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Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA

Isaac W. Park · Mark D. Schwartz

Abstract In recent years, a growing body of evidence has emerged indicating that the relationship between flowering phenology and climate may differ throughout various portions of the growing season. These differences have resulted in long-term changes in flowering synchrony that may alter the quantity and diversity of pollinator attention to many species, as well as altering food availability to pollenivorous and nectarivorous animal species. However, long-term multi-season records of past flowering timing have primarily focused on temperate environments. In contrast, changes in flowering phenology within humid subtropical environments such as the southeastern USA remain poorly documented. This research uses herbarium-based methods to examine changes in flowering time across 19,328 samples of spring-, summer-, and autumn-flowering plants in the southeastern USA from the years 1951 to 2009. In this study, species that flower near the onset of the growing season were found to advance under increasing mean March temperatures (-3.391 days/°C, $p=0.022$). No long-term advances in early spring flowering or spring temperature were detected during this period, corroborating previous phenological assessments for the southeastern USA. However, late spring through mid-summer flowering exhibited delays in response to higher February temperatures (over 0.185 days/°C, $p \leq 0.041$ in all cases). Thus, it appears that flowering synchrony may undergo significant restructuring in response to warming spring temperatures, even in humid subtropical environments.

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Introduction

It is well-documented that the timing of flowering among spring, summer, and autumn species differ in their responses to ongoing climate changes (Wolkovich et al. 2012; Fitter and Fitter 2002; Fitter et al. 1995; Menzel et al. 2001; Sparks et al. 2000). Phenological records across a majority of long-term European and North American datasets (Wolkovich et al. 2012) indicate that the timing of flowering across a wide array of plant species has advanced more rapidly in early spring than among late spring or summer in response to warming temperatures in recent decades (Fitter and Fitter 2002). Such differences in relative timing of early and late-flowering species in recent years may disrupt a variety of key ecological processes, including pollinator attention to many plant species (Hegland et al. 2009; Wall et al. 2003). These changes may strengthen weak synchronies among co-occurring species, reducing pollination and fruiting success through increased interspecific pollen transfer and limited pollinator attention to each species (Waser 1978). Conversely, the weakening of existing synchronies may lead to periods of floral "drought", in which fewer species are in flower, and pollen and nectar availability to nectarivorous or pollenivorous species are reduced (Aldridge et al. 2011; Memmott et al. 2007; McKinney et al. 2012). Such changes may also disrupt facilitative interactions among species that use simultaneous, multi-taxa floral displays to increase pollinator attention (Staggemeier et al. 2010; Tachiki et al. 2010).

However, phenological records capable of examining such differences among spring, summer, and autumn flowering have typically focused on areas with cooler continental or maritime environments above 38° in latitude (Fitter et al. 1995; Fitter and Fitter 2002; Menzel et al. 2001; Sparks et al. 2000; Wolkovich et al. 2012), on fully tropical environments (Borchert 1996; Borchert et al. 2004; Brearley et al. 2007; Opler et al. 1976; Rivera and Borchert 2001), or on dry

subtropical (Mediterranean) climates (Gordo and Sanz 2005, 2010; Peñuelas et al. 2004; Spano et al. 1999). In comparison, multi-seasonal records of flowering phenology are sparse among humid subtropical ecosystems, particularly in the northern hemisphere. Thus, the potential for similar disruptions among spring, summer, and autumn phenology across humid subtropical regions such as the southeastern USA remains largely unknown.

This lack of data among lower temperate and subtropical latitudes is rendered even more problematic by the fact that this region represents a transitional space between cool temperate and tropical climates, both of which have been found to display radically different relationships between climate and phenology. In mesic regions, inter-annual changes in temperature are well-documented to explain the majority of variation in flowering phenology (Fitter et al. 1995; Chuine and Cour 1999; Menzel 2003; Miller-Rushing and Primack 2008; Primack et al. 2004; Sherry et al. 2007; Sparks et al. 2000; Wolfe et al. 2005). The timing of spring and summer flowering within temperate and dry subtropical environments have typically been found to advance most strongly in response to increasing temperatures during the 1–3 months prior to flowering (Estrella et al. 2007; Fitter and Fitter 2002; Kottek et al. 2006; Gordo and Sanz 2005, 2010; Spano et al. 1999). However, evidence indicates that some species and phenophases in dry subtropical or Mediterranean regions may be more responsive to changes in precipitation than temperature (Peñuelas et al. 2004).

