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Impacts of Spatial, Environmental, and Compositional Differences on Community-level Flowering Phenology

Isaac William Park

University of Wisconsin-Milwaukee

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**Impacts of Spatial, Environmental, and
Compositional Differences on Community-
Level Flowering Phenology**

by

Isaac Park

A Dissertation Submitted in Partial

Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

In Geography

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May 2014

ABSTRACT

IMPACTS OF SPATIAL, ENVIRONMENTAL, AND COMPOSITIONAL DIFFERENCES ON COMMUNITY- LEVEL FLOWERING PHENOLOGY

by

Isaac Park

The University of Wisconsin-Milwaukee, 2014

Under the Supervision of Professor Mark D. Schwartz

This dissertation investigates three important topics related to flowering phenology throughout the United States. First, this work evaluates the utility of herbarium records for estimating historical variation in community-level flowering phenology, and evaluate the relationship of such estimates to satellite-derived greenup timing at regional scales. This dissertation then reconstructs historical variations in flowering phenology throughout the spring, summer, and autumn across South Carolina for the years 1951 through 2009. These estimates will then be compared to seasonal temperature variations throughout this period. Finally, this dissertation develops novel herbarium-based methods to separate intraspecific phenological variations over space from changes in flowering time derived from differences in community composition, and evaluate the contributions of compositional differences to spatial variation in community-level flowering times throughout the early, mid, and late portions of the growing season and across a variety of temperate

environments within the continental United States.

The results of these inquiries demonstrate that phenological information included in digital herbarium archives can produce annual phenological estimates correlated to satellite-derived green wave phenology. Examinations of historical flowering throughout South Carolina also determined that species that flower near the onset of the growing season advanced under increasing mean March temperatures, while late spring through mid-summer flowering exhibited delays in response to higher February temperatures. Thus, although no long-term phenological trends were detected, these findings indicate that flowering synchrony may undergo significant restructuring in response to warming spring temperatures, even in humid subtropical environments. Examinations of composition-derived phenological variation over space determined that, although typically smaller than intraspecific variations, composition-derived shifts in flowering time explained up to 49.3% of overall phenological variation, and were the most responsive to differing climate conditions within xeric regions and among late-flowering species. These results demonstrate that interspecific differences in flowering time play a significant role in determining the composition of the plant community over space. Additionally, these findings indicate that impacts of flowering phenology on community assemblage are most severe within xeric regions and throughout the late-flowering portion of the plant community.

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LIST OF ABBREVIATIONS

DOY- Day of Year

LAI- Leaf Area Index

MODIS- Moderate Resolution Imaging Spectrometer

SI-x- Enhanced Spring Index

SOS- Start of Season

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1. Introduction

As evidence of rapid climate change continues to mount, the study of phenology, or the timing of seasonal life history events, has emerged as a crucial tool for monitoring the effects of climate variations on the biosphere (Schwartz, 2003). However, progress in discerning the differences in the component phenology of the various plant communities, or the relevance of differences in the composition of the plant community over space in generating observed differences in flowering phenology at landscape and regional scales has been limited. As many of the ecologically relevant aspects of phenology involve changes in the relative phenological timing between species (Wall *et al.*, 2003; Hegland *et al.*, 2009), the ability to examine such differences is vital to predicting the population and community level effects of climate changes on the biosphere (Chaine & Beaubien, 2001; Morin *et al.*, 2007). Similarly, understanding the proportion of spatial phenological variation at regional scales that results from transitions in species composition as opposed to variable phenological timing within individual species has critical implications to the fitness and range limitation of plant species under future climate regimes (Craine *et al.*, 2012). To date, however, phenological observations have been largely unable to address these issues due to limitations in scale, taxonomic diversity, or ability to discriminate among taxa within existing observational methodologies.

This work will explore novel methods for addressing these difficulties through the use of herbarium records. It will focus on the following topics: 1) Validating the efficacy of herbarium samples as a source developing multispecies

phenological indices that are capable of evaluating the phenological variation at both interannual and multidecadal scales; 2) Examining changes in flowering time among over 1900 species of spring, summer, and autumn flowering plants in previously undocumented regions of the southeastern United States; and 3) Determining the contributions of compositional differences to observed spatial variations in community-level flowering times throughout the early, mid, and late portions of the growing season and across a variety of temperate environments. This work will both contribute new information to our understanding of phenological variations within ecosystems, as well as provide new methods to assist in further developing our understanding of phenological science.

This work will be divided into three separate research sections dealing with the specific projects that acted as subcomponents to this overall endeavor and represented the progressive methodological development of this work: 1) the extent to which interannual variation in satellite-derived green wave phenology is connected to variations in mean flower timing as observed among herbarium records; 2) an examination of long-term patterns of variation in flowering phenology among taxa with differing flowering seasonality and their relationship to annual climate conditions and phenoclimate models of bloom timing; and 3) an examination of the relative contributions of compositional differences and intraspecific phenological variation to observed spatial variations in community-level flowering times throughout the early, mid, and late portions of the growing season and across a variety of temperate environments. While presented as largely self-contained research projects, and addressing quite distinct research questions,

each of these projects acted as a methodological 'stepping' stone to subsequent projects through the development and verification of increasingly sophisticated methods for extracting new information from historical records.

2. Digital herbarium archives as a spatially extensive, taxonomically discriminate phenological record; a comparison to MODIS satellite imagery

2.1 Abstract

This study demonstrates that phenological information included in digital herbarium archives can produce annual phenological estimates correlated to satellite-derived green wave phenology at a regional scale ($R=0.183$, $p=0.03$). Thus, such records may be utilized in a fashion similar to other annual phenological records and, due to their longer duration and ability to discriminate among the various components of the plant community, hold significant potential for use in future research to supplement the deficiencies of other data sources as well as address a wide array of important issues in ecology and bioclimatology that cannot be easily addressed using more traditional methods.

2.2 Introduction

In the face of growing concerns about the effects of changes in climate, phenology, or the study of the timing of seasonal biological events, has emerged as one of the clearest and most responsive mechanisms for exploring the relationship between climate conditions and the biosphere (Schwartz, 2003). However, as phenological science progresses toward the development of long-term assessments and predictive models of regional and continental phenological change, the limitations of existing phenological records are becoming increasingly apparent.

Satellite imagery, the predominant source of data for phenological modeling at regional or continental scales (Reed *et al.*, 2009; White *et al.*, 2009), is limited

both by its inability to discriminate among plant taxa and by the comparatively recent development of satellite systems capable of phenological monitoring. The other robust source of spatially extensive phenological data in North America, the lilac-honeysuckle network established by Caprio, provides data as far back as 1957, but includes only three non-native taxa and is restricted to regions with a sufficient chilling period for those species to grow (Schwartz, 2003). Thus, neither data source is able to discriminate among specific components of the plant community. While additional phenological records exist that are capable of analyzing the different phenological responses of multiple species (Abu-Asab *et al.*, 2001; Cook *et al.*, 2007), they are typically local in scale and are of limited utility in addressing regional phenological variability.

Herbaria, or collections of pressed plant samples collected to document taxonomic diversity, represent an increasingly popular phenological record uniquely suited to address both of these concerns. Many previous studies have indicated that herbarium records within highly localized, well-sampled locations produce similar estimates of long-term phenological changes to those produced by in-situ observation (Primack *et al.*, 2004; Bolmgren & Lunnberg, 2005; Miller-Rushing *et al.*, 2006; Robbirt *et al.*, 2011). However, the process of assessing the phenological status and location of each sample is extremely time consuming. With the exception of the few studies that use digital herbarium databases (Gallagher *et al.*, 2009; Neil *et al.*, 2010) or consider only intra-annual phenological patterns without incorporating interannual changes, (Boulter *et al.*, 2006; Zalamea *et al.*, 2011), the resulting limitations in sample size have restricted most phenological

studies using herbarium data to either single species (Lavoie & Lachance, 2006; Gaira *et al.*, 2011; Robbirt *et al.*, 2011; Zalamea *et al.*, 2011), or highly local areas (Primack *et al.*, 2004). Additionally, this has thus far limited herbarium-based studies of interannual phenological variation to a decadal or multi-decadal resolution. The advent of digital archiving efforts among an increasing number of herbaria will facilitate analysis of the vast wealth of phenological data they represent and allow the full usage of such records for spatially extensive, taxonomically discriminate examinations of phenological change. Further, this may also allow a finer temporal resolution than has previously been considered possible with such records.

However, as most samples are collected during flowering, herbarium records are primarily useful in evaluating that phenophase. Additionally, most databases include simple binary notation as to whether each sample is flowering/not flowering and fruiting/not fruiting, severely limiting their utility in estimating the timing of specific events such as date of first flower. Spatial information is also rarely registered in a standardized fashion below county level, restricting the spatial resolution possible when utilizing large numbers of records. Additionally, many annual gaps occur at a county level, and some spatial collection biases may occur in highly heterogeneous areas (Loiselle *et al.*, 2008). While these records do include virtually all species documented in an area, some groups of plants, such as graminoid (grasslike) species, are unsuitable for assessment through digital herbarium records due to a lack of accurate phenological assessment among those

taxa, and species of particular taxonomic interest or those having charismatic blooms may be more commonly collected than other co-occurring species.

Despite these issues, such records provide a unique window into the responses of the plant community to climate variation, and may facilitate the use of herbarium records as a measure of overall ecosystem phenology capable of detecting variations not only at a multidecadal scale, but also at interannual resolutions that require evaluation of a previously prohibitive number of samples each year.

2.3 Research Questions

This study will demonstrate that A) digital herbarium records retain a significant amount of explanatory power over wide spatial scales even when pooled across a broad array of species and that B) interannual variations in phenological timing derived from digital herbarium records are sufficiently correlated to other ecosystem-wide measures of phenological variation (in this case, MODIS derived greenup estimates) to represent a robust measure of ecosystem-level plant phenology across a wide range of plant species.

2.4 Data and Methods

Herbarium records were acquired with permission from the herbaria of Clemson University, the University of South Carolina, and Florida State University, for a total of 5,949 observed flowering specimens collected from 2000-2009. Satellite imagery consisted of all MODIS 5 leaf area index (LAI) 8-day composite images within South Carolina from the years 2000-2009 (507 images in total) from the Land Process Distributed Archive Center (<https://lpdaac.usgs.gov/>). As this

work crosses a wide array of vegetation types, MODIS LAI algorithms were considered preferable to NDVI or EVI as they account for qualitative differences in vegetation structure (Knyazikhin *et al.*, 1999; Myneni *et al.*, 2002), and provide a more structural measure of vegetation.

2.4.1 Image Preparation and Estimation of Greenup Timing

After the exclusion of cloud-contaminated pixels, all images were overlaid with a vector-based 3km fishnet grid. Each grid cell was assigned to the county in which its center fell, and mean LAI values in each cell were computed for each image.

Rate of change in LAI was determined by calculating a linear slope for each 40-day period (5 successive images) using a rectangular window function. For each cell, greenup was estimated to occur at the midpoint of the 8-day composite image located in the center of the 40-day time series producing the highest positive slope, with an implicit 4-day uncertainty. County-level averages of greenup timing were then calculated across all counties and years. Due to false estimations of LAI increase in late fall caused by cloud contamination, only 40-day windows with at least one uncontaminated pixel in 4 out of the five composite images were considered.

2.4.2 Herbarium Data Preparation and Correlation Analysis

First, observations of spore-bearing and graminoid (grasslike) species were excluded from analysis due to unreliable phenological assessments. Average observed flowering dates among all observations were then calculated for each remaining species. In order to exclude winter-flowering species and remove errors caused by occasional second flowering in fall by some spring flowering species (I.

