.

Fourth, we predict differences in changes in phenology among different plant growth forms (trees, shrubs and forbs; Prediction 4). Growth forms vary in rooting depth as well as access to sunlight and nutrients. As such, changes in the availability of these resources can impact growth forms differentially, resulting in varying impacts to their leaf out and flowering timing. Recent work shows that tree phenology may be shifting more quickly than the phenology of understory forbs in this region (Heberling et al., 2019), though comparisons in phenological change among growth forms has been limited to only a handful of studies (e.g., Calinger et al., 2013; Crimmins et al., 2010, 2011; Heberling et al., 2019).

Fifth, we predict that species in urban locations will show a greater advancement in their phenology than their rural counterparts (Prediction 5). More developed areas tend to exhibit higher temperatures in a phenomenon termed the urban heat island effect. Leaf and flowering phenology are frequently advanced in urban areas compared to nearby less developed areas (Bornstein, 1968; Imhoff et al., 2010; Neil & Wu, 2006; Zhang et al., 2004), and this effect is especially exaggerated at higher latitudes (Li et al., 2019).

Finally, we predict that insect-pollinated species will exhibit greater advancement in first flower dates due to selection promoting earlier flowering to maintain synchrony with pollinators (Prediction 6; Calinger et al., 2013; Fitter & Fitter, 2002). Pollination syndrome is a key factor to explore because of the importance of climate change impacts on plant-pollinator mutualisms (Forrest, 2015; Gérard et al., 2020; Kudo & Cooper, 2019). However, differences in phenological shifts among pollination syndromes are rarely evaluated due to the scarcity of data sets with adequate representation of wind-pollinated species.

2 | MATERIALS AND METHODS

2.1 | Historical and contemporary networks

From 1826 to 1872, a network of academies/sites managed by the New York State Regents collected meteorological and/or phenological data across hundreds of sites in the state of New York (NY). During the first period of the network (1826–1850), data were collected at over 70 sites spanning more than two-thirds of NY counties. In 1850, the effort was harmonized with, and helped inspire, the newly launched Smithsonian Institution's national network of meteorological observers (historical precursor to the National Weather Service). New sites were selected, others fell away and refined protocols were adopted. During the second period of the network (1851–1872), the number of Regents/Smithsonian sites following the refined protocols grew into the hundreds, spanning nearly every county in NY. The effort in NY remained strong until the US Civil War when data collection significantly waned.

Based on data in the summary reports of the Regents/Smithsonian network, well over 500 observers collected data in NY during its timespan (Hough, 1872; Smithsonian Institution, 1869). The historical data set was rediscovered and compiled in 2014 by the Hawthorne Valley Farmscape Ecology Program, then digitized and standardized in collaboration with the New York Phenology Project in 2016 (Progress of the Seasons, 2017).

The New York Phenology Project (NYPP), part of the USA National Phenology Network (USA-NPN, a national-scale, volunteer-driven phenology observation effort; Rosemartin et al., 2014), has more than 30 organized, institution-based sites while also supporting individual 'backyard' phenology observers across the state. Approximately 200 individuals contributed observations to the contemporary data set (which spans 2009–2017). The sites in the network are independent but share resources and training and use targeted species lists and protocols supplied by the founding institution, Community Greenways Collaborative, and the USA-NPN. The sites are not exactly co-located with sites included in the historical network but are nearby. Sampling frequency appears similar in the two time periods—daily-weekly frequency—based on descriptions of protocols and our analyses of the data.

2.2 | Data preparation and protocols

The historical phenology data set was compiled from multiple books and formats. The data were entered in their original form by hand, then subsequently proofed and standardized to conform to current scientific names and the USA-NPN phenophases descriptions (Appendix S1). The historical and contemporary data sets both contain the most data for the phenophases (life cycle stages) known as 'breaking leaf bud' (green leaf tips visible) and 'open flower' (reproductive parts visible), which were defined nearly identically in the two time periods (see Appendix S1 for specific details on protocols, data sheets and data preparation for both time periods). Volunteers can accurately identify and record these two phenophases for most species, resulting in data appropriate for analysis (Fuccillo et al., 2015). The breaking leaf bud phenophase was only included for 1851-on when standardized leafing protocol was in use network-wide. Contemporary observations were collected using the USA-NPN protocols for plant phenology monitoring (Denny et al., 2014).

The primary focus of the historical network was weather observations, and thus nearly all locations with phenology data have paired weather data. We digitized and used monthly mean temperature data (which were averaged from daily temperature means and published in summary reports) (Hough, 1855, 1872; Lawson, 1851; United States et al., 1840; United States and Lawson, 1855). We supplemented the historical temperature data set with data from

Fort Columbus in New York City (1826–1854), recorded as part of a system of meteorological observations at army stations at the time. Protocols for historical temperature data collection, including the hourly protocols and daily mean calculation methods, are in Appendix S1. The contemporary temperature data were NOAA Online Weather Data monthly normals (NOWData, 2017). The historical and contemporary temperature data were selected based on the following criteria: all temperature data had to be from weather stations located in a region that contained a cluster of historical and modern phenology monitoring sites, be within 25 km distance and within 50 m of elevation from one another and have contiguous records representing the hardiness zones and times of the phenology data used (years 1826–1861 and 2009–2017). We defined and calculated January–April temperatures (JAT) as the mean monthly temperatures for January through April following Miller-Rushing and Primack (2008), Primack et al. (2004) and Schwartz (1998).

2.3 | Data treatment

Each phenology record consists of the date (day of year; DOY) when the first leaf or flower of a species was observed at a particular location in a particular year. We refer to these records from here on as first leaf date (FLD) and first flower date (FFD). In this study, we used only data for species for which we had phenology observations for more than 3 years in each time period and at least 12 observations total for each phenophase. These criteria are similar to those used in studies of regional multi-species phenology based on herbarium specimens (e.g., Calinger et al., 2013; Everill et al., 2014) and single site historical comparisons (Miller-Rushing & Primack, 2008). The species that lacked species or phenophase cross-over were removed (there were initially 909 species total between the two time periods so they were pared down drastically to meet our minimum requirement). Data from 1862 to 1872 did not meet our criteria for inclusion in this paired species analysis (data collection had significantly waned by this point due to the Civil War, so coverage was extremely spotty). The final data set consisted of 36 species (11 forbs, 13 small trees/shrubs and 12 trees) at 154 locations (66 historical and 88 contemporary locations of which 35 are organized phenology monitoring programs and 53 are independent sites), with general overlap across a large geographic region with a range of highly urbanized sites to very rural sites (Figure 1). Most of the 36 species met more than the minimum requirement for observations, and all species-specific results mentioned in the discussion are limited to species with more than 60 observations to better address yearly and spatial variation. Data were categorized into two time periods: historical (1826–1861) and contemporary (2009–2017).

