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Hiding in plain sight: combining field-naturalist observations and herbarium records to reveal phenological change

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Abstract

As the climate warms, northern ecosystems are experiencing warmer winters and seasonal climatic shifts. Vascular plants are expected to respond to climate change by adjusting flowering or seeding periods. To determine how a native mixed-wood boreal floral assemblage has responded to warming temperatures over the 20th century, we collated historical observations made by field-naturalists as well as voucher data from the Thunder Bay region of Ontario, Canada. Combining these datasets, we performed regression analyses on 11 species of spring-flowering vascular plants to evaluate temporal trends and used spring cumulative growing degree day ($sGDD_0$) to determine the influence of climate on flowering times. Four species showed consistent positive temporal trends (i.e., flowered later with time), while four species (three of which also demonstrated temporal trends) showed negative trends with $sGDD_0$ (i.e., flowered earlier with an increased number of degree days above 0°C). The unexpected observation of later flowering times but predicted observation of earlier blooming with increased $sGDD_0$ indicates that the inclusion of climate metrics may be necessary to determine the response of native vascular plants to the onset of changes in their environment. These observations were not statistically significant when field-naturalist or herbarium voucher data were analyzed separately, possibly due to low statistical power. Combining data from both sources, however, revealed common responses to climate warming among species within an ecoregion.

Key words: Climate change; phenology; Ontario; boreal mixed woods; angiosperms

Introduction

Anthropogenic activity is unequivocally altering global climate, with significant and observable effects on ecosystems (Hoegh-Guldberg and Bruno 2010; Woodward *et al*. 2010; Burrell *et al*. 2020). The earth's climate has increased 0.74°C on average over the last 100 years, and the Intergovernmental Panel on Climate Change (IPCC) projects a continued rise of 0.2°C in each following decade (Trenberth *et al*. 2007; IPCC 2018). Rising global temperatures have many environmental side effects, among them the melting of polar ice caps, increased drought, and unpredictable extremes for regular climatic events such as El Niño and La Niña (Fischer and Knutti 2015; Stott 2016; Teng *et al.* 2016; Jia *et al*. 2019). These abiotic climatic changes affect organisms living in these environments in ways that are acute, long-term, or both (Rodenhouse *et al*. 2009; Last *et al*. 2011; Pecl *et al*. 2017). Perhaps the most likely to be affected, especially in northern latitudes, are organisms reliant on temperature-specific cues to time their lifecycles.

Climate-change-related temperature increases are most pronounced in temperate, Antarctic, and Arctic regions, with the most dramatic changes expressed as increases in mean winter temperature and a contraction of the length of winter (e.g., Beaumont *et al.* 2011; Guzzo *et al.* 2017). These climatic changes have the potential to alter a variety of seasonally dependent phenotypes in plants, animals, and other organisms, such as timing of migration, reproduction, food acquisition, and frequency of reproductive bouts (Both *et al*. 2010; Bussière *et al*. 2015; Goulson *et al*. 2015; Green 2017; Tao *et al*. 2018). Decoupling or mis-timing of these cues can result in a variety of deleterious

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outcomes including reproductive failure (Williams *et al*. 2014; Tao *et al*. 2018), changes in energetic coupling (Guzzo *et al*. 2017), or mismatches in responses of different trophic levels to different environmental cues leading to reduced energy transfer and decreased survival (e.g., Winder and Schindler 2004). An adaptive response to these outcomes is to migrate to cooler latitudes, which may have an effect on the pre-existing flora and fauna of that region (Schmidt *et al.* 2012). Species that are reliant on environmental cues are thus dependent on their ability to adapt to new climatic norms, respond by phenotypic plasticity, or their ability to migrate to new habitats to survive.

Phenology, the study of the seasonal lifecycle of organisms, will play a role in determining how these organisms adapt to a warming environment. Phenological cues can either be independent of climate (e.g., number of daylight hours) or climate dependent (e.g., soil temperature, type or amount of precipitation). While equatorial ecosystems often rely on predictable changes in the moisture regime with largely stable temperatures (Borchert 1996; Marques *et al.* 2004), temperate organisms are often reliant on the onset of spring to initiate their lifecycles, signalled by snowmelt, increased daylight hours, and warmer temperatures. The ability to capitalize on these conditions is often critical to an organism's ability to survive and produce offspring.

In plants, climatic challenges related to phenology may be greater than in animals (Cleland *et al*. 2007). While shifts in elevational or latitudinal distributions are predicted for both animals and plants to maintain an optimal thermal environment, the reliance of vascular plants on seeding success for this distributional shift (rather than active individual movement) is an intrinsically slower process; extirpations of local populations have been observed in several species as individual plant populations fail to adapt to new climatic conditions (Wiens 2016). Previous studies of vascular plant phenology have shown that consecutive warmer springs result in earlier flowering (Fitter *et al*. 1995; Miller-Rushing and Primack 2008; Beaubien and Hamann 2011a; Panchen *et al*. 2012), but patterns are not consistent across taxa, variably showing earlier, delayed, or neutral responses to increasingly warm springs (Cook *et al*. 2012; Ziello *et al*., 2012; Hart *et al*. 2014; Hufft *et al*. 2018; Panchen and Gorelick 2017). Of the temperate vascular plants previously studied, those that bloom in early spring often show an increased sensitivity to mild winters and early-arriving springs, blooming days earlier than their late spring or summer counterparts (Lavoie and Lachance 2006; Miller-Rushing and Primack 2008; Willis *et al*. 2010; Ellwood *et al*. 2013).

To determine if and how assemblages of plants are responding to climate change, long-term datasets are critical. Museums hold a wealth of information that can be used to address phenology; vouchers of botanical specimens provide a record of location, range, and flowering stage. Collected over many years, they also provide a valuable account of plant phenology and occurrence through both time and space. However, herbarium collections can show biases, including curator bias towards particular taxa or a tendency for vouchers to be collected from only accessible locations (Willis *et al*. 2017). In spite of these biases, herbarium vouchers often form the basis of historical phenological studies in plants (Everill *et al*. 2014; Panchen *et al*. 2014, 2019; Park and Schwartz 2015; Riera *et al*. 2015; Daru *et al*. 2018; Park *et al*. 2019), which can also be coupled with short-term citizen science observations or field studies (Morisette *et al.* 2009; Spellman and Mulder 2016). Along these lines, amateur field-naturalist (hereafter simply field-naturalist) records can provide another source of information that remains largely unmined for potentially informative phenological data (Miller-Rushing *et al*. 2012).