In contrast, the timing of flowering throughout tropical regions is often insensitive to temperature variations (Borchet 1994). Instead, the flowering phenology in such regions is often more closely related either to seasonal changes in daylength or insolation (Calle et al. 2010), or to changes in moisture availability (Borchert 1996; Borchert et al. 2004; Brearley et al. 2007; Opler et al. 1976).

Regions with humid subtropical climates, such as the southeastern USA, represent a poorly documented transitional zone between tropical regions in which plant phenology is predominantly dictated by insolation (Calle et al. 2010) or rainfall (Brearley et al. 2007) and temperate regions in which temperature plays the dominant role in determining plant phenology (Fitter et al. 1995; Fitter and Fitter 2002; Sparks et al. 2000). Such regions are characterized by mild winters (mean daily temperatures typically above 0 °C during coldest month) with occasional frosts, but lack the pronounced dry season of Mediterranean climates.

Short-term records of flowering phenology in humid subtropical regions throughout both southern Brazil (Marques et al. 2004) and the southeastern USA (Abu-Asab et al. 2001; Funderburk and Skeen 1976) imply that flowering phenology in those environments is more closely related to temperature than to precipitation. However, two of these studies were unable to evaluate any long-term

divergences among seasonal components of the plant community due to their short duration (1996–1998 in Brazil, 1967–1971 in GA, USA), and the third examined only spring-flowering species (Abu-Asab et al. 2001). Therefore, the effects of climate changes on the synchrony of flowering throughout spring, summer, and autumn in these areas are largely unknown, as is the nature of the climate cues that may affect the timing of flowering across the various seasons.

This study addresses the lack of long-term phenological data in humid subtropical environments through the construction of a long-term phenological record detailing the timing of flowering across spring, summer, and autumn throughout the state of South Carolina in the southeastern USA from the year 1951 to 2009. Specifically, the following questions will be addressed: (1) Do plant species with different flowering seasonalities display different patterns of inter-annual variation in South Carolina? (2) Have species that flower during different portions of the growing season exhibited differing long-term phenological trends from 1951 to 2009 within humid subtropical climates? (3) Do species that flower during different portions of the growing season exhibit divergent responses to varying climate conditions in humid subtropical climates? (4) Is flowering phenology in this region dictated by similar climate cues as have been documented in colder temperate environments? (5) Do species that flower during different portions of the growing season exhibit differing levels of spatial autocorrelation? (6) Do variations in sampling intensity result in systematic biases towards earlier or later estimates of community-level flowering phenology?

Materials and methods

This study made use of extensive digital herbarium records drawn from the digital archives of the Clemson University herbarium, the University of South Carolina herbarium, and the herbarium of Florida State University. Previous studies have shown that herbarium-derived records produce similar estimates of long-term phenological change to those produced by direct observation (Miller-Rushing et al. 2006; Diskin et al. 2012) and can be used to evaluate spatial changes in flowering phenology over wide areas (Diskin et al. 2012; Lavoie and Lachance 2006; Zalamea et al. 2011). Because such data allow analyses to incorporate information across an unparalleled diversity of plant species, herbarium records are also uniquely suited to evaluate community-level phenological patterns among the majority of species in a region. However, herbarium collections rarely repeat across the same locations and individuals every year and are often influenced by short-term research projects that may have variable spatial or taxonomic foci. Thus, annual

gaps occur in the record for most species; and even in years where some data are present, many taxa may not include sufficient records for species-level phenological analysis.

Thus, with some notable exceptions (Callinger et al. 2013), most studies utilizing herbarium records have been limited to evaluating either a small set of highly collected species (Gaira et al. 2011; Diskin et al. 2012; Lavoie and Lachance 2006) or restricted to localized areas of particularly intense collection (Miller-Rushing et al. 2006; Panchen et al. 2012; Primack et al. 2004). Similarly, evaluations of phenological change have generally been limited to decadal or multi-decadal scales in order to minimize the effects of spatial variability or annual gaps in collection (Diskin et al. 2012; Panchen et al. 2012; Primack et al. 2004).

