Advancing Leaf-Out and Flowering Phenology is Not Matched by Migratory Bird Arrivals Recorded in Hunting Guide's Journal in Aroostook County, Maine

Authors: Caitlin McDonough MacKenzie, Jason Johnston, Abraham J. Miller-Rushing, William Sheehan, Robert Pinette, et. al.

Source: Northeastern Naturalist, 26(3) : 561-579

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/045.026.0309

2019 NORTHEASTERN NATURALIST 26(3):561–579

Advancing Leaf-out and Flowering Phenology is not Matched by Migratory Bird Arrivals Recorded in Hunting Guide's Journal in Aroostook County, Maine

Caitlin McDonough MacKenzie[1,*], Jason Johnston[2], Abraham J. Miller-Rushing[3], William Sheehan[4], Robert Pinette[5], and Richard Primack[6]

Abstract - Historical records have the potential to temporally and spatially expand ecological studies to places and periods that garnered the attention of earlier naturalists. Few historical or contemporary scientific studies have examined the local-to-regional ecological effects of climate change in northern Maine. Recently uncovered journals of L.S. Quackenbush, a hunting guide in mid-20th century Aroostook County, ME, provide an opportunity to incorporate new historical ecological data into climate change research.The leaf-out and flowering phenology observations in the Quackenbush journals are closely tied to spring temperatures and match the direction, though not the magnitude, of changes found in southern New England. Comparisons of Quackenbush's bird records to contemporary observations are less straightforward, but help fill an important gap in regional migratory bird phenology studies. Quackenbush's routine observations, recorded daily in a rural outpost in northern Maine, provide an important contribution to climate change research in a data-poor region and highlight a type of record that may be available in other rural areas.

Introduction

Ecologists are increasingly using historical records to measure the impact of anthropogenic climate change on biological communities. Natural history collections, herbaria, photographs, and journals have contributed valuable ecological data to these studies (Cleland et al. 2007, Ledneva et al. 2004, Miller-Rushing et al. 2006, Panchen et al. 2012, Primack and Miller-Rushing 2012, Vellend et al. 2013). Historical data on phenology—the timing of seasonal biological events—are abundant thanks to dedicated naturalists who routinely recorded events like annual first flower and spring arrival of migratory songbirds. Historical records of phenological events that are cued by temperature allow ecologists to track the response of organisms to changes in the climate over decades or even centuries (Ellwood et al. 2013, Fitter and Fitter 2002). Changes in spring phenology have proven to be visible and readily accessible measures of the ecological effects of climate change (Parmesan and Yohe 2003, Root et al. 2003). Demonstrated phenological responses to climate

[1]Climate Change Institute, 210 Sawyer, University of Maine, Orono, ME 04469. [2]Department of Biology, University of Maine at Presque Isle, 181 Main Street, Presque Isle, ME 04769. [3]US National Park Service, Acadia National Park, Bar Harbor, ME 04609. [4]1125 Woodland Center Road, Woodland, ME 04736. [5]Professor Emeritus, University of Maine at Presque Isle, 18 Melden Drive, Brunswick, ME 04011. [6]Department of Biology, Boston University, 5 Cummington Mall, Boston, MA 02215. [*]Corresponding author - caitlin.mcdonough@maine.edu.

Manuscript Editor: Robert Bertin

change include shifts in the timing of leaf-out, flowering, and migratory bird arrivals (Ellwood et al. 2010, 2013; Polgar and Primack 2011). These phenological responses have been documented across the globe and studied in depth in southern New England where historical records are abundant (Cleland et al. 2007, Primack and Miller-Rushing 2012).

Complete long-term records of leaf-out, flowering, and migratory bird phenology for a single location are rare; few naturalists consistently noted these events over long time periods and even fewer had their diaries archived. Henry David Thoreau and Aldo Leopold are examples of naturalists whose archived journals have been surveyed for use in climate change research (Ellwood et al. 2013, Primack and Miller-Rushing 2012). Thoreau's phenology charts for leaf-out, flowering, and migratory bird arrivals sparked a 21st century renaissance of phenology monitoring in Concord, MA (Primack and Miller-Rushing 2012). Comparing Thoreau and his contemporaries' records to present-day data reveals large advances in the leaf-out and flowering phenology observed in the temperate deciduous forests of Concord (Miller-Rushing and Primack 2008, Polgar et al. 2014). In contrast, the spring arrivals of migratory birds have shown far less plasticity in studies from Concord, Mt. Auburn Cemetery (Cambridge, MA), and Manomet Bird Observatory (Plymouth, MA); bird migrations appear to be less responsive to local temperature variation and are affected by a wider range of environmental factors (Ellwood et al. 2010, Ledneva et al. 2004).

Despite the wealth of information about spring phenology from southern New England, northern New England remains understudied in terms of the ecological impacts of climate change. Northern New England, where the leading edge of temperate deciduous forest meets the ecotone with boreal forest, is expected to experience more rapid warming than the rest of the contiguous US (Karmalkar and Bradley 2017). Although the northeastern US is generally rich in natural history records, northern Maine is recognized as a "cold spot" for floristic records and herbarium sampling (Daru et al. 2017, McDonough MacKenzie et al. 2019a).