Park, personal obs.), all flowering samples collected more than 150 days after median flowering were removed, as were taxa with average flowering prior to day 45 or after day 310. Remaining samples included 5,949 samples across 1185 species, which represented the majority of non-graminoid species found within South Carolina across all growth habits and counties in South Carolina. Average flower timing was then calculated within each county for each year, and correlation analysis was conducted between MODIS-derived greenup estimates and average flowering blocked by county and year. Data was present within all counties for at least one year of the study period (Fig. 2.1). In order to identify the correlation of the two metrics across spatial and interannual variation independently, correlation analyses were also conducted when pooled among counties and years.

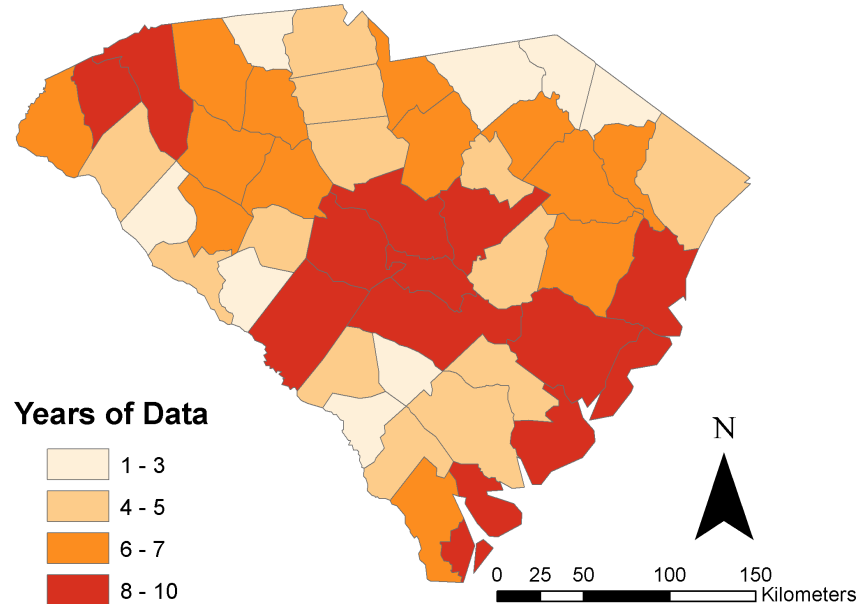


Figure 2.1. Years of herbarium data among South Carolina counties from 2000 to 2009.

2.5 Results

MODIS-derived greenup timing was significantly correlated to herbarium-derived flower timing over 2000-2009 ($R=0.183$, $p=0.03$, $df=267$). Although similar correlation was detected when only interannual variation was considered, ($R=0.221$, $p=0.568$ $df=9$, Fig. 2.2) neither interannual nor spatial correlation ($R=0.107$, $p=0.107$ $df=46$), when considered singly, were statistically significant due to the reduction in degrees of freedom in these cases.

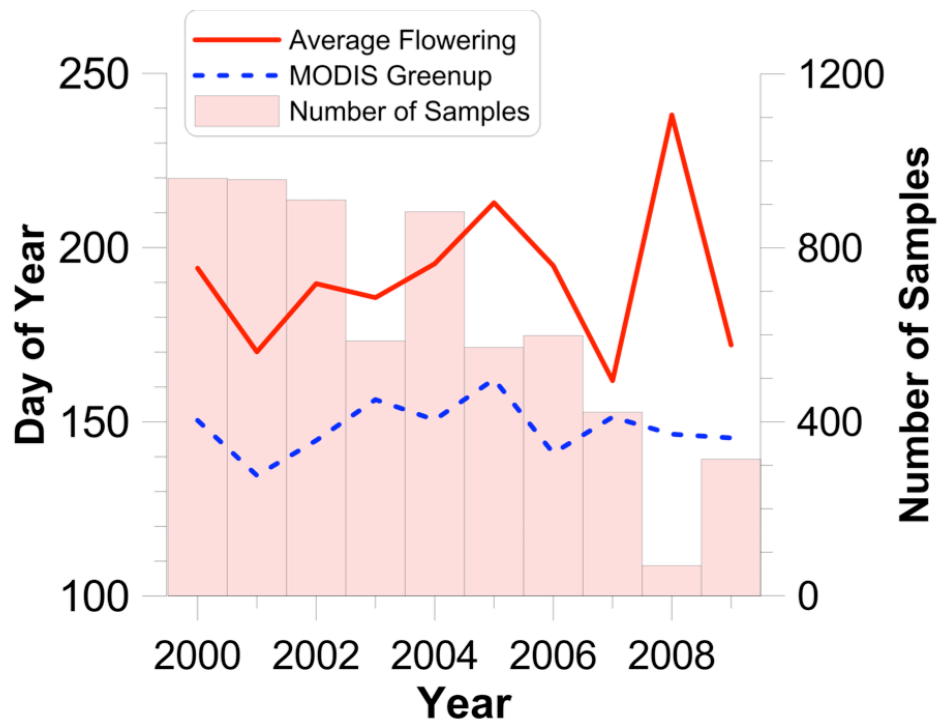


Figure 2.2 Solid lines indicate average flowering time estimated from herbarium records, while dotted lines indicate MODIS-derived greenup estimates. Bars indicate the number of herbarium samples collected in flower each year.

2.6 Discussion

These results indicate that multi-taxa analysis of herbarium records are capable of detecting interannual changes in phenological timing despite the various

limitations inherent in herbarium records. Given the paucity of samples in 2008 along with the extreme estimated phenology from that year (Fig. 2.2), smoothing or exclusion of poorly sampled years may be required. However, such deficiencies may be somewhat comparable to data quality issues present in other data sources, such as the cloud contamination of satellite imagery. While the limited span of satellite records and the large number of missing years within the herbarium records for some counties (Fig. 2.1) prevented useful analysis of spatial variation, additional work incorporating the full duration of herbarium collections will address this issue.

Given the promising nature of this preliminary study, future work should expand to address a variety of important issues that cannot be easily addressed by existing techniques. First, herbarium records may be used in conjunction with life history and physiological data to determine the relative importance of factors such as phylogeny, morphology, drought and shade tolerance, or annual or perennial life cycles to patterns of historical phenological variations. Consideration of various components of the plant community may also be used to contextualize the relationship of other phenological measures such as satellite imagery to specific components of the plant community. Because of their ability to evaluate myriad species' phenology independently and examine phenology over wide areas, these records also possess a unique capability to evaluate the relative roles of inter- and intra-species phenological plasticity on regional and continental patterns of landscape phenology. Finally, as many collections date back to the late 1800s, such records may be used to extend our historical record of North American phenology. As more herbaria across the country digitize their holdings, such records may play a

unique role in the development of a continental, and eventually global, assessment of the history of our biosphere's relationship to changes in climate.

3. Long-term herbarium records reveal temperature dependent changes in flowering phenology in the southeastern United States

3.1 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 United States remain poorly documented. This research uses herbarium-based methods to examine changes in flowering time across 21,676 samples of spring-, summer-, and autumn-flowering plants in the southeastern United States 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/ $^{\circ}\text{C}$, $p=0.022$). No long-term advances in early spring flowering or spring temperature were detected during this period, corroborating previous phenological assessments for the southeastern United States. However, late spring through mid-summer flowering exhibited delays in response to higher February temperatures (over 0.185 days/ $^{\circ}\text{C}$, $p\leq 0.041$ in all cases). Thus,

it appears that flowering synchrony may undergo significant restructuring in response to warming spring temperatures, even in humid subtropical environments.

3.2 Introduction

Recent evidence increasingly shows that the timing of flowering among spring, summer, and autumn differ in their responses to ongoing climate changes (Fitter *et al.*, 1995; Sparks *et al.*, 2000; Menzel *et al.*, 2001; Fitter & Fitter, 2002; Wolkovich *et al.*, 2012). 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 under warming temperatures in recent decades than in late spring or summer (Fitter & 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 (Wall *et al.*, 2003; Hegland *et al.*, 2009). 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 (Mommott *et al.*, 2007; Aldridge *et al.*, 2011; 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; Sparks *et al.*, 2000; Menzel *et al.*, 2001; Fitter & Fitter, 2002; Wolkovich *et al.*), on fully tropical environments (Opler *et al.*, 1976; Borchert, 1996; Rivera & Borchert, 2001; Borchert *et al.*, 2004; Brearley *et al.*, 2007), or on dry subtropical (Mediterranean) climates (Spano *et al.*, 1999; Peñuelas *et al.*, 2004; Gordo & Sanz, 2005, 2010). In comparison, multi-seasonal records of flowering phenology are sparse among humid subtropical ecosystems (Köppen climate class Cfa, (Kottek *et al.*, 2006)), 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 United States 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, interannual changes in temperature are well documented to explain the majority of variation in flowering phenology (Fitter *et al.*, 1995; Chuine & Cour, 1999; Sparks *et al.*, 2000; Menzel, 2003; Primack *et al.*, 2004; Wolfe *et al.*, 2005; Sherry *et al.*, 2007; Miller-Rushing & Primack, 2008). Both spring and summer flowering phenology among 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 (Spano *et al.*, 1999; Fitter & Fitter, 2002; Gordo & Sanz, 2005; Kottek *et al.*, 2006; Estrella *et al.*, 2007; Gordo & Sanz, 2010). However evidence indicates that some species and phenophases in dry subtropical or Mediterranean regions (Köppen Climate class Csa/Csb, (Kottek *et al.*, 2006)) 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 (Borchert, 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 (Opler *et al.*, 1976; Borchert, 1996; Borchert *et al.*, 2004; Brearley *et al.*, 2007).

Regions with humid subtropical climates, such as the southeastern United States, 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; Sparks *et al.*, 2000; Fitter & Fitter, 2002). 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 United States (Funderburk & Skeen, 1976; Abu-Asab *et al.*, 2001) 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 Georgia, 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.

3.3 Research Questions

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 United States for the years 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 variations in sampling intensity result in

systematic biases towards earlier or later estimates of community-level flowering phenology?

3.4 Data 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 (Lavoie & Lachance, 2006; Zalamea *et al.*, 2011; Diskin *et al.*, 2012). 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.

For these reasons, most studies utilizing herbarium records have been limited to evaluating either a small set of highly-collected species (Lavoie & Lachance, 2006; Gaira *et al.*, 2011; Diskin *et al.*, 2012), or restricted to localized areas of particularly intense collection (Primack *et al.*, 2004; Miller-Rushing *et al.*,

2006; Panchen *et al.*, 2012). 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.

By pooling data across a wide array of species that share similar flowering seasonality (over 1900 species), 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 across all taxa that typically flower during each season. Unlike methods that focus on the onset or peak of flowering for a given species (Fitter *et al.*, 1995; Miller-Rushing *et al.*, 2008; Amano *et al.*, 2010; Diskin *et al.*, 2012), 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, 2003; Menzel *et al.*, 2006; 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 the majority 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), indicating a successful capture of inter-annual variation.

3.4.1 Data Preparation

The vast majority of herbarium samples used in this study were collected while in flower, producing an extensive dataset regarding flowering phenology. Samples were most commonly collected for each species in the period immediately following first bloom (I.W. Park, unpublished data), 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. Thus, only samples listed as ‘in flower’ were utilized.

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

misabeled or represented the occasional second flowering of spring species during “false springs” in late autumn (I. 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 60-year, statewide flowering normals for each species.

Using these estimates of normal values, all species were then assigned to one of seven thirty-day timing classes from early spring (DOY 70 to 99, Mar. 11 to Apr. 9) to early autumn (DOY 250 to 279, Sept. 7 to Oct. 6), with spring and summer each divided into early, mid, and late periods (Table 3.1). 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 thirty-day periods. Nevertheless, only 25 species with mean flowering dates prior to day 70 (Mar. 11-12) or after day 279 (Oct. 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 winter flowering species and other problematic samples, 21,676 samples remained across 1924 species. Each remaining timing class included between 683 and 3650 samples and at least 93 species (Table 3.1).