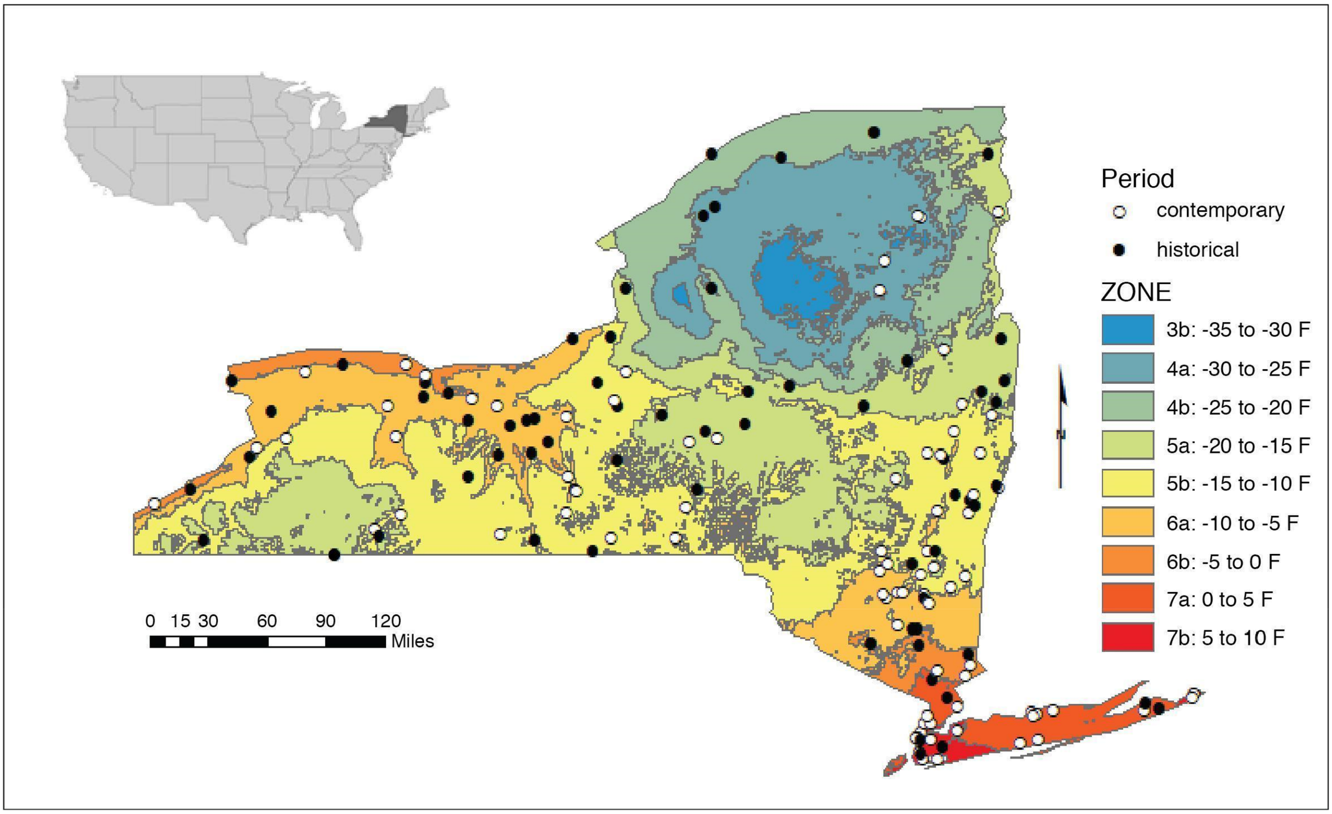

FIGURE 1 Geographic projection map of historical and contemporary phenology monitoring sites across New York, USA, with contemporary US Department of Agriculture Hardiness Zones indicated from the year 2012 (USDA, 2012). Historical locations ($n = 66$) are indicated by black circles and contemporary locations ($n = 88$) by white circles. Historical time period spanned years 1826–1861, and contemporary time period spanned years 2009–2017.

We used temperature data from the period between 1826 and 1861 to match the period of phenology data in the analysis. For all analyses that included JAT as a variable, we used data from the location with the most complete data in our record: New York City (NYC). New York City had three historical and three contemporary weather stations with the complete monthly records needed to create JAT for both time periods (historical stations: Erasmus Hall, Fort Columbus and Union Hall; contemporary stations: Central Park, LGA Airport and JFK Airport). No other region in New York State had complete monthly records for both historical and contemporary time periods for the length of time covering the phenology observations. NYC as a region also contained the largest volume of phenology data from both time periods, so we determined it would be the best overall fit to evaluate changes in phenology with paired temperature data. However, to ensure that variation in JAT in NYC provided a reasonable approximation of variation in JAT in other areas of the state, we tested the correlation among JAT for three cities with historical and contemporary weather stations, one each from three of the current major United States Department of Agriculture (USDA) Hardiness Zones in New York State (New York City = zone 7, Kingston = zone 6, Albany = zone 5), for our period of study. These three sites do not constitute a formal statewide sampling (and do not include rural sites) but did allow us to assess whether JAT in NYC could be extrapolated to other areas of the state at different hardiness zones and latitudes. JAT at these three locations were highly correlated ($r > 0.85$, $p < 0.001$ for all pairwise correlations; see Results for detailed correlation results), so these data were used in all statistical models that included temperature as a variable.

2.4 | Explanatory variables

Based on prior results of single-site studies or regional herbarium specimen-based studies, we included several categorical variables, in addition to JAT, that likely contribute to, or mediate, changes in flowering and leaf phenology: hardiness zone (as a proxy for local climate and local adaptation), species, time period, seasonality, growth form and urban–rural classification (Calinger et al., 2013; Miller-Rushing & Primack, 2008; Wolkovich et al., 2014). We also separately explored changes in phenology between the two time periods for tree species with differing pollination syndromes (wind- and insect-pollinated) by season (all forbs and shrubs were insect-pollinated).

USDA Hardiness Zones 4–7 (USDA, 2012) represented variation in climate (and associated local adaptation) across locations (Figure 1). Latitude and elevation are often used in analyses of phenology as proxies of spatial variation in climate, but in New York, the influence of the Great Lakes, the Atlantic Ocean and the concentration of urbanized areas in the southern portion of the state confound the relationships among climate, latitude and elevation, making hardiness zone a better proxy for spatial variation in climate, as reflected by maps of climate normals from Northeast Regional Climate Center (NRCC, 2010). We defined seasonality as: early spring (1 March to 30 April, DOY 60–120), late spring (1 May to 1 June, DOY 121–152) or summer (2 June to 15 July, DOY 153–196); dates were chosen a priori based on general categorization (i.e., spring ephemerals, summer flowers) and species assigned to categories based on their mean flowering or leafing across the data set. These categories reflect seasons with different selection pressures on phenology and previously observed differences in phenological responses to climate change (Calinger et al., 2013; Rathcke & Lacey, 1985; Wolkovich et al., 2014). We used data from USDA PLANTS (USDA, 2019) to assign species to plant growth form categories (i.e., forb, small tree/shrub or tree). Urban–rural classification was assigned by compiling census data for locations from both time periods and assigning each location an urban or rural status as it is described in the census data as defined by the current U.S. Census Bureau criteria (U.S. Census Bureau, 2010). This broad categorization is based on current census definitions and so does not consider changes to the criteria used to designate urban and rural areas historically, thus changes in urban locations may be amplified by magnitude of urbanization (and the associated urban heat island effect) in some locations between the two time periods. Pollination syndrome was classified for tree species as insect- or wind-pollinated based on the USDA Tree Atlas (Prasad et al. 2007), and corroborating literature review. Pollination syndrome differences were only comparable across time periods for trees (forbs and shrubs in the data set are all insect-pollinated).

2.5 | Statistical analyses

We assessed changes in temperature and phenology over time to get a baseline of change between time periods. We used linear regression to analyse change in JAT over the full study period (1826–2017; prediction 1). We then tested all our predictions about phenology by creating four different multi-factor general linear mixed effects models (*variance component structure*, *restricted maximum likelihood*) for each phenophase (first flower date = FFD and first leaf date = FLD) with DOY as the response variable (which we will describe in detail below), following them up with post-hoc tests and per species tests to determine what factors or species drove the trends. We explored whether the timing of flowering and leafing changed between the historical period (1826–1861) and the contemporary period (2009–2017) for all species combined by including time period in the general linear mixed effects models (Models 1 and 2), followed up with a Tukey HSD. We also examined species individually via t-test to assess the Day of Year (DOY) change between periods and to explore how species vary in the magnitude of their responses between time periods (Prediction 1). We report the critical alpha, $p < 0.05$, as well as critical alpha after Bonferroni correction in the per-species table for first flower date then for first leaf date. We report these values both across hardiness zones as well as separated by hardiness zones to help evaluate variation in distributions across hardiness zones.

To test the predictions of the influence of temperature and the additional explanatory variables on variation in phenology (Predictions 2–5), we included temperature in the four general linear mixed effects models. To specifically examine species response to temperature and to explore to what extent species variation between time periods was related to temperature and urbanization, our third model (Model 3) included species as a fixed variable interacting with temperature and urbanization. To visualize how closely species variation tracked temperature variation, we also ran a linear regression to determine relationships between mean January–April temperature (JAT) and first flowering date (FFD) for eight of the most commonly observed species in the historical data set (selected by determining which species from the three growth forms had the highest sample sizes). This is a commonly used metric for measuring phenological response to temperature.