Field-naturalist observations have been made for centuries, often with a goal of determining timing and location of agricultural harvest, but also with an interest in observing the natural world. Perhaps the most famous North American example is Henry David Thoreau's recording of natural events in and around Walden Pond, in Concord, Massachusetts (Miller-Rushing and Primack 2008). Detailed individual accounts like Thoreau's are the exception, but in the 20th century we see the rise of organized groups of field-naturalists who often recorded local natural events over time. This practice continues in the form of citizen science projects including the USA Phenology Network (https://www.usanpn.org/usa-national-phenology-network), and the Canada PlantWatch program (https://www.naturewatch.ca/plantwatch/).

Northwestern Ontario, located on edge of the boreal Canadian Shield, presents a unique opportunity to determine how phenology is changing in a previously understudied part of Canada, with records of vascular plant phenology available through written records kept by the Thunder Bay Field Naturalists (TBFN; https://tbfn.net), as well as in the holdings of the Claude Garton Herbarium (LKHD) at Lakehead University. In Canada, studies that use historical or herbarium data to examine changes in phenology are growing in number. Several have been conducted in the last 30 years that have examined climatic effects on seasonality of herbaceous plants in Quebec, Alberta, and regions of the high Arctic (Lavoie and Lachance 2006; Houle 2007; Beaubien and Hamann 2011a; Kharouba *et al*. 2014; Panchen and Gorelick

2017; Prevéy *et al.* 2017; Park *et al.* 2019). To date, no study of this nature has been conducted in northwestern Ontario and we believe this to be the first study to use long-term phenological records kept by the TBFN.

The goal of our study was to determine climate-related phenological changes in early-flowering vascular plants from several common plant families in northwestern Ontario. As no work of this nature has been done in the region, we chose a variety of angiosperm taxa well represented in both herbarium and field-naturalist datasets from different families. We hypothesize that the earliest blooming species will be the most sensitive to changes in climate and will flower significantly earlier through time.

Methods

Study area

Northwestern Ontario is located on the Canadian Shield and is bounded by the U.S. Minnesota border and the Great Lakes to the south, Hudson's Bay to the north, Manitoba to the west, and Timmins, Ontario, to the east (Figure 1). The Thunder Bay region, where many of the collections or observations included here were made, encompasses ~103 722 km^2 and is composed of several large tracts of Canadian Crown land that transitions from southern mixed-wood forests into boreal forest. These forests are dominated by birch (*Betula* spp.), poplar (*Populus* spp.), spruce (*Picea* spp.), pine (*Pinus* spp.), and various shrubs (alder, willow [*Salix*]). The understorey is largely herbaceous, with 119 families of vascular plants present (TBFN 2015).

Climate data

Historical daily average temperatures were obtained from Environment and Climate Change Canada (ECCC; Government of Canada 2019) from five weather stations within a 25 km radius of the city of Thunder Bay (Figure 1), the area in which 70% of the herbarium vouchers were collected ($n = 271/399$) and 100% of the naturalist observations were made (see below). Recorded temperatures in this area span almost 140 years, from 1878 to 2017. Where multiple

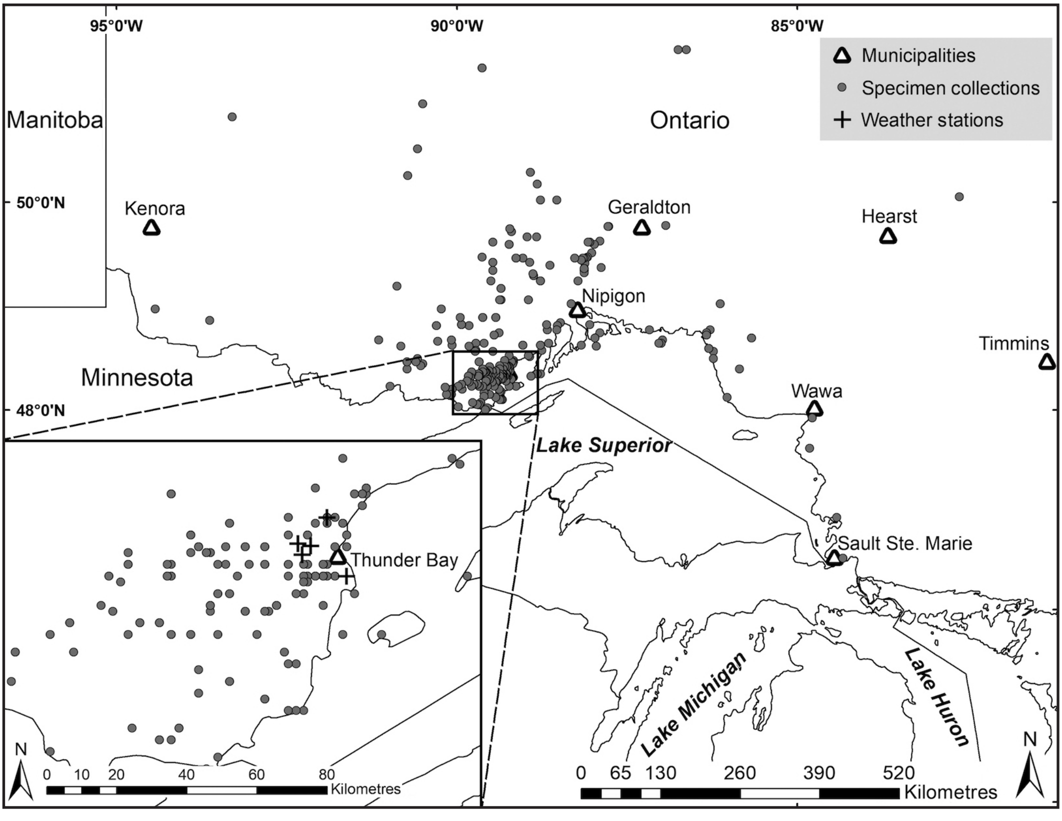

FIGURE 1. Map showing Thunder Bay region with collection localities of included vouchers. Of the 399 vouchers from the Claude Garton Herbarium (LKHD) included, 29 lacked GPS co-ordinates and are not shown here. Weather stations are denoted with a cross.

daily temperatures from several stations were recorded, we used the average value of all stations with useable data (i.e., those not flagged as erroneous by ECCC). Although the first and last phenological observations in our dataset occurred in 1932 and 2006, respectively, we included all available climatic data in this region to attempt to capture possible changes in the long-term climate record. Mean annual temperature was estimated as the 365-day average of daily means.