Herbarium Collections						
		Date Range (Calendar)	Date Range (DOY)	# Samples	# Species	Years of data
Native						
	Overall	Mar 11-Oct 6	70-279	21676	1924	59
	Early Spring	Mar 11-Apr 9	70-99	683	93	32
	Mid- Spring	Apr 10-May 9	100-129	3704	259	54
	Late Spring	May 10-Jun 8	130-159	2209	248	50
	Early Summer	Jun 9-Jul 8	160-189	3000	236	51
	Mid- Summer	Jul 8-Aug 7	190-219	2964	289	52
	Late Summer	Aug 8-Sept 6	220-249	3069	292	49
	Early Fall	Sept 7-Oct 6	250-279	3699	287	52

Table 3.1. Species diversity and number of samples present in all timing classes. Calendar dates correspond to non-leap years.

Departures in mean flowering time from 60-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. Annual estimates of statewide, multitaxa departures from flowering normals were then calculated by averaging all species-level departures within each year (Fig. 3.1). 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 5 species and covered at least 5 of South Carolina's 46 counties were included for analysis.

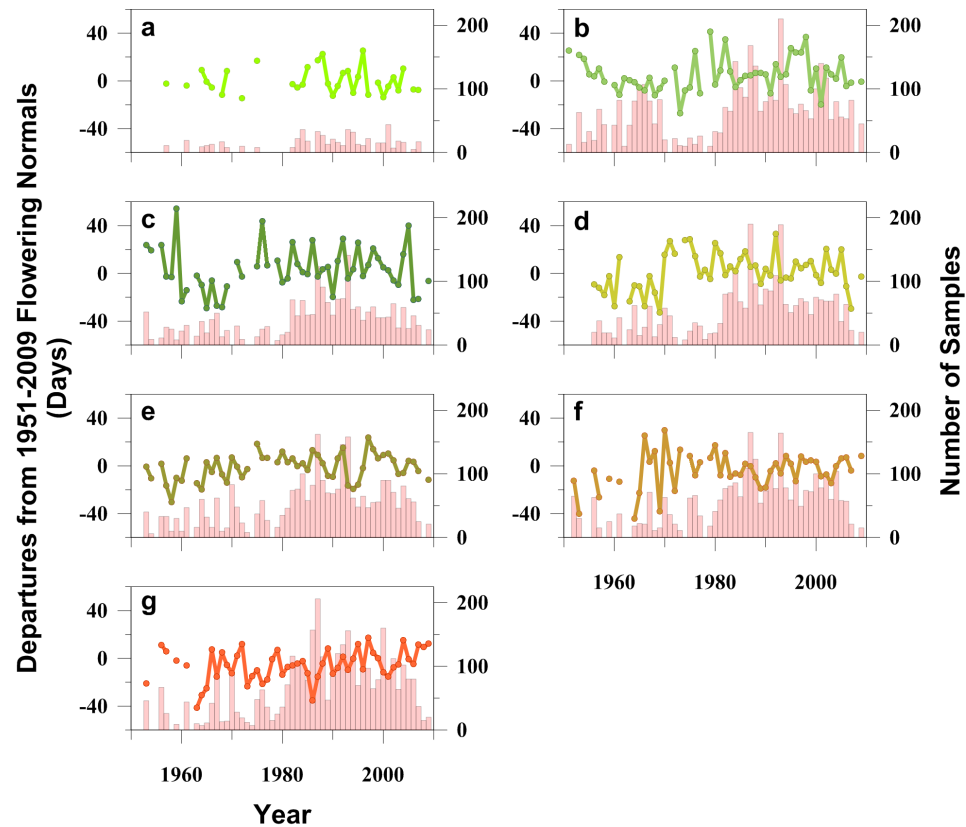


Figure 3.1. Departures from 1951-2009 flowering normals and annual sample counts among early spring (2a), mid-spring (2b), late spring (2c), early summer (2d), mid-summer (2e), late summer (2f), and early fall (2g) flowering species. Lines indicate mean annual departures from 1951-2009 phenological normals, while bars indicate the number of samples available annually within each timing class.

Temperature and precipitation data used in this study were acquired from the United States Historical Climatology Network. Data were utilized from all 13 stations within South Carolina that included at least 50 years of data from 1951 to 2009 (Fig. 3.2).

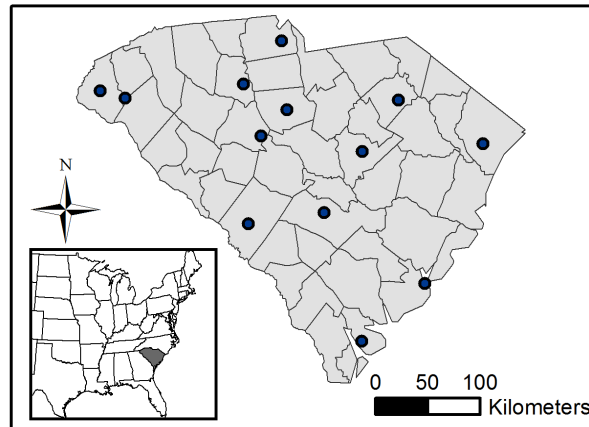


Figure 3.2 Location and size of overall sample area. Circles represent the location of stations providing meteorological data in South Carolina. Sampled area is indicated in grey.

3.4.2 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 60-year phenological normals. Long-term trends in flowering time within each timing class were then evaluated using linear regression analysis on annual, multitaxa statewide departures from phenological normals over the entire study period. Inter-annual variations in flowering phenology were related to 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 60-year phenological normals and the corresponding number of samples from which each annual estimate was derived. In order to evaluate the relationship between low sample sizes and increased variability in estimates of annual departures (without directional bias), bivariate correlations were also conducted between the absolute values of annual phenological departures and corresponding annual sample sizes.

3.5 Results

Partial correlations of annual variation in flowering time among all timing classes indicated a gradual transition in the pattern of flowering from mid-spring through late summer. Variations in flowering time throughout the mid-season were strongly correlated to the timing of previous and subsequent timing classes ($p \leq 0.005$ in all cases, Table 3.2). However, neither early spring nor early autumn flowering was significantly correlated to the timing of flowering in any other season (Table 3.2).

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

Table 3.2. Seasonal correlations in annual departures from 1951-2009 flowering normals. Bold text indicates statistically significant correlation.

Significant spatial autocorrelation throughout South Carolina was detected only among late-summer flowering species ($R^2=0.109$, $p=0.017$, Table 3.3). No significant spatial autocorrelation was detected throughout any other season.

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

Table 3.3. Spatial autocorrelation of mean flowering time by county. df = 46 in all cases. Bold text indicates statistically significant spatial autocorrelation.

Early spring flowering was found to advance in response to increases in March temperature (-3.391 days/ $^{\circ}\text{C}$, $R^2=0.220$, $P=0.007$, $df=31$, Fig. 3.3a), 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/ $^{\circ}\text{C}$, $R^2=0.171$, $p=0.003$, $df=49$, Fig. 3.3b), early summer (2.282 days/ $^{\circ}\text{C}$, $R^2=0.083$, $p=0.041$, $df=50$, Fig. 3.3c), and mid-summer (1.852 days/ $^{\circ}\text{C}$, $R^2=1.04$, $p=0.019$, $df=51$, Fig. 3.3d). No significant relationships were detected between variations in mean monthly temperature and the timing of flowering among mid-spring, late summer, or autumn-flowering species.

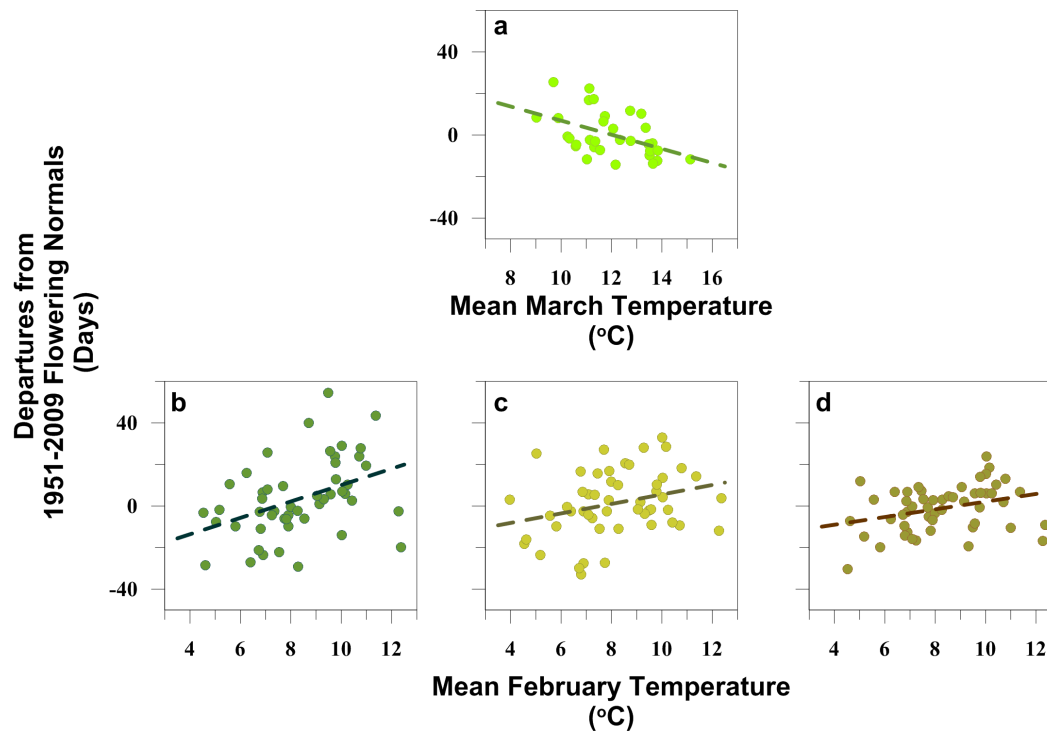


Figure 3.3. Relationships between departures from 1951-2009 flowering normals and mean monthly temperatures among early spring (3.3a), late spring (3.3b), early summer (3.3c) and mid-summer (3.3d) flowering species. Phenological variations within each timing class are compared to mean temperatures within the month to which they exhibited significant correlation.

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 3.4). 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 somewhat 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 ($R^2 < 0.001$, $p = 0.715$, $df = 340$).

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

Table 3.4. Linear trends in departures from 1951-2009 flowering normals. Bold text indicates statistically significant correlation.

3.6 Discussion

These results demonstrate a striking disconnect in the patterns of inter-annual variation by species which flower during the middle of the growing season and those which 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 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 (Fitter *et al.*, 1995; Fitter & Fitter, 2002; Primack *et al.*, 2004; Menzel *et al.*, 2005; Estrella *et al.*, 2007). However, while studies in cooler regions typically found that temperatures within the 1-3 months prior to flowering played the largest role in determining the timing of mid- and late-season flowering (Fitter *et al.*, 1995; Sparks *et al.*, 2000; Fitter & Fitter, 2002; Estrella *et al.*, 2007), temperature variations near the onset of the growing season 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 & Smith, 1986).

Although hampered by limited data collection among the earliest flowering species, this study also supports previous model-based predictions that the Southeastern U.S. 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 U.S. (Abu-Asab *et al.*, 2001; Cayan *et al.*, 2001; Ledneva *et al.*, 2004; Primack *et al.*, 2004; Wolfe *et al.*, 2005; Schwartz *et al.*, 2013) and Europe (Menzel & Fabian, 1999; Menzel *et al.*, 2006; Schwartz *et al.*, 2006; Diskin *et al.*, 2012). While some trends towards later flowering were detected among 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 quite different patterns of mid-season phenological variation occur within the southeastern United States than have previously been documented in northern and western portions of North America or in Europe. This finding underscores the importance of evaluating phenological change throughout the entire growing season when documenting regions that have not previously been the focus of long-term phenological records.

