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Herbarium specimens can reveal impacts of climate change on plant phenology; a systematic review of methods and applications

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Studies in plant phenology have provided some of the best evidence for large-scale responses to recent climate change. Over the last decade, more than thirty studies have used herbarium specimens to analyze changes in flowering phenology over time. In this review, we summarize the approaches and applications used to date. Reproductive plant phenology has primarily been analyzed using two summary statistics, the mean flowering day of year and first flowering day of year, but mean flowering day has proven to be a more robust statistic. Three types of regression models have been applied to test for changes in phenology; flowering day regressed on year, flowering day regressed on temperature, and temperature regressed on year. Most studies analyzed the effect of temperature by averaging temperatures from three months prior to the date of flowering, but other approaches may be suitable in some cases. On average, published studies have used 55 herbarium specimens per species to characterize changes in phenology over time, but in many cases fewer specimens were used. Geospatial grid data is increasingly being used for determining average temperatures at herbarium specimen collection locations, allowing testing for finer scale correspondence between phenology and climate. Multiple studies have shown that inferences from herbarium specimen data are comparable to findings from systematically collected field observations. Herbarium specimens are expected to become an increasingly important resource for analyzing plant responses to climate change. As temperatures continue to rise globally, there is a need to understand phenological rates of change in response to warming and implications of these changes, especially in tropical environments where phenological studies are thus far generally lacking.

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Herbarium specimens can reveal impacts of climate change on plant phenology; a systematic review of methods and applications

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Abstract

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Studies in plant phenology have provided some of the best evidence for large-scale responses to recent climate change. Over the last decade, more than thirty studies have used herbarium specimens to analyze changes in flowering phenology over time. In this review, we summarize the approaches and applications used to date. Reproductive plant phenology has primarily been analyzed using two summary statistics, the mean flowering day of year and first flowering day of year, but mean flowering day has proven to be a more robust statistic. Three types of regression models have been applied to test for changes in phenology; flowering day regressed on year, flowering day regressed on temperature, and temperature regressed on year. Most studies analyzed the effect of temperature by averaging temperatures from three months prior to the date of flowering, but other approaches may be suitable in some cases. On average, published studies have used 55 herbarium specimens per species to characterize changes in phenology over time, but in many cases fewer specimens were used. Geospatial grid data is increasingly being used for determining average temperatures at herbarium specimen collection locations, allowing testing for finer scale correspondence between phenology and climate. Multiple studies have shown that inferences from herbarium specimen data are comparable to findings from systematically collected field observations. Herbarium specimens are expected to become an increasingly important resource for analyzing plant responses to climate change. As temperatures continue to rise globally, there is a need to understand phenological rates of change in response to warming and implications of these changes, especially in tropical environments where phenological studies are thus far generally lacking.

Introduction

Carl Linnaeus pioneered the study of phenology when he outlined methods for investigating the association between flowering and climate (Puppi 2007). The word “phenology” originates from botanist Charles Morren who introduced the term around 1850 to describe his observational studies of yearly flowering (Demarée 2009). Early field studies of plant phenology have been thoroughly reviewed by van Schaik et al. (1993), Fenner (1998) and Forrest et al. (2010). Long-term field observations have provided a valuable resource for analyzing phenological responses to climate change (Walther et al. 2002; Parmesan & Yohe 2003). A growing need for historical data that allows for the exploration of ecological implications of climate change has prompted researchers to look to herbarium specimens as a resource for long-term flowering data. The first study to use herbarium specimens to understand phenological responses to climate change was published by Primack et al. (2004). A few phenology studies such as Borchert et al. (1996) and Rivera & Borchert (2001) used herbarium specimens to study flowering periodicity, but not in the context of climate change. Primack et al. (2004) used 372 specimen records (1885-2002) and found peak flowering had advanced approximately eight days over the last century. Primack et al. (2004) noted that the method of using herbarium specimens may be useful for plants with either short flowering durations or long flowering durations and for plants from unique ecosystems such as mountain peaks or islands. Between 2004 and 2017, more than 30 studies were published using herbarium specimens to examine changes in phenology in response to climate change. An early criticism of the method was that plants preserved as herbarium specimens might not have been collected during their peak flowering season, potentially biasing interpretations (Lamoureux 1972). In response, authors later found that large sample sizes afforded by herbarium specimens, and the use of mean flowering times, can yield valid inferences, even if specimens were not collected at the time of peak flowering (Primack 2004; Bertin 2015). Additional criticisms of collector bias and plant size choice were also found to be overcome by appropriate statistical analyses, especially when mean flowering times were used as the variable of interest, rather than date of first flowering (Robbirt et al. 2011; Davis et al. 2015).