All five stations were used to generate a complete dataset with daily average temperatures and very few stations had periods of overlap with regard to data availability. As most observations were concentrated in the Thunder Bay region, we used mean daily temperatures from this area as indicative of climate in the region generally. Given the broad temporal (e.g., annual averages) scale of our analysis, minor regional deviations in microclimate across our study region were assumed to be negligible. To validate this assumption, we compared mean annual temperatures between our dataset and one at the IISD Experimental Lakes Area, 600 km west of Thunder Bay (date range of comparison 1970 to 2013). The relationship between estimates from both stations (forced through the origin) was not significantly different from 1:1 ($t_{43} = 1.43$, $P = 0.07$), suggesting that the Thunder Bay weather stations were representative of the region generally.

Because many early spring-flowering plants are thought to rely on temperature cues to begin their phenological cycle, we use cumulative growing degree days (GDD) greater than 0°C over the spring period ($sGDD_0$ hereafter). Cumulative GDD are used to measure the ambient air temperature above a threshold temperature from germination or reactivation in perennial species to a given life stage, here peak flowering of spring plants. Although GDD is a measure of ambient air temperature, it has been used as a metric of phenology and growth patterns to determine the importance of climate in dictating the life history of many taxa, including fishes, insects, and plants (Neuheimer and Taggart 2007; Mulder *et al*. 2017).

As minimum growth temperatures for our species are not known, we set our base temperature at 0°C, the minimum temperature at which most C3 plants are able to grow (Dürr *et al*. 2015). A lower temperature threshold of 0°C has been used elsewhere in plant growth investigations that include early flowering plants (Abrami 1972). Further, it has been demonstrated that root development in cold-adapted species (including species of Ranunculaceae and Asteraceae, well represented in our study; Table 1) begins at between 0 and 1°C (Nagelmüller *et al*. 2017). As all the plants under investigation here are early ephemerals adapted to begin growth in cold environments shortly after snow melt, the common reference point of 0°C was assumed to be suitable across all species, and also provides comparable estimates across species.

We defined "spring" as the period from 1 February to 31 May. These dates were chosen because (a) few non-zero GDD values were observed between 1 January to 1 February in the study region over the period investigated (indeed, including January had no impact on our $sGDD_0$ estimates; data not shown), (b) this span of time included the typical flowering period for all species studied, and (c) the inclusion of months after the known blooming period has been shown to weaken the statistical relationship between temperature and flowering timing in other phenological

Table 1. Species used in climate trend evaluations, Thunder Bay Region, Ontario, Canada. Number of observations from Thunder Bay Field Naturalists (TBFN) newsletters and vouchers at the Claude Garton Herbarium (LKHD) are indicated.

Family	Species	Common name	Range of years evaluated	TBFN (*n*)	LKHD (*n*)
Ranunculaceae	*Anemone quinquefolia* L.	Wood Anemone	1933–1983	19	85
Ranunculaceae	*Caltha palustris* L.	Yellow Marsh Marigold	1948–1992	19	50
Montiaceae	*Claytonia caroliniana* Michaux	Carolina Spring Beauty	1937–1992	17	109
Ericaceae	*Epigaea repens* L.	Trailing Arbutus	1954–1994	14	63
Rosaceae	*Fragaria vesca* L.	Wild Strawberry	1949–1991	17	43
Ranunculaceae	*Hepatica americana* (de Candolle) Ker Gawler	Round-lobed Hepatica	1949–1992	22	50
Asteraceae	*Petasites frigidus* (L.) Fries	Coltsfoot	1933–1992†	23	94
Salicaceae	*Salix discolor* Muhlenberg	Pussy Willow	1949–1981	15	171
Papaveraceae	*Sanguinaria canadensis* L.	Bloodroot	1932–1994	29	66
Violaceae	*Viola pubescens* Aiton	Yellow Violet	1950–2003	12	72
Violaceae	*Viola selkirkii* Pursh ex Goldie*	Selkirk's violet	1933–2003	0	155

*LKHD data only; only three TBFN observations available, none noted as "in bloom".

†2017 outlier removed.

studies of temperate vascular plants (Mulder *et al.* 2017). To calculate $sGDD_0$, mean daily temperatures greater than 0°C were summed from 1 February to 31 May. We additionally estimated GDD_0 to bloom, where the cumulative GDD_0 was estimated for each year that blooms were observed for each species.

Phenological data

We focussed our study on 11 species of perennial angiosperms from eight families found in northwestern Ontario (Table 1). These species were chosen as they represented the plants with the greatest number of records between TBFN and herbarium datasets, and also showed the earliest flowering patterns in the region. It should be noted that herbarium collections and observations do not cover the entire defined Thunder Bay region; most of these data originate from the southern townships east and west the city. Of the 11 included species, all are herbaceous with the exception of Pussy Willow (*Salix discolor* Muhlenberg), which is woody and usually the first to flower locally.

Herbarium vouchers were used to score flowering through time in the 11 chosen species. When a voucher had more than one specimen, these were scored individually and treated as individual observations in the dataset. All herbarium vouchers studied (n = 399; Table S1) are housed in LKHD. While most specimens had an associated latitude and longitude, a small number of older vouchers did not (Table S1). We identified those associated localities that fell within the Thunder Bay region using maps. If a locality was outside of this region or could not be identified due to vague locality description (n = 29), it was not included. The pressing quality of vouchers can vary, so only specimens with clear stages of flowering were scored and included in the herbarium dataset. Collection dates for focal plant species began in 1932 and end in 2006.

All field-naturalist observations (n = 190; Table S1) were made by members of the TBFN. This organization has kept phenological records as part of their membership newsletters from 1947 to present; newsletters are digitized and publicly available on their website (https://tbfn.net/). Three to five newsletters have been published each year, with each issue containing a detailed section on member-reported local phenology of plants, birds, and other wildlife. For angiosperms, the recorded data were most often first flowering of the year, alongside notable locations of rare species; occasionally senescence was noted as well. For our dataset, we included only spring observations in which the state of the plant was explicitly stated (e.g., "in flower"). When a notation of phenological state included flowering, it was assumed that peak flowering was being observed. Recorded sightings by the TBFN are focussed primarily in the city of Thunder Bay (formerly two separate towns, Fort William and Port Arthur) and the nearby townships of Dorion, Neebing, and Oliver-Paipoonge (Table S1).