In the mid-20th century, a hunting guide named L.S. Quackenbush in Oxbow, ME, kept detailed journals of the annual dates of first leaf-out, first flowering, and the earliest spring sightings of migratory birds. Quackenbush carefully recorded daily notes and observations from his walks through the small plantation of Oxbow in his journal. Though he was not a formally trained scientist, his consistent observations and orderly record-keeping lend credibility to his abilities as a naturalist. In the late 1950s, he organized his journals into tables of first flowering, first leaf-out, and first bird arrivals by species and year. After Quackenbush's death in 1959, his journals, including these tables, were donated to Acadia National Park and archived at College of the Atlantic in Bar Harbor, ME.

Through these records of phenological events, the Quackenbush journals provide a unique opportunity to study the ecological effects of climate change and climatic variation in northern Maine. The rural region of Aroostook County, ME, where Quackenbush lived, has been minimally studied in research on climate change due to its remote location, low population density, and relative lack of historical data or active ecological research sites. While there have been a few recent studies on spring phenology in Maine, these have excluded this region. For example, recent research of migratory bird arrival dates explicitly excludes Aroostook County (Wilson 2007, Wilson et al. 2000), or includes relatively few observations (Wilson 2017), and a regional study using pheno-cams to monitor leaf-out dates extends only as far north as Howland Forest in central Maine (Richardson et al. 2009). In Aroostook County, ornithologist W. Sheehan has recorded migratory bird arrival dates since 1993. Recently, J. Johnston and R. Pinette began monitoring spring leaf-out and flowering in Presque Isle for a suite of species observed by Quackenbush. Our study is among the first to analyze changes in migratory bird and plant phenology in Aroostook County and draws on the fieldwork of Quackenbush and Sheehan.

The historical data captured in the Quackenbush journals from 1940 to 1959 and comparisons to modern data collected between 1993 and 2012 allow us to explore how the timing of biological events has shifted in the temperate deciduous and mixed conifer forests of northern Maine over the past 70 y. Although spring phenology in temperate deciduous forests has been extensively studied in southern New England, northern Maine is comparatively much less developed, closer to the temperate–boreal ecotone, and is more likely to experience the rapid warming expected at high latitudes (Fernandez et al. 2015, Karmalkar and Bradley 2017). The objectives of this work were to: (1) quantify the responsiveness of the timing of leaf-out and flowering to spring temperatures in the temperate deciduous and mixed conifer forests of Oxbow, ME; (2) determine if migratory birds arrive earlier now than in the past; and (3) compare the phenological shifts observed in northern Maine to patterns of leaf-out, flowering, and migratory bird arrivals noted in southern New England. In addition, this project provides an example of the value of unconventional data sources in phenology research, while expanding the study of spring phenology from southern New England north to Aroostook County, ME.

Field-site Description

Quackenbush made observations in the unincorporated town of Oxbow Plantation (46.4186°N, 68.4900°W) in Aroostook County, ME. He was born around 1879 and moved to Oxbow Plantation sometime in the late 1930s. His house and barn still stand at 1550 Oxbow Road. His daily journal entries document the weather, ice on the Oxbow River behind his house, and natural history observations from walks around Oxbow, beginning in February 1940 and ending on 31 August 1959. The area behind his home and the surrounding town are largely undeveloped mixed hardwood and conifer forests and rough fields, with streams, a river, and few buildings. Dominant tree species include *Populus tremuloides* (Quaking Aspen), *Fagus grandifolia* (American Beech), *Abies balsamea* (Balsam Fir), and *Betula papyrifera* (Paper Birch). Aroostook County covers 17,687 km^2, and the traditional mainstays of the county's economy are agriculture and forest products (Judd 1984). Hunting and fishing are also important in the local economy of Oxbow today (J. Johnston, pers. observ.). The population of Aroostook County was 94,436 in 1940 and 70,055 in 2013; in 2010, the population of Oxbow was 66 (US Census 2010).

Methods

We transcribed Quackenbush's phenological observations into spreadsheets, limiting our analysis to species with at least 10 y of data for first leaf-out and first flowering, and at least 5 years of data for bird first arrivals. Our data set for first flowering comprised 15 species with observations over 12 y, during the period from 1945 to 1957. Our dataset for first leaf-out comprised 10 species with observations over 16 y, from 1940 to 1955 (Table 1).

Our dataset for migratory birds comprised 8 species with observations of first arrivals over 17 y, from 1941 to 1957 (Table 1). We were able to match our migratory bird dataset with recent observations of the same 8 species recorded by ornithologist W. Sheehan over 17 y, during the period 1993–2012. Sheehan, a dedicated birder, has kept track of first arrivals throughout Aroostook County for 2 decades. He observes birds several times per week, mainly in the Presque Isle area which is about 64 km northeast of Oxbow. The area included in Sheehan's observations is much larger than the area examined by Quackenbush, but this is the only available comparative dataset.

