


Historical floras reflect broad shifts in flowering phenology in response to a warming climate

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Abstract. Organisms across the globe are experiencing shifts in phenological events as a result of ongoing climate change. Recently, a variety of novel methods have been applied in order to fill gaps in the phenological data set, in which records often have a patchy temporal, spatial, and/or taxonomic resolution. Here, I tested whether changes in flowering phenology could be detected through the months of flowering stated in 11 guides to the Swedish flora published over a period of 220 yr (1798–2018), focussing on 241 plant species (approximately 8% of the Swedish flora), and accounting for the large increase in herbarium records that have occurred over the same period. Despite the coarse, monthly scale of flowering times reported, historical floras and wildflower guides may hold potential to fill temporal and taxonomic gaps in the plant phenological data set. However, factors other than climate may also influence any apparent phenological shifts over time. Here, flowering was found to start earlier (0.49 d/decade), end later (0.71 d/decade), and carry on longer (1.19 d/decade), with flowering length also associated with increases in the regional temperature anomaly during the 20th century (0.11 months/°C). First flowering occurring earlier in 71% of species (14% showing a significant negative trend), 68% of species ceased flowering later (20%), and 80% flowered for longer (29%). Detected phenological shifts also appeared to be related to species' flowering seasonality. Later-flowering species were found to flower later and for longer, while increasing temperatures appeared to drive stronger responses both in flowering onset in early-flowering species and in flowering cessation in later-flowering species. Although potential issues exist regarding the largely unknown ways by which authors have determined flowering times and the coarseness of the data, historical floras may be a useful resource in phenological and climate change research, with the potential to both identify and compare the broad climatic responses of a region's entire flora over long time periods, as well as filling gaps in an otherwise patchy data set.

Key words: climate change; flora; flowering; historical ecology; phenology; spring; time series.

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INTRODUCTION

Together with shifts in species distributions (Chen et al. 2011, Freeman et al. 2018) and the rearrangement of species within communities (Devictor et al. 2012, Auffret and Thomas 2019), shifts in phenological events are one of the main fingerprints of anthropogenic climate change on

the natural world (Parmesan and Yohe 2003, Root et al. 2003, Poloczanska et al. 2013). In response to warming temperatures over the past decades, plant species have been found to exhibit earlier bud-burst, flowering and fruit ripening, and longer growing seasons (Menzel and Fabian 1999, Fitter and Fitter 2002, Menzel et al. 2006, CaraDonna et al. 2014), insects have emerged

earlier (Roy and Sparks 2000, Bartomeus et al. 2011), and birds have shown earlier migration and breeding behavior (Kullberg et al. 2015, McDermott and DeGroot 2016). Shifts in the timings of life-history events have also been linked to species responses to climate change in terms of distributional shifts (Amano et al. 2014, Macgregor et al. 2019).

It is clear that phenological data are a valuable resource for understanding ecological responses to a changing climate at both the species and the community level. However, such data sets are generally quite patchy. Long time series of phenological data are often limited to a single observer at a specific location (Fitter and Fitter 2002, Bolmgren et al. 2013), while efforts to harness community science to increase geographical coverage, such as the USA National Phenology Network (<https://www.usanpn.org/>), the UK's Nature's calendar (<https://naturescalendar.woodlandtrust.org.uk/>), and its Swedish equivalent (<https://www.naturskalender.se>) are constrained to a more recent time period and a specific set of study species and events that are easily recognizable to the wider public. Large phenological data sets containing many species over long time periods therefore contain a mixture of a relatively small number of species that are well-documented in time and space, and a majority of species with comparatively few records and/or locations (Menzel et al. 2006, Amano et al. 2010). In order to fill geographic, temporal, and/or taxonomic gaps in phenological information, there have been a number of recent developments using novel means such as reviewing live television footage (De Frenne et al. 2018) and analyzing internet traffic through species' Wikipedia pages (Mittermeier et al. 2019). Since the turn of this century, there has also been a sharp rise in the use of herbarium and museum specimens to track shifts in phenological events over time (Willis et al. 2017). The increasingly large data sets used in such studies have allowed for generalizations to be made across the whole flora for large areas (Park 2014, Pei et al. 2015), as well as more detailed analyses of change across in groups of focal species (Munson and Long 2017, Daru et al. 2019). Recent advances in machine-learning technology provide further potential for herbaria-based phenology research by automating the processing of specimens (Pearson et al. 2020).