Collection of vascular plants by herbarium staff occurred from 1932 until 1994, and on a yearly basis until the 1970s, when collections began to decline. In all, herbarium records encompass ~60 years of data. Likewise, the TBFN newsletters contain phenological records of local vascular plant species from 1948 until the 1980s when the records began to be less regularly reported in the newsletters. Each of the species included in the study was represented within both datasets except Selkirk's Violet (*Viola selkirki* Pursh ex Goldie), which was found in LKHD records only.

Phenological coding

A variety of approaches have been used to determine the stage of phenology in flowering plants, especially with respect to herbarium vouchers (Everill *et al.* 2014; Rawal *et al.* 2015; Willis *et al.* 2017; Hufft *et al.* 2018). We numerically coded our plants based on an eight-stage phenological scale, starting with first leaf out (1) and ending with fall senescence (8; Table 2), adapting and expanding on coding stages proposed by Haggerty and Mazer (2008). Collection dates were

TABLE 2. Coded stages of phenology used to determine flowering stage used in the study, Thunder Bay region, Ontario, Canada.

Stage of phenology	Description
1	Leaf buds present but not opened
2	First leaf is fully expanded
3	Entire plant is leaf out with only buds present
4	First flower is fully open
5	Peak flowering is occurring (largest floral display, >50% of flowers on individual plants are open)
6	Last flower
7	Fruit maturity and/or seed dispersal
8	Leaves are withered and discoloured (senescence)
X	Status cannot be determined from voucher or observation

converted to numerical day of year to facilitate analysis of phenological trends across years. Because our main interest was determining if the timing of blooms in early-flowering species was responding to variation in spring conditions, and to provide comparable data between datasets, we focussed on peak flowering (stage 5), the period during which 50% or more of the present flowers are open simultaneously on a given individual plant. Peak flowering has been used to measure phenological changes in response to climate change and is thought to be a more accurate predictor of population response time than first flowering events as it represents a measure of central tendency of the bloom period, rather than the extreme of first flowering date (Miller-Rushing and Primack 2008; CaraDonna *et al.* 2014; Zhang *et al.* 2018). Finally, while other stages of phenology are important and classically understudied (e.g., autumn; see Gallinat *et al.* 2015), most of the LKHD collections and TBFN observation included were gathered in spring or summer, not allowing the inclusion of any other developmental stage of the plants to be considered here.

On herbarium vouchers with multiple individual plants included on a single voucher, plants were each coded individually, with the assumption that they represented collections of individuals from the same population. If the entire record for the plant in a given year was a single voucher with single or multiple plants in bloom, this was used to estimate peak flowering date. We calculated a weighted average of the day of year for peak bloom only if multiple vouchers occurred in the same year, using the proportion of individuals at peak flowering on the voucher as our weighting term. Weighted means were calculated using the *summarize* function in R (version 3.6.2, R Core Team 2019) package "dplyr" (Wickham 2011).

Bloom records from TBFN newsletters (Table S1) were entered by hand from newsletters. Each botanical record made by the TBFN was assigned a stage of flowering, if noted, on the eight-stage scale. The phenological stage code assigned to each year was then assigned a binary code; 1 for peak flowering and 0 for any other stage. If no observation of phenological stage was included, the record was coded with an "X" to denote stage unknown. Similar to herbarium specimen data, dates of recorded sightings were converted into numerical day of year.

Because Wild Strawberry (*Fragaria vesca* L.) blooms multiple times through the season, we limited the reported bloom dates to those occurring prior to 20 July (day of year 200), given that we were primarily interested in the patterns of spring blooming of plants. For both LKHD and TBFN datasets in the Thunder Bay region, the number of observations for each species included varied between datasets, ranging from three (Selkirk's Violet, TBFN) to 171 (Pussy Willow, LKHD; Table 3).

Statistical analyses

Analyses were conducted using R (version 3.6.2, R Core Team 2019). Mean dates of flowering and GDD_0 for each species were estimated (Table 3). Temporal trends in climate data (mean annual air temperature, $sGDD_0$) were evaluated using linear regression. To determine relationships between day of year of peak bloom and year of collection, a simple

TABLE 3. Estimated mean day of bloom and mean growing degree days (GDD) greater than 0°C (units of degree days) to bloom across all observations in the Thunder Bay region, Ontario, Canada. GDD_0 to bloom estimated as the sum of daily temperatures above zero until observed bloom date in a given year; mean across all years with reported bloom dates are presented. *n* = sample size are shown for both the Thunder Bay Field Naturalist (TBFN) and Claude Garton Herbarium (LKHD) datasets.

Species	Mean day of bloom	SE	Mean GDD_0 to bloom	SE	Total peak flowering	
					TBFN (*n*)	LKHD (*n*)
Wood Anemone	144 (24 May)	± 3.2	288	± 28	11	22
Yellow Marsh Marigold	150 (30 May)	± 3.3	376	± 39	18	28
Carolina Spring Beauty	136 (16 May)	± 2.4	129	± 17	12	23
Trailing Arbutus	139 (19 May)	± 3.5	249	± 18	11	18
Wild Strawberry	148 (28 May)	± 5.8	410	± 66	6	16
Round-lobed Hepatica	135 (15 May)	± 2.5	215	± 22	15	32
Coltsfoot	135 (15 May)	± 2.7	238	± 23	18	34
Pussy Willow	117 (27 Apr)	± 8.1	135	± 26	8	11
Bloodroot	133 (13 May)	± 2.0	205	± 20	14	37
Downy Yellow Violet	151 (31 May)	± 2.9	380	± 32	14	20
Selkirk's Violet*	148 (28 May)	± 2.5	338	± 31	0	14

*Only herbarium records.

regression was applied to each species using the peak bloom time estimated for each year. When simple linear regression was applied to only LKHD and TBFN datasets separately, they tended to have weak or nonexistent trends for all species; therefore, only the combined dataset trends are reported here. The combined datasets were examined to determine the relationship between peak bloom and sGDD$_0$ using linear regression. Assumptions of homogeneous and normally distributed residuals were evaluated visually and data transformations were applied to peak bloom time when necessary to satisfy these assumptions (Table 3). Relationships were reported as significant for all P below a critical alpha of 0.1. We chose this more liberal threshold to help emphasize commonalities of temporal trends among species apparent in the data, which, given their consistency in both direction and magnitude across several species (see Results), we believe are unlikely to result from spurious associations. Where significant patterns were observed, the mean predicted change over the period investigated for each species was calculated. For each species, between one to five years had observations from both datasets. We used these data with observations from both datasets to conduct a paired t-test across all species to determine how closely the TBFN and LKHD records compared to one another.