We used correction factors to transform the data and allow community-wide comparisons among years when not all species were observed (Ellwood et al. 2010). We calculated correction factors for the migratory bird community as the difference between the mean first arrival date of all species and the mean first arrival date of each species. For example, Quackenbush recorded the spring arrival of Eastern Kingbirds in 8 y, with a mean arrival date of 20 May. Across all 8 bird species in our dataset, the mean arrival date observed by Quackenbush was 23 May; thus the correction factor for Eastern Kingbirds in the dataset is 3 days, which we added to the arrival date every year in which Quackenbush observed the Eastern Kingbird. Correction factors are a common transformation in studies that leverage uneven historical data to explore community-level changes; this eliminates the problem of observations of different species in different years (Gallinat et al. 2018, Miller-Rushing et al. 2006, Primack et al. 2004). We calculated correction factors for each species in our 4 datasets: Quackenbush bird arrivals, Sheehan bird arrivals, Quackenbush leaf-out, and Quackenbush flowering.

We used 2-sample *t*-tests to compare the arrival dates of each bird species between the historical and contemporary time periods. For plant phenology, we calculated the relationships between phenology and spring temperatures based on mean monthly temperature data from the nearest weather station, in Presque Isle (~64 km from Oxbow), from the NOAA National Climatic Data Center. When we employed Bejamini–Hochberg corrections for all sets of analyses to reduce the risk of Type I errors, our results did not change; thus, we report uncorrected *P*-values below.

We used linear regressions to analyze the relationship between phenological events, such as dates of migratory bird arrival, flowering, and leaf-out, and mean temperatures in the preceding months. For each taxon, we correlated the date of the phenological event with the mean monthly temperatures of the month of the event and the preceding months (typically January through April). From those correlations, we found the month(s) for which the mean temperatures were best correlated with each phenological event (Miller-Rushing and Primack 2008). In the case of migratory bird arrivals, we considered the whole dataset (Quackenbush and Sheehan), and also analyzed each time period separately in case differences in methods between the 2 observers masked a relationship between arrival date and spring temperatures. All analyses were conducted in R (R Core Team 2017).

Table 1. Species included in our analysis of spring phenology from Quackenbush's journal. Scientific names are the most likely species based on Quackenbush's notes of common names, local herbarium specimens, field visits to Oxbow, and the authors' local natural history knowledge. *n* Quackenbush = the number of years in which each species' phenological event was recorded by Quackenbush during the period 1940–1959 and *n* Sheehan = the number of years in which migratory bird first arrivals for each species was recorded by Sheehan during 1993–2012.

	n	
Species	Quackenbush	Sheehan
Migratory bird arrivals		
Tyrannus tyrannus L. (Eastern Kingbird)	8	14
Petrochelidon pyrrhonota Vieillot (Cliff Swallow)	7	12
Empidonax minimus Baird (Least Flycatcher)	5	14
Setophaga caerulescens Gmelin (Black-throated Blue Warbler)	8	11
Vireo olivaceus L. (Red-eyed Vireo)	6	13
Zonotrichia leucophrys Forster (White-crowned Sparrow)	10	13
Setophaga coronata coronata L. (Myrtle Warbler)	10	15
Setophaga pensylvanica L. (Chestnut-sided Warbler)	12	15
First flowering observations		
Trillium erectum L. (Red Trillium)	12	
Amelanchier sp. (shadbush)	12	
Viola renifolia Gray (White Violet)	10	
Fragaria virginiana Duchesne (Wild Strawberry)	11	
Viola sororia Willd. (Blue Violet)	11	
Taraxacum officinale (L.) Weber ex F.H. Wigg (Dandelion)	11	
Malus pumila Miller (Apple)	11	
Cornus canadensis L. (Bunchberry)	10	
Maianthemum canadense Desf. (Canada Mayflower)	11	
Ranunculus sp. (buttercup)	11	
Cornus sericea L. (Red Osier Dogwood)	11	
Daucus carota L. (Wild Carrot)	11	
Sisyrinchium sp. (blue-eyed-grass)	11	
Rosa sp. (wild rose)	11	
Genus unknown (daisy)	11	
First leaf-out observations		
Populus tremuloides Michx. (Quaking Aspen)	16	
Betula papyrifera Marshall (Paper Birch)	16	
Ostrya virginiana (Mill.) K. Koch (American Hophornbeam)	12	
Acer saccharum Marshall (Sugar Maple)	10	
Acer pensylvanicum L. (Striped Maple)	12	
Fagus grandifolia Ehrh. (American Beech)	10	
Quercus rubra L. (Red Oak)	13	
Abies balsamea (L.) Mill. (Balsam Fir)	10	
Populus grandidentata Michaux (Large-tooth Aspen)	11	
Fraxinus americana L. (White Ash)	11	

We compared these records from Maine to similar phenological records from Concord, MA, to determine if species were responding in a similar way to warming spring temperatures. We considered species-level rates of phenological sensitivity to be different if the coefficients of regressions (d/°C) and standard errors for the same species in Concord and in Oxbow did not overlap.