By incorporating information from a wide array of taxa (>1,700 species) with flowering phenologies that range from early spring through the end of the growing season, this study demonstrates that herbarium records can be used to develop annual as well as multi-decadal estimates of flowering phenology at regional scales. This method allows a much larger annual sampling than is available for any single species. In exchange, however, it sacrifices the ability to detect specific events such as first flowering or peak bloom by individual species. Instead, it produces general estimates of variation in flowering time among all species that share similar flowering seasonality, through averaging annual departures from each species' long-term flowering normal (mean observed timing from 1951 to 2009) across all taxa that typically flower during each season. Unlike methods that focus on the onset or peak of flowering for a given species (Diskin et al. 2012; Amano et al. 2010; Miller-Rushing et al. 2008; Fitter et al. 1995), the resulting estimates of flowering time may be thought of as reflecting variation in the "mean center" of flowering across the entire community. Unlike previous studies that examined multiple phenophases (Menzel et al. 2006; Menzel 2003; Estrella et al. 2007), this method does not necessarily reflect changes in the timing of other events such as budburst or end of season leaf senescence. However, this does ensure that seasonal comparisons of variation in flowering phenology are not conflated with fruiting or vegetative events that are qualitatively distinct. Further, by pooling data broadly across a wide array of species in each season, the influence of atypical phenological response by any individual species on estimates of community-level trends is minimized. Preliminary work using similar methods has indicated that this approach can produce estimates of inter-annual variations in flowering phenology that correlate to satellite-derived green-wave phenology (Park 2012). Although that work did not attempt to discern seasonal differences in phenological response, it did demonstrate that such methods are capable of producing meaningful estimates of inter-annual phenological variation.

Data preparation

The vast majority of samples available throughout the herbaria utilized in this study were collected while in flower (97.1 % of samples with listed phenological data). Thus, although only samples listed as "in flower" were analyzed in this study, this dataset still allowed examination of reproductive phenology across a highly diverse (>1,700 species) group of taxa. Anecdotal evidence indicated that samples were most commonly collected for each species in the period immediately following first bloom, although samples could be listed as in flower as soon as floral buds began to open and until the senescence of the petals (D. Damrel, personal communication). Other phenophases such as leaf development, fruiting, or autumn leaf coloration were less well-represented.

Further, as sampling of trees, shrubs, and invasive species was quite limited, only samples of native forb species were included for analysis. As reduced sample availability outside of South Carolina and prior to 1951 hampered the consistency of these records, only samples collected within South Carolina between the years 1951 and 2009 were evaluated.

The date of collection for each sample was converted into a single day of year (DOY) value from 1 (January 1st) to 366 (December 31st on leap years). Mean observed collection dates for each species were then calculated across all samples that were collected while in flower. In order to eliminate samples that were mislabeled or represented the occasional second flowering of spring species during "false springs" in late autumn (I. W. Park, personal obs.), samples collected in flower more than 150 days after mean flowering of their respective species were removed. The mean date across which all remaining samples were collected in flower was then recalculated for each species to form 59-year, statewide flowering normals for each species.

Using these estimates of normal values, all species were then assigned to one of seven 30-day timing classes from early spring (DOY 70–99, Mar 11–Apr 9) to early autumn (DOY 250–279, Sept 7–Oct 6), with spring and summer each divided into early, mid, and late periods (Table 1). Thirty-day timing classes were considered optimal as they produced a manageable number of classes that could be mapped intuitively onto relatively narrow portions of the growing season, included a substantial number and diversity of samples within each class, and roughly coincided with the onset and termination of the growing season throughout this region. However, it should be noted that these date ranges indicated only the general seasonality of a species. Individual samples, however, often fell outside of these 30-day periods. Nevertheless, only 25 species with mean flowering dates prior to day 70 (March 11–12) or after day 279 (October 6–7) were observed. These taxa were presumed to represent species that flowered outside of the normal growing season and were not analyzed due to low sample availability (58 samples total). After removal of