Results

Mean annual air temperature increased significantly from 1878 to 2017 ($F_{1,135}$= 14.4, P = 0.0002, r^2 = 0.1), increasing by 1.04°C over the nearly 140-year period on average (Figure 2a; see Table S2 for raw data). Similarly, we also observed an increase in sGDD$_0$ with time ($F_{1,138}$ = 15.8, P = 0.0001, r^2 = 0.1), increasing by 86.8 degree days on average over the nearly 140-year period investigated (Figure 2b). There was a significant positive relationship between sGDD$_0$ and mean annual air temperature ($F_{1,135}$ = 90.9, P < 0.0001, r^2 = 0.4; Figure 2c).

The 11 species included in this study were all confirmed to be early blooming, with mean peak bloom dates ranging between 27 April for Pussy Willow and 31 May for Downy Yellow Violet (*Viola pubescens* Aiton), and mean sGDD$_0$ ranging between 129 (Carolina Spring Beauty [*Claytonia caroliniana* Michaux]) and 410 degree days (Wild Strawberry; Table 3). One hundred fifty-nine vouchers (of 399) showed 359 individual specimens during their peak flowering period (stage 5); 116 of 190 TBFN observations were recorded as "in bloom".

In four of the 11 species evaluated (Table 4, Figure 3), we observed a substantial lag in peak bloom over time. This trend was observed in Wood Anemone (*Anemone quinquefolia* L.: 38-day delay on average from 1952 to 1983), Bloodroot (*Sanguinaria canadensis* L.: 19-day delay from 1932 to 1994), Carolina Spring Beauty (29-day delay from 1937 to 1992), and Wild Strawberry (53-day delay from 1949 to 1992). Wood Anemone showed a significant

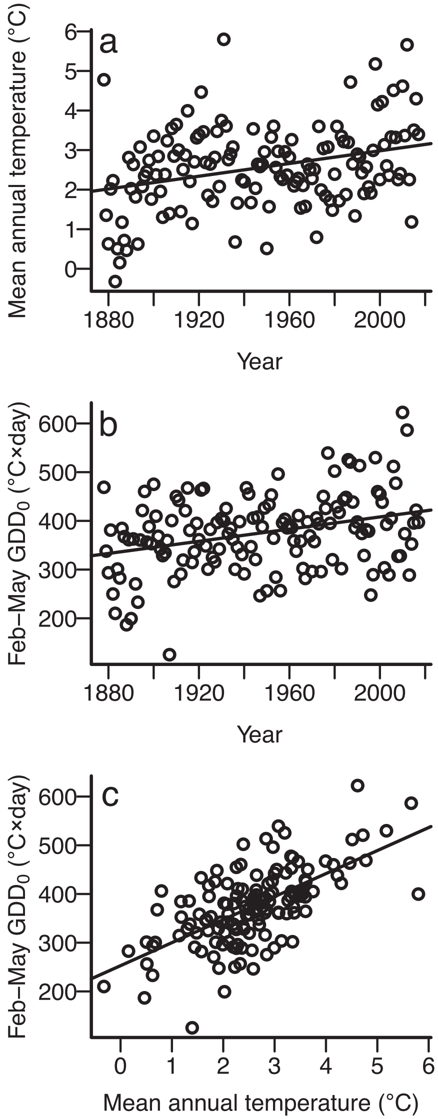

FIGURE 2. Changes in climate in the Thunder Bay region over the past ~130 years. a. Mean annual temperature in the region has increased ($F_{1,135}$= 14.4, P = 0.0002, r^2 = 0.1), with increasing variability since ca. 1960. b. Growing degree days >0°C between February and May (describing thermal conditions in the spring in the region) have also increased during the same period ($F_{1,138}$ = 15.8, P = 0.0001, r^2 = 0.1). c. Spring cumulative growing degree day (SGDD$_0$) is positively related to mean annual temperature in the region ($F_{1,135}$ = 90.9, P < 0.0001, r^2 = 0.4).

TABLE 4. Statistical results for evaluations of trends over time and with spring GDD_0 (growing degree days from February to May greater than 0°C), Thunder Bay region, Ontario, Canada. Statistically significant relationships ($P < 0.1$) are in bold.

Species	Trend with year		Trend with spring GDD >0°C	
	Test statistic	*P*	Test statistic	*P*
Wood Anemone*	**$F_{1,15}$ = 20.40**	**<0.01**	**$F_{1,20}$ = 3.54**	**0.08**
Yellow Marsh Marigold	$F_{1,26}$ = 0.08	0.77	$F_{1,26}$ = 0.00	0.95
Carolina Spring Beauty	**$F_{1,21}$ = 8.80**	**0.01**	**$F_{1,21}$ = 5.08**	**0.04**
Trailing Arbutus	$F_{1,16}$ = 0.11	0.74	$F_{1,16}$ = 0.14	0.71
Wild Strawberry	**$F_{1,14}$ = 3.30**	**0.09†**	**$F_{1,14}$ = 3.25**	**0.09**
Round-lobed Hepatica	$F_{1,30}$ = 0.10	0.76	**$F_{1,30}$ = 7.44**	**0.01**
Coltsfoot	$F_{1,32}$ = 0.17	0.69	$F_{1,32}$ = 0.56	0.46
Pussy Willow	$F_{1,9}$ = 1.21	0.30	$F_{1,9}$ = 0.13	0.73
Bloodroot	**$F_{1,35}$ = 5.34**	**0.03**	$F_{1,35}$ = 0.33	0.57
Downy Yellow Violet	$F_{1,18}$ = 1.02	0.33	$F_{1,18}$ = 0.59	0.45
Selkirk's Violet	$F_{1,12}$ = 0.02	0.88	$F_{1,12}$ = 0.13	0.72

*Trend excludes data earlier than 1950.
†Results for log-transformed data.