The most common approach found in studies using herbarium specimens follows the model set by Primack et al. (2004). This approach can be summarized as collecting flowering dates from herbarium specimens, collecting long-term temperature data from an independent source, and then using regression analyses to analyze correlations and rates of change over time (Primack et al. 2004; Miller-Rushing et al. 2006; Gallagher et al. 2009; Robbirt et al. 2011; Gaira et al. 2011; Molnár et al. 2012; Panchen et al. 2012; Park 2012; Primack and Miller-rushing 2012; Li et al. 2013; Calinger et al. 2013; Hart et al. 2014; Rawal et al. 2015; Park & Schwartz 2015). Linear regression models are the most widely used statistical models in field studies investigating flowering phenology (Zhao et al. 2013). The studies in this review mostly used three types of linear regression models to show evidence of associations between phenology and climate change (Table 1). These studies regressed flowering day on temperature, flowering day on year, temperature on year, or some combination of these with multiple regression models. Results from these models address whether flowering day was earlier in the year when temperatures were warmer, whether flowering day was earlier in the year over time, and whether temperatures were warmer over time. Around 30% of the studies in this review used all three types of regression models in their analyses (Table 1). Approximately 82% of the studies modeled flowering day on year to show long-term changes in flowering (Table 1). About 64% of studies modeled the effect of temperature on flowering day and a different 64% modeled long-term changes in temperature (Table 1).

These studies have primarily been conducted with specimens from herbaria in temperate latitudes such as the Eastern Himalayas (Gaira et al. 2011; Li et al. 2013; Gaira et al. 2014; Hart et al. 2014), Southern Australia (Gallagher et al., 2009; 2012; Rawal et al., 2015), Northern Europe (Robbirt et al. 2011; Diskin et al. 2012; Molnár et al. 2012), and North America (Primack et al. 2004; Lavoie and Lachance 2006; Miller-Rushing et al. 2006; Primack 2009; Neil et al. 2010; Panchen et al. 2012; Park 2012; Primack and Miller-rushing 2012; Searcy 2012; Calinger et al. 2013; Park 2014; Park & Schwartz 2015; Bertin 2015; Davis et al. 2015). Although studies by Borchert (1996) and Zalamea et al. (2011) analyzed flowering periodicity in tropical plants using herbarium specimens, we found no study to date that has used herbarium specimens to analyze effects of recent climate change in a tropical region. In this review, we examined how studies chose sample sizes, flowering specimens, temperature averages and geographical scale in their analyses. We also examined how these studies validated the use of herbarium specimens and provide suggestions for methods to be used in future studies.

Survey Methodology

We worked between 2015 and 2017 to compile and review studies that used herbarium specimens to assess climate change and flowering phenology. The time period of the database search was between 2004 and 2015. Studies were eligible for this review if they met three main criteria. Studies must have sampled herbarium specimens, analyzed associations with climate change, and assessed flowering phenology. We searched Web of Science (1900 – present), JSTOR (1665 – present) and Google Scholar for studies containing the terms; herbarium, specimen, phenology, and climate change. We only selected studies that met the all three eligibility criteria. The methods of each study were reviewed for; sample size, determining flowering status of specimens, approach to determining temperatures, geographic variation, and any validations of the use of herbarium specimens (e.g. comparisons to field observations). Findings were then categorized into subheadings and a synthesis of each category is discussed. The reviewed papers were also categorized into studies that regressed flowering day on temperature, flowering day on year, or temperature on year and percentages were reported for each. Sample size data was also collected from the reported sample sizes of each individual study and summarized.