Table 1 Number of species and samples present in all timing classes

Herbarium collections

	Date range (calendar)	Date range (DOY)	No. of samples	No. of species	Years of data
Overall	Mar 11–Oct 6	70–279	19,328	1,704	59
Early spring	Mar 11–Apr 9	70–99	683	93	32
Mid-spring	Apr 10–May 9	100–129	3,704	259	54
Late spring	May 10–Jun 8	130–159	2,209	248	50
Early summer	Jun 9–Jul 8	160–189	3,000	236	51
Mid-summer	Jul 8–Aug 7	190–219	2,964	289	52
Late summer	Aug 8–Sept 6	220–249	3,069	292	49
Early autumn	Sept 7–Oct 6	250–279	3,699	287	52

Calendar dates correspond to non-leap years

winter flowering species and other problematic samples, 19,328 samples remained across 1,704 species. Each remaining timing class included between 683 and 3,704 samples and at least 93 species (Table 1).

Departures in mean flowering time from 59-year normals were then calculated for each species within each year and county of South Carolina by subtracting annual mean timing of each species from that species' statewide mean timing across the entire study period. All species that were observed in fewer than 3 years were then excluded, and annual estimates of statewide, multi-taxa departures from flowering normals were then calculated by averaging all species-level departures within each year and across all counties (Fig. 1). In order to ensure that all estimates included at least a minimal taxonomic diversity and comprised multiple sampling expeditions, only annual estimates that comprised at least five species and covered at least five of South Carolina's 46 counties were included for analysis.

Climate data

Temperature data used in this study were acquired from the United States Historical Climatology Network (Lawrimore et al. 2011). Statewide monthly mean temperature data were calculated using all 13 stations within South Carolina that included at least 50 years of data from 1951 to 2009 (Fig. 2).

Data analysis

In order to examine broad patterns of spatial variation in flowering phenology, mean flowering dates were calculated within each county and timing class (averaged over the years 1951 to 2009), and spatial correlations were evaluated using the Moran's I statistic according to an inverse distance weighting method embedded in ArcGIS. The relationships in inter-annual phenological variation among the various timing classes were also examined through bivariate correlation analysis of the annual, statewide multi-species departures

from 59-year phenological normals. Long-term trends in flowering time within each timing class were then evaluated using linear regression analysis on annual, multi-taxa statewide departures from phenological normals over the entire study period. Inter-annual variations in flowering phenology throughout South Carolina were also related to statewide mean monthly temperatures from January through September using stepwise linear regression.

In order to evaluate the hypothesis that varying sample sizes resulted in systematic biases towards earlier or later estimates of annual flowering time, bivariate correlation analyses were also conducted between annual departures from 59-year phenological normals and the corresponding number of samples from which each annual estimate was derived. Additionally, the relationship between small sample sizes and increased variability in estimates of annual departures (without directional bias) was also examined through evaluations of bivariate correlations between the absolute values of annual phenological departures and corresponding annual sample sizes.