4. Impacts of differing community composition on flowering phenology throughout warm temperate, cool temperate, and xeric environments

4.1 Abstract

Flowering phenology is well documented to restrict the distribution of many plant species. However, community-level shifts in flowering time may occur either through exclusion of species with unsuitably early or late flowering for local conditions (composition-derived phenological shifts), or through intraspecific phenological responses to climate variations over space. Although these mechanisms have quite different ecological implications, the relative contribution of composition-derived phenological shifts remains largely unknown. Therefore, determining the magnitude of composition-derived phenological variation is crucial to understanding the relationship between phenology and community assemblage over space, and to predicting the impacts of future climate change. This study will develop novel, herbarium-based methods to determine the contributions of compositional differences to observed spatial variations in community-level flowering times throughout the early, mid, and late portions of the growing season and across a variety of temperate environments throughout the United States.

Although typically smaller than intraspecific variations, composition-derived shifts in flowering time explained up to 49.3% of overall phenological variation. Composition-derived changes in flowering time among late-flowering species also explained the greatest proportion of overall variation and were the most responsive to differing climate conditions. Xeric regions also exhibited composition-derived

phenological shifts that were stronger and more closely tied to climate conditions (R^2 up to 0.553) than other regions. These results indicate that interspecific differences in flowering time play a significant role in determining the composition of the plant community over space. However, the impact of flowering phenology on community assemblage varies considerably among seasons and climate regions, and appears to be strongest among xeric regions and among late-flowering species.

4.2 Introduction

The reproductive timing of plant species has been well documented to vary in response to changes in environmental conditions, both over space and interannually. The ability of individual species to adapt their phenology either plastically or genetically to differing environmental conditions has been found to impact both the range limits (Chuine & Beaubien, 2001; Morin *et al.*, 2007) and persistence (Willis *et al.*, 2008) of many species, while differences in climate conditions may influence both composition (Morin *et al.*, 2007; Craine *et al.*, 2012) and invasibility (Willis *et al.*, 2010) of the plant community. However, when viewed from a community perspective, changes in mean phenological timing (pooled across a representative sample of local species) may occur either through phenological adaptations by individual species to varying conditions, or through systematic changes in the composition of the plant community towards species with consistently earlier or later flowering times. These two mechanisms represent quite distinct ecological processes with very different implications for the composition of the plant community as a whole, but their relative contributions to overall patterns

of community-level phenology remain poorly understood. Therefore, in order to interpret the repercussions of future climate variation on the plant community, it is essential to separate the mechanisms by which spatial variations in phenology occur, and to determine the contributions of intraspecific and composition-derived phenological variation to overall community-level phenological variations.

To date, the majority of phenological research has focused on phenological responses to differing environmental conditions that occur within a single species (i.e. intraspecific phenological variation, Fig. 4.1a), and do not incorporate the effects of variations in the composition of the plant community. Intraspecific phenological responses may occur either through A) phenotypic plasticity, or the ability of plants to adapt their phenological timing to various climate conditions through physiological, behavioral, or morphological mechanisms that do not require genotypic variation (Bradshaw, 1965), or B) local genetic adaptations resulting from selective pressure towards differing phenologies among populations that inhabit areas with distinct climate conditions (Olsson & Agren, 2002; Jonzén *et al.*, 2007; Vitasse *et al.*, 2009a; Vitasse *et al.*, 2009b). Unfortunately, it is often quite difficult to disentangle interpopulation genetic adaptations from plastic phenological responses to differing conditions over space (Donnelly *et al.*, 2012), and this study will not attempt to distinguish between these two forms of intraspecific phenological variation.

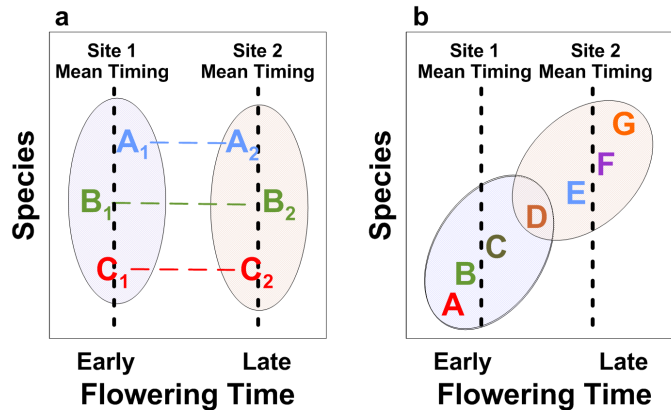


Figure 4.1. Models of purely intraspecific (1a) and purely composition-derived (1b) phenological variation over space. Species are denoted by capital letters. Locations are denoted by numerals, and community composition at each location is indicated by ellipses. Vertical dashed lines represent mean phenological timing for each location.

In contrast to phenological adaptations that occur within individual species, however, are changes in community-level phenology that result from differences in the mean flowering time across all species that collectively form the plant community at different locations over space. As the plant community changes over space or in response to climate gradients, species with maladapted traits or environmental tolerances may be filtered out of the plant community and replaced with different species that exhibit more suitable traits for the local environment (Keddy, 1992). In similar fashion, species with unsuitable flowering phenology for a given location may be excluded, resulting in changes in the composition of the plant community that shift preferentially towards species that intrinsically flower earlier or later as local conditions dictate (Fig. 4.1b). Such systematic shifts in the composition of the plant community over space have been found to result in community-level differences in mean flowering time across all species present in each location. Being driven purely by compositional differences, such variation

occurs independently of phenological plasticity within individual species (Craine *et al.*, 2012). Community-level patterns of phenology across different locations may thus be affected both by differing intraspecific responses by species that are common across both locations, and by the exclusion of species with flowering phenology that is unsuitable to local conditions at either location (e.g. composition-derived changes) (Primack *et al.*, 2009; Craine *et al.*, 2012). Individual species are typically capable of plastic phenological responses only to climate conditions that are historically present in their native ranges, but may be limited in their ability to adapt to more extreme conditions (Sparks *et al.*, 2000; Morin *et al.*, 2010). Hard limits in the range of climate conditions across which each species is capable of persisting are also typically present (Chaine & Beaubien, 2001; Morin *et al.*, 2007; Chaine, 2010). Unsuitable timing of flowering and fruiting that results in cold damage to reproductive tissues or premature termination of fruit development has been implicated as the primary mechanism for these climatic range limits, indicating that differences in flowering phenology are critical to changes in the composition of the plant community over space (Morin *et al.*, 2007). Thus, it is likely that intraspecific changes in flowering time, which cannot account for changes in community composition, represent only a portion of the overall phenological variation that occurs across broad climate gradients.

These two mechanisms also represent quite distinct processes with very different implications for the composition of the plant community. Composition-derived variations in community-level flowering phenology reflect the systematic exclusion of species that cannot adapt their reproductive timing to suit a given

environment (resulting in timing that is too early or too late) and their replacement by other taxa that exhibit more suitable reproductive timing. In contrast, phenological change that occurs intraspecifically represents the ability of individual species to adapt their phenology (plastically or through local genetic adaptation) in order to remain suitable across a range of environments without being excluded due to unsuitable reproductive timing. Increased intraspecific adaptation among the majority of species in a location would therefore be expected to reduce phenologically-driven disruptions to community composition, while composition-derived phenological change directly reflects phenologically-driven changes in community composition over space.

Thus, it is clear that simple examinations of community-level phenological variation that do not distinguish between these two mechanisms are limited in their ability to evaluate the relationships between community composition and reproductive phenology. Differences in community-level flowering time that result purely from systematic shifts in the composition of the plant community have been detected among both cold-temperate perennial grasslands in North America (Craine *et al.*, 2012) and among assemblages of species in bog, woodland, and disturbed communities throughout Franklin County, Maine (Heinrich, 1976). Despite this, composition-derived phenological variation has rarely been examined separately from intraspecific variation, and its relative contributions to overall patterns of community-level phenology remain poorly understood. Further, no systematic comparison of intraspecific and composition-driven phenological change has been conducted at a spatial scale that is sufficient to extrapolate to regional and

continental processes, or that is capable of comparing the role of such changes in community composition across broad climate regions.

Nevertheless, it is well documented that under changing climate conditions, plant species must typically either adapt plastically, evolve rapidly to meet the changing environmental conditions, or face local extinction and replacement by species that are better adapted to the local environment (Aitken *et al.*, 2008). Research into phylogenetic patterns of species loss have already detected preferential decreases in abundance and increases in the risk of local extinction among those taxa with the lowest plasticity in flowering time under interannual climate variations and progressive warming in the Boston Area (Willis *et al.*, 2008). Additionally, process-based models have indicated that the primary climatic constraints on the ranges of temperate tree species arise from unsuitable timing of flowering and fruiting (Morin *et al.*, 2007). Thus, it is clear that the timing of reproductive phenology is closely tied to the composition of the plant community over space. Understanding the magnitudes of intraspecific and composition-derived changes in flowering phenology over space is crucial to evaluating how rapidly the composition of those communities is likely to shift under future climate changes.

Previous studies have also determined that the magnitude and direction of intraspecific phenological responses to climate cues vary significantly among the early, middle, and late portions of the growing season (Fitter *et al.*, 1995; Miller-Rushing & Primack, 2008; Gordo & Sanz, 2010; Wolkovich *et al.*, 2012; Mazer *et al.*, 2013). Similarly, phenological sensitivity to temperature variations is often milder among warm temperate and subtropical regions than cool temperate regions

(Borchert *et al.*, 2005) while xeric regions often exhibit delayed phenology in response to late rainfall (Ghazanfar, 1997; Peñuelas *et al.*, 2004; Gordo & Sanz, 2010). Thus, it is quite plausible that relative contributions of intraspecific variation and phenologically deterministic shifts in species composition to patterns of overall variation in flowering time may differ both seasonally and among regionally distinct climate zones. Unfortunately, large-scale examinations capable of evaluating the magnitude of intraspecific and compositional changes in flowering phenology across broad regions and wide environmental gradients are lacking. Such large-scale studies are necessary, however, to determine the relative importance of compositional changes in flowering time to the assemblage of the plant community at continental and global scales, as well as to forecast the severity of phenologically-driven disruptions to the composition of existing plant communities under additional climate change. This study will remedy this deficiency, and will leverage novel, herbarium-based methods to separate the contributions of intraspecific and composition-derived phenological variations to the overall timing of community-level flowering throughout the growing season, and to evaluate the relative magnitudes of intraspecific and composition-derived shifts in flowering phenology along climate gradients throughout warm temperate, cool temperate, and xeric environments.

4.3 Research Questions

This research will address the following questions; A) Do systematic, phenologically deterministic changes in the composition of the plant community over space account for a significant portion of overall spatial variation in flowering

time throughout temperate environments at regional and continental scales? B)

Does the proportion of overall spatial variation in flowering time that can be explained through intraspecific variations differ among the early, middle and late-flowering portions of the plant community, or among xeric, warm temperate, and cool temperate environments? C) Does the proportion of overall spatial variation in flowering time that can be explained through the effects of changes in community composition differ among the early, middle and late-flowering portions of the plant community, or among xeric, warm temperate, and cool temperate environments?

D) Do intraspecific variations in flowering time exhibit different responses to seasonal temperature variations during the early, middle, and late portions of the growing season, or among xeric, warm temperate, or cool temperate environments?