Specimen sample sizes

Sample size, or the number of specimens used per species, varied across studies (Table 1). The minimum number of specimens used per species was occasionally as low as two or three records (Searcy 2012). Miller-Rushing & Primack (2008) used field data and found that small sample sizes led to biased estimators of first-flowering dates, but mean flowering day was not biased by sample sizes. Moussus et al. (2010) investigated sample sizes by simulating 10 known phenological estimators such as mean flowering day and first-flowering date. After comparing known phenological shifts from simulated sample data with shift estimations from models using the same data, Moussus et al. (2010) concluded that first-flowering dates were inaccurate and showed much a greater variability than mean flowering day. Low sample sizes prompted Bertin (2015) to provide a detailed analysis of how sample size affected mean, median, range, early flowering and late flowering summary statistics. In random simulations comparing sample sizes, mean flowering day values deviated less than five days for species with as few as four samples (Bertin 2015). Bertin (2015) concluded that the mean was a more robust measure of phenology than other estimators of early flowering. Bertin (2015) also showed that by increasing the sample size to 20, mean flowering times deviated only one to two days.

Some studies using herbarium data have set a minimum number of herbarium specimen samples per species or a minimum time range for collections to more accurately estimate phenologies and change over time. Calinger et al. (2013) and Gallagher et al. (2009) set a minimum of 10 specimens in order to meet statistical assumptions of different models. Molnár et al. (2012), eliminated a species from analyses because collections only yielded dates across an eight year time span and Park & Schwartz (2015) eliminated species with records that spanned less than three years. Neil et al. (2009) organized species into functional groups (spring ephemerals, spring shrubs, fall ephemerals, winter-spring ephemerals, and winter-spring shrubs) in order to overcome the problem of low sample size for each species. Responses of individual species within these functional groups varied greatly however and the aggregated data showed some significant trends.

If phenology varies across a species' geographic range, it may be necessary have a larger number of specimens In order to analyze species distributions using herbarium specimens, van Proosdij et al. (2016) found that the minimum number of herbarium specimen samples should be between 14 and 25 depending on the geographical range of the species. The van Proosdij et al. (2016) study used simulated species to assess the minimum herbarium samples required for acceptable model performance in both virtual and real study areas. Some species with narrow geographical ranges could be modeled with as few as 14 herbarium records while wide ranging species could be satisfactorily modeled with a minimum of 25 records (van Proosdij et al. 2016). Based on these studies, we recommend caution when interpreting results from samples sizes with fewer than 30 records (Miller-Rushing et al. 2008; Moussus et al. 2010; Bertin 2015). The average sample size across studies in this review was about 55 samples per species (Table 1.). We also recommend using a minimum of 10 herbarium records per species when conducting regression analyses and the mean day of year should be used rather than first flowering, especially with small samples sizes (Calinger et al. 2013; Gallagher et al. 2009).

Determining flowering status of specimens

Studies have often simply recorded the presence or absence of flowers on herbarium specimens. However, some studies used more detailed criteria to assess flowering specimens. Diskin et al. (2011) used a scoring system to categorize the stages of flowering on each specimen. Calinger et al. (2013) only used specimens with more than 50% of flower buds in anthesis to help ensure that the samples were in peak flowering. For a species with an inflorescence, Davis et al. (2015) only counted specimens as "flowering" if greater than 75% of flowers were open.

Haggerty et al. (2012) provided a primer to help phenology researchers collect data from herbarium specimens. Haggerty et al. (2012) stated that researchers must assume the stem on the herbarium sheet represents the flowering phenophase for the entire plant.

Studies in temperate regions have used varying methods to account for long flowering durations. For example, Molnár et al. (2012) and Bertin (2015) excluded species that flowered outside of the peak flowering season of the region, defined as the period from late-spring to early-summer. Molnár et al.

(2012) removed a species because its peak flowering date was in September and focused on 40 other taxa that had flowering peaks from in spring and early-summer. The excluded species was a strong outlier and it was suggested that autumn climate events may affect species differently than spring climate events (Molnár et al., 2012). Park (2012) also removed outlier records when flowering records fell outside the peak regional flowering season. Flowering records before day 45 and after day 310 on the 365 day year were removed from analyses to reduce biases caused by winter flowering species. Additionally Park (2012) removed records that were 150 days after the median flowering date for each species to reduce errors caused by any second flowerings that can happen in autumn months.