Results

Correlations of annual variation in flowering time among all timing classes indicated that patterns of flowering phenology vary substantially throughout the growing season. Variations in flowering time from late spring to late summer were strongly correlated to the timing of previous and subsequent timing classes ($p \leq 0.005$ in all cases, Table 2). Thus, these analyses also indicate a gradual transition from mid-spring to late summer patterns of flowering rather than sharp divergences among patterns of seasonal flowering. In contrast, neither early spring nor early autumn flowering was significantly correlated to the timing of flowering in any other season (Table 2). Significant spatial autocorrelation throughout South Carolina was detected only among late summer-flowering
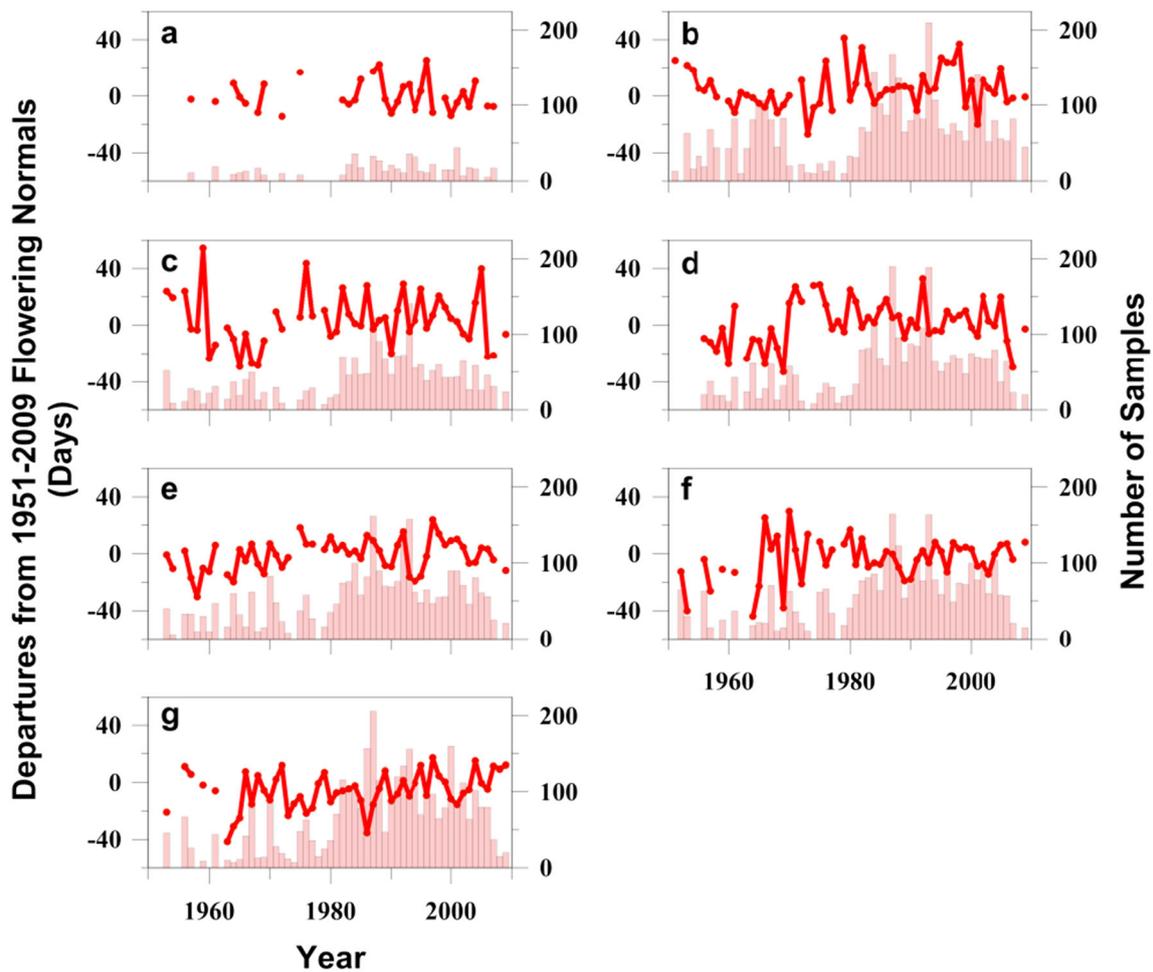
Fig. 1 Departures from 1951 to 2009 flowering normals and annual sample counts among early spring (**a**), mid-spring (**b**), late spring (**c**), early summer (**d**), mid-summer (**e**), late summer (**f**), and early autumn (**g**) flowering species. *Lines* indicate mean annual departures from 1951 to 2009 phenological normals, while *bars* indicate the number of samples available annually within each timing class