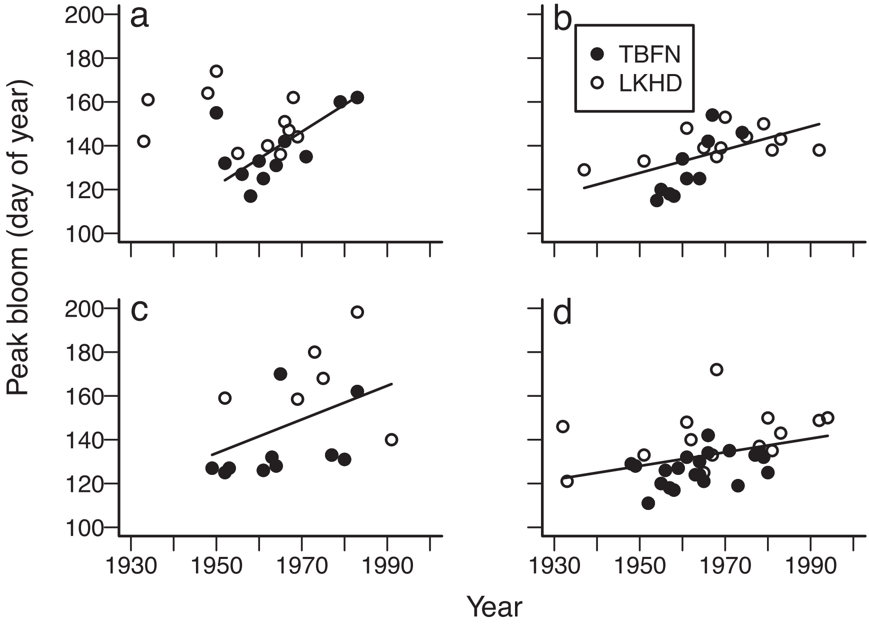

FIGURE 3. Plants in the Thunder Bay region, Ontario, Canada demonstrating significant positive changes in flowering phenology over time. a. Wood Anemone (*Anemone quinquefolia*), demonstrating a significant positive relationship from 1950–1983 only ($F_{1,15}$ = 20.4, P = 0.0004, r^2 = 0.58, β = 1.23). b. Carolina Spring Beauty (*Claytonia caroliniana*, $F_{1,21}$ = 8.8, P = 0.007, r^2 = 0.3, β = 0.5303). c. Wild Strawberry (*Fragaria vesca*, $F_{1,14}$ = 3.3, P = 0.092, r^2 = 0.19, β = 0.0051 from log-transformed bloom date). d. Bloodroot (*Sanguinaria canadensis*, $F_{1,35}$ = 5.34, P = 0.027, r^2 = 0.13, β = 0.3125). TBFN = data collected from the Thunder Bay Field Naturalists, LKHD = data collected from the Claude Garton Herbarium, Lakehead University.

relationship, but only with the exclusion of any observations made before 1950, which appeared distinctly separate from the distribution of the rest of the data series for that species (Figure 3a). There was a weak positive trend for Wild Strawberry ($F_{1,14}$ = 3.1, P = 0.098); applying a log-transformation improved the fit slightly (Table 4, Figure 3c). Collectively, the mean predicted peak bloom of the four species showing strong trends was delayed 35 days between 1932 and 2006. The other six species evaluated demonstrated no significant trends (Table 2). Contrary to our predictions, no early blooming plants included in this dataset demonstrated a significant relationship of earlier blooming over the time series.

Across all species investigated, comparison of the LKHD and TBFN datasets in years when both were represented revealed that LKHD blooming dates tended to be nine days later on average than TBFN records (t_{28}= 2.28, P = 0.03).

Flowering as a function of sGDD₀

Yearly cumulative $sGDD_0$ was negatively related to peak flowering for four species evaluated (Table 4; Figure 4): Round-lobed Hepatica (*Hepatica americana* (de Candolle) Ker Gawler), Wood Anemone, Wild Strawberry, and Carolina Spring Beauty. Each of these species showed a significant negative trend with an increase in cumulative $sGDD_0$. With a higher quantity of cumulative thermal energy in spring, plants tended to have earlier peak blooms (Round-lobed Hepatica 24 days earlier; Wood Anemone 22 days earlier; Wild Strawberry 33 days earlier; Carolina Spring Beauty 18 days earlier). Collectively, the peak bloom of these species decreased a predicted mean of 21 days as cumulative $sGDD_0$ increased between 214 and 246 degree days.

Discussion

Changing phenology of the Thunder Bay region

Regardless of the analysis applied (either simple regression of flowering over time or response to $sGDD_0$), several angiosperms in the Thunder Bay region of northwestern Ontario were observed to have changed their flowering times in a consistent and predictable fashion in response to a warming climate. However, these metrics showed a perceived conflict in trend direction. In analyses that examine only changes in peak flowering over time, species showing a significant trend were unexpectedly observed to delay their flowering over time rather than advancing bloom time as we originally hypothesized. In contrast, but matching expectations, we observed earlier blooming with a greater accumulation of $sGDD_0$.

Trends in flowering phenology

Contrary to the trend we expected—earlier blooming periods with warmer springs—each of the species showing significant relationships reached peak bloom later in the year rather than earlier, from anywhere between 19 and 52 days (Wood Anemone and Wild Strawberry, respectively) over the entire time period evaluated. Of the four species that flowered later through time, Bloodroot and Carolina Spring Beauty