Documentation of regional and national floras has occurred for centuries, especially since the publication of the Linnean system of taxonomy (Linné 1758). Historical records are an important resource in ecology (Vellend et al. 2013), and data extracted from floras are increasingly being used to assess change in species occurrences (MacKenzie et al. 2019), diversity (Nielsen et al. 2019), distributions (Kosanic et al. 2018), and composition in relation to environmental changes such as climate and land use (Tyler et al. 2018, Auffret and Thomas 2019). Many historical floras, along with most modern wildflower guides, also contain information on flowering times (Withering 1776, Liljeblad 1798, Thomé 1905), but it has not yet been investigated whether these flowering times have changed over time.

The long time periods covered, along with national floras and wildflower guides generally being designed to catalogue all or the majority of a region's species, mean that these sources may hold the potential to fill an important taxonomic and temporal gap in plant phenological data. This in turn might contribute toward a more complete view of phenological responses to climate change, as well as facilitating the study of what kinds of species exhibit responses. For example, a strong focus on spring events may affect our understanding of how (and when) many species respond to a warming climate (Gallinat et al. 2015, Parmesan and Hanley 2015), while many species may instead exhibit distributional shifts rather than phenological change (Amano et al. 2014). However, such tomes are not designed to document standardized phenological information, and in addition to the broad, monthly scale of the flowering times given, there may be factors that could confound the interpretation of any temporal changes in flowering phenology. Herbarium samples are a likely source of information for authors, especially in the past when long-distance travel was slow and it would have been otherwise difficult to gather information about flowering times across regions and countries. As cumulative numbers of herbarium specimens have increased over time, this larger pool of source material would reveal more intraspecific variation in flowering (i.e., examples of earlier and later flowering) that could result in apparent shifts in phenology in later floras. In countries or regions with strong and/or long

climatic gradients, an increase in the botanical exploration of areas at the ends of such gradients could also result in changes in flowering onset and cessation over time that is not related to climate change (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008). It is therefore important to identify and account for such potential biases and limitations when developing novel methods of using historical data for new purposes (Meineke et al. 2018, Panchen et al. 2019).

In this study, I extracted the flowering times specified for 241 plant species from a range of historical Swedish floras and wildflower plant-identification guides covering a period of 220 yr. Considering potentially confounding effects, I wanted to find out: (1) Are previous findings of earlier flowering start, later cessation, and an extended flowering period reflected in changes in the broad, monthly flowering times given in floras and wildflower guides over time? (2) Do apparent phenological changes relate to year of publication and to regional temperature

(change)? (3) Do interspecific differences in apparent phenological responses over time differ according to when in the season species usually flower?

MATERIALS AND METHODS

Sources and species

I found 20 scientific floras or wildflower guides (hereafter floras), published from 1745 until 2018, covering Sweden only, or Sweden together with other Nordic countries (Table 1). Of these, 11 were found to be suitable for tracking phenological change over time, in that they contained the majority of all plant species known to Sweden at the time of publication and indicated the month or months of flowering for most species. The remaining books either did not give flowering times, or only gave one month, meaning that it was uncertain whether the month given was the start or peak flowering, or even if this was consistent across species.

Table 1. Swedish floras and wildflower guides.

Year	Name	Focal region	Reference	Omission
1745	Flora Suecica	Sweden	Linne (1745)	A
1798	Utkast till Svensk flora	Sweden	Liljeblad (1798)	
1820	Handbok i Skandinaviens flora	Scandinavia	Hartman (1820)	
1867	Svenska växternas naturhistoria	Sweden	Nyman (1867)	
1883	Svensk flora [för skolor]	Sweden	Krok and Almquist (1883)	A
1901	Sveriges Flora	Sweden	Neuman and Ahlfvengren (1901)	
1905	Bilder ur Nordens Flora	Nordic	Lindman (1905)	A
1918	Svensk fanerogamflora	Sweden	Lindman (1918)	
1922	Skandinaviens flora	Scandinavia	Holmberg (1922)	C
1944	Svenska Växter i text och bild	Sweden	Ursing (1944)	
1950	Floran i färg	Sweden	Bolin and von Post (1950)	
1953	Nordisk kärlväxtflora	Nordic	Hylander (1953)	A
1958	Vår svenska flora i färg	Sweden	Hultén and Anthon (1958)	
1963	Norsk og Svensk flora	Sweden & Norway	Lid (1963)	B
1965	Vår flora i färg	Sweden	Elvers and Anthon (1965)	A
1992	Den Nordiska Floran	Nordic	Mossberg et al. (1992)	
1992	Nordens flora	Nordic	Nylén (1992)	B
1997	Den virtuella floran (website)	Sweden	Anderberg and Anderberg (http://linnaeus.nrm.se/flora/)	
2000	Flora Nordica	Nordic	Jonsell et al. (2004)	C
2018	Nordens flora	Nordic	Mossberg and Stenberg (2018)	