Several other studies removed taxa with long flowering durations to reduce variance among species. Bertin (2015) excluded native weedy species with flowering durations from spring to fall. Gallagher et al. (2009) only used species with a flowering duration of less than three months. Panchen et al. (2012) chose to use only species with clear beginning and ending points to investigate long and short flowering duration. Panchen et al. (2012) found that plants with shorter flowering durations required smaller sample sizes to produce significant results when regressing flowering day on year. Other studies such as Calinger et al. (2013) and Lavoie & Lachance (2006) disregarded the effect of flowering duration and noted the results of Primack et al. (2004), which reported no bias associated with long or short flowering durations when mean estimations are analyzed. Plants in tropical regions often have long flowering durations (van Schaik 1993; Fenner 1998), but as long as flowering is not continuous throughout the year, methods applied to temperate regions should also yield valuable insight into effects of climate change on phenology in the tropics.

Averaging temperatures

The foundational study by Primack et al. (2004) used temperature averages from three calendar months prior to the specimen flowering date, with the assumption that flowering date is a function of temperatures experienced in past months. Field investigations such as Fitter et al. (1995) have shown temperature averages from different sets of months preceding flowering affect flowering phenology in different ways. More recently, Calinger et al. (2013) chose to regress the month of flowering with temperature averages from each of the 11 months prior to flowering. They found that temperature averages from three months prior to the date of flowering showed the strongest correlations with flowering (Calinger et al. 2013). Robbirt et al. (2011) investigated temperature averages for three sets of temperature averages over three -month long intervals and also found that three months prior to flowering had the most predictive power. Similarly, Rawal et al. (2015) regressed flowering for each species on temperature averages from 1, 3, 6, 9, and 12 months prior to flowering, because responses can vary by species. Rawal et al. (2015) also found that mean temperatures three months prior had the greatest influence on flowering time for all species.

Other studies have used average temperatures from spring months because spring temperatures generally have the most predictive power for flowering date (Miller-Rushing & Primack 2008; Primack et al. 2009; Robbirt et al. 2011; Calinger et al. 2013; Park 2014; Park & Schwartz 2015). Bertin (2015) found an interesting trend that supported the effect of spring temperatures. Bertin (2015) found that the earlier a species' mean flowering time occurred in the spring, the more the species' mean dates had shifted toward an earlier day of year over time. Robbirt et al. (2011) also found the highest correlations of flowering day with spring temperature averages across March, April and May. Calinger et al. (2013) found significant changes in flowering in response to average spring temperatures (February-May) but not in response to summer temperatures (June to September). Gaira et al. (2011) found the highest correlations between flowering and temperatures in earlier months from December-February in a Himalayan perennial herb. As an alternative to using mean monthly temperatures, Diskin et al. (2011) investigated the averages of temperature anomalies, or deviations from the overall long-term mean, for

2, 3, and 6 month periods from January to June and found the averages from six months prior to flowering had the strongest correlations.

Park (2014) used temperature averages across three month periods from early spring to late summer and found a similar trend. Temperature averages were organized into early, mid, and late seasonal classes within the months of February to October. Park (2014) found warming temperatures had affected species in the early spring class more than other classes. Park & Schwartz (2015) also used early, mid and late seasonal classes for spring and summer and found that mid-season phenology events should be modeled differently than early or late season events.

Hart et al. (2014) used annual temperatures and temperatures from each season (spring, summer, fall, and winter) and found significant correlations for annual and fall temperature averages, but with opposite effects. Hart et al. (2014) discussed that warmer fall temperatures may delay the chilling requirement for Rhododendron species, resulting in a delay in flowering while warmer annual temperatures will lead to advances in flowering overall.

Other studies found annual temperature means were as useful as spring temperatures. Davis et al. (2015) found similar results between spring and annual temperature averages and used annual averages in analyses. Gallagher et al. (2009) also used annual temperature means for analyses and explained that seasonal means were correlated with annual means.