Fig. 2 Location and size of overall sample area. *Circles* represent the location of stations providing meteorological data in South Carolina. Sampled area is indicated in *gray*
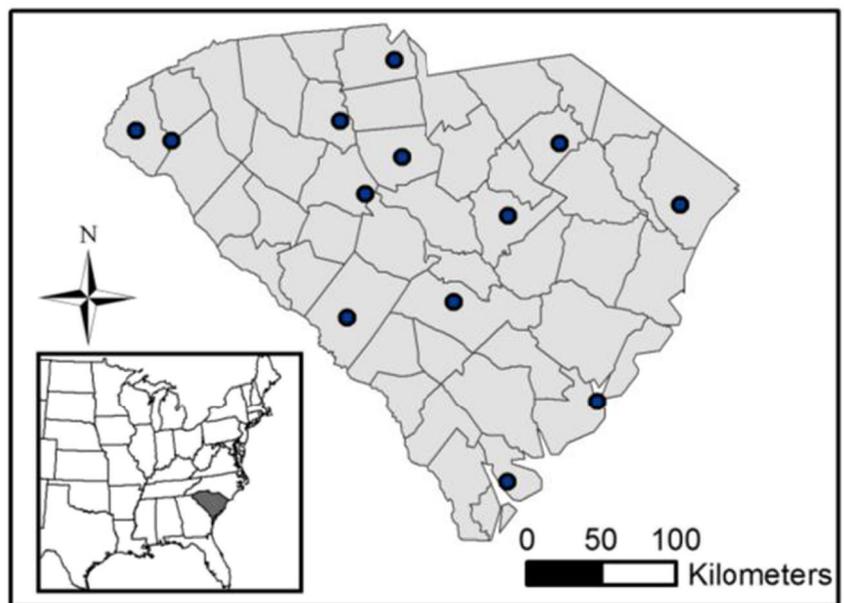
Table 2 Seasonal correlations in annual departures from 1951 to 2009 flowering normals

Correlations in flowering over time		Early spring	Mid-spring	Late spring	Early summer	Mid-summer	Late summer
Mid-spring	Correlation	0.108					
	p value	0.557					
	df	32					
Late spring	Correlation	0.212	*0.556*				
	p value	0.243	*<0.001*				
	df	32	*48*				
Early summer	Correlation	0.265	0.216	*0.395*			
	p value	0.143	0.140	*0.005*			
	df	32	48	*48*			
Mid-summer	Correlation	0.037	0.114	0.210	*0.567*		
	p value	0.840	0.432	0.142	*<0.001*		
	df	32	50	50	*49*		
Late summer	Correlation	−0.170	−0.048	0.106	0.228	*0.416*	
	p value	0.353	0.752	0.485	0.128	*0.003*	
	df	32	46	46	46	*48*	
Early autumn	Correlation	−0.300	0.268	0.079	−0.093	−0.072	0.224
	p value	0.096	0.066	0.596	0.525	0.624	0.127
	df	32	48	47	49	49	48

Values in italic indicate statistically significant correlation

species ($R^2=0.109$, $p=0.017$, Table 3). No significant spatial autocorrelation was detected throughout any other season.

Early spring flowering was found to advance in response to increases in March temperature (−3.391 days/°C, $R^2=0.220$, $p=0.007$, $df=31$, Fig. 3a), although no significant correlations were detected to mean monthly temperature in any other month. Higher February temperatures were also associated with delayed flowering throughout both late spring (3.943 days/°C, $R^2=0.171$, $p=0.003$, $df=49$, Fig. 3b), early summer (2.282 days/°C, $R^2=0.083$, $p=0.041$, $df=50$, Fig. 3c), and mid-summer (1.852 days/°C, $R^2=1.04$, $p=0.019$, $df=51$, Fig. 3d). No significant relationships were detected between variations in mean monthly temperature and the timing of

Table 3 Spatial autocorrelation of mean flowering time by county

Spatial autocorrelation		
Flowering class	Moran's I	p value
Early spring	−0.040	0.906
Mid-spring	−0.059	0.809
Late spring	0.142	0.237
Early summer	−0.001	0.879
Mid-summer	0.254	0.059
Late summer	*0.330*	*0.017*
Early autumn	0.171	0.192

$df=46$ in all cases

Values in italic indicate statistically significant spatial autocorrelation

flowering among mid-spring-, late summer-, or autumn-flowering species.

No long-term trends towards earlier or later flowering time were detected within early, mid-, or late spring, or among early summer-flowering species from 1951 to 2009. Mild but significant trends towards later flowering were present among mid-summer, late summer, and autumn-flowering communities (at least 0.132 days/year in all cases, Table 4). However, no linear trends were detected in mean monthly temperatures in any month from January through September over the same period ($p>0.207$, $df=58$ in all cases).