Notes: Scandinavia covers Denmark, Sweden, Norway, and Finland, while the Nordic region also includes Iceland and the Faroe Islands. First editions were sourced in almost all cases; Liljeblad (1798) was first published in 1792, while Bolin and von Post (1950) was first published earlier in 1950 and only contains changes to the illustrations. Rows in boldface indicate those floras used in the analysis. Reasons for omission: A, no flowering times given; B, only one month given for flowering; C, flora was never/has not been completed.

Two hundred and forty-one species were analyzed in this study, which is approximately 8% of the total number of plant species in Sweden. Forty-two of these were phenology species, for which the species' Swedish or binomial scientific name indicates that it is related to flowering phenology (e.g., *Convallaria majalis*, *Scorzoneroides autumnalis*, *Geranium sylvaticum*—Swedish: *Midsommarblomster*), or are species for which the public is encouraged to report data for the Swedish phenology network (including *Anemone nemorosa*, *Tussilago farfara*, *Betula pendula*), many of which correspond to the species that are well-documented in large-scale phenology data sets (Amano et al. 2010). Next, 200 species (arbitrarily chosen to ensure robust results given limited time) were randomly selected using the function `sample` in the statistical environment R 3.4 (R Development Core Team 2018), from the pool of species that are present in at least 5% of 5 × 5 km grid squares in at least 5 of the 18 Swedish provinces (of total 29) for which province-level plant atlas data are available (Appendix S1: Fig. S1, Auffret and Thomas 2019). This was to ensure that these random species were relatively common and widespread and would therefore be more likely to be present in as many national floras as possible. For each species in each flora, the month of flowering start and flowering cessation were recorded, and flowering length was deduced by calculating (month of flowering cessation – month of flowering start) + 1. For example, a flowering time stated as May–June would have a two-month flowering time. When a species could not be found in a particular flora, synonyms of both Swedish and binomial scientific names were used to search for the species under another name. One random species (*Taraxacum sect. Borea*) was not presented in any flora, resulting in the 241 analyzed species.

Accounting for confounding methodological effects

None of the floras clearly stated where the raw information used to determine the flowering times were collected. One flora (Neuman and Ahlfvengren 1901) stated that flowering times generally followed that of a previous flora (Hartman 1820), although the more recent flora contained 41 additional species (of the 241 analyzed species), and identical flowering times are only apparent for 34% of the species documented in

both floras. Additionally, Mossberg and Stenberg (2018) share two authors with an earlier flora (Mossberg et al. 1992), in which identical flowering times were given for 91–94% of species depending on metric (start, cessation, or length), with differences in both directions (i.e., earlier/later, longer/shorter) for the remaining species. Both the above examples had another flora published in between those with potential duplication in flowering times, which should help to reduce bias in detecting any phenological shifts.

To quantify the potential for confounding factors in resulting from an increasing pool of source material available to authors of floras, I collated two additional sets of data. First, I searched the Swedish national library's online catalogue (<http://libris.kb.se/>) to find the publication date for the earliest provincial flora (i.e., book that documents the flora of a province) from Sweden's provinces (Appendix S1: Table S1 and Fig. S1). I then used the Swedish Meteorological and Hydrological Institute's open-access gridded climate data (<https://www.smhi.se/data>) to calculate mean July temperatures for each of the 4-km grid squares for the 1961–1990 reference period. For each province, I then extracted the maximum and minimum values to give a broad estimation of where they lie on the country's climate gradient. This revealed that by the time of the publication of the second national flora with phenological information (1820), the full climatic range of Sweden had already been documented in the form of a provincial flora. Therefore, the geographic extent of botanical exploration across Sweden's climate gradient is unlikely to be a confounding factor.