Results

Migratory birds

Mean monthly temperatures for March and April did not change significantly between the historical (1941–1957) and contemporary time periods (1993–2012; both months: $P = 0.179$, March: $P = 0.331$, April: $P = 0.187$). The historical mean monthly temperature for March and April was 0.02 °C (standard deviation [SD] = 1.6 °C; maximum = 3.7 °C, minimum = -2.3 °C); the contemporary mean monthly temperature of March and April was 0.76 °C (SD = 1.5, maximum = 4.1° C, minimum = -1.7 °C).

During the historical period of observation by Quackenbush (1941–1957), the average date of arrival for our suite of 8 bird species was 23 May. Arrivals varied from 19 April (Eastern Kingbird in 1957) to 29 June (Red-eyed Vireo in 1945). During the contemporary period of Sheehan's observations (1993–2012), the same 8 bird species arrived significantly earlier, on 14 May ($P < 0.001$). Contemporary bird arrivals varied from 20 April (Yellow-rumped Warbler, 2012) to 23 June (Red-eyed Vireo, 2007). Arrivals varied from year to year in both historical and contemporary observations. From species-level *t*-tests, we found that 4 of the 8 bird species arrived significantly earlier ($P < 0.05$) in contemporary observations, that is, the mean arrival dates over the 17 contemporary years for each species are earlier than the mean arrival dates over the 17 historical years; these species were the Chestnut-sided Warbler, Least Flycatcher, Yellow-rumped Warbler, and White-crowned Sparrow. None of the bird species displayed a later mean arrival date in contemporary observations as compared to historical observations.

There was no significant relationship between the mean annual arrival of the 8 bird species and the mean temperature of March and April ($P = 0.697$); that is, average bird arrivals were not correlated with mean spring temperatures (Fig. 1). We did not find a statistically significant relationship between temperature for any months between January and May and arrival dates. We also found no relationship between mean annual arrivals of the 8 bird species and mean spring temperatures in either the historical ($P = 0.353$) or the contemporary observations ($P = 0.507$).

When we examined each species individually, the arrival dates of 2 species were significantly correlated with the mean temperature in the Presque Isle area during the months prior to their arrival. The arrival of Least Flycatchers was correlated with mean March, April, and May temperatures ($P = 0.004$, $R^2 = 0.40$); the arrival of White-crowned Sparrows was correlated with mean April and May temperatures ($P = 0.006$, $R^2 = 0.31$) (Table 2). Least Flycatchers arrived 3.7 d earlier for each 1

°C increase in mean March, April, and May temperatures (standard error [SE] = ±1.1), while White-crowned Sparrows arrived 2.8 d earlier for each 1 °C increase in mean April and May temperatures (SE = ±0.9).

Flowering phenology

During the historical period of observation by Quackenbush, the average date of first flower for our suite of 15 species was 2 June. The date of first flower averaged across all 15 species was correlated with mean April temperatures ($P < 0.001$, $R^2 = 0.70$, $F = 23.73$). The average date of flowering advanced by 2.5 d for each 1 °C (SE = 0.5) increase in mean April temperature (Fig. 1).

Of the 15 species in our analysis, the date of first flower for 12 species was significantly correlated with the mean temperature in the Presque Isle area during months prior to flowering; 9 species were significantly correlated with mean April temperatures, and 3 with mean May temperatures. All 12 species flowered earlier in warmer years, with advances varying from 2.1 d/°C (*Ranunculus* [Buttercup]) to 4.8 d/°C (*Cornus sericea* [Red Osier Dogwood]) (Table 2).