We could not address all our hypotheses in a single model analysis for each phenophase because (a) some of the predictors covaried with each other (e.g., the variance inflation factor indicated that growth form and seasonality could not be in the same model; similarly species had to be a random factor in three of the models because of multicollinearity) and (b) pollination syndrome only pertains to trees in flower whereas the other models include all growth forms. To avoid complications from strong collinearity, we separated some variables into separate analyses and ran four different models. Table 1 summarizes those questions that are addressed in each of the different analyses, as reflected in the model analysis output tables. We included hardiness zone as a random factor in the models as it is not a specific variable of interest related to our six predictions (but functions as a proxy for local climate and controls for spatial variation). We also included species as a random factor in Models 1 and 2 as species cannot be a fixed factor alongside seasonality or growth form due to multicollinearity.

In Model 1, which also evaluates our prediction for seasonality, we included the fixed predictor variables of period (historical versus contemporary), JAT (continuous), urban–rural setting (urban versus rural) and seasonality (flowering in early spring, late spring or summer) and their interactions with temperature (for all categorical variables). In Model 2, which also evaluates our predictions for growth form, we included the fixed predictor variables of period (historical versus contemporary), JAT (continuous), urban–rural setting (urban versus rural) and growth form (forb, shrub or tree) and their interactions with temperature. We used Tukey HSD for pairwise comparisons to assess degree of change between periods (reporting DOY change).

In Model 3, focusing on species response to temperature and exploring to what extent species variation between time periods related to temperature and urbanization, we included species as a fixed variable, urban–rural (fixed), temperature (continuous), their interactions as predictor variables and hardiness zone as a random effect. As these three mixed effect models included urbanization, we also followed these tests up with *t*-tests individually for species with an $N > 20$ for each phenophase classified by rural and urban locations to get the DOY change between periods (as we did for species change between time periods in prediction 1).

In Model 4, focusing on the relationship between temperature and pollination syndrome, we included explanatory variables JAT (temperature), pollination syndrome (fixed, categorical: insect versus wind pollinated) and the interaction between JAT and pollination syndrome; hardiness zone was a random effect. We

TABLE 1 Table showing which analysis tables address each of our central questions (the predictions associated with the questions are also listed). FFD = examined for first flower date, FLD = examined for first leaf date; × temp = the interaction between temperature and the factor was also examined; × spp = the model also includes the interaction between species and the factor.

Questions addressed	Table 2, Model 1	Table 3, Model 2	Table 4, Model 3	Table 5, Model 4
Time period: Is there advancement in phenology over the period of record (historic versus contemporary)? (Prediction 1)	FFD, FLD	FFD, FLD		
Temperature: Are changes in phenology associated with increasing temperatures? (Prediction 2)	FFD, FLD	FFD, FLD	FFD, FLD	FFD, FLD
Seasonality: Do species active earlier in the spring season show greater advancement in phenology than species active later in the season (and is there an interaction with temperature)? (Prediction 3)	FFD, FLD × temp			
Growth form (functional group): Do changes in phenology differ among trees, shrubs and forbs (and is there an interaction with temperature)? (Prediction 4)		FFD, FLD × temp		
Urbanization: Do species in urban locations show a greater advancement in their phenology than their rural counterparts (and is there an interaction with temperature, or species)? (Prediction 5)	FFD, FLD × temp	FFD, FLD × temp	FFD, FLD × spp	
Pollination syndrome: Do insect-pollinated species exhibit greater advancement in first flower date (and is there an interaction with temperature)? (Prediction 6)				FFD, FLD × temp
Species: To what extent do different species vary in their phenological responsiveness and sensitivity to temperature (and is there an interaction with temperature)? (Crosscutting all predictions)	(as random factor)	(as random factor)	FFD, FLD × temp	(as random factor)

explored this pollination syndrome prediction separately because this analysis was limited to trees (all shrubs and forbs were insect-pollinated) and thus had a smaller sample size and could not be included with the other models. We also evaluated each predictor variable via linear regression to examine each variable's relationship to temperature over time and conducted pairwise comparisons of each explanatory variable via Tukey HSD to determine the DOY change between time periods. We evaluated data for equality of variances and normality of residuals. Data for FFD included years 1826–1861 and data for FLD included years 1851–1859. All data were evaluated with the statistical software package SAS, JMP v. 16.

3 | RESULTS

3.1 | Changes over time (prediction 1)

3.1.1 | Changes in temperature across time periods (1826–2017)

January–April Temperatures (JAT) warmed substantially statewide between 1826 and 2017, as indicated by three measures. First, a time series in New York City revealed a relatively steady warming trend, beginning in 1880 (Figure 2), consistent with regional analyses of warming (Horton et al., 2014). Second, combined JAT at three locations (New York City, Kingston and Albany) in different hardiness zones (zones 7, 6 and 5, respectively) warmed by an average of 1.0°C (1.8°F) between historical (1826–1861) and contemporary (2009–2017) time periods (t = 1.94, N = 25, p = 0.028, NYC = 3.96°F, Kingston = 0.33°F, Albany = 1.2°F). Third, temperatures at three locations in New York City warmed by 2.5°C (4.6°F) between historical and contemporary time periods (t = 4.81, N = 45, $p < 0.001$). Despite the greater magnitude warming in New York City, interannual variation in JAT in New York City—the site of our longest temperature time series—was representative of interannual variation at other cities in the state: JAT in New York City, Kingston and Albany were highly correlated over the study period ($r > 0.91$, N = 24, $p < 0.001$) for all pairwise correlations; specifically, historical stations: Kingston-Albany r = 0.85, Kingston-NYC r = 0.92, NYC-Albany r = 0.91; and contemporary stations: Kingston-Albany r = 0.98, Kingston-NYC r = 0.98, NYC-Albany r = 0.98).

3.1.2 | Changes in phenology across time periods (1826–2017)

Time period was a significant factor for both phenophases in Models 1 and 2 (Tables 2 and 3). FFD and FLD both advanced significantly from the historical (1826–1861) to contemporary (2009–2017) time periods. FFD advanced 10.6 days (Tukey HSD $p < 0.0001$), while FLD advanced 19.0 days (Tukey HSD $p < 0.0001$). Individual species showed variation in average FFD and FLD difference across time periods (Appendix S2: Tables S1 and S2). Approximately 85% of species evaluated showed advanced flowering in the contemporary period and approximately 60% (19 of 31) of those earlier flowering times were statistically significant via t-test ($p < 0.05$). FLD was even more uniform: all species showed earlier FLD in the contemporary time period and approximately 80% of those (18 of 19 species) were statistically significant via t-test ($p < 0.05$; Appendix S2: Table S2). Figure 3 highlights the 12 species most commonly observed per phenophase to illustrate the changes in phenology for these data-rich species (Figure 3a,b).

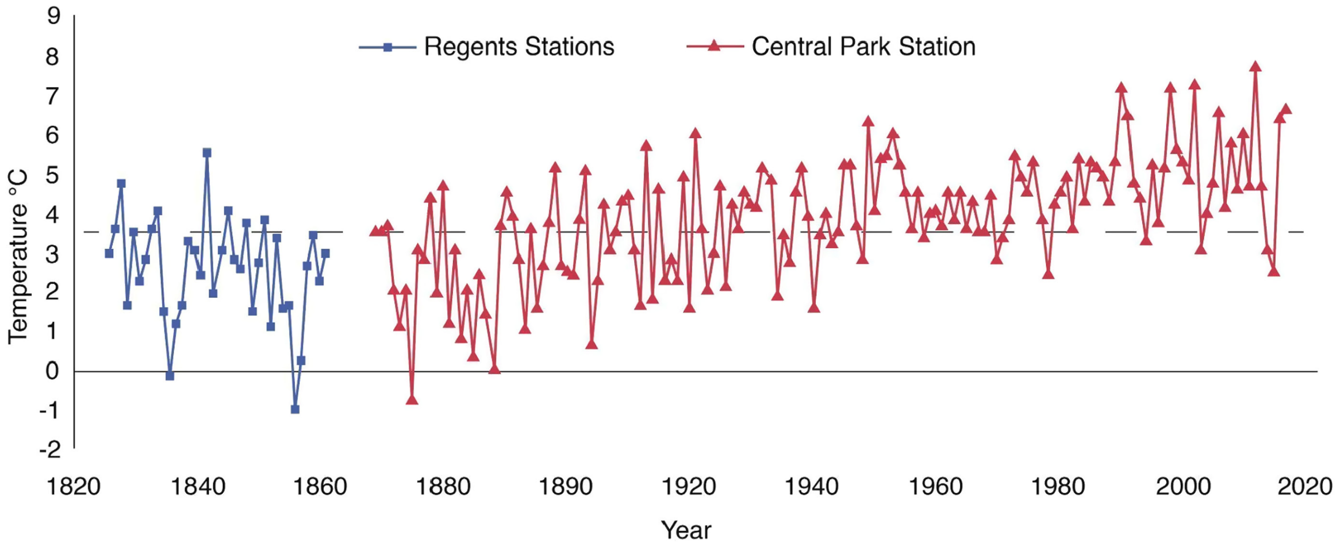

FIGURE 2 January–April temperatures (JAT) at three sites in New York City 1826–2017. Blue squares represent years 1826–1861, compiled from regents and army station data. Red triangles represent years 1869–2017 from Central Park, downloaded from NOAA Online Weather Data (NOWData, 2017). The dash-dot line shows the mean January–April temperature for the entire dataset, 1826–2017 (3.7°C).