To investigate the potential effect of the increase in volume of herbarium records in driving apparent shifts in flowering phenology, I downloaded the entire digitized herbarium record of Sweden, consisting of more than 1.65 million records (<http://herbarium.emg.umu.se/>). Relatively few of the digitized records include scans of the pressed plants themselves, so it is not known to what extent collected specimens are in flower. The digitization of the herbarium records is ongoing at the six regional herbaria that contribute to the national collection, with 46% of records digitized so far. Although the digitized catalogue is far from complete, digitization has not occurred in any strong taxonomic or

chronological order across herbaria. Plotting the fluctuations in collections over time (Appendix S1: Fig. S2), the patterns broadly follow that of other herbaria around the world, with a strong increase in collections from the late 19th century, decreasing in the mid-late 20th century, and another resurgence in recent decades (Daru et al. 2018, Meineke et al. 2018, Panchen et al. 2019). Therefore, I assume that the digitized records generally reflect the increase of herbarium records available to the authors of floras over time. As above, the database included records from the warmest and coolest provinces prior to 1820. I calculated the cumulative increase in the number of records over time, both in terms of the total number of records, and for each of the 241 study species individually. Species names were harmonized according to the Swedish taxonomic database (<http://www.dyntaxa.se>). This information was then included in the models below.

Data analysis

To assess change in flowering phenology over time as a whole, I created linear mixed-effects models with Gaussian-error distributions for each of (1) month of flowering start, (2) month of flowering cessation, and (3) flowering duration (in months), with year of publication of the flora as a predictor variable. To account for the potential confounding effect of increases in herbarium samples, this was added as an additional fixed predictor variable. However, due to the strong (97%) correlation between year and herbarium records, I adopted the sequential regression approach (Graham 2003, Dormann et al. 2013). First, a Gaussian-error linear model (function: *lm*) regressed cumulative herbarium records against year of publication of the studied floras, and the residuals of that model were added as a fixed predictor in the main mixed model. Species and flora were included as non-nested random effects. The structure of each of the three models in R's *lme4* package (function: *lmer*; Bates et al. 2014) was thus:

$$\text{Month} \sim \text{Year} \mid \text{Residual Herbarium} \\ \mid (1 \mid \text{Flora}) \mid (1 \mid \text{Species})$$

To assess phenological change in relation to climate, I used the CRUTEM4 database (Jones et al. 2012), which contains global monthly

temperature anomalies from the 1961 to 1990 reference period at a 5-degree resolution from 1850 to present. As these were the best historical climate data that were available, I could therefore only include floras from Neuman and Ahlfven-gren (1901) and onward for this part of the analysis. For each flora, I approximated the climate in the time leading up to publication by averaging the annual temperature anomaly from CRUTEM4 across the nine 5-degree grid squares covering Sweden for the 30 yr up to and including the year of the flora's publication (e.g., climate for the flora from 1901 was characterized by the average climatic anomaly 1872–1901). I then built linear mixed-effects models with the same structure as above, replacing year of publication with the calculated temperature anomaly, and running the sequential regression approach again for the subset of floras being studied. Both sets of models (year and temperature) were built using the entire 241-species data set, as well as with phenology and random subsets of species separately, to assess any differences in strength or direction of responses among groups. For all models, bootstrapped 95% confidence intervals were calculated, and conditional and marginal R^2 values were calculated (method: Nakagawa and Schiel-zeth 2013; R-implementation: Lüdecke et al. 2021).

For species-level responses, I included only species that were listed in at least five floras, which gives a minimum possible time period of 57 yr. This resulted in 221 species (204 species for the shorter time period possible for temperature analysis). For each species, I created Gaussian-error linear models (function: *lm*) where month of flowering start, cessation, and duration were response variables, and year of publication or temperature as a predictor variable, along with the residual effect of herbarium records calculated as above, separately for each species. To explore how different types of species might be exhibiting phenological shifts over time, the slopes of the species-level linear models for both year and temperature models were used as the response variable in a set of Gaussian linear models (function: *lm*) with flowering season as a predictor variable (1 = early, flowering starts in May or earlier, 64 species; 2 = mid, flowering starts June or July, 170 species; 3 = late, flowering starts in August or later, seven species).

Information for this variable is taken from the first flora in which each species is listed. Although not ideal, using the earliest possible flora means that flowering seasonality is extracted from a flora before any apparent phenological shift has occurred, while 86% of analyzed species first appeared in one of the first two floras (1798 and 1820) for the analysis over time, while 98% of species in the temperature analysis were present in the earliest flora (1901). In both the case of the whole data set and the species-specific responses, model estimates and confidence intervals were converted from months per year to days per decade. This is both to aid interpretation by the reader by avoiding low numbers with several decimal places that characterize the former and to aid comparison with other studies which usually use the latter.