Although low sample sizes were mildly associated with more extreme annual departures from phenological normals ($R^2=0.04$, $p<0.001$, $df=340$), no significant biases towards early or late timing were detected in relation to differing sample sizes ($R^2<0.001$, $p=0.715$, $df=340$). When restricted to years that included at least 60 samples per timing class, sample size showed no significant relationship to increased annual departures from phenological normals. However, this restriction eliminated the majority of the available annual data (retaining only 20 years per season on average) and was therefore not applied to this work. Additionally, correlation analyses between annual estimates of date of first collection in flower, date of last collection in flower, and mean flowering date for each species found that mean flowering date was more strongly correlated to the timing of first collection ($R^2=0.753$, $p<0.001$, $df=70$) than to last collection in flower ($R^2=0.463$, $p<0.001$, $df=70$), confirming anecdotal observations among collectors which indicated that samples were
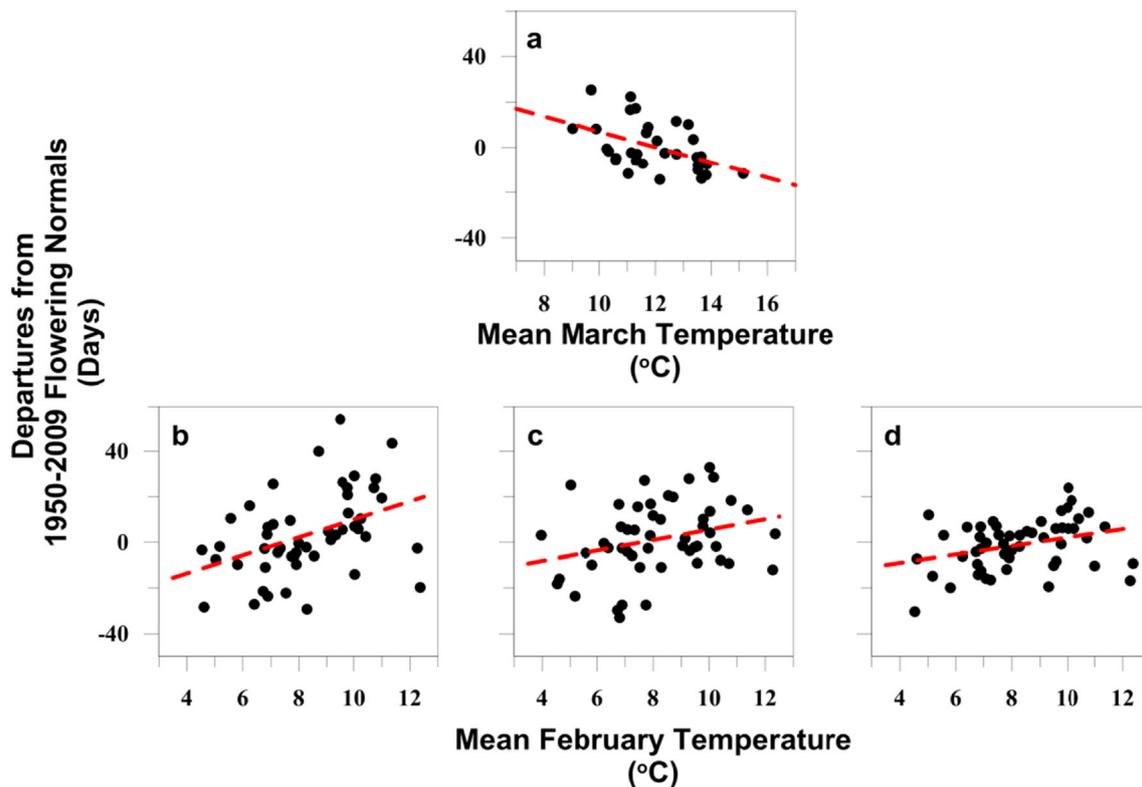
Fig. 3 Relationships between departures from 1951 to 2009 flowering normals and mean monthly temperatures among early spring (**a**), late spring (**b**), early summer (**c**), and mid-summer (**d**) flowering species. Phenological variations within each timing class are compared to mean temperatures within the month to which they exhibited significant correlation

most often collected during the period immediately after the onset of flowering, when reproductive structures were in the best physical condition.