TABLE 2 Results of general linear mixed effects model 1 describing the relationship between response variables (a) first flower date (FFD) and (b) first leaf date (FLD) (as measured by day of year, DOY) across all species and explanatory variables: January–April temperature (JAT): mean temperature in January–April (°C); time period: historical (1826–1872) versus contemporary (2009–2017); seasonality: early spring (DOY 60–120), late spring (DOY 121–152), and, for first flower only, summer (DOY 153–196); urban–rural setting; and their interactions with JAT, with hardiness zone (as designated by US Department of Agriculture) and with species as random effects. Significant *p*-values are in bold

(a) First flower date

Fixed effects	df	df Den	*F*	*p*
January–April temperature (continuous)	1	2390	103.19	**<0.0001**
Seasonality (categorical)	2	27.62	58.76	**<0.0001**
Temperature × seasonality	2	2396	15.03	**<0.0001**
Time period (categorical)	1	2403	7.662	**<0.0001**
Temperature × urban–rural	1	2383	4.90	**0.0269**
Urban–rural (categorical)	1	2364	0.87	0.3509
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone	28.68	9.61	40.82	0.4823
Species	88.15	28.25	25.09	**0.0004**

(b) First leaf date

Fixed effects	df	df Den	*F*	*p*
Time period (categorical)	1	1809	86.83	**<0.0001**
January–April temperature (continuous)	1	1827	25.43	**<0.0001**
Urban–rural (categorical)	1	1825	15.17	**<0.0001**
Seasonality (categorical)	1	27.49	15.33	**<0.0005**
Temperature × urban–rural	1	1836	0.12	0.7241
Temperature × seasonality	1	36.54	4.75	0.8493
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone	77.55	26.13	68.18	0.2341
Species	15.00	5.05	6.36	**0.0184**

TABLE 3 Results of general linear mixed effects model 2 describing the relationship between response variables (a) first flower date (FFD) and (b) first leaf date (FLD) (as measured by day of year, DOY) across all species and explanatory variables: January–April temperature: mean temperature in January–April (°C); time period: historical (1826–1872) versus contemporary (2009–2017); growth form: tree, small tree/shrub or forb; urban–rural setting; and their interactions with JAT, with hardiness zone (as designated by US Department of Agriculture) and with species, as random effects. Significant *p*-values are in bold.

(a) First flower date

Fixed effects	df	df Den	*F*	*p*
January–April temp.	1	2378	166.20	**<0.0001**
Temperature × growth form	2	2380	7.19	**0.0008**
Time period	1	2385	9.33	**0.0023**
Temperature × urban–rural	1	2378	3.63	**0.05361**
Growth form	2	28.04	1.13	0.3362
Urban–rural	1	2385	0.7569	0.3844
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone	28.12	4.42	41.44	0.4823
Species	433.20	65.76	24.37	**0.0002**

(b) First leaf date

Fixed effects	df	df Den	*F*	*p*
January–April temp.	1	1833	83.06	**<0.0001**
Time period	1	1801	93.62	**<0.0001**
Urban–rural	1	1819	14.51	**0.0001**
Temperature × growth form	1	1836	0.07	0.0883
Growth form	1	23.78	0.29	0.5925
Temperature × urban–rural	1	1832	0.03	0.8542
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone (random)	48.5	17.5	28.7	0.0915
Species (random)	15.3	5. 5	1.6	**0.0279**

3.2 | Changes in phenology in response to temperature

3.2.1 | Changes in FFD and FLD in response to JAT (prediction 2)

FFD and FLD tended to advance as JAT warmed, FFD by 3.3 days/°C (FFD: $r^2 = 0.07$, slope = −3.3 days/°C, $p < 0.001$) and FLD by 3.0 days/°C ($r^2 = 0.13$, slope = −3.0 days/°C, $p < 0.001$) (Figure 4). FFD and FLD varied significantly across species in response to temperature. The mixed effects Model 3 showed that both the species by temperature interaction and the species by urban–rural setting interaction were significant for both FFD and FLD, with species advancing at different rates in response to temperature and urbanization (Table 4). Additionally, in the regression analysis, the relationships between FFD and JAT for eight of the most commonly observed tree, small tree/shrub and forb species in our data set show that warmer temperatures were associated with earlier FFDs for all eight species ranging from 2.4 days earlier/°C for *Erythronium americanum* (dogtooth violet) to 6.3 days earlier/°C for *Ulmus americana* (American elm) (Figure 5, Appendix S2: Table S3).

3.2.2 | Influence of functional groups and urbanization on changes in FFD and FLD (seasonality, growth form, urban–rural and pollination syndrome) (predictions 2–6)

First flower date

January to April temperature (JAT) had a very strong influence on phenology, stronger than any other factor in the models for FFD (Tables 2a