E) Do the effects of changes in community composition on community-level flowering time along seasonal temperature gradients differ among the early, middle, and late portions of the growing season, or among xeric, warm temperate, or cool temperate environments?

4.4 Methods

4.4.1 Data Sources

Records of flowering phenology used in this study were drawn from the digital archives of the herbaria of Clemson University, the University of South Carolina, Florida State University, Arizona State University, the University of Arizona, the University of California-Riverside, the University of Texas, and the Rocky Mountain Herbarium. This record included samples of trees, shrubs, and herbaceous species collected from the years 1890 to 2012. Only samples that were

collected in flower and documented the county of collection were included.

Graminoid (grasslike) species were excluded due to a lack of discrimination between flowering and fruiting phenophases throughout most digital records. In order to ensure that only regions with sufficient sampling were included, only data in states that included over 1500 samples were evaluated based on empirical observation of sampling intensity. After all unusable data were excluded, the remaining record included 823,033 samples over a total of 24,105 species among 750 counties and 16 states, covering over 2.5 million square km (Fig. 4.2).

Nevertheless, this sample was still restricted to those areas in which significant herbarium records were digitally available, and thus covered only 18% of the continental United States. Temperature data used in this study were drawn from U.S. climate normals (1971-2000) developed by the PRISM Climate group (Prism Climate Group, 2004). Köppen Climate classification data was drawn from the 2006 world map of Köppen-Geiger climate classification (Kottek *et al.*, 2006).

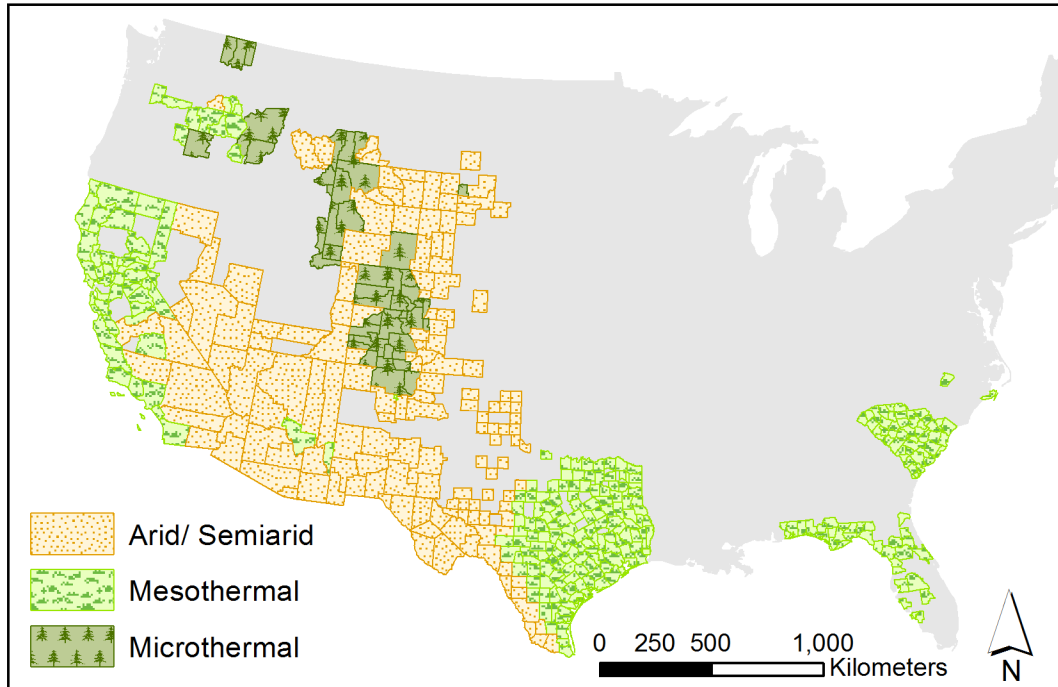


Figure 4.2 Study area and climate regions.. Mesothermal (warm temperate) regions corresponded to regions Köppen class C, while microthermal corresponded to Köppen class D.

4.4.2 Climate Classes

Each county was assigned to one of three climate classes based on the Köppen-Geiger climate type that covered the majority of each county. Arid and semiarid counties were placed into a single “xeric” class (Köppen classes BWk, BWb, BSk, BSh). Humid subtropical (Cfa), dry subtropical (Csa, Csb), and maritime (Cfb) regions were combined into a “warm temperate” class, while hemiboreal (Dfb, Dsb) and boreal (Dfc) regions, along with two high-altitude alpine (ET) counties were combined into a single “cool temperate” class (Fig. 4.2).

4.4.3 Seasonal Classes

As patterns of flowering phenology may vary significantly throughout the growing season (Bradley *et al.*, 1999; Menzel, 2000; McEwan *et al.*, 2011), it was

necessary to separate all species into seasonal classes for comparative analysis. Classes were assigned by calculating the mean DOY (Day of Year) in which samples of each species were collected in flower (Park, 2012) within each state for each species. Each species was then placed into one of seven quantile classes based on the relative order of flowering (from earliest to latest) of all species within each state. Seasonal classes were developed at the state level to ensure a sufficiently robust list of species for accurate ranking, while still compensating for major regional variations in the duration and onset of the growing season. Seven classes were empirically determined to be necessary for separation of mid-season flowering from early and late-season flowering, which exhibited significantly different properties. However, this also resulted in the generation of intermediate classes that incorporated elements of both early, mid, and late season flowering. Thus, only data from the second, fourth, and seventh seasonal classes, which typified the major differences in intraspecific and composition-derived flowering phenology that occurred throughout the early, middle, and late portions of the growing season will be presented here. Data from the second-earliest class, which exhibited similar patterns of variation to the earliest class, is presented in preference to the earliest class due to significantly improved sampling intensity in the second seasonal class.

4.4.4 Pairwise Comparisons

As examinations of intraspecific and composition-derived phenological differences required identification of those species that remained common over space and those species that were excluded from various locations, it was necessary to develop novel methods in order to examine each element of phenological

variation separately. Thus, all analysis of spatial variation throughout this study was conducted through pairwise comparisons of mean flowering times between each possible pair of counties using MATLAB. This permitted precise identification of all species that were common across each pair of locations as well as those species that were not, allowing a separation of the effects of intraspecific and compositional changes in flowering time throughout the study area. This method also facilitated comparisons of flowering phenology among all locations that included sufficient phenological documentation regardless of their proximity or dissimilarity of climate conditions, and was therefore not restricted to comparisons between adjacent or climatically similar locations.

4.4.5 Calculating Overall Differences in Flowering Time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time (represented by the mean collection date of all flowering samples) was calculated for each species that was present within each county. The average timing of all species within a given class was then calculated for each county. In order to facilitate comparisons in flowering time among locations, pairwise differences in mean overall flowering time were calculated among each possible pair of counties, resulting in a measurement of the difference in overall flowering time among each pair of locations. This metric represents an estimate of the actual differences in flowering phenology over space, and incorporates the effects of both intraspecific and compositional changes over space.

4.4.6 Isolating Intraspecific Differences in Flowering Time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time of each species (represented by the mean collection date of all flowering samples) in a given timing class was calculated within each county. For each possible pair of counties, all species that were present in both locations were then selected. For each of the two counties being compared, a community-level mean flowering time was then calculated based on the flowering times of only those species that were present within both counties. Differences in the resulting averages were then computed. Thus, by evaluating identical sets of species in each location, this metric isolated intraspecific phenological variation and excluded the effects of changes in species composition between each pair of counties.

4.4.7 Isolating Composition-Derived Differences in Flowering Time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time of each species (represented by the mean collection date of all flowering samples) in a given timing class was calculated across all samples throughout its entire range. This resulted in a single estimate of flowering time for each species that was not influenced by any intraspecific responses to varying environmental conditions over space. For each possible pair of counties, all species that were present in only one of the two counties were then selected. For each of the two counties being compared, a community-level mean flowering time was then calculated based on the flowering times of only those species that were not shared with the other county. Differences

in the resulting averages were then computed. Thus, by eliminating the effects of local environmental variation on the flowering times of each species, this metric isolated composition-derived differences in flowering time and excluded the effects of intraspecific phenological variation. It should be noted that while the proportion of species that were shared among each pair of counties was highly variable, the relative proportion of shared to unshared species had no significant impact on the overall magnitude of composition-derived phenological differences ($R^2 < 0.001$, $p = 0.419$, $df = 26113$).

4.4.8 Analysis

The relationships of intraspecific and composition-derived variations in flowering phenology to variations in overall flowering time within each season and climate region were evaluated through linear regression analyses conducted within each seasonal class and climate region, as well as throughout the entire study area.

Additionally, intraspecific and composition-derived variations in flowering time within each season were compared to differences in county-level mean temperature estimates (based on 1971-2000 normals) over the three-month period to which they showed the strongest relationship using linear regression analysis. As temperature variations during the same periods were most closely related to flowering times in each season across all climate regions, this resulted in comparisons of early season (class 2) flowering to mean temperatures from February to April, of mid-season (class 4) flowering to mean temperatures from May to July, and of late season (class 7) flowering to mean temperatures from August to October.

However, because of the pairwise nature of the methods used to estimate intraspecific and composition-derived differences in flowering time, estimates of intraspecific and composition-derived flowering phenology required a sufficient diversity of both shared and unique species within each county pair to represent mean, multispecies trends across the plant community. Therefore, all county pairs that included fewer than ten species that were shared across both counties or fewer than twenty species that were unique to each of the two counties were excluded from analysis. Despite this restriction, comparisons were still possible among surprisingly distant communities, and included county pairs separated by over 4500 km, and over 11.5 degrees in latitude. Further, this requirement appeared to be sufficient to eliminate biases through variable sample intensity among locations, as the number of collections showed no significant effect on timing estimates ($R^2 < 0.001$, $p = 0.717$, $df = 2132$). Previous studies have also confirmed that herbarium-based estimates of flowering phenology typically exhibit minimal collector bias and can accurately predict in-situ observations of flowering time (Miller-Rushing *et al.*, 2006; Bowers, 2007; Robbirt *et al.*, 2011; Zalamea *et al.*, 2011). As this record evaluated spatial rather than temporal phenological variation and therefore pooled samples over many decades and collectors at each location, resulting estimates of intraspecific or composition-derived variation in flowering phenology should be particularly resistant to the influence of collector bias or variable sampling intensity.

4.5 Results

4.5.1 Contributions to observed variation in overall flowering time

Intraspecific variations in flowering time were closely related to overall variations in flowering time, explaining over 50% of observed variation in overall flowering in all cases and over 75% of overall early-season variation (Fig. 4.3, Table 4.1).

Regression analysis also found that intraspecific changes in flowering time were similar in magnitude to overall variations in flowering time, and actually exceeded the mean overall responses in flowering time during the early and middle portions of the growing season (Fig. 4.3, Table 4.1).