We recommend investigating the effect of temperature by analyzing averages from multiple sets of months prior to flowering for each species rather than using only spring or only annual temperatures (Diskin et al. 2011; Robbirt et al. 2011; Calinger et al. 2013). Caution should be taken when analyzing temperature averages from the same months prior to flowering for all species when flowering month varies by species. For example, when analyzing the effect of temperature averages from three months prior for all species, Calinger et al. (2013) found that for many species, flowering was correlated with temperatures three months earlier, yet for species with an earlier mean flowering day in April, January temperatures (three months prior to flowering) did not predict flowering date; instead, temperature averages from the months of February, March and April were better predictors for those species.

Geographic variation

Among species that have broad geographic ranges, differences in climate in different parts of the species' range can complicate attempts to correlate a species' flowering day with temperature. Several methods have been used to account for climate variability across a species' range. An early study by Lavoie & Lachance (2006) investigated the effects of climate variation on the phenology of Coltsfoot (Tussilago farfara L.) across a range of about 10,000 km2 in Quebec, Canada. Temperature data from 88 meteorological stations were averaged together across this range. To account for early snow cover melt in the southern part of this range, flowering dates from individuals in southern locations were normalized with individuals in northern locations by subtracting extra periods of snow cover from individuals in the north. The adjusted dates indicated flowering occurred 33 days earlier over the last century while original (unadjusted) dates indicated flowering occurred 19 days earlier over the last century.

While the study by Lavoie & Lachance (2006) adjusted actual dates for analyses, more recent studies mostly account for climate variation using georeferenced climate data at various scales. Calinger et al. (2013) accounted for climate variation across Ohio by using temperature averages from 10 US Climate Divisions across the state, each about 8,000 km2. A total of 344 Climatic Divisions were established across the contiguous United States in 1895 in order to monitor climate records more accurately. These divisions have now accumulated about 100 years of climate records (Guttman & Quayle 1996). A later study by Park (2014) used average temperatures across the U.S. county where each specimen was collected.

Other studies accounted for climate variation across longitude, latitude, or elevation. Robbirt et al. (2011) analyzed the geographical effect of longitude and found that flowering occurred 4.86 days earlier per degree of longitude in a westward direction across the southern coastal counties of England (Robbirt et al. 2011). A later study by Bertin (2015) used Hopkins' bioclimatic law to normalize dates on specimens. Hopkins' (1918) generally stated that for every increase in a degree of latitude, or increase of 121.92 m elevation, the life history events of plants and animals were delayed by four days. Bertin (2015) found consistencies with Hopkins' bioclimatic law using latitude and elevation and chose to normalize flowering dates by adding expected phenological deviations from both latitude and elevation. Gaira et al. (2011) also analyzed climate variation using elevation when temperature data were not available, assuming a 6.5°C change in temperature per 1000 m change in elevation in the Himalayan region.

Other studies used temperature averages across large regions. Li et al. (2013) used temperature data that was averaged from 36 meteorological stations across the Tibet Autonomous Region. Molnár et al. (2012) used temperature averages from 10 meteorological stations across Hungary and stated that the data were statistically indistinguishable across stations (~93,030 km²). Park & Schwartz (2015) averaged temperatures from 13 stations across South Carolina, USA (~82, 931 km²). A later study by Robbirt et al. (2014) used temperature averages from an area between Bristol, Preston, and London, across the United Kingdom (~17, 000 km²). Robbirt et al. (2014) used geographical divisions called Watsonian vice-counties specifically delineated for the purposes of collecting scientific data, much like the US Climate Divisions. Robbirt et al. (2014) found temperature averages were sufficient because climate variation across the Watsonian vice-counties used in their study did not significantly differ.

In order to more accurately estimate temperature averages across a region, recent studies have used Geographical Information Systems (GIS) to project finer-scale climate layers across a region and extract temperature data from specific Global Positioning System (GPS) points. A study by Gallagher et al. (2009) referenced GPS locations for each specimen and extracted the temperature averages at specimen GPS points from a gridded map of temperature averages across Australia (~5 km2 resolution). A study by Rawal et al. (2015) also used the nearest data point from gridded climate averages across Victoria, Australia. A recent study by Edward & Still (2008) analyzed the climate envelopes of grasses by assigning GPS points to herbarium specimen locations in order to extract temperature averages from gridded climate maps (250m2 resolution). Studies using GPS data are able to account for climate variation with higher resolution, although accuracy still depends on the underlying empirical data and modeling approach used to generate GIS climate layers.