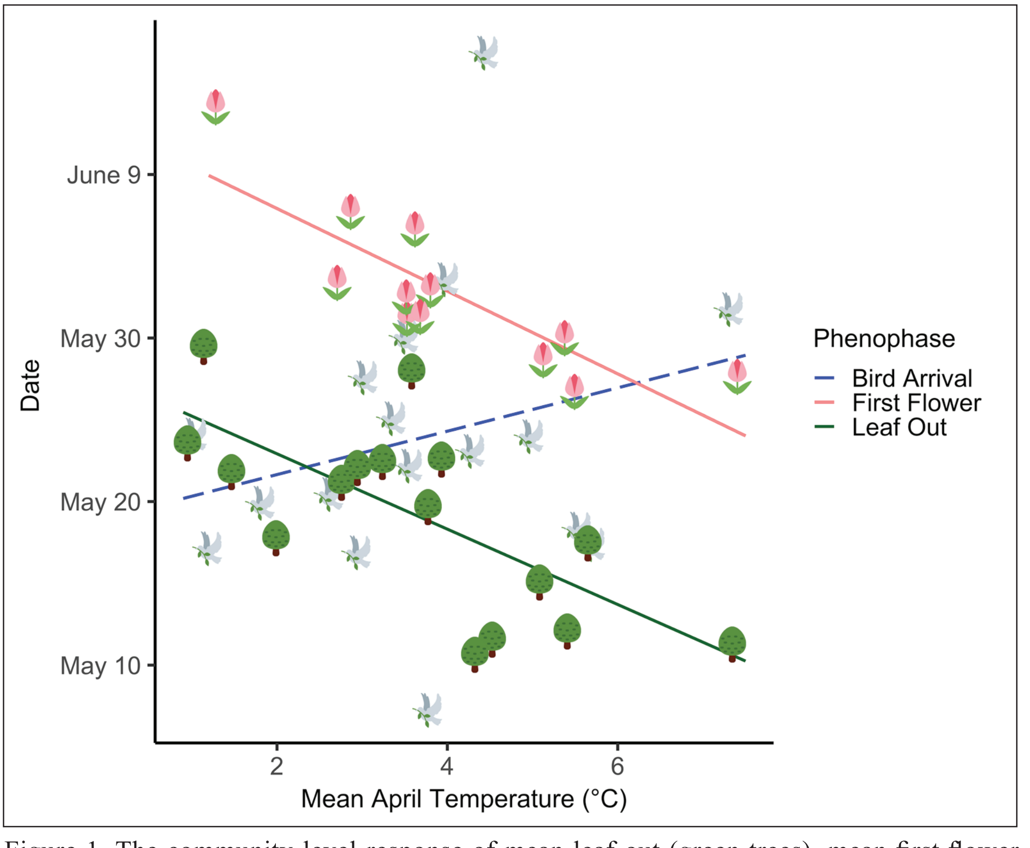

Figure 1. The community-level response of mean leaf-out (green trees), mean first flower (pink tulips), and mean migratory bird arrival date (grey doves) to mean April temperatures (°C) from the records of L.S. Quackenbush. Linear models for each phenophase shown in solid lines for significant ($P < 0.05$) models (leaf-out and flowering) and the dashed lines for the non-significant bird arrival model.

Leaf-out phenology

During the period of observation by Quackenbush (1940–1955), the average date of leaf-out for our suite of 10 plant species was 19 May. The date of average first leaf-out for these 10 species was correlated with mean April temperatures ($P = 0.003$, $R^2 = 0.49$, $F = 13.47$). The date of average first leaf-out advanced by 2.3 d for each 1 °C increase in mean April temperature (SE = 0.6) (Fig. 1).

Of the 10 species, the date of leaf-out of 6 species was significantly correlated with the mean temperature in the Presque Isle area during months prior to leaf-out; 5 species were significantly correlated with mean April temperatures, and 1 (*Fraxinus americana* [White Ash]) with mean May temperatures. All 6 species leafed out earlier in warmer years, with advancements varying from 2.3 d/°C (*Acer saccharum* [Sugar Maple]) to 4.5 d/°C (Paper Birch) (Table 2).

Table 2. Results of linear models of species-level phenological responses to spring temperatures (°C). An asterisk (*) denotes a significant *P* value. Standard error for regression coefficients is included in parentheses in days/°C column.

Species	Mean arrival date	Model	*P* value	R^2	Days/°C	*n*
Bird arrivals						
White-crowned Sparrow	11 May	April–May	0.006*	0.31	-2.8 (0.9)	23
Least Flycatcher	19 May	March–May	0.004*	0.40	-3.7 (1.1)	19
Flowering						
Red Trillium	12 May	April	0.000*	0.86	-3.9 (0.5)	12
Shadbush	19 May	April	0.000*	0.75	-4.5 (0.8)	12
Wild Strawberry	21 May	April	0.002*	0.69	-3.1 (0.7)	11
White Violet	21 May	April	0.005*	0.64	-3.9 (1.0)	10
Apple	28 May	April	0.011*	0.53	-2.9 (0.9)	11
Bunchberry	6 Jun	April	0.016*	0.54	-3.7 (1.2)	10
Dandelion	24 May	April	0.016*	0.50	-3.0 (1.0)	11
Canada Mayflower	7 Jun	April	0.021*	0.46	-3.5 (1.2)	11
Daisy	21-Jun	May	0.023*	0.46	-3.5 (1.3)	11
Red Osier Dogwood	11 Jun	May	0.027*	0.44	-4.8 (1.8)	11
Wild Rose	20-Jun	May	0.028*	0.43	-4.4 (1.7)	11
Buttercup	9 Jun	April	0.041*	0.39	-2.1 (0.9)	11
Wild Carrot	12 Jun	April	0.062	0.34	-1.6	11
Blue Violet	22 May	April	0.188	0.18	-1.5	11
Blue-eyed-grass	15 Jun	May	0.268	0.13	-2.8	11
Leaf-out						
Paper Birch	12 May	April	0.000*	0.65	-4.5 (0.9)	16
Quaking Aspen	11 May	April	0.001*	0.57	-4.3 (1.0)	16
Sugar Maple	15 May	April	0.017*	0.53	-2.2 (0.8)	10
American Hophornbeam	15 May	April	0.021*	0.43	-2.4 (0.9)	12
Striped Maple	17 May	April	0.024*	0.41	-2.4 (0.9)	12
Ash	31 May	May	0.044*	0.38	-3.0 (1.3)	11
Balsam Fir	24 May	April	0.074	0.34	-2.1	10
Large-tooth Aspen	28 May	May	0.125	0.24	-2.8	11
Red Oak	23 May	April	0.177	0.16	-1.2	13
American Beech	20 May	April	0.316	0.13	-1.2	10