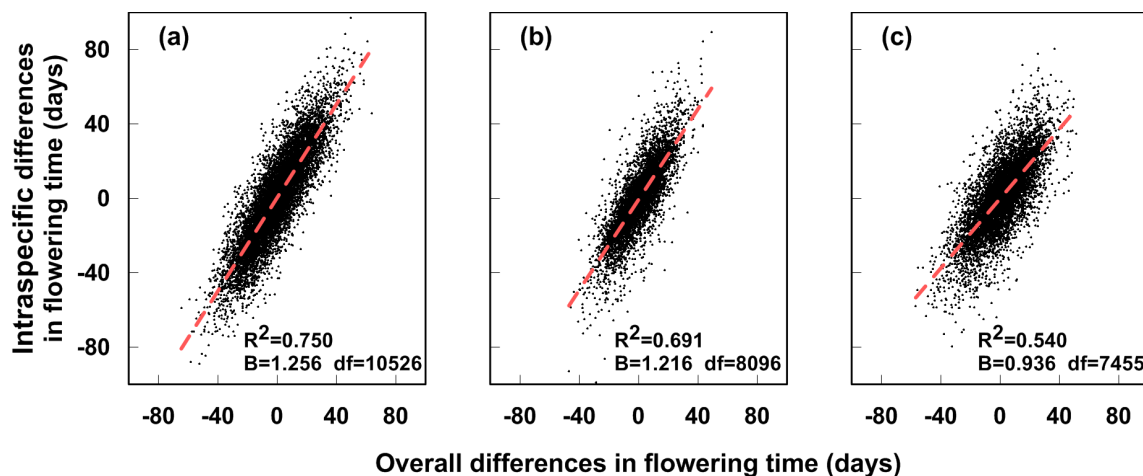


Figure 4.3. Intraspecific versus overall differences in flowering phenology over space among early flowering (4.3a) mid-season flowering (4.3b) and late-flowering portions of the plant community (4.3c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend.

Intraspecific versus Overall Variation in Timing of Flowering		Overall	Xeric	Warm Temperate	Cool Temperate
Early Season					
	% Explained Variance	75.1%	78.7%	69.2%	76.0%
	Δ Plastic/ Δ Overall	1.256	1.244	1.170	1.018
	P Value	<0.001	<0.001	<0.001	<0.001
	# Samples	10527	1194	6311	26
Mid-Season					
	% Explained Variance	69.1%	77.1%	58.3%	86.9%
	Δ Plastic/ Δ Overall	1.216	1.271	1.204	1.151
	P Value	<0.001	<0.001	<0.001	<0.001
	# Samples	8097	1400	1857	1172
Late Season					
	% Explained Variance	54.0%	58.5%	53.4%	53.3%
	Δ Plastic/ Δ Overall	0.936	0.877	0.930	1.061
	P Value	<0.001	<0.001	<0.001	<0.001
	# Samples	7456	987	5283	14

Table 4.1. Contributions of plastic phenological variation to overall differences in flowering time within xeric, warm temperate, and cool temperate environments. Significant correlations were indicated using bold text.

In contrast, linear regressions of differences in composition-derived and overall flowering times found that composition-derived variations in flowering time were smaller than variations in overall observed flowering ($B < 0.343$ in all cases, Figs. 4.4, 4.5, Table 4.2) and explained under 50% of overall variation in flowering (up to 49.3% among early-flowering, xeric communities, Table 4.2).

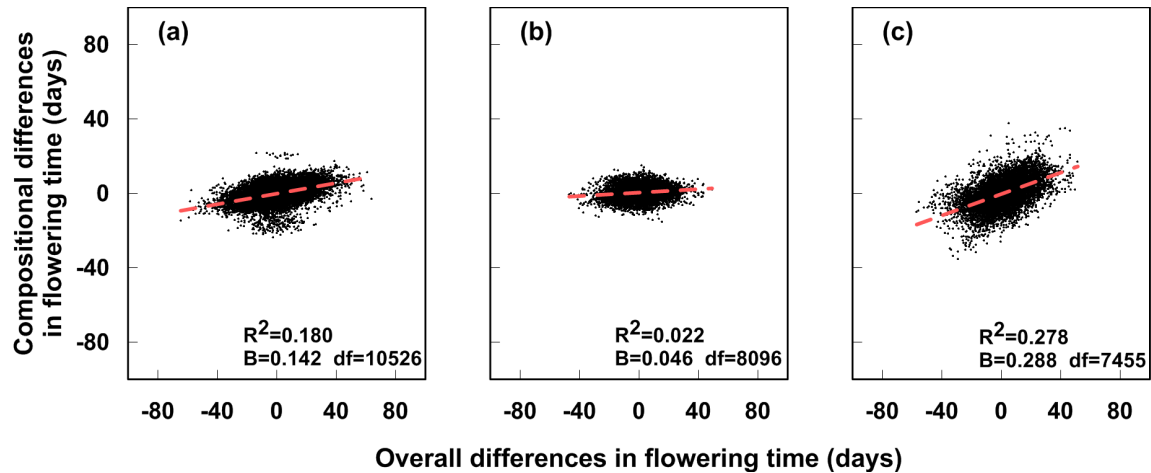


Figure 4.4. Compositional versus overall differences in flowering phenology over space among early flowering (4.4a), mid-season flowering (4.4b), and late-flowering portions of the plant community (4.4c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. B is used here to indicate the slopes of linear relationships between composition-derived and overall phenological variations.

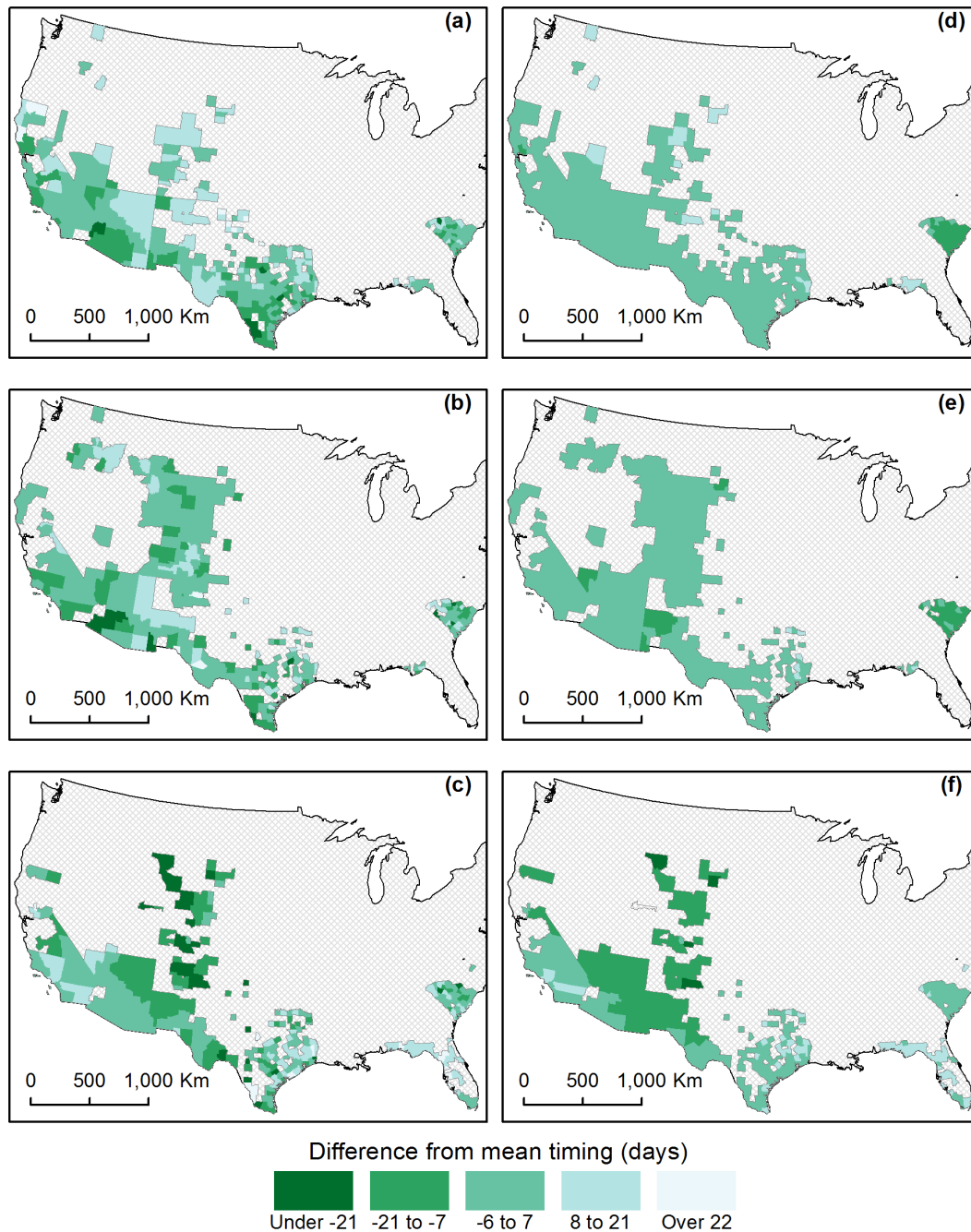


Figure 4.5. Overall variations in flowering time over space among early flowering (4.5a) mid-season flowering (4.5b) and late-flowering portions of the plant community (4.5c) as derived from mean flowering dates of each species within each county, as well as composition-derived variations in flowering time over space among early flowering (4.5d) mid-season flowering (4.5e) and late-flowering portions of the plant community (4.5f) as derived from estimates of mean flowering dates across all taxa as derived purely through the mean flowering of each species within a county across its entire documented range.

Compositional versus Overall Variation in Timing of Flowering		Overall	Xeric	Warm Temperate	Cool Temperate
Early Season					
% Explained Variance		18.0%	49.3%	6.8%	22.2%
Δ Compositional/ Δ Overall		0.14	0.20	0.10	0.34
P Value		<0.001	<0.001	<0.001	0.013
# Samples		10527	1194	6311	26
Mid-Season					
% Explained Variance		2.2%	0.4%	4.3%	5.3%
Δ Compositional/ Δ Overall		0.046	-0.020	0.054	0.084
P Value		<0.001	0.018	<0.001	<0.001
# Samples		8097	1400	1857	1172
Late Season					
% Explained Variance		27.8%	20.7%	30.3%	15.3%
Δ Compositional/ Δ Overall		0.288	0.344	0.248	0.254
P Value		<0.001	<0.001	<0.001	0.150
# Samples		7456	987	5283	14

Table 4.2. Contributions of composition-derived phenological variation to overall differences in flowering time within xeric, warm temperate, and cool temperate environments. Significant correlations were indicated using bold text.

However, the relationship between composition-derived and overall variations in flowering time often remained highly significant, and exhibited considerable seasonal variation. Composition-derived differences in flowering time also showed minimal contributions to differences in overall flowering time during the middle portion of the growing season (Fig. 4.4b), but explained over 25% of the observed variation among late-flowering species ($R^2=0.278$, Fig. 4.4c, Table 4.2). Examinations of spatial patterns of composition-derived variation in late-season flowering phenology were also surprisingly similar in both distribution and magnitude to overall patterns of variation in flowering time (Figs. 4.5c, 4.5f).

The role of composition-derived phenological changes in determining overall variations in flowering time also appeared to vary considerably among climate regions. Composition-derived variations in early-season flowering were minimally connected to overall flowering times in warm temperate areas, but were strongly correlated to overall early-season flowering in xeric regions, explaining nearly 50% of the observed variation ($R^2=0.493$, $B=0.205$, $p<0.001$, Table 4.2). Interestingly, composition-derived variations in early spring flowering in xeric regions also exhibited strong correlation to intraspecific variation ($R^2=0.40$, $p<0.001$, $df=1195$), even though such relationships were modest ($R^2\leq 0.081$) throughout all other seasons and regions.

4.5.2 Responses to seasonal temperature variations

Across the entire study area, early-season flowering exhibited rapid intraspecific shifts towards earlier flowering under warmer February to April temperature ($R^2=0.433$, $B=-0.4.532$ Days/ $^{\circ}\text{C}$, $p<0.001$, Fig. 4.6a, Table 4.3). In

comparison, mid-season flowering exhibited milder shifts towards earlier flowering in response to increasing May-July temperature ($R^2=0.144$, $B=-0.1673$ Days/ $^{\circ}\text{C}$, $p<0.001$, Fig. 4.6b, Table 4.3). While late-season flowering did show significant intraspecific shifts towards later flowering in response to increasing temperatures from August to October, correlations between intraspecific variations in flowering time and differences in autumn temperature were minimal ($R^2=0.042$, $B=1.306$ Days/ $^{\circ}\text{C}$, $p<0.001$, Fig. 4.6c, Table 4.3). Intraspecific responses to temperature variations within each season were consistently lower in warm temperate regions than either xeric or cool temperate regions (Table 4.3). Additionally, cool temperate regions exhibited substantially stronger responses to temperature variations by both mid- and late season flowering than occurred in either other climate region, although estimates of late-season responses may be somewhat unreliable due to the small sample size in cool temperate regions (Table 4.3).