We recommend using the most spatially precise temperature data available, such as climate divisions (Calinger et al. 2013; Robbirt et al. 2015) rather than state or region averages (Li et al. 2013; Park & Schwartz 2015). Using GPS specimen data to identify local climate conditions from GIS climate layers (Gallagher et al. 2009; Edward & Still 2008) is also now generally more precise and convenient in comparison to making generic and coarse-scale corrections for latitude, longitude or elevation (Gaira et al. 2011; Robbirt et al. 2011; Bertin 2015). If temperature averages from larger areas are used, we recommend testing for climate variability across smaller divisions before using averages across the larger area (Lavoie & Lachance 2006; Molnár et al. 2012; Robbirt et al. 2015).

Validation: herbarium specimens versus field observations

Field data are often combined with herbarium specimen data in analyses, allowing for comparison and sometimes allowing for validation of conclusions based on herbarium data (Primack et al., 2004; Miller-Rushing et al. 2006; Bertin 2015). Primack et al. (2004) used herbarium specimens to find a "historic" flowering mean and then used field data to find a "current" flowering mean (Primack et al., 2004). The historic mean derived from specimens was compared to the current mean from field data in order to determine if there was a statistical difference in mean flowering between the two time periods. Primack et al. (2004) found that the flowering duration of each species was statistically indistinguishable between herbarium and field data and therefore concluded that herbarium and field data were compatible. Studies by Miller-Rushing et al. (2006) and Bertin (2015) also compared historical averages with current averages using herbarium specimens for historical data and field samples for current data. Miller-Rushing et al. (2006) found that results from herbarium specimens alone differed from the combined data by only about one day.

An early study by Borchert, (1996) found that herbarium specimen data produced slightly longer flowering durations than field data, but noted that durations were mostly similar overall. Borchert, (1996) and Rivera & Borchert (2001) found that phenology data from field sites largely overlapped that of herbarium specimens with only slight differences. The negligible differences between herbarium specimen data and field data in these studies helped justify the use of herbarium specimen data to analyze phenology in more recent studies. Nevertheless, several more recent studies specifically compared phenology estimates from field data to those made from herbarium specimens.

Bolmgren & Lonnberg (2005) compared herbarium specimen data directly to field data and found the two data sets were overall highly correlated with only minor differences. For example, herbarium specimens showed a slightly earlier mean flowering for spring-flowering plants than field data, but the difference was not significant (Bolmgren & Lonnberg, 2005). Later studies by Robbirt et al. (2011) and Davis et al. (2015) also primarily focused on testing the validity of using herbarium specimen data. Robbirt et al. (2011) used a principal axis regression analysis to compare herbarium derived peak-flowering dates with field derived peak-flowering dates and found a high degree of correlation. Robbirt et al. (2011) discusses how the high degree of correlation between herbarium and field data also supports the notion that geographically different records will not significantly alter the robustness of either data set. A study by Davis et al. (2015) used a paired t test to compare mean first flowering day between herbarium specimen and field data and found no statistical difference. Davis et al. (2015) concluded that both specimen and field data could be combined and used as a whole.

In order to increase sample sizes, Molnár et al. (2012) added about 2000 field observations to about 5000 herbarium records, resulting in 70% herbarium records for the study. Similarly, Panchen (2012) added about 2000 field records to about 1500 herbarium records, for a total of 43% herbarium records for the study. Searcy (2012) combined herbarium specimen and field data and then split the combined data into two time periods (1863–1935 and 1994–2008). Despite criticisms, herbarium specimen data have been shown to produce similar enough results to field data that herbarium specimen data are now widely accepted in phenological studies.