Comparison to southern New England

In Concord, MA, average spring (March–May) temperatures have warmed from 5.5 °C (1852–1858) to 6.3 °C (1878–1902) to 8.8 °C (2004–2012), while mean first date of flowering for 32 common species advanced from 15 May to 10 May to 4 May, respectively (Ellwood et al. 2013). At the community level, first flowering date in Concord advanced faster (d/°C) than in Oxbow, though the standard errors for these regression coefficients overlapped (Table 3). However, the plant communities at the 2 sites are comprised of different species, so a species-level comparison is more appropriate. Flowering phenology for 3 species (*Cornus canadensis* [Bunchberry], *Maianthemum canadense* [Canada Mayflower], and *Fragaria virginiana* [Wild Strawberry]) were studied both in Oxbow and Concord (Ellwood et al. 2013, Miller-Rushing and Primack 2008). The sensitivity of these species (days flowering advanced/°C) was comparable in the 2 locations: the standard errors for the regression coefficients of Bunchberry and Wild Strawberry overlapped, and the standard error for our calculated shift in Canada Mayflower flowering includes the estimate for Miller-Rushing and Primack's (2008) Canada Mayflower coefficient (Table 4).

As in flowering, our findings of changes in leaf-out in Maine matched results in southern New England, clearly displaying earlier leaf-out dates in warmer years. At the community level, leaf-out in Concord advanced much faster (6.1 d/°C mean temperature in March–April) than in Oxbow (2.3 d/°C mean temperature in April) (Table 3). The standard error for our regression coefficient did not overlap with rates reported from Concord (Polgar et al. 2013), or a region-wide analysis of leaf-out from herbarium specimens (advancing 3.2 d/°C mean temperature in April) (Table 3; Everill et al. 2014). The herbarium study (Everill et al. 2014) found that annual variations in temperature were the most powerful explanatory variable to predict date of leaf-out and used mean April temperatures in a simple linear model, matching our April model in Oxbow, ME.

Compared to plant phenology, trends in migratory bird arrivals were less clear across the region. In Concord, MA, a compilation of migratory bird arrivals observed by local naturalists that spans 157 y from Thoreau to 2007 found no change in arrival dates when observations before 1973 were compared to observations after 1988 (Ellwood et al. 2010). A study utilizing the journal of one amateur naturalist in Middleborough, MA, from 1970 to 2002 found 5 migratory bird species (of 16 in the analysis) with statistically significant trends toward earlier spring arrivals (Ledneva et al. 2004). Six of the Quackenbush bird species were included in these studies from southern New England (Table 5). Direct comparisons between our results and these studies reveal inconsistent relationships between arrival dates and spring temperatures.

Discussion

We found that plants in Aroostook County, ME, leaf out and flower earlier in warmer years. These shifts match the direction, but not the magnitude, of phenological sensitivity observed in Concord, MA. In both southern and northern New

Table 3. Results of linear models of phenology and spring temperatures from the New England region. An asterisk (*) denotes a significant P-value and ns stands for not significant ($P > 0.05$). Where available, standard error for regression coefficients is included in parentheses in days/°C column.

Linear model	Time period	Temperatures	n	P value	R^2	Days/°C	Citation
Bird arrival							
Manomet	1970–2002	March, April, May	32	<0.05*	0.13–0.30	-0.1 -0.36	Miller-Rushing et al. 2008b
Mt Auburn Cemetery volunteers	1980–2004	March, April	30	0.023*	0.01	-1.10	Miller-Rushing et al. 2008c
Concord from Thoreau to Corey	1851–2007	March, April	22	<0.001*	0.15	-0.77	Ellwood et al. 2010
Kathleen Anderson, Middleborough, MA	1970–2002	February, March	16	<0.05*	0.24–0.43	-2.5–6.2	Ledneva et al. 2004
Quackenbush	1940–2012	March, April	9	0.286	ns	ns	This study
Flowering							
Hosmer	1878–1902	January, April, May	296	<0.001*	0.84	-3.28	Miller-Rushing and Primack 2008
Thoreau, Hosmer, Miller-Rushing	1852–2008	January, April, May	43	<0.001*	0.61	-3.07	Miller-Rushing and Primack 2008
Thoreau, Hosmer, Miller-Rushing, (native species)	1852–2008	January, April, May	33	<0.001*	0.59	-2.93	Miller-Rushing and Primack 2008
Thoreau, Hosmer, Ellwood (native species)	1852–2012	March, April, May	32	<0.001*	0.75	-3.16 (0.35)	Ellwood et al. 2013
Quackenbush	1945*1957	April	15	<0.001*	0.70	-2.53 (0.5)	This study
Leaf-out							
Polgar field study	2009–2012	March, April	3	<0.001*	0.75	-6.10	Polgar et al. 2013
Polgar experimental warming	2009–2010	March, April	3	<0.01*	0.47	-2.10	Polgar et al. 2013
Polgar remote sensing	2003–2011	March, April	4	0.01*	0.70	-3.70	Polgar et al. 2013
Everill herbarium specimens	1834–2008	April	1558	<0.001*	0.15	-3.22	Everill et al. 2013
Quackenbush	1940–1955	April	10	<0.001*	0.49	-2.30 (0.6)	This study

England, plants are more responsive to spring temperatures than migratory bird arrivals, underscoring a common potential asynchrony between these trophic levels.