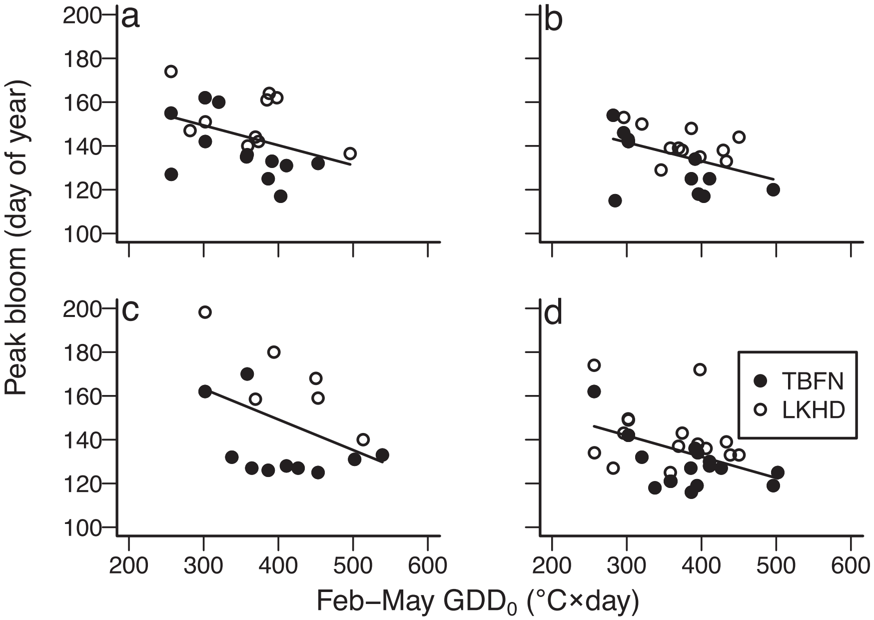

FIGURE 4. Plants in the Thunder Bay region, Ontario, Canada demonstrating significant negative changes in flowering phenology with growing degree days >0°C between February and May. a. Wood Anemone (*Anemone quinquefolia*, $F_{1,20}$ = 3.54, P = 0.08, r^2 = 0.15, β = –0.985). b. Carolina Spring Beauty (*Claytonia caroliniana*, $F_{1,21}$ = 5.08, P =0.035, r^2 = 0.2, β= –0.0860). c. Wild Strawberry (*Fragaria vesca*, $F_{1,14}$ = 3.25, P = 0.09, r^2 = 0.19, β = –0.1396). d. Round-lobed Hepatica (*Hepatica americana*, $F_{1,30}$ = 7.44, P = 0.011, r^2 = 0.2, β = –0.0968). TBFN = data collected from the Thunder Bay Field Naturalists, LKHD = data collected from the Claude Garton Herbarium, Lakehead University.

flower briefly before tree leaf-out (Vezina and Grandtner 1965; Schemske 1978), whereas Wild Strawberry and Wood Anemone have longer flowering periods that continue after the canopy closes (Swink 1952; Eriksson and Ehrlén 1991). The delay in flowering for these species varies, with Carolina Spring Beauty and Bloodroot changing by 0.5 to 0.3 days per year, respectively (five to three days per decade) and Wood Anemone and Wild Strawberry delaying their flowering by 1.2 days per year (~12 days per decade over the period observed). These four plants are among the earliest flowering vascular plants seen in the Thunder Bay area (Table 3).

Other published work has noted species with conflicting trends over time. While the majority of published studies record earlier flowering times in response to warming temperatures, a minority of previous studies have recorded delayed or no change in flowering for some species, particularly in response to warm fall or winter temperatures (Sherry *et al*. 2007; Hart *et al*. 2014). Additionally, while some species do not shift their first flowering or peak bloom, last flowering may be delayed (e.g., CaraDonna *et al*. 2014; Parmesan and Hanley 2015). Although no trends are detected for some of the species included in our dataset, it is possible that their response to changing climate is not occurring with peak flowering but rather with delayed onset of the last bloom, fruiting periods, or senescence, which we were unable to evaluate in our study with the data available.

It is possible that the delay in flowering noted here could also be the result of a plastic response to winter temperature, specifically vernalization, a process through which overwintering plants use cold temperature cues to time their flowering (Williams *et al*. 2015). Vernalization is cumulative, so that the number of days below a certain temperature must be met before the angiosperm responds to warm temperatures by flowering. During winters that have mild mean temperatures, plants that rely on this process will not meet their cumulative cold degree requirements to respond to an earlier spring with a delay in their flowering time. Indeed, warming mean annual temperatures in northwestern Ontario and across Canada are largely attributable to warmer winters (Guzzo *et al.* 2017; Myers-Smith *et al*. 2019). Non-significant results for species included in our dataset could be the result of vernalization requirements not being met, as demonstrated in the analysis by Cook *et al*. (2012) of temperate early-flowering plants in the United Kingdom. However, the conflicting trends we report with $sGDD_0$ regressions, along with lack of research conducted on the vernalization of native North American plants, make it difficult to conclusively say that a cold winter temperature threshold is a requirement of the plants included in our study. Further, of the 11 species assessed, four species of three different families—three of which show delayed flowering in the simple temporal regression—showed a response to an increased number of growing degree days above 0°C; Wood Anemone, Round-lobed Hepatica, Wild Strawberry, and Carolina Spring Beauty all reached an earlier peak bloom with a greater accumulation of $sGDD_0$.

While early North American studies of local phenology largely sought to characterize the timing of flowering over short timescales (e.g., Swink 1952; Vezina and Grandtner 1965), researchers now have the ability to examine long-term trends over larger timescales in accordance with climate data. Here, we see that the inclusion of GDD provides evidence consistent with predictions, and context for an otherwise surprising result when considering temporal trends only. The similarity of significant trends among species suggests that the patterns observed are real and not spurious. Our results suggest that using metrics (e.g., temporal trends alone) that do not also consider biological responses to environmental cues may result in incorrect inferences. While later flowering in these species may be evidence of vernalization, data required to evaluate this possibility are lacking. Instead, our predicted results of earlier blooming with $sGDD_0$ are consistent with expectations due to increased thermal accumulation.

In the species that show significant but conflicting trends in temporal and $sGDD_0$ analyses, other work shows that when temperature is accounted for, these species bloom earlier in response to warmer climate. For example, Wood Anemone has flowered increasingly earlier in the southern part of its range, in conjunction with mild winters (Abu-Asab *et al.* 2001; Panchen *et al*. 2012). Canadian populations of another early-flowering species in the same family, Prairie Pasqueflower (*Pulsatilla nuttalliana* (de Candolle) Berchtold ex J. Presl), similarly showed a two-day decrease in flowering per decade in conjunction with thermal time models (Beaubien and Hamann 2011a). Carolina Spring Beauty shows similar sensitivity to earlier springs. Previously, only one study has examined the Canadian phenology of Carolina Spring Beauty, but without accounting for the influence of temperature (Vezina and Grandtner 1965). However, spring beauty (*Claytonia* spp.) is a North American genus that has demonstrated earlier blooming time with correspondingly early snowpack melt (Panchen *et al*. 2012; Gezon *et al*. 2016). Although snow melt data were not available for analysis in our study, others have demonstrated its correlation with earlier flowering times, especially in plants reliant on this abiotic factor as a primary cue (Lavoie and Lachance 2006; Lambert *et al*. 2010; Bjorkman *et al*. 2015).