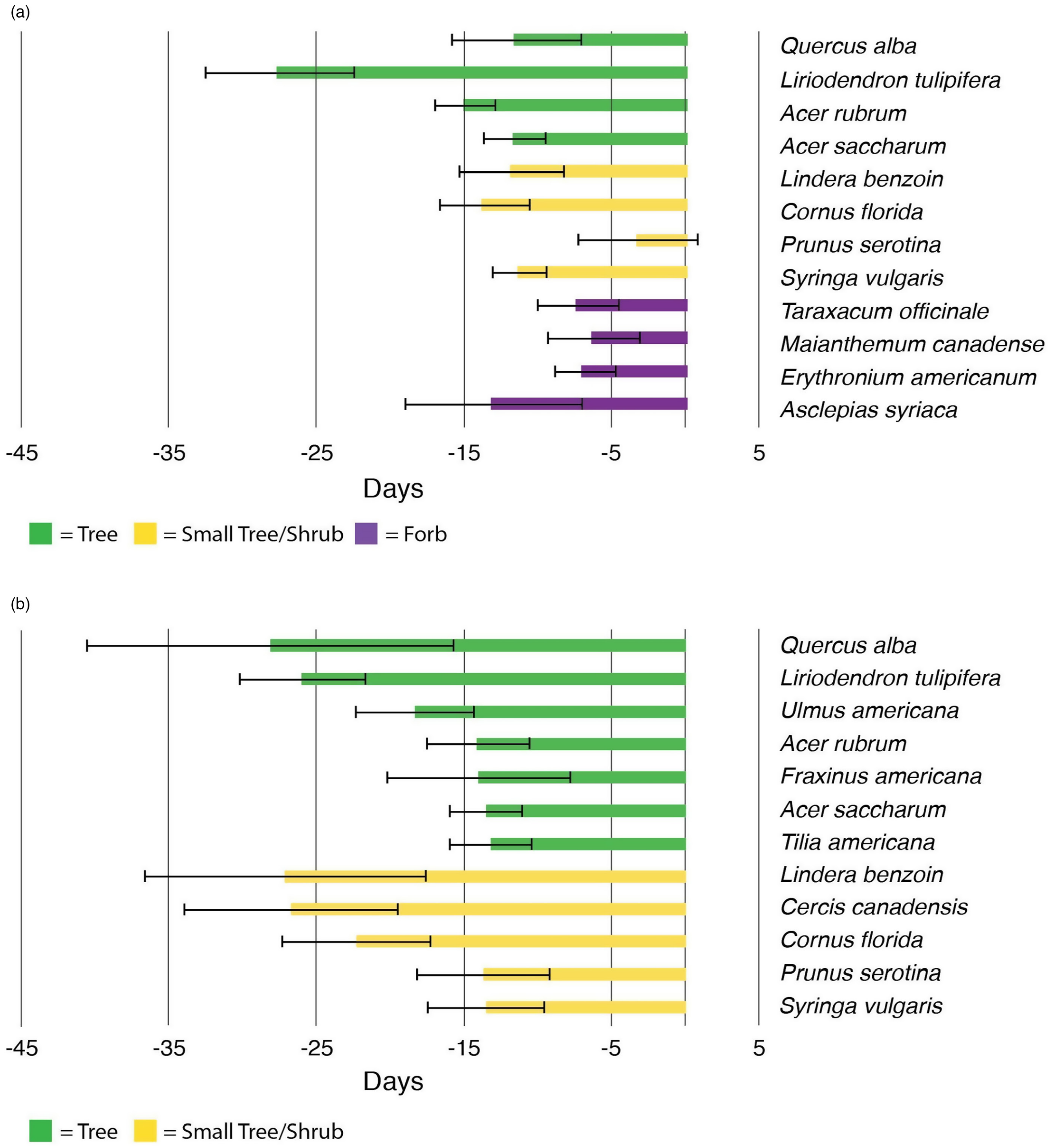

FIGURE 3 Change in (a) first flowering date (FFD) and (b) first leaf date (FLD) of individual species grouped by growth form (green = tree, yellow = small tree/shrub, purple = forb) for species with sample sizes greater than 60 (except FLD for *Cercis* $n = 23$, *Tilia* $n = 35$, and *Ulmus* $n = 41$), in at least two hardiness zones (with the exception of *Cercis*). Analysis for change between time periods was by *t*-test (results in Appendix S2: Tables S1 and S2). Error bars are SE.

and 3a). Seasonality, time period, temperature by seasonality and urban–rural by temperature all significantly influenced FFD (Table 2a). For FFD, early spring species were more responsive to changes in temperature than late spring species (3.8 days/°C for early spring species, versus 1.7 days/°C for late spring species, and no significant change for summer species, as indicated by the significant interaction between JAT and seasonality ($r^2 = 0.193$, slope = −3.7 days/°C, $p < 0.0001$, $r^2 = 0.039$, slope = −1.67 days/°C, $p < 0.0001$). Early spring flowering advanced by 11.4 days in the contemporary period (Tukey HSD $p < 0.0001$), late spring flowering advanced by 3.2 days (Tukey

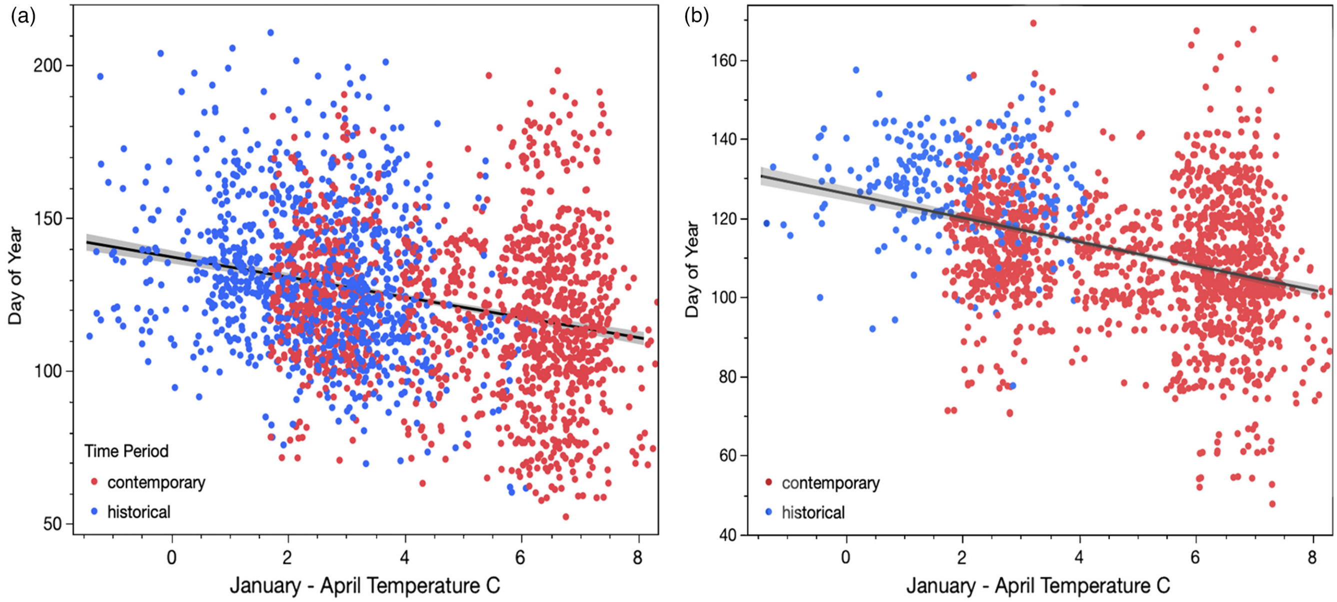

FIGURE 4 Relationships between JAT and (a) first flowering date (FFD) and (b) first leafing date (FLD) across all species. FFD and FLD tended to advance as JAT warmed, FFD by 3.3 days/°C (FFD: $r^2 = 0.07$, slope = −3.3 days/°C, $p < 0.001$) and FLD by 3.0 days/°C (FLD: $r^2 = 0.13$, slope = −3.0 days/°C, $p < 0.001$). Best fit lines are shown (shading is SE).

TABLE 4 Results of general linear mixed effects model 3 describing the relationship between response variables (a) first flower date (FFD) or (b) first leaf date (FLD) and explanatory variables: January–April temperature (JAT), urban–rural setting and species as fixed factors. Significant *p*-values are in bold.

(a) First flower date				
Fixed effects	**df**	**df Den**	***F***	***p***
January–April temp.	1	2319	88.03	**<0.0001**
Urban–rural	1	2301	3.98	**0.0461**
Species	30	2316	137.70	**<0.0001**
Temperature × species	30	2316	4.21	**<0.0001**
Urban–rural × species	30	2316	2.67	**<0.0001**
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone	52.49	22.03	29.15	0.0718
(b) First leaf date				
Fixed effects	**df**	**df Den**	***F***	***p***
January–April temp.	1	1790	130.52	**<0.0001**
Species	18	1791	9.35	**<0.0001**
Temperature × species	1	1790	2.56	**0.0003**
Urban–rural × species	18	1792	2.00	**0.0073**
Urban–rural	1	1752	0.39	0.5314
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone	60.60	22.59	35.47	0.0875

HSD 0.0023) and summer flowering showed no significant DOY difference between time periods. FFD was more responsive to temperature for trees (4.5 days/°C) and shrubs (4.1 days/°C) than forbs, as indicated by the significant interaction term between JAT and growth form ($r^2 = 0.11$, slope = −4.5 days/°C, $p < 0.0001$; $r^2 = 0.16$, slope = −4.1 days/°C, $p < 0.0001$; $r^2 = 0.0002$, slope = −0.17 days/°C, $p = 0.68$, respectively). The change between time periods was greater for trees (19.5 days) and small trees/shrubs (17.1 days) than for forbs (6.2 days) (Tukey HSD $p < 0.001$).

Both models showed a significant interaction between urban–rural designation and temperature for FFD (Tables 2a and 3a). FFD was more responsive to temperature in urban areas than rural areas ($r^2 = 0.09$, slope = −3.8 days/°C, $p < 0.0001$; $r^2 = 0.05$, slope = −2.70 days/°C, $p < 0.0001$, respectively). FFD advanced 8.7 days on average in rural settings, versus 11.9 days on average between time periods showing a 3-day advancement in the contemporary time period for plants in urban settings relative to rural settings (Tukey HSD $p < 0.0001$). Some species showed strong differences in how much FFD changed between urban and rural areas. For example, FFDs for *Acer rubrum*, *Liriodendron tulipifera* and *Syringa vulgaris* advanced more between time periods in urban areas than in rural areas (Appendix S2: Table S4). However, *Acer saccharum* and *Ulmus americana* showed the opposite tendency.