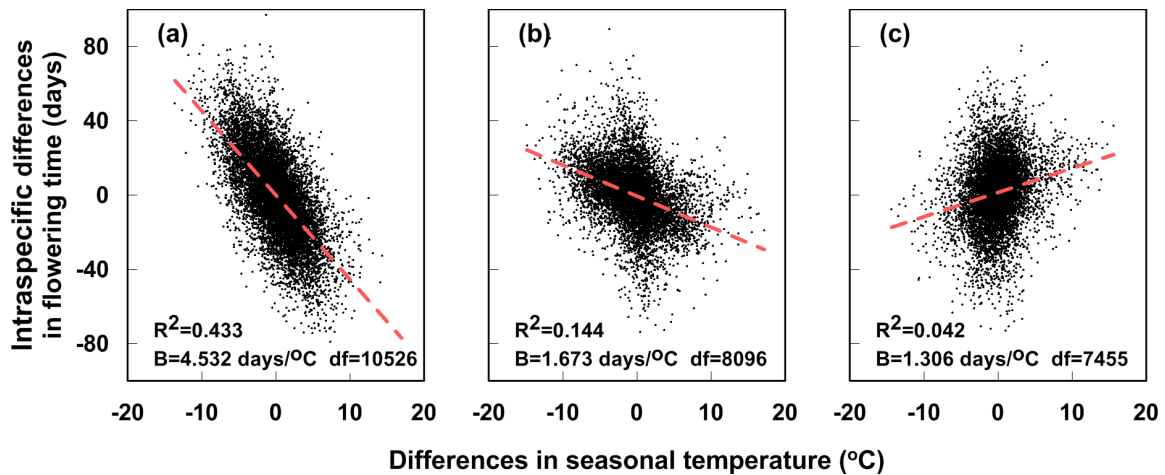


Figure 4.6. Intraspecific responses to differences in seasonal temperature among early flowering (4.6a), mid-season flowering (4.6b), and late-flowering portions of the plant community (4.6c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. B is used here to indicate the slopes of linear relationships between intraspecific phenological timing and seasonal temperature variations.

Intraspecific Responses to Spatial Variations in Temperature		Overall	Xeric	Warm Temperate	Cool Temperate
Early Season					
% Explained Variance		43.3%	55.3%	31.3%	51.8%
Days/°C		-4.53	-4.20	-4.36	-2.26
P Value		<0.001	<0.001	<0.001	<0.001
# Samples		10527	1194	6311	26
Mid-Season					
% Explained Variance		14.4%	13.2	5.1%	39.1%
Days/°C		-1.673	-1.526	-1.911	-2.237
P Value		<0.001	<0.001	<0.001	<0.001
# Samples		8097	1400	1857	1172
Late Season					
% Explained Variance		4.2%	9.6%	1.8%	73.2%
Days/°C		1.306	0.975	0.934	2.413
P Value		<0.001	<0.001	<0.001	<0.001
# Samples		7456	987	5283	14

Table 4.3. Intraspecific phenological responses in flowering time to spatial variations in seasonal temperature throughout xeric, warm temperate, and cool temperate environments. Early season flowering was compared to mean temperature from February to April. Mid-season flowering was compared to mean temperatures from May to July, and late season flowering was compared to mean temperature from August to October. Significant correlations were indicated using bold text.

While intraspecific responses to seasonal temperature variations were typically strongest among early-flowering species, composition-derived responses to changing temperatures were strongest among late-flowering species (Fig. 4.7). Although early and mid-season compositional responses to temperature variations were significantly weaker and less deterministic than intraspecific responses, late-season composition-derived shifts towards later flowering time among locations with warmer temperatures from August through October were both more consistent ($R^2=0.258$) and more rapid ($B=1.39$ days/ $^{\circ}\text{C}$) than intraspecific responses to autumn temperature changes (Figs. 4.6c & 4.7c, Table 4.4).

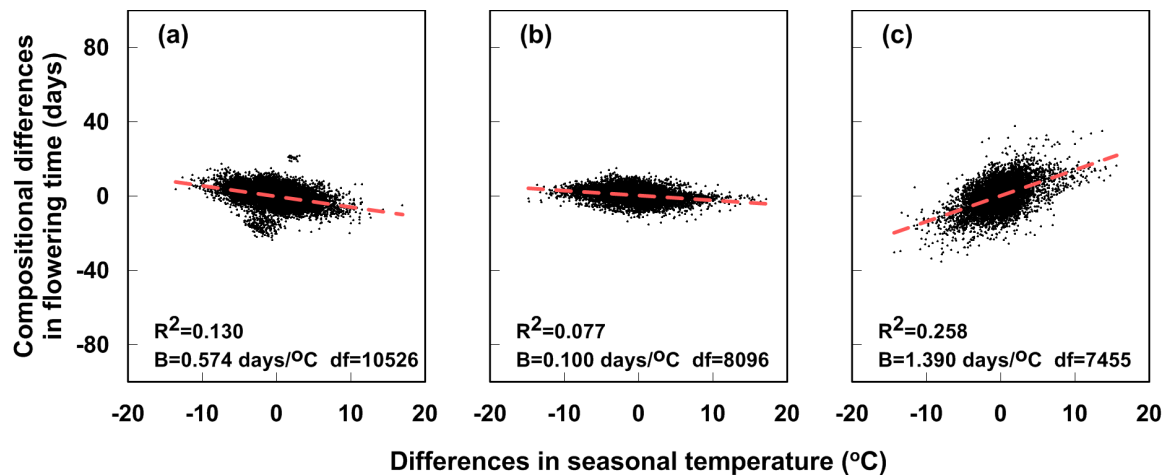


Figure 4.7. Compositional responses to differences in seasonal temperature among early flowering (4.7a), mid-season flowering (4.7b), and late-flowering portions of the plant community (4.7c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. B is used here to indicate the slopes of linear relationships between composition-derived phenological timing and seasonal temperature variations.

Compositional Responses to Spatial Variations in Temperature		Overall	Xeric	Warm Temperate	Cool Temperate
Early Season					
% Explained Variance		13.0%	34.0%	2.0%	29.0%
Days/°C		-0.57	-0.69	-0.30	-1.06
P Value		<0.001	<0.001	<0.001	<0.004
# Samples		10527	1194	6311	26
Mid-Season					
% Explained Variance		7.7%	7.0%	7.2%	<0.1%
Days/°C		0.10	-0.265	-0.534	-0.001
P Value		<0.001	<0.001	<0.001	0.153
# Samples		8097	1400	1857	1172
Late Season					
% Explained Variance		25.8%	49.4%	9.0%	37.9%
Days/°C		1.390	1.583	1.001	0.812
P Value		<0.001	<0.001	<0.001	<0.015
# Samples		7456	987	5283	14

Table 4.4. Compositionally-derived phenological responses in flowering time to spatial variations in seasonal temperature throughout xeric, warm temperate, and cool temperate environments. Early season flowering was compared to mean temperature from February to April. Mid-season flowering was compared to mean temperatures from May to July, and late season flowering was compared to mean temperature from August to October. Significant correlations were indicated using bold text.

Additionally, both early and late-season compositional responses to temperature variations were strongest in xeric regions, and not only exhibited much more deterministic responses to temperature variations than occurred through intraspecific variations (Tables 4.3 & 4.4) but also exhibited much more rapid delays in late-season flowering ($B=1.583$ Days/ $^{\circ}\text{C}$, Table 4.3) than occurred through intraspecific responses ($B=0.975$ Days/ $^{\circ}\text{C}$, Table 4.4). However, composition-derived phenological responses to differing temperatures during the middle portion of the growing season remained minimal throughout all regions ($R^2 \leq 0.077$, Fig. 4.7b, Table 4.4), as well as within warm temperate regions throughout all seasons ($R^2 \leq 0.09$ in all cases, Table 4.4).

4.6 Discussion

Collectively, it is clear that both intraspecific and composition-derived changes contribute significantly to the overall pattern of spatial variation in flowering timing that occurs throughout the United States, and that isolating composition-derived phenological variation reveals important differences in community-level phenology and its relationship to community composition along environmental gradients. Intraspecific variations in flowering time are sufficient to explain the majority of overall variation in flowering time throughout all seasons and within each climate region, although the percentage of overall variation in flowering times that could be explained purely through intraspecific responses were greatest in spring and reduced among later portions of the bloom display. In contrast, however, the magnitude of composition-derived phenological changes

differed significantly both among climate regions and along a seasonal gradient. Therefore, these results indicate that phenological timing plays a significantly more important role in determining the composition of some plant communities than others, and that such communities may experience more rapid phenologically-driven changes in composition through species loss, invasions, or range shifting under additional climate change than other communities that exhibit lower composition-derived shifts in flowering phenology.

While intraspecific variation explained the majority of overall spatial variations in flowering time, reduced intraspecific responses to temperature variations were detected later in the growing season, particularly among late-flowering species. This supports previous in-situ research that found reduced intraspecific responses to temperature variations during the mid- and late portion of the growing season (Fitter *et al.*, 1995; Gordo & Sanz, 2005; Cook *et al.*, 2012). Similarly, in-situ examinations of mean responses to interannual temperature variations throughout North America and Europe found that autumn flowering species exhibited milder and more variable responses to interannual temperature variations than spring flowering species (Wolkovich *et al.*, 2012).

In contrast to intraspecific variations, however, composition-derived phenological differences exhibited stronger responses to temperature variations over space and explained a larger percentage of variation in overall flowering time among late-flowering species. Collectively, these results indicate that the portion of the plant community that flowers towards the end of the growing season may experience a higher degree of phenologically-driven range limitation than species

that flower earlier in the year. Phenological studies that only examine intraspecific phenological variation may therefore underestimate the magnitude of responses to climate change in late-season flowering phenology.

Mid-season flowering typically exhibited the mildest composition-derived phenological variation, and explained only a small percentage of observed variation in overall flowering. This pattern is compatible with previous research into the mechanisms underlying phenologically-derived range limitation, as most species were found to be range limited either by cold damage to flowering structures through late frosts, to which early-flowering species would be most vulnerable, or by cold damage to fruiting structures prior to seed maturation, to which late flowering species would be most susceptible (Morin *et al.*, 2007; Chuine, 2010). Thus, it appears that additional warming is less likely to produce phenologically-driven changes in the composition of that portion of the plant community which flowers during late spring or summer.

In addition to seasonal differences, the role of flowering phenology in determining community composition also appeared minimal throughout warmer temperate regions. As warm temperate regions represented the region with the mildest climate, this may reflect a region where cold or drought damage to poorly timed blooms are often insufficient to exclude those species. Thus, it appears likely that warm temperate regions may be less prone to phenologically enforced changes in composition than xeric or cool temperate regions, and may be more resilient to future climate changes.

In xeric regions, however, the plant community appears to be highly susceptible to phenologically enforced changes in composition, as xeric regions exhibited the most rapid composition-derived changes in the timing of both early and late-season flowering across a temperature gradient. Composition-derived phenological changes among early flowering species were also strongly responsive to both temperature shifts, and highly correlated to overall phenological variations. Interestingly, it would also appear that composition-derived phenological changes among early flowering species in xeric regions were also strongly correlated to intraspecific shifts in flowering time. Collectively, this may reflect an increased pressure to avoid frost damage (Inouye, 2008) and drought (Ghazanfar, 1997; Peñuelas *et al.*, 2004; Gordo & Sanz, 2005; Prieto *et al.*, 2008; Gordo & Sanz, 2010; Mission *et al.*, 2011; Ferdenández-Martínez *et al.*, 2012) within xeric regions that enforces highly coherent flowering times among early-flowering species.