The consistent but conflicting trends and non-responsiveness of some species we observed could also be the result of small sample sizes. Panchen *et al.* (2012), studying changing phenology of plants in the Philadelphia region, found that for the 150-year span of their study, species with short flowering periods showed significant results with 60 observations, while longer flowering species required up to 100 observations to show significant changes. When assessing TBFN and LKHD data together, the average number of observations per species was 50, which is slightly below both these thresholds. However, the species which showed significant trends for temporal or temperature-based analyses all had between 31 (Wild Strawberry) and 62 (Bloodroot) observations, indicating that despite smaller sample sizes of peak flowering records, there is still a strong enough trend to detect consistent changes in phenology. Species that did show significant phenological responses also varied in bloom period, from short- to longer-blooming periods. This suggests that there are other dynamics influencing the response of these plants.

It is also possible that some of the differences we observed are population-level adaptations or a plastic species response to differences in climate, where some populations have become more attuned to vernalization or temperature cues than others (Panchen *et al.* 2017; Prevéy *et al.* 2017). However, studies of phenology across native ranges of North American vascular plants do not regularly address differences in flowering time by populations. Additionally, many range oriented studies focus on expansion, contraction, or shifts, but have not examined the *in situ* differences between existing populations. Of the few studies that have addressed phenological differences at a latitudinal gradient, significant differences in requirements for germination and flowering have been observed, with more northern populations achieving smaller size and flowering earlier, compared to more southern populations achieving larger size and later flowering (van Dijk *et al.* 1997; Weber and Schmid 1998; Olsson and Ågren 2002). Here, what evidence of population level plasticity does exist is also conflicting; while many vascular plants readily respond to temperature cues (Nicotra *et al.* 2010; Schmidt *et al.* 2012; Tansey *et al.* 2017), others demonstrate no appreciable differences (Vitasse *et al.* 2009; Phillimore *et al.* 2012). It is evident that additional studies examining population-level phenological plasticity are necessary to tease apart these trends.

Importance of climatic metrics in local phenology studies

While climatic variables are important in characterizing phenology, the choice of environmental cue should be based on the life history of the organisms under consideration. Other approaches include snow melt (Lavoie and Lachance 2006), air temperature and moisture (Reed *et al.* 2019), and year-to-year climatic variability (Büntgen *et al.* 2012). Given that climatic effects vary over latitude and ecosystem, any of these metrics may provide an avenue to measure changes in flowering phenology and should be used in conjunction with phenological studies when such data are available. However, although a variety of approaches can be taken, GDD (sometimes referred to as thermal time models) does show consistency in the ability to predict the change over time for several thermally-dependent organisms across a broad range of taxa (Bonhomme 2000; Beaubien and Hamann 2011b; Lester *et al.* 2014). Additionally, understanding general flowering trends with GDD for early blooming species (Table 3) provides metrics for evaluating other phenological patterns across latitudinal gradients (Ross *et al.* 2021).

Source data

Without the combination of both locally collected field-naturalist observations and the herbarium records included in our study, sample sizes were too small to reveal reliably significant trends for all 11 species. Although many previous studies have included citizen science projects conducted over the short-term, the incorporation of long-term field-naturalist records to either augment existing data or as a data source on their own is still a relatively new practice (Miller-Rushing *et al.* 2012). As herbaria and museums become increasingly digitized, the combination of these two data sources has the potential to greatly expand our understanding of how biota respond to global climate change. While many studies of phenology attempt to cover large areas (Lavoie and Lachance 2006; Panchen and Gorelick 2017) or include thousands of specimens (Gordo and Sanz 2005; Hart *et al.* 2014), these types of studies often require vouchers from other herbaria or other records to bolster their datasets. For small herbaria, augmenting voucher data with naturalist observations may go further to reveal the responses of local ecosystems to climate that may otherwise go unnoticed.

Interestingly, in years when both TBFN and LKHD records were available, bloom times in the LKHD vouchers were nine days later on average than TBFN flowering times. It is unclear why this might be. Regardless, the delays in blooming reported here are all longer than nine days over the periods investigated, suggesting that the trends observed were real and unlikely an artefact of systematic differences between datasets. Further, the distribution of data from both datasets in species that demonstrate trends does not appear to be biased over the time periods investigated (Figure 3), further reducing the possibility that bias in datasets might be contributing to observed results.

Our study suggests that field-naturalist data can contribute to long-term, ongoing studies of phenology. Current projects, such as the USA-National Phenology Network (USA-NPN), use citizen scientist data to track phenological change across North America, as well as archival datasets that are accessible to both researchers and the public (https://www.usanpn.org/results/dataset-list). These retroactive contributions to monitoring projects can help strengthen trends across time and space for researchers who are concerned with changing phenological norms. Additionally, they also can help to increase data coverage in areas where there may be few collections but written personal or organizational records exist.

Conclusion

While climate change is a global phenomenon, the impacts are felt locally. Our study demonstrates the value of both regional herbaria and long-term field-naturalist records in helping reveal the effects of climate change on a local level, and for the first time, uses data collected in the northwestern Ontario region to determine how vascular plants are responding to changing climate. We found that a small number of early-flowering vascular plants showed a response to warming seasons, but also that these trends oppose one another in temporal and climatic analyses. Lastly, our study supports the maintenance of local herbaria and the continuance of field-naturalist observations as essential resources for local phenological studies. Recording local phenological changes also provides a unique opportunity for institutions (such as herbaria) to partner with the public. Phenology is an accessible field: records are easy to keep for those without scientific training, allowing researchers, citizen scientists, and other organizations to work together to interact with, monitor, and manage their surrounding ecosystems.

Author Contributions

Conceptualization: E.S.L.; Investigation: E.S.L.; Formal Analysis: G.M. and M.D.R.; Writing – Original Draft: E.S.L. and M.D.R.; Writing – Review and Editing: E.S.L., M.D.R., and G.M.

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SUPPLEMENTAL MATERIALS:

FIGURE S1. Collections per decade for all species included in the study for both the Thunder Bay Field Naturalists (TBFN) and Claude Garton Herbarium (LKHD) datasets.

TABLE S1. Voucher table for all Claude Garton Herbarium and Thunder Bay Field Naturalists specimens and observations used in this study

TABLE S2. Climate data used to evaluate phenological changes in spring blooming perennials.