For pollination syndrome, JAT and the interaction between JAT and pollination syndrome were both significant (Table 5). Insect-pollinated trees were more sensitive to temperature than wind pollinated trees ($r^2 = 0.15$, slope = −5.5 days/°C, $p < 0.0001$; $r^2 = 0.004$, slope = −0.7 days/°C, $p = 0.30$, respectively). Pairwise comparisons show that insect-pollinated tree species advanced their FFD more than wind pollinated species between time periods, by 27.4 days versus 8.1 days, respectively (Tukey HSD $p < 0.0001$). The complete regression statistics for the relationship between FFD and JAT are in Appendix S2: Table S5; Tukey test statistics for differences between periods are in Appendix S2: Table S6.

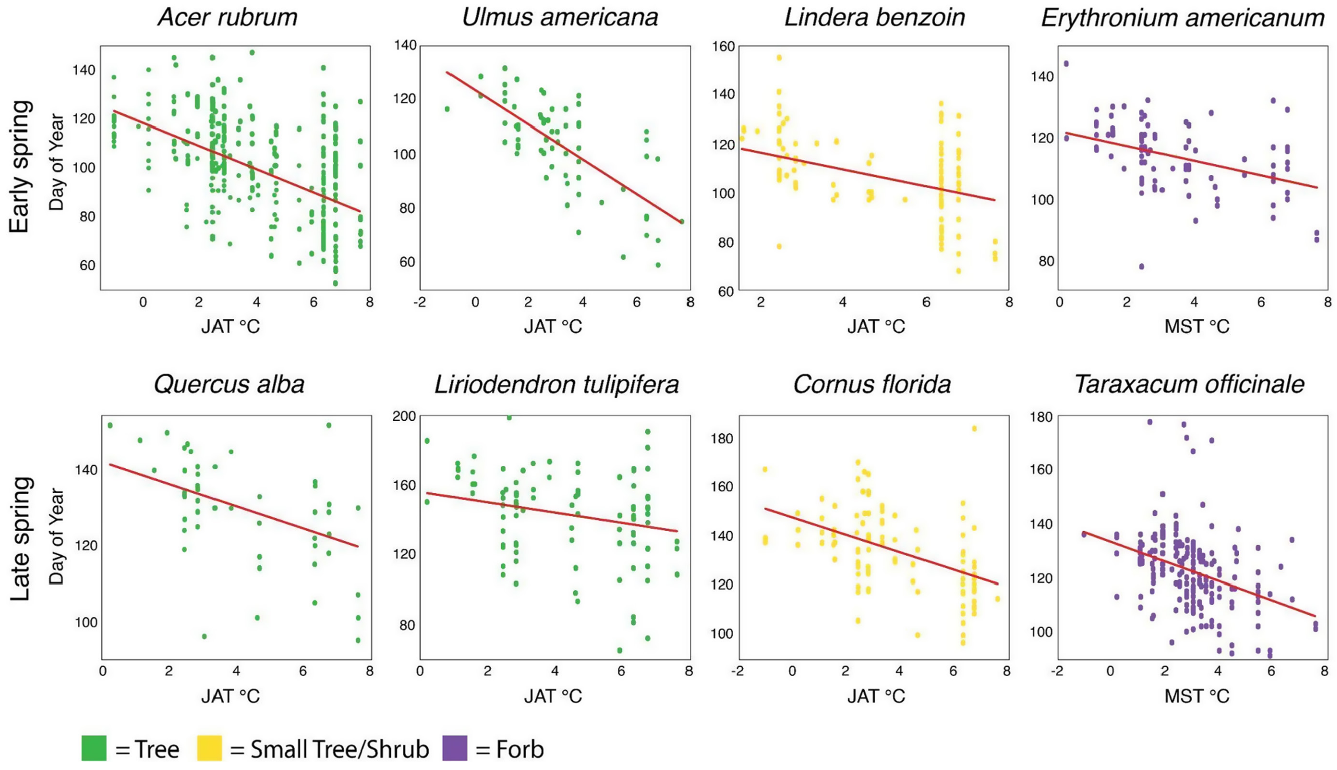

FIGURE 5 Relationships between mean January–April temperature (JAT) and first flowering date (FFD) for eight of the most commonly observed species in our data set, grouped by seasonality (early spring and late spring) and growth form (green = tree, yellow = small tree/shrub, purple = forb), as indicated by linear regression. Observations are from the historical time period. Each point represents one observation of FFD at one location in 1 year. Best fit lines shown here (Appendix S2: Table 5).

TABLE 5 Results of general linear mixed effects model 4 describing the relationship between the response variable first flower date (FFD) and explanatory variables (a) time period and (b) January–April temperature, along with pollination syndrome (fixed) and hardiness zone (random), across tree species. First flower date (FFD), measured by day of year, DOY; time period: historical versus contemporary; January–April temperature: mean temperature in January–April (°C); pollination syndrome: wind or insect. Significant *p*-values are in bold

Fixed effects	df	df error	*F*	*p*
Jan-April temp.	1	1033	37.07	**<0.0001**
Temperature × pollination syndrome	1	1073	25.90	**<0.0001**
Pollination syndrome	1	1073	2.03	0.1546
Random effects	**Variance component**	**%**	**SE**	**Wald *p*-value**
Hardiness zone (random)	20.0	2.73	16.3	0.2197

First leaf date

January to April temperature, time period and urban–rural designation all had significant effects on phenology for FLD in both models (Tables 2b and 3b). Seasonality was significant on its own, but not in relationship to temperature (Table 2b). Pairwise comparisons show that trees and shrubs advanced in the contemporary period by 16.8 and 15.4 days for early spring and late spring species respectively (Tukey HSD, $p < 0.0001$). Growth form was statistically non-significant overall in the model ($p < 0.08$); however, the linear regression showed a significant relationship to temperature ($r^2 = 0.12$, slope = −3.2 days/°C, $p < 0.001$; $r^2 = 0.13$, slope = −2.9 days/°C, $p < 0.001$, for shrubs and trees respectively) and pairwise comparisons show that trees and shrubs both advanced in the contemporary time period (trees by 19.6 and shrubs by 16.7 days) (Tukey HSD $p < 0.0001$). The interaction term for urban–rural designation and species for FLD was significant with species as a fixed effect (Table 4). First leaf date in urban areas appear more sensitive to temperature than in rural areas ($r^2 = 0.14$, slope = −3.3 days/°C, $p < 0.0001$; $r^2 = 0.13$, slope = −2.6 days/°C, $p < 0.0001$, respectively). Pairwise comparisons show that leaves advanced in urban areas by 20.9 days versus 17.2 days in rural areas showing a 3.7 day advancement in the contemporary time period for plants in urban settings relative to rural settings (Tukey HSD $p < 0.0001$). FLD also had variable trends across species (Appendix S2: Table S4). FLDs for *Acer saccharum*, *Cornus florida*, *Liriodendron tulipifera* and *Quercus alba* all advanced more in urban areas, but *Acer rubrum* and *Tilia americana* showed the opposite trend (Appendix S2: Table S4). More complete regression statistics for the relationship between FLD and JAT are in Appendix S2: Table S5; Tukey test statistics for differences between periods are in Appendix S2: Table S6.

4 | DISCUSSION

This plant phenology data set spanning nearly two centuries is exceptional for its combination of traits: a large-scale, multi-species, multi-site comparison of standardized, ground-collected phenology observations with paired weather data that both predates and extends well into human-caused perturbation of Earth's climate system. The temporal depth and taxonomic breadth of this record has enabled us to extend and strengthen findings regarding phenology changes from this region. Results from this study show large phenological differences from the beginning to almost two centuries after industrialization, including strong effects of urbanization and greater advancement in flowering for early-season species, and for trees and shrubs, particularly those that are insect-pollinated. Moreover, the historical observations were collected by a trained citizen science network similar in structure and observation protocols to the contemporary USA-NPN, vividly illustrating the utility of public participation in science research to build data sets rich with potential for discovery.