RESULTS

Considering all species together, the flowering times stated in Swedish floras have gradually become earlier over time, in line with a warming climate (Fig. 1, Appendix S1: Table S2). Based on

the parameter estimate of the linear mixed-effects model, the shift in start of flowering occurred at a rate of 0.49 d per decade (95% confidence intervals 0.31–0.65), or more than one and a half weeks across the 220-yr time period. Stated flowering times in the floras became later on average over time, 0.71 d per decade across the 220-yr period (95% CI 0.51–0.85), and the total duration of flowering increased by 3.75 weeks (1.19 d per decade, 95% CI 0.85–1.51). Flowering times also started earlier with increasing annual temperatures since 1901, with flowering start occurring 0.11 months (or 3.39 d, calculated as parameter estimate months per $^{\circ}\text{C} \times 30.4$) earlier per degree Celsius increase in the temperature anomaly (95% CI 0.015–0.2). Models did not indicate a relationship for flowering cessation or duration with increasing temperatures. Model outputs for phenology and random subsets of species followed the same trends as each other and the data set as a whole (Appendix S1: Table S2).

Species-level analysis of flora-derived flowering phenology indicated that—consistent with

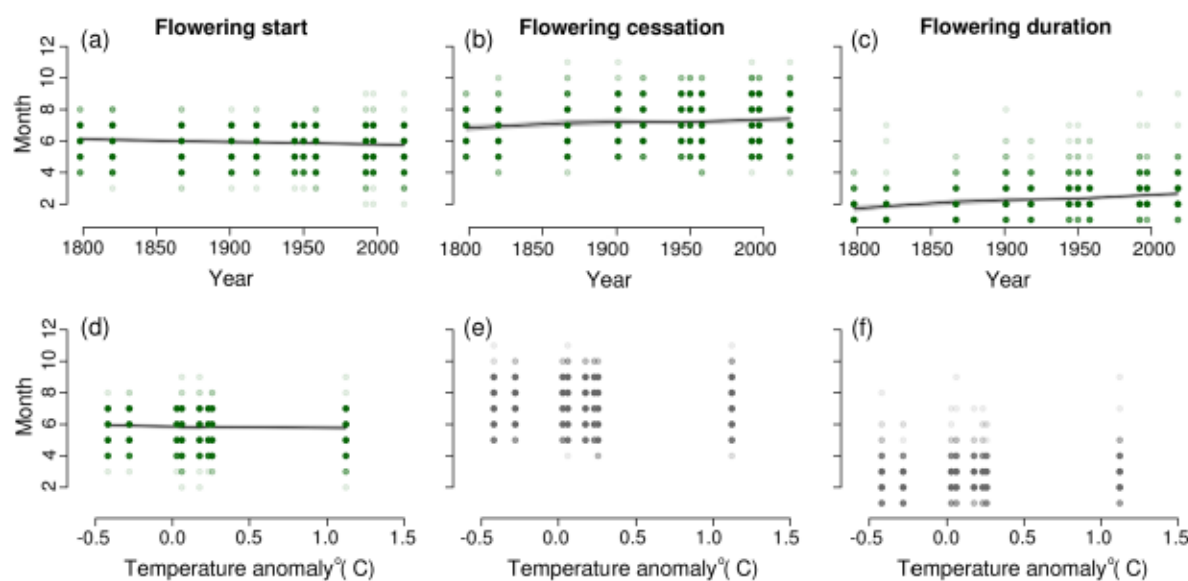


Fig. 1. Phenological change in 241 plant species over 220 yr assessed from wildflower guides and scientific floras, correcting for the influence of increasing herbarium records over time. Points are months of flowering start, cessation, and length (cessation minus start plus one) over time. Shaded areas show 95% bootstrapped confidence intervals around trend lines from linear mixed models, for those models where confidence intervals did not cross zero. Panels (a–c) plot flowering phenology against year of publication (1798–2018), while panels (d–f) plot flowering against Sweden's temperature anomaly from the 30 yr preceding publication of each book (1901–2018 only due to available temperature data).

the all-species model—the majority of species exhibited earlier flowering start, later cessation of flowering, and a longer flowering season over time, according to the flowering times stated in the studied floras (Figs. 2, 3). Of the 222 species for which analysis was possible, more than two-thirds of species (158, 71%) were found to start flowering earlier over time, as indicated by a negative parameter estimate from the linear model. Of these, 30 (14%) were shown to be significant in the expected direction (parameter estimate P -value <0.05). Flowering ceased later in 68% of species (20% significantly) and lasted longer in 80% of species (29% significantly). The majority of all significant trends were in the expected direction, with 83% of significant trends in flowering start being negative, and 88% and 97% of significant trends being positive for flowering cessation and duration, respectively. A significant shift of at least one response (start, cessation, duration) in the expected direction was exhibited in 39% of species.