Global trends in spring phenology

L.S. Quackenbush's observations add Aroostook County, ME, to the list of locations with observation-based phenological datasets. The phenological trends captured in Quackenbush's journals match global shifts in spring events, echoing the global ecological effects of climate change while bringing attention to an understudied corner of the New England region.

We found that Quackenbush's dates of first flower and leaf-out were highly correlated with mean April temperatures in the mid-20th century (Fig. 1). In Oxbow, date of first flower advanced 2.5 d/°C, while date of leaf-out advanced 2.3 d/°C. These results from Aroostook County agree with the general trends in spring plant phenology observed globally in temperate deciduous forests. Shifts

Table 4. Species-level linear models of flowering phenology and spring temperatures from the New England region. An asterisk (*) denotes a significant *P*-value. Where available, standard error for regression coefficients is included in parentheses in days/°C column.

Species	Temperature	*P* value	Days/°C	R^2	Citation
Bunchberry	April	0.016*	-3.7 (1.2)	0.54	This study
Bunchberry	January, March, April	<0.05*	-4.4	0.62	Miller-Rushing and Primack 2008
Bunchberry	March, April, May	<0.01*	-3.3 (0.9)	0.36	Ellwood et al. 2013
Canada Mayflower	April	0.021*	-3.5 (1.2)	0.46	This study
Canada Mayflower	January, March, April	<0.05*	-3.4	0.63	Miller-Rushing and Primack 2008
Wild Strawberry	April	0.002*	-3.1 (0.7)	0.69	This study
Wild Strawberry	March, April, May	<0.001*	-4.2 (1.4)	0.33	Ellwood et al. 2013

Table 5. Species-level linear models of migratory bird phenology and spring temperatures from the New England region. An asterisk (*) denotes a significant *P*-value.

Species	Temperature	*P* value	Days/°C	Citation
Black-throated Blue Warbler	March, April	0.702	-0.25	This study
Black-throated Blue Warbler	March, April	0.003*	-3.67	Miller-Rushing et al. 2008c
Chestnut-sided Warbler	March, April	0.925	-0.12	This study
Chestnut-sided Warbler	March, April	0.556	-0.96	Miller-Rushing et al. 2008c
Eastern Kingbird	March, April	0.456	-1.07	This study
Eastern Kingbird	March, April	0.228	-0.47	Ellwood et al. 2010
Least Flycatcher	March, April	0.005*	-3.22	This study
Least Flycatcher	March, April	0.090	3.66	Miller-Rushing et al. 2008c
Least Flycatcher	March, April, May	0.175	-0.13	Miller-Rushing et al. 2008b
Red-eyed Vireo	March, April	0.551	-1.21	This study
Red-eyed Vireo	March, April	0.717	0.18	Ellwood et al. 2010
Red-eyed Vireo	March, April	0.034*	-3.84	Miller-Rushing et al. 2008c
Red-eyed Vireo	March, April, May	0.158	-0.06	Miller-Rushing et al. 2008b
White-crowned Sparrow	March, April	0.258	-1.09	This study
White-crowned Sparrow	March, April	0.124	-3.17	Miller-Rushing et al. 2008c

in flowering dates are a well-documented response to changes in spring temperatures; this trend has been found in observational records and experimental manipulations in temperate deciduous and boreal forest sites across the globe (Miller-Rushing and Primack 2008, Rice et al. 2018, Wolkovich et al. 2012). Observational data, experimental studies, and remote-sensing data similarly connect advancing leaf-out dates and green up with warming spring temperatures (Cleland et al. 2007, Korner and Basler 2010, Polgar et al. 2013). Though plant phenology studies are widespread, few have recorded both leaf-out and flowering data at the same site (but see Ettinger et al. 2018, McDonough MacKenzie et al. 2019b). Oxbow, ME, is unique: the Quackenbush journal provides records on both leaf-out and flowering phenology—as well as migratory bird arrivals—from a site that is generally overlooked in phenology research.