4.1 | Leaf and flower phenology has advanced dramatically with increasing spring temperatures; shifts vary by species

As expected, across 36 plant species representing a range of functional groups examined across New York State, most flower and leaf earlier in recent years (2009–2017) than they did in the early and middle parts of the 19th century (1826–1861 for FFD and 1851–1859 for FLD). On average, plants flowered 10.5 days earlier and leaf 19 days earlier—with some species flowering up to 27 days earlier and leafing up to 31 days earlier over that time period. Most of this change is coincident with warming mean January–April temperatures (JAT) over that time; JAT warmed by 2.5°C in NYC and by 1.0°C when averaged across three representative urban sites between the historical and contemporary periods. Warming in NYC was likely accelerated relative to other parts of the state because of the warming effects of high urbanization.

The magnitude of phenological changes observed across New York State, flowering and leafing on average 3 days/°C earlier, supports and strengthens the trend described by other studies in the northeastern United States by extending the period of record back in time (Cook et al., 2008; Cook, Wolkovich, & Parmesan, 2012; Everill et al., 2014; Melaas et al., 2016; Miller-Rushing & Primack, 2008; Morin et al., 2009; Park et al., 2019; Polgar et al., 2014; White et al., 2014). A notable result from this data set is the high degree of variation in the magnitude of change among species and phenophases. Not all species are responding to climate change in the same ways: some species have shown no obvious change, while others are dramatically advancing or delaying the timing of their development. The variation found here reinforces results found in nearly all community-level studies of changes in phenology (Craine et al., 2012; Diez et al., 2012; Rafferty et al., 2020) but adds specificity in terms of individual species phenological sensitivity, some of which have not been assessed in other studies. Additionally, leaf out appears to be advancing more rapidly over time than flowering between time periods, although both show similar responses to temperature. The differential rate of change between leaf out and flowering, whether driven primarily by temperature or by other synergistic factors influencing changes over time (i.e., urbanization), can create disruptions in ecological interactions such as pollinators and herbivores and the plants on which they rely as food sources, especially when the magnitude of the advance is substantial (Kharouba et al., 2018; Kharouba & Wolkovich, 2020; Samplonius et al., 2021). Similar disruptions can occur between canopy and understory plants and other types of mutualistic interactions (Heberling et al., 2019). For example, we documented an advance in leaf out of 27 days in *Lindera benzoin*, the obligate host of the spicebush swallowtail butterfly; a change of this magnitude could have major impacts on swallowtail populations. *Cornus florida* (flowering dogwood) and *Liriodendron tulipifera* (tulip tree), both important late spring nectar sources, now flower 14 and 27 days earlier on average, respectively, than in the 19th century. *Asclepias syriaca* (common milkweed), a key late-season nectar source and a member of the obligate genus host for the migratory monarch butterfly, flowers 13 days earlier on average. These species-specific results can help direct targeted research and efforts to restore ecosystem function in managed landscapes (i.e., planting efforts on behalf of pollinators).

4.2 | Seasonality and growth form both strongly influence changes in flowering, but leafing patterns for these functional groups are less clear

For flowering, early-season species tended to show particularly rapid advancement and strong responses to temperature, a result consistent with other studies in the region and elsewhere (Cook, Wolkovich, Davies, et al., 2012; Miller-Rushing & Primack, 2008; Park et al., 2019). Such changes can lead to an extension of the flowering season and shifts in the timing of resource availability (Aldridge et al., 2011; Diez et al., 2012). As predicted, temperature-driven differences in phenology for different flowering times advanced more for some growth forms than others. First flower date was more responsive to temperature for trees and shrubs than for forbs, and trees showed the greatest change between time periods, which confirm and amplify results from a recent study from this region (Heberling et al., 2019).

The changes we saw in timing of leafing between time periods did not consistently support our hypothesis that earlier season species would show a greater rate of advancement. Early-season species advanced slightly more than late-season species between periods (1.4 days), but the relationship to temperature was not significant. Individual species variation for both early- and late-season species may be obscuring the trends found in other studies. The species that showed the greatest rate of change between periods had high proportions of individuals from urban locations in both time periods, which may point to other global change factors such as soil moisture, light pollution and nitrogen pollution affecting individual species independent of their seasonality (Meng, 2021). The analysis of the change in timing of leafing between time periods and the two growth forms also did not strongly support our hypothesis that trees would show a greater advancement. However, trees appear to be advancing slightly more than shrubs overall, 19.6 versus 16.7 days respectively, and there is a notable but not statistically significant relationship with temperature. The synergistic effects of urbanization may be obscuring the ability to detect more significant functional group patterns overall in this particular analysis, but future studies may be able to reveal which other factors are driving changes in leaf out.

4.3 | Urban locations show greater advancement in leafing and flowering than rural areas

As predicted, we found that plants in urban areas are shifting phenology at a greater rate than those in rural areas, likely driven by more rapid warming in urban areas. For example, our data show that *L. benzoin* leafs out 18 days earlier in rural areas and 31 days earlier in urban areas, and *Syringa vulgaris* (common lilac) leafs out 9 days earlier in rural areas and 20 days earlier in urban areas. This type of pattern is already causing urban areas to become 'islands' of early phenology (Zhang et al., 2004) and may further isolate urban plant populations from rural populations in the future. These islands could facilitate responses to climate change for migratory species (Tryjanowski et al., 2013) or could contribute to phenological mismatches as urban areas become increasingly disconnected from surrounding landscapes. Phenological reproductive isolation of urban populations could also facilitate evolution within these populations; speciation is already being seen in some urban populations (Yakub & Tiffin, 2017).

In addition to temperature, plant phenology is affected by water availability, nutrients, light and other factors (Meng et al., 2021; Rathcke & Lacey, 1985). Concentrations of carbon dioxide, ozone, nitrogen oxides and other pollutants, soil moisture and level of artificial light all have changed with industrialization and increasing urbanization and have been shown to affect phenology (Meng, 2021; Wohlfahrt et al., 2019). Indeed, our analyses identified that the time period of the data (historical versus contemporary) has a strong effect, particularly on leafing, despite the fact that temperature was also accounted for in the models. This result suggests that temperature was not the only influential global change factor at play that changed phenology from the early industrial revolution to now. Furthermore, average temperatures for a season may not be the only or even most important factor determining flowering and leaf timing; the amplitude of minimum and maximum temperatures also can be important (De Rességuier et al., 2020), especially in urban areas.

4.4 | Insect-pollinated species are advancing phenology more than wind-pollinated species

Our analysis uniquely suggests a potential difference in phenological responsiveness due to pollination syndrome (wind- or insect-pollination) with ground-collected historical data over a large geographic region. Insect-pollinated tree species showed a greater phenological advancement than wind-pollinated trees in the contemporary time period, bearing out our prediction. Insect-pollinated trees may be experiencing greater selection for temperature sensitivity because of their year-to-year need to coincide with insect pollinators (Calinger et al., 2013; Fitter & Fitter, 2002; Kudo et al., 2008; Wiegmann & Waller, 2006).

Many trees and shrubs provide a large proportion of nectar for pollinators due to their size and abundance of flowers, particularly during the early spring season (Vaughan & Black, 2006). Too much phenological sensitivity to temperature change however, in trees and shrubs specifically, could have dire consequences for pollinators if pollinators are not responding synchronously. In the ecosystems detailed in this study, *A. rubrum* is the first major nectar plant of the spring and both native pollinators and honeybees are dependent on this first flush of nectar (Batra, 1985; Southwick & Southwick, 1986). Our study found that *A. rubrum* is flowering more than 2 weeks earlier on average in the contemporary time period and that its flowering has a strong relationship to JAT. If this crucial nectar source responds to warm temperatures in late winter/early spring and pollinator species do not respond synchronously or frost kills the initial flowers, local pollinator populations could be severely impacted by this one species alone. Because our sample size was limited due to only including trees and having a limited number of tree species, we were not able to explore the influence of species as a factor in this model. Future studies should include a higher number of species to further validate these results.