These results clearly show that herbarium records may be used successfully to evaluate the magnitude of intraspecific and composition-derived shifts in flowering phenology in response to changing climate conditions over space, and to represent a way to estimate the magnitude of disruption to the composition of existing plant communities under additional climate change that would result from changes in optimal reproductive timing. Unlike previous methods, which relied upon in-situ observation (Craine *et al.*, 2012), this method may easily be extended to any region that includes significant digital herbarium records and some form of spatial temperature and climate characterization, and may also be further expanded to continental and global scales as herbarium records are digitally processed and

become available. While this study primarily focused on broad climate regions throughout North America, these results also have significant implications for a range of temperate environments and may easily be adapted to any region of the globe for which both significant herbarium records and basic climate information are available.

Still, this research represents only a preliminary examination of the mechanisms underlying spatial variations in flowering phenology throughout North America. Further research will expand this work to evaluate the magnitude of intraspecific and compositional variations in flowering phenology among plants that exhibit differing morphologies and physiological adaptations. A fuller understanding of the mechanisms which underpin observed patterns of variation in flowering phenology is critical to predicting the resilience of the plant community to future climate perturbations. Thus, future work will expand this method to also separate intraspecific variations in flowering time into variations caused through either phenotypic plasticity or interpopulation genetic adaptation. While this work remains at the preliminary stages, it is clear that community-level changes in flowering phenology are closely tied to changes in the composition of the plant community over space. Evaluation of the various mechanisms that contribute to spatial differences in community-level flowering phenology represents a critical next step forward in predicting future changes in the ranges and local persistence of plant species that occur throughout the globe.

5. Conclusions and Future Research

This dissertation examined three core issues relating to community-level flowering phenology and the use of herbarium records in phenological research. In chapter 2, comparisons of herbarium-based metrics with MODIS-derived greenup estimates determined that meaningful year-to year predictions of community-level variation in flowering phenology can be constructed from herbarium data. Chapter 3 leveraged this finding to provide new insights into the relationships between multi-seasonal reproductive phenology across the plant community and climatic variations throughout portions of the Southeastern United States that were previously lacking in long-term phenological data. Finally, chapter 4 presented novel methods to evaluate the relationship between spatial variations in plant community composition, variation in community-level reproductive phenology, and the role of changes in local biodiversity in producing community-level phenological change along climate gradients.

In addition to a number of methodological advances, this dissertation yielded multiple findings that contribute significantly to our understanding of plant reproductive phenology. Chapter 3 determined that flowering during both the onset of the growing season and throughout late spring and summer were influenced primarily by temperature variations during February and March. Further, this work determined that seasonal changes in patterns of interannual phenological variation occurred gradually throughout the mid-portion of the growing season, but that flowering among both the earliest and latest-flowering species exhibited quite dissimilar patterns of annual variation than occurred during

any other season. Further, this work confirmed previous model-based phenological estimates, which indicated that no long-term changes had occurred throughout the Southeastern U.S. over the past 50 years. In addition, it was determined that composition-derived changes in flowering time explained the greatest proportion of overall variation among late-flowering species. Similarly, the composition of the portion of the plant community that flowers during the later portions of the growing season was also found to be quite responsive to differing climate conditions, particularly within xeric environments. Thus, while the impact of flowering phenology on community assemblage varies considerably among seasons and climate regions, it appears that the plant community is likely the most susceptible to phenologically-enforced disruptions to local composition within xeric regions and among late-flowering species, and the most resilient within warm temperate regions and among species that flower during the mid-portion of the growing season.

Collectively, this work has shed light on previously unexplored aspects (both spatial and conceptual) of plant reproductive phenology. Further, the techniques developed through the course of this dissertation open new avenues to explore not only historical patterns of phenological variation, but the relationship of plant reproductive phenology to critical ecological processes. In the future, this work will expand to evaluate impacts of composition-derived phenological variations on additional processes such as species persistence, invasibility, and the rate of change in local assemblage along climate gradients. The methods developed here may also be adapted to additional taxa outside of the plant community, particularly fungal

collections, which primarily occur through collection of fruiting structures, and arthropod collections, which may be related to the timing of migration, pupation and larval development, or spring emergence. Perhaps most importantly, it may be possible to integrate the methods developed here for evaluating compositionally-derived phenological variation with predictive modeling techniques in order to develop the first standardized, global indices for estimating phenologically-driven disruption to plant community composition under various models of projected climate change.

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7. Curriculum Vitae

Education

Ph. D. May 2014 Geography
University of Wisconsin-Milwaukee, Milwaukee, WI
G.P.A. 4.00

M.S. 2009, Plant and Environmental Science
Minor: Experimental Statistics
Clemson University, Clemson, SC
G.P.A. 4.00

B.A. 2004, Liberal Arts
St. John's College, Santa Fe, NM
G.P.A. 3.12

Research Interests: phenology, landscape ecology, community ecology, plant physiology, population ecology, biogeography, bioclimatology, remote sensing, citizen science

Refereed Publications:

Park, I. W. (In Press) Impacts of differing community composition on flowering phenology throughout warm temperate, cool temperate, and xeric environments. *Global Ecology and Biogeography*

Park, I. W. (2012) Digital herbarium archives as a spatially extensive, taxonomically discriminate phenological record; a comparison to MODIS satellite imagery. *International Journal of Biometeorology* 56(6): 1179-1182

Park, I. W., S. J. DeWalt, E. Siemann, and W. Rogers (2012) Differences in cold hardiness between introduced populations of an invasive tree (*Triadica sebifera*) in the southeastern United States. *Biological Invasions* 14(10): 2029-2038

Additional Professional Publications:

Ribbens, E., I. W. Park (2011) The Wired Herbarium: Phenology Data. *The Vasculum* 6: 10-11

In Review:

Park, I. W., Schwartz, M. D. (in review) Long-term herbarium records reveal temperature dependent changes in flowering phenology in the Southeastern United States. In review at *International Journal of Biometeorology*

Liu, L., Liu, L., Liang L., Donnelly, A., Schwartz, M. D., Park, I.W. (in review) Differential response of spring land-surface phenology to interannual and altitudinal temperature variations in the Tibetan Plateau grasslands. In review at *Chinese Science Bulletin*.

In Preparation:

Park, I.W., Tonkyn, D. (in preparation) How many species are there? Methods for teaching species richness estimation.

Invited Oral Presentations:

2009 **Park, I. W.**, S. J. DeWalt, E. Siemann, and W. Rogers. "Potential for introduced-range expansion of Chinese tallow tree (*Triadica sebifera*) in the Southeastern United States" Horticulture Departmental Seminar, Clemson University

Contributed Oral Presentations: (in all cases the first author was the presenter)

2014 **Park, I. W.** "Impacts of differing community composition on flowering phenology throughout temperate environments" Association of American Geographers, Tampa, FL

2013 **Park, I. W.** "Patterns of spring, summer, and fall flowering phenology using digital herbarium records: Identifying the role of compositional changes over space" Ecological Society of America, Minneapolis, MN

Park, I. W. "Flowering phenology across North America" Association of American Geographers, Los Angeles, CA

2012 **Park, I. W.** "Examining patterns of spring, summer, and fall flowering phenology using herbarium records" Phenology 2012, Milwaukee, WI

Park, I. W. "A plant for all seasons: Examining patterns of spring, summer, and fall flowering phenology across South Carolina" Ecological Society of America, Portland, OR

Park, I. W. "Relating herbarium records to satellite phenology: Problems and potential " Association of American Geographers, New York, NY

- 2011 **Park, I. W.** "Phenological patterns in digital, multi-taxa herbarium records across the Southeastern United States" Association of American Geographers, Seattle, WA
- 2008 **Park, I. W.,** S. J. DeWalt, E. Siemann, and W. Rogers. "Range expansion potential of four populations of Chinese tallow tree (*Triadica sebifera*) throughout South Carolina" Ecological Society of America, Milwaukee, WI

Poster Presentations: (in all cases the first author was the presenter)

- 2007 **Park, I. W.,** S. J. DeWalt, E. Siemann, and W. Rogers. "Effect of Winter Conditions on Germination of Four Chinese Tallow Tree Genotypes in Coastal, Midlands, and Upstate Areas of South Carolina." Ecological Society of America, San Jose, CA
- 2006 **Park, I. W.,** and S. J. DeWalt. "Germination of Four Chinese Tallow Tree Genotypes In Coastal, Midlands, and Upstate Areas of South Carolina." Southeastern Population Ecology and Evolutionary Genetics Conference, Greensboro, NC

Professional Organizations:

Ecological Society of America
 Association of American Geographers
 -Biogeography Specialty Group
 -Climate Specialty Group
 -Remote Sensing Specialty Group
 International Society of Biometeorology

Awards and Fellowships:

- 2013-2014 University of Wisconsin-Milwaukee Distinguished Dissertator Fellowship
 Amount awarded: \$16,500
- 2013 Association of American Geographers Biogeography Specialty Group Student Paper Competition, (1st place)
 Amount Awarded: \$100
- 2011-2013 University of Wisconsin Mary J. Read Travel Fellowship
 Amount Awarded: \$3400
- 2011 Association of American Geographers Climate Specialty Group Student Paper Competition, (3rd place)
 Amount Awarded: \$100
- 2010-2013 University of Wisconsin Mary J. Read Fellowship
 Amount awarded: \$5000
- 2009-2010 University of Wisconsin-Milwaukee Graduate School Fellowship
 Amount awarded: \$14,000
- 2009-2010 University of Wisconsin-Milwaukee Chancellor's Fellowship
 Amount awarded: \$5000

Work Experience:

University of Milwaukee-Wisconsin, Department of Geography, Milwaukee, WI

- Lecturer for GEOG 120-Our Physical Environment; Spring 2014
- Project manager for NSF-sponsored observation of spring and autumn phenology among northern Wisconsin forest species; 2012-2013 (Mark. D. Schwartz, PI)
- Lab Instructor for GEOG 405/605-Cartography; Spring 2012
- Lab Instructor for GEOG 120-Our Physical Environment; Fall 2011
- Lab Instructor for GEOG 215-Introduction to GIS; Fall 2010

Clemson University, Department of Biological Sciences, Clemson, SC

- Lab Instructor for Biological inquiry for non-majors lab; Fall 2007, 2008
- Lab Instructor for Biology of Plants lab; Spring 2006-Spring 2008

Professional Activity:

- 2013 USA National Phenology Network Seasonal Timing workshop invited participant
- 2012-2013 Copy-editor: Phenology: an integrative environmental science, Vol 2. Ed: M. D. Schwartz
- 2012 Chair: Tree Phenology Contributed Oral Session, Phenology 2012, Milwaukee, WI
- 2011 Reviewer: Ecography
- 2010-2012 Web Maintenance, International Society of Biometeorology Homepage
- 2009-2010 USA National Phenology Network 2009 & 2010 annual meeting invited participant (plant division)

Additional Professional Training

- 2013 PyOhio 2013 Pycamp python programming workshop July 22-26
- 2008 Scientific illustration workshop at Highlands Biological Station July 7-12

Technical Expertise:

- Statistical: SAS, SPSS
- Programming: Python
- GIS/Remote Sensing: ArcGIS, IDRISI, ERDAS Imagine, Hoboware
- Sensors/Hardware: Spectrasuite/Jaz spectrometry, Hoboware (Light/temp sensors)