Species-level models did not show such clear directional relationships to temperature anomalies since 1901, with around half of species showing earlier flowering start, later cessation, and a longer flowering duration, and only a handful significantly. There was, however, a significant relationship between changes in stated flowering times and flowering seasonality (Table 2). Species that flower later in the season had greater delays in flowering cessation over time and with increases in temperature, compared to earlier-flowering species (positive relationship between species-level parameter estimate and flowering seasonality). Later-flowering species were also found to have a longer flowering duration over time, while earlier-flowering species flowered earlier in response to increasing temperatures (Table 2).

DISCUSSION

This study indicates that it may be possible to use historical scientific floras and wildflower guides to track shifts in flowering phenology in a changing climate. Flowering times stated in wildflower guides were found to start earlier over time, as well showing an association with the climate warming that has occurred over the same period. This broad, national-scale directional shift is consistent with previously published work

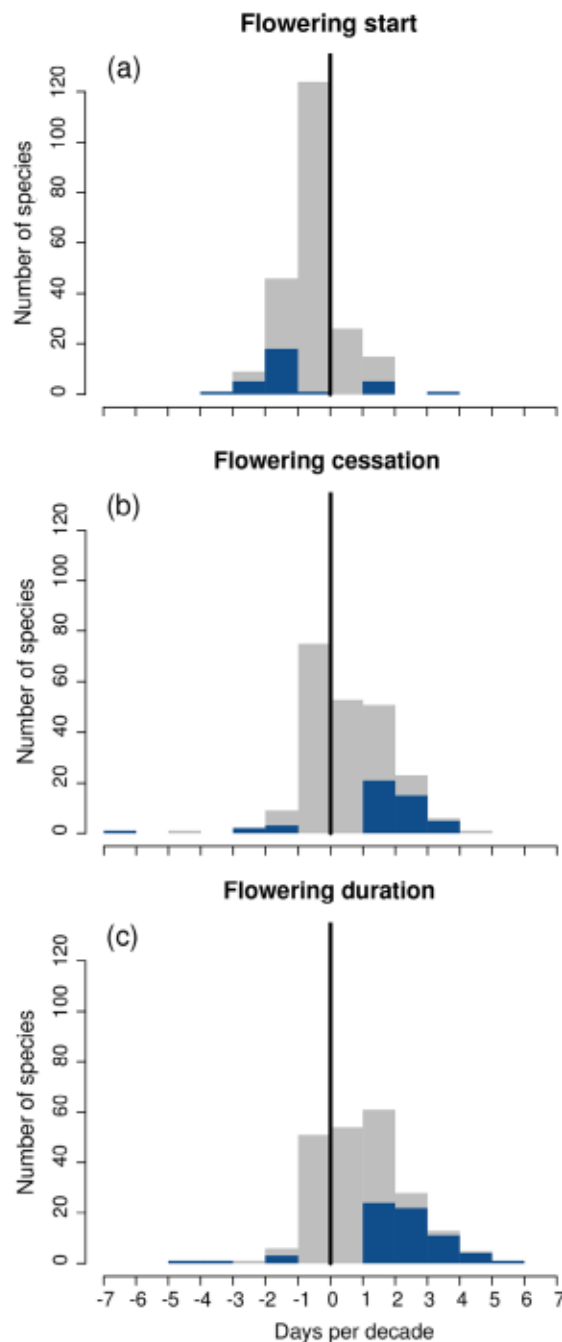


Fig. 2. Phenological shifts over time for 222 species as assessed from scientific floras and wildflower guides, calculated from the slope of linear models assessing change in flowering against year of publication, where (a) shows flowering start, (b) shows flowering cessation and (c) shows flowering duration. Gray bars show all species, while blue bars indicate those where linear models indicated a significant ($P < 0.05$) association between flowering and year.