4.5 | Limitations

Though these data sets are extensive and have provided solid evidence of phenological change over time, there are limitations that present challenges. The historical data set is spotty in some locations, and there is a lack of phenology data in this comparison between 1862 and 2009. Further, the historical locations that reported phenology observations in a given year vary per species and are not exactly the same locations as in the contemporary period. Though we found no major inconsistencies between historical time period phenology protocols in our preliminary analyses, historical phenology data were collected under slightly different protocols, and the lack of exact protocol match between the historical and contemporary time periods could contribute to variance in the data set. The use of monthly means as a coarse evaluation of temperature change over time also does not consider meteorological equipment and protocol differences among sites and time periods. Finally, temperature change and differences between urban and rural areas may be confounded by factors such as magnitude of urbanization or localized climate changes due to land use over the study period (Bonan, 1999; Burakowski et al., 2016). Despite the limitations, clear and significant patterns emerge from these data, demonstrating their utility and robustness. To strengthen the predictive power of phenology data, future citizen science studies should include other measurable factors that affect phenology in addition to temperature, especially in the context of the effects of urbanization and land use changes over time.

4.6 | Conservation implications

Species that appear to be particularly sensitive (or insensitive) to changes in spring temperatures may be able to serve as indicator species to help identify conservation priorities, or be targeted as species that should be planted more widely (for example, planting species with high nectar value as urban street trees to aid pollinator conservation endeavours). Notable species that are widely found in natural and cultivated settings, appear phenologically sensitive and have high value to wildlife include *C. florida*, *A. rubrum* and *U. americana*, all of which flowered about 2 weeks earlier in the contemporary period. Alternatively, species with phenologies that do not appear to be responding to changes in temperature may be particularly prone to declining in abundance, potentially due to limited plasticity or adaptability (Cleland et al., 2012; Willis et al., 2008), though this does not apply in all ecosystem types (Block et al., 2020; Iler et al., 2019). Many of the early-season spring ephemerals evaluated in this study are examples of species that do not appear to be as sensitive to changing temperature and have advanced their phenology by a week or less in the contemporary period (i.e., *M. canadense*, *E. americanum*). Together, these community-level and species-specific results will inform ecologists and resource managers who are exploring and managing the ecological and evolutionary impacts of phenological changes among organisms (Enquist et al., 2014; Morellato et al., 2016).

The differences we found in phenological change among functional groups (seasonality and growth form) and phenophases between time periods suggest that interactions between different canopy levels may change, possibly affecting species that compete for light to support early-season growth and photosynthesis, and those that rely on light in the understory during flowering (Heberling et al., 2019; Hudson et al., 2017; Kudo et al., 2008; Sercu et al., 2017). We found that first leaf date for many of the common tree species in New York's contemporary second growth forests have advanced by about 2–4 weeks. The fact that these tree species are leafing out dramatically earlier will produce earlier shade and therefore could affect the early spring understory. Indeed, some early-season spring ephemeral forbs show only minor changes in flowering time. Reduced light from early canopy closure can reduce overall fitness (Heberling et al., 2019). Such selection pressure (or plasticity) could drive some of these species to advance phenology faster, but that could increase their vulnerability to late-season frosts (Augspurger, 2013; Inouye, 2000). Our findings of distinct patterns of phenological responsiveness among functional groups support our prediction and add to the limited number of studies globally that have evaluated variations in phenological sensitivity at the functional group level (Crimmins et al., 2010, 2011; Keller et al., 2011; Miller-Rushing & Primack, 2008).

Understanding how plant phenological responses to warming vary among species, across regions, and over long time scales is an important step in predicting future ecological responses to climate change (Lewis et al., 2022; Piao et al., 2019). At regional and landscape scales, as in this study, plant phenology can influence migration, pollination and ecosystem processes such as carbon, water and nutrient cycling (Peñuelas et al., 2009). Understanding how factors such as urbanization, seasonality and growth form influence phenological sensitivity to warming is critical to forecasting future changes in phenology and their ecological impacts. Such insights can inform and direct targeted research and efforts to restore ecosystem function in natural and managed landscapes (i.e., pollinator habitat restoration, invasive species management).

4.7 | Insights from unique volunteer-based data sets

The two data sets evaluated in this study are novel in that they were both contributed primarily by non-professionals and follow similarly rigorous observation protocols. To our knowledge, no other phenology data set dating from the early industrial period exists from North America using standardized protocols and encompassing multiple decades, species and sites. Because of these features, this historical data set is well-suited for pairing with modern phenology observations and enables a more thorough evaluation of phenological change among species than previously documented for this region. In particular, the diversity present in the data set has enabled an assessment of variation in changes among species as well as pollination syndrome, a trait not typically evaluated in evaluations of phenological change. Phenology data with similar temporal depth and taxonomic breadth originating in the United Kingdom have revealed critically important findings regarding differential changes among species (Büntgen et al., 2022).

The full historical data set we describe here has a taxonomic richness that we did not fully address in this study, given our data requirements to match the modern plant phenology data. The fully digitized data set has the potential to yield many more comparative analyses and cross-sector collaborations, with this first analysis able to serve as a foundational model for methodologies that can be used when comparing or joining large-scale citizen science data sets.

The findings from this evaluation also have value for shaping current and future citizen scientist phenology monitoring efforts. In particular, this evaluation demonstrates species that can effectively be tracked by non-professionals, targeting phenophases with known accuracy (Fuccillo et al., 2015). Our findings also suggest species that might be given priority when starting or revising citizen science phenology programs. The volume of observers and large spatial scales of citizen science projects can cover more ground than scientists alone and can simultaneously provide social and educational benefits for the participants (McDonough MacKenzie et al., 2020; Spellman & Mulder, 2016). They can also be organized along environmental gradients to capture responses to key variables (e.g., McDonough MacKenzie et al., 2019). Collectively, the insights derived from this historical data set and its modern counterpart can serve as a model to validate the importance of long-term monitoring. The volunteer observers of today are building the data sets needed for the future to track the mechanisms and consequences of climate change.

5 | CONCLUSIONS

Our data show a strong signal of phenological change in response to climate change across a large geographic region. Our data add a critical piece to the growing literature describing both temperature and phenological change: we add earlier (pre-1850s) temperature and flowering data and a broader spatial scale of community-level phenology data than exists from any other observational data set in North America. Previously comparable data were primarily available from herbarium specimens, which are highly valuable, but also have known sampling biases (Daru et al., 2018). We are not aware of any older historical-contemporary comparative phenology study that uses historical data from an organized citizen science network which closely matches newer data collected by the USA National Phenology Network and other phenology networks around the world (Denny et al., 2014).

Our findings validate and amplify patterns found in other studies in this region, as well as strengthen ecological forecasting potential by extending the period of record available for both ground-truthed temperature and phenology data. Based on our results, forecasts may anticipate strong effects of urbanization on phenology and stronger changes in flowering for early-season species and for trees and shrubs, particularly those that are insect-pollinated. Our results also highlight the potential for mismatches and other community-level changes in interactions—such as shifts in plant-pollinator, plant-herbivore or plant-plant relationships—to occur locally and along urban–rural and other climate gradients. Our analyses suggest several ways phenological variation can create demographic and population impacts across time scales. We also identified species and groups of species (e.g., insect-pollinated trees) that might be used as indicators of changes in phenology and those that might be further impacted by future warming. Collectively, these data deepen our understanding of climate change impacts, creating rich opportunities for further experimental work and modelling. By bringing the efforts of a historical network into a contemporary context we explicitly illustrate how long-term monitoring and citizen science efforts are invaluable for ecological forecasting and discovery.

AUTHORS' CONTRIBUTIONS

K.F.B., A.D. and C.R.V. conceived of the initial project and compiled and digitized the data sets; K.F.B. led the data preparation with assistance from A.D., T.M.C. and L.L.A.-D.; K.F.B. led the analysis and evaluated and interpreted results with support from T.M.C., C.E.d.R., A.D., C.R.V., L.L.A.-D. and T.N.R.; K.F.B. drafted the manuscript and all authors contributed critically to the drafts (specifically CDR) and gave the final approval for publication. The authors have no conflicts of interest with respect to this publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to report.

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DATA AVAILABILITY STATEMENT

The data used in this analysis is archived in Figshare https://doi.org/10.6084/m9.figshare.13232243 (Fuccillo Battle et al., 2022).

ORCID

Kerissa Fuccillo Battle https://orcid.org/0000-0002-9152-1965
Anna Duhon https://orcid.org/0000-0002-0817-705X
Conrad R. Vispo https://orcid.org/0000-0003-3899-0620
Catherine E. de Rivera https://orcid.org/0000-0002-3526-0668

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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