Discussion

These results demonstrate a substantial disconnect in the patterns of inter-annual variation by species which flower during the middle of the growing season and those which

Table 4 Linear trends in departures from 1951 to 2009 flowering normals

Long-term trends in flowering time (1951–2009)

Flowering class	Trend (days/year)	R^2	p value	df
Early spring	−0.022	0.001	0.870	31
Mid-spring	0.066	0.006	0.565	53
Late spring	0.028	0.001	0.864	49
Early summer	0.208	0.042	0.149	50
Mid-summer	*0.091*	*0.079*	*0.043*	*51*
Late summer	*0.132*	*0.080*	*0.049*	*48*
Early autumn	*0.111*	*0.107*	*0.018*	*51*

Values in italic indicate statistically significant correlation

flower near the growing season's onset (early spring) or termination (autumn). While flowering phenology transitions gradually from mid-spring through late summer patterns of inter-annual variation, phenological variations among the earliest and latest groups of species exhibited no correlation to any other season. This division was compounded by the fact that early spring-flowering species exhibited an inverse response to late spring through mid-summer species under warming temperatures near the onset of the growing season. Thus, this study clearly demonstrates that mid-season phenological events must be modeled quite separately from early spring and autumn phenology, which have historically been the primary focus of such work. Novel climate metrics focused specifically on modeling mid- and late-season phenology may be necessary to accurately predict variations in the timing of mid-season flowering.

Nevertheless, early spring flowering phenology in South Carolina does appear similarly responsive to spring temperature cues as species in cooler temperate environments (Primack et al. 2004; Menzel et al. 2005; Estrella et al. 2007; Fitter and Fitter 2002; Fitter et al. 1995). However, while studies in cooler regions have found significant influences on phenological timing by monthly temperature up to 5 months preceding flowering (Amano et al. 2014; Sparks et al. 2000), temperatures within the 1–3 months prior to

flowering typically played the largest role in determining the timing of mid- and late-season flowering (Estrella et al. 2007; Fitter and Fitter 2002; Fitter et al. 1995; Sparks et al. 2000). Furthermore, warming temperatures during the months immediately preceding flowering were primarily associated with earlier flowering onset even among late spring- and summer-flowering species in England (Sparks et al. 2000; Estrella et al. 2007). In contrast, temperature variations near the onset of the growing season (February and March) appear to be the primary determinant for reproductive phenology among both spring and summer-flowering species in South Carolina. As this region experiences warmer conditions and shorter winter periods than the sites of most previous temperate phenological studies, it is possible that warmer conditions in February would be more likely to result in unfulfilled chilling requirements, thereby delaying flowering among species that flower in mid-season (Cannell and Smith 1986). It is also possible that, despite evidence that the "mean flowering" estimates used in this study are primarily influenced by the onset of flowering, this metric is less sensitive to temperature variations in the period immediately preceding bloom than the more commonly used observation of first flowering dates.

Although somewhat hampered by limited data collection among the earliest flowering species, this study also supports previous model-based predictions that the southeastern USA has not experienced significant shifts towards earlier springs in recent decades (Schwartz et al. 2013), in contrast to well-documented patterns throughout both the northern and western USA (Schwartz et al. 2013; Primack et al. 2004; Cayan et al. 2001; Wolfe et al. 2005; Ledneva et al. 2004; Abu-Asab et al. 2001) and Europe (Menzel and Fabian 1999; Schwartz et al. 2006; Menzel et al. 2006; Diskin et al. 2012). While some trends towards later flowering were detected among mid-summer, late summer, and autumn-flowering communities, such trends were mild and could not be attributed to long-term warming during any portion of the year.

Collectively, these results imply that flowering phenology throughout much of the growing season in South Carolina is responsive to temperature variations. However, it is also clear that these responses are often distinct from those previously detected in cooler environments, particularly during late spring and summer. This work also demonstrates that herbarium records may be sufficient to evaluate both yearly and long-term patterns of variation in flowering phenology in areas where other historical records are unavailable. Additionally, this data corroborates previous studies that detected no collection-dependent bias towards early or late flowering among herbarium-based estimates of flowering phenology (Loiselle et al. 2008). Although these methods lack the precision of traditional in situ-based observational studies, this work clearly demonstrates that patterns of mid-season phenological variation within the southeastern USA are quite different from previously documented variations among northern and western portions of North America and Europe. This finding underscores the importance of evaluating phenological change throughout the entirety of the growing season when documenting warmer regions that have not previously been the focus of long-term phenological records.

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