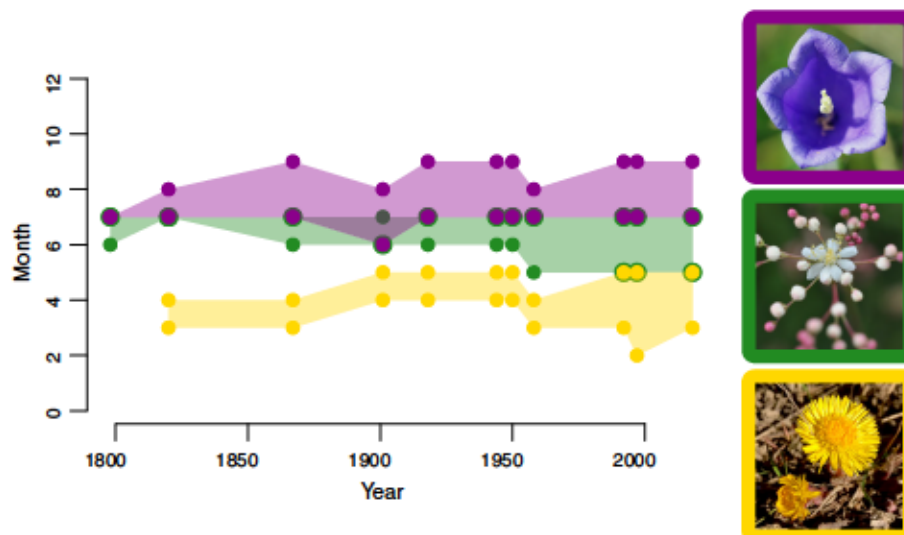


Fig. 3. Examples of species-level phenological shifts over time as extracted from national floras, where points show months of flowering start and cessation and polygons show flowering period. *Campanula rotundifolia* (upper, purple) is a mid-season flowering, randomly selected species that showed significantly later-flowering cessation and increasing flowering duration over time; *Filipendula vulgaris* (middle, green) is a mid-season randomly selected species that was shown to flower earlier and for longer; *Tussilago farfara* (lower, yellow) is an early-flowering phenology species with later-flowering cessation and longer flowering duration over time.

Table 2. Effect of flowering seasonality (early, mid, or late flowering, coded on an ordinal scale 1–3) on species-level phenological shifts over time (year; 1798–2018) and in response to climate change (temperature; 1901–2018).

Variable	Estimate	SE	<i>t</i>	<i>P</i>	Model <i>R</i> ²
	Year				
Flowering start	−0.0002	0.00041	−0.48	0.63	0.001
Flowering cessation	0.0016	0.00057	2.81	0.0055	0.035
Flowering duration	0.0018	0.00062	2.92	0.0039	0.037
	Temperature				
Flowering start	0.16	0.055	2.98	0.0032	0.042
Flowering cessation	0.3	0.065	4.61	<0.001	0.0394
Flowering duration	0.13	0.076	1.77	0.079	0.015

Notes: Each row represents a different general linear model, in which the response variable is the species-level shift over time or change in temperature and the predictor variable is flowering seasonality. Estimate is the change in phenological shift (months per year or °C) that occurs when moving across categories of flowering seasonality from early to late flowering. Bold rows indicate models where the predictor variable is significant ($P < 0.05$).

from across the globe based on exact observations of first flowering at the local level (Parmesan and Yohe 2003, Menzel et al. 2006, Bolmgren et al. 2013), despite the coarse, 12-point monthly scale of the input data. The method also supported a generally less-studied fingerprint of climate change on plant phenology, that of later-flowering cessation, which along with changes in fruiting and leaf senescence can show how phenological shifts are not only confined to the spring (Menzel and Fabian 1999, CaraDonna et al. 2014, Gallinat et al. 2015, Pearse et al. 2017).