Conclusions

The use of herbarium specimens for the investigation of flowering phenology has grown considerably during the past decade. As efforts to produce digital copies of specimens and label information have amassed large datasets, new approaches for analyzing responses to climate change are becoming available. Studies using herbarium specimens have become an asset for long-term climate change vulnerability assessment. Studies using herbarium specimens have also begun to analyze the effects of climate change on community composition (Miller-Rushing & Primack 2008, Park 2014) coevolved plant pollinator relationships (Molnár et al. 2012; Robbirt et al. 2014) functional groups (Miller-Rushing & Primack 2008; Panchen et al 2012; Calinger et al. 2013) and phylogenetic relationships (Bolmgren & Lonnberg 2005; Molnár et al. 2012; Primack and Miller-rushing 2012).

While studies using herbarium specimen data to analyze long-term changes have been limited to temperate regions, future studies could use circular statistics to analyze long-term phenological changes in tropical regions (Fisher 1993; Morellato et al. 2010). Circular statistics have been used to analyze flowering phenology in several tropical field studies, but these studies lacked long-term climate change analyses (Novotny & Basset 1998; Morellato et al. 2000; Cruz et al. 2006; Rogerio & Araujo 2010;

Tesfaye et al. 2011; Nadia et al. 2012; Nazareno & dos Reis 2012; Staggemeier et al. 2012; Carvalho & SartorWe2015; Kebede & Isotalo 2016). Although small sample sizes have been used in early studies of phenology, various factors, such as long flowering duration or wide geographic range, may require larger sample sizes. Based on recent validations, mean estimations of peak flowering should be used rather than first flowering because estimates of first flowering from herbarium specimens are more variable. The use of GPS data appears to be the way forward for the advancement of methods in the study of phenology. GPS point data will allow for correspondence with higher resolution temperature data in climatically diverse geographical regions. Studies using herbarium specimen data will continue to help us understand the impact of recent climate change on plant reproductive phenology. Future studies are needed on the importance of phylogenetic signals and plasticity in order to further improve our understanding of adaptation and resilience to climate change, and herbarium specimens offer promise in understanding effects of climate on other aspects of plant phenology such as fruit ripening and spring leaf emergence, the timing of which has important implications for higher trophic levels, which may include rare animals dependent on plant resources.

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Table 1(on next page)

Table1

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Methods of studies; The column "Flw Day ~ Temp" represents studies that conducted a type of regression analysis with flowering day (Flw Day) as the dependent variable and temperature average (Temp) as the independent variable. This follows for columns using a tilde (~) which include the independent variable "Year". The "$\Delta \bar{x}$" symbol represents studies that analyzed a difference in the mean flowering day between Historic and Current time period groups rather than using a type of regression analysis.

species	specimens	specimen per species	authors	year	geographic region	(flw day ~ temp)	(flw day ~ year)	(temp ~ year)
1	117	117	Gaira et al.	2011	Eastern Himalayas		x	x
1	NA	NA	Gaira et al.	2014	Eastern Himalayas	x	x	x
1	192	192	Robbirt et al.	2011	Northern Europe	x		
5	158	32	Rawal et al.	2015	Southern Australia	x	x	
5	540	108	Diskin et al.	2012	Northern Europe	x	x	x
20	371	19	Gallagher et al.	2009	Southern Australia	x	x	x
20	1108	55	Davis et al.	2015	North America	x	x	x
28	1587	57	Panchen et al.	2012	North America	x	x	
36	460	13	Hart et al.	2014	Eastern Himalayas	x		x
>37	372	10	Primack et al.	2004	North America	x	x	x
39	216	6	Lavoie & lachange	2006	North America		x	x
39	5424	139	Molnár et al.	2012	Northern Europe		x	x
41	909	22	Li et al.	2013	Eastern Himalayas	x	x	x
42	142	3	Miller-Rushing et al.	2006	North America	x	x	x
43	NA	NA	Primack & Miller-Rushing	2012	North America		x	x
87	NA	NA	Neil et al.	2010	North America		x	
141	5053	36	Calinger et al.	2013	North America	x		x
186	30,000	161	Bertin	2015	North America		$\Delta \bar{x}$	x
370	1125	3	Searcy	2012	North America		$\Delta \bar{x}$	
1185	5949	5	Park	2012	North America		x	
>1700	19,328	11	Park	2014	North America	x		
24,105	823,033	34	Park & Schwartz	2015	North America	x	x	