Although the direction of phenological shifts matched expectations in relation to a changing climate and existing research, rates of change were somewhat lower than those previously reported. Here, onset of flowering was estimated to be approximately half a day per decade earlier, considering all 241 species together. Values from other large syntheses include an earlier onset of spring in Europe by 2.5 d per decade (Menzel et al. 2006) and 2.3 d per decade globally (Parmesan and Yohe 2003), while a plant community at a single locale in the UK showed that flowering onset was on average 4.5 d earlier per decade during the

second half of the 20th century (Fitter and Fitter 2002). The most likely reason for this discrepancy is the coarse scale of the input data. Because the temporal resolution of the flowering times is one month, shifts in flowering phenology of up to four weeks are required for the shift to be detectable. This would in many cases lower the rates of some shifts and leaving many undetected, resulting in relatively small changes over time averaged across species. An additional reason for the relatively slow shifts exhibited over time could be the long time period of the data set, meaning that slower changes in the early 19th century in both climate (Jones et al. 2012) and plant phenological response (Amano et al. 2010) result in a relatively low rate of change over the 220-yr period examined. The rate of phenological change derived from floras from the 20th century onward in terms of flowering start as a function of temperature was more closely matched to existing observational records. The rate of 3.39 d earlier flowering per °C for all species, and 4.77 d per °C for the phenology subset of species is within the range of published estimates using different methods to track phenological change at the regional, national, and international scale (Amano et al. 2010, Wolkovich et al. 2012, Calinger et al. 2013, Thackeray et al. 2016).

The analysis at the species level similarly showed a general trend toward earlier flowering start, later cessation of flowering, and a longer flowering duration (Fig. 2). For the same likely reasons as above, the coarse input data meant that rates of change were generally lower than previously published analyses, and the fractions of species showing significant shifts were relatively low. While the 71% of species flowering earlier is generally comparable to previous analyses, the 14% of species exhibiting significant shifts was lower than the 30% or more that is often reported (Parmesan and Hanley 2015, Menzel et al. 2020), but comparable to the 16% found by Fitter and Fitter (2002). Nonetheless, 39% of species showed an expected directional shift in flowering, and the 83% of significant trends in flowering start over time following the direction expected by regional climate change was relatively high (Rosenzweig et al. 2008, Parmesan and Hanley 2015).

In addition to the coarse, monthly resolution of the input data that may have affected or prevented the detectability of trends in many species, the results showed that there are other factors that

need to be considered with using flora data to analyze phenological change. The (intuitively) high correlation between cumulative number of herbarium samples and year of flora publication means that the author of each flora had an increasingly large amount of material at their disposal, exhibiting a potentially larger variation in flowering. Even though the phenological signal of change over time was still evident when controlling for this increase, not considering such potentially confounding factors could result in an exaggeration of the magnitude of phenological shifts over time, or any relationship to increasing temperatures. It is also important to note that herbarium records themselves can be biased in terms of location and time of collection, and the identity of species and collector (Daru et al. 2018, Panchen et al. 2019). Although this study did not directly interpret flowering phenology from herbarium specimens, an indirect effect of these biases on those who compiled the floras that were studied cannot be discounted. The potential issue of increased botanical exploration confounding apparent phenological shifts (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008) did not appear to be relevant in the current study. Sweden's climate gradient was documented by a regional flora as well as with herbarium records an early stage, but could affect results in other countries or regions without such a long history of (documented) botanical exploration. Ideally, floras and wildflower guides would contain information about how flowering times were determined, though this is unfortunately rarely the case. Doing so would allow for a more accurate quantification and consideration of any confounding factors affecting apparent phenological shifts.

This study shows that if such potentially confounding factors can be confidently accounted for, historical floras hold some potential to fill large taxonomic gaps in the global phenological data set. In particular, it means that the majority of a nation or region's flora can be examined for apparent phenological changes. Historical floras can also stretch back long time periods to potentially fill gaps in the knowledge of long-term phenological shifts (Withering 1776, Liljeblad 1798, Thomé 1905). Indeed, the broad, monthly scale of the flowering times given in these sources means that long time periods are necessary in order to detect relatively small shifts, and

there are likely many species in this study for which real phenological shifts went undetected. It also means that future work will need to develop statistical corrections for comparing rates of phenological change from national floras to those from single populations or sites and with other sources of data (Pearse et al. 2017).

Going forward, the main potential for this method probably lies in comparing varying rates of phenological change across a large number of species. Here, I showed that seasonality in flowering times was related to differing magnitudes of shifts over time and in response to increasing temperatures. Future work could improve our understanding how phenological shifts relate to functional traits and habitat associations, as well as examining relationships or trade-offs of phenological shifts with other responses to climate, such as range expansion or retraction (Parmesan and Hanley 2015, Bell et al. 2019, Macgregor et al. 2019).

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DATA AVAILABILITY

Flowering times from the historical floras are deposited to the Swedish National Data Service: <http://doi.org/10.5878/m49-wx18>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3683/full>