The migratory bird species we analyzed in Quackenbush's journals have shifted their spring arrivals earlier, from 23 May in the mid-20th century to 14 May today, but this shift is not correlated with spring temperatures (Fig. 1). Globally, patterns in migratory bird arrival phenology are less consistent than patterns in plant phenology. Shifts in the arrival dates of migratory birds were among the first documented signs of the ecological effects of climate change in the late 20th century (Parry et al. 2007, Walther et al. 2002). Although migratory birds generally advanced their arrival dates over time and in response to warming temperatures, these arrival dates may not be shifting fast enough to keep up with changes in the phenology of the birds' insect food sources, and there is potential for trophic mismatches in phenology (Visser 2016, Visser and Both 2005). For example, in eastern North America, mist-netting data from Pennsylvania and Ontario calculated advancing spring bird migration at 1 d/°C, while *Syringa vulgaris* L. (Lilac) flower dates in the same area were 3 times more responsive to spring temperatures (Marra et al. 2004). We observed a similar divergence in phenological sensitivity here: the plants in Aroostook were responsive to spring temperatures, while migratory birds were not (Fig. 1).

Aroostook County vs. New England

Adding Aroostook County to the list of locations with phenology datasets facilitates new research, including comparing phenological change across sites within the same region. Recent research documenting variation in phenological shifts at the population level has opened new questions around intraspecific variation and phenological plasticity (McDonough MacKenzie et al. 2018, Prevéy et al. 2017, Vitasse et al. 2017). These variations have implications for range shifts and invasions; if plants are responding to climate change at different rates in d/°C across their range, some populations may be more or less vulnerable to climate change.

The Quackenbush journals reveal trends in flowering and leaf-out phenology that match the direction of phenological shifts observed in southern New England, but at a slower rate. In Quackenbush's Oxbow, the date of first flower advanced 2.5 d/°C; in Thoreau's Concord, the date of first flower advanced 3.2 d/°C (Ellwood et al. 2013). Leaf-out advanced 2.3 d/°C in Oxbow, and 6.1 d/°C in Concord (Polgar et al. 2013). Our community-wide comparisons were limited because our study comprised different species than those in Concord, but we also found evidence at the species-level that plants in Oxbow may be less responsive than their conspecifics in Concord (Table 4).

Our results contrast with our expectation that higher latitudes (i.e., northern Maine) will experience greater phenological changes than lower latitudes (i.e. southern New England), as more intense warming is predicted to occur at higher latitudes (Bertin 2008). Reviews of global phenology data disagree if higher latitude sites are generally experiencing greater phenological shifts (Parmesan 2007, Root et al. 2003). Within the New England region, plant phenology in Concord seems more responsive to spring temperatures (i.e., advancing at a greater rate in d/°C) than the same species in Acadia National Park, ME (McDonough MacKenzie et al. 2019b). Why is plant phenology in Concord advancing at a faster rate? This response could be an artifact of the study period and/or land-use history. Perhaps northern Maine in the mid-20th century did not experience enough interannual variation in spring temperatures to reveal a stronger advancing phenology trend. Indeed, a review of observational studies of plant phenology found that the most pronounced flowering and leaf-out shifts have been recorded since the 1970s and 1980s (Bertin 2008). The divergent land-use histories of southern New England and northern Maine may also explain the paradoxical latitudinal signal of more responsive phenology. Plant communities in Concord have been exposed to development pressures and urban heat-island effects that are absent from Oxbow (Primack et al. 2009).

It is also possible that our comparisons captured a true difference and that populations in southern New England simply have a stronger response to changes in temperature. More northern populations may experience greater risk of frost damage if their phenology shifts in response to "false spring" events (Augspurger 2009, Inouye 2008, Muffler et al. 2016). In contrast, species in in southern New England have a longer growing season in which to recover from spring frost damage but may be under greater pressure to compete for light availability and visibility to pollinators through shifting phenology (Heberling et al. 2019). Continued monitoring in Aroostook county and other northern sites could help clarify (or dispute) differences in rates of response between plants in northern and southern New England.

Quackenbush's journals allow us to explore trends in spring arrivals of migratory birds over the past 70 y; these data are an invaluable compliment to the ongoing study of migratory bird arrivals across Maine, led by H. Wilson (Colby College, Waterville, ME). Aroostook county is traditionally underrepresented in the observations collected by Wilson, and the biophysical region including Oxbow has been excluded from a series of state-wide analyses, in part due to lack of data (Wilson 2007, Wilson et al. 2000), or included with many fewer observations (Wilson 2017). Analyses of arrival dates for migratory breeding birds in Maine found that the majority of species showed no significant difference in arrival date across the state: arrival times were generally synchronized within Maine, regardless of the location of the observer. However, species without synchronized arrival dates tended to have significantly later arrival dates in northern Aroostook county (Wilson 2017, Wilson et al. 2000). When we compared observations collected by volunteers from the excluded biophysical region (i.e., Aroostook County) to our results, the species in Quackenbush's journals were too sparsely represented in Wilson's data for statistical analysis (H. Wilson, pers. comm.). We also compared the Quackenbush data with bird arrival records from southern New England and found few species-level significant relationships between arrival date and spring temperatures scattered among 4 studies; no species had more than one study identifying a significant trend indicating a generally weak association between arrival phenology and temperature (Table 5).

Across New England, there is a clear trend in advancing leaf-out and flowering phenology. In contrast, migratory bird arrivals do not seem to be shifting as consistently or rapidly as the plant phenologies in the region. As these trophic levels respond to climate change at different rates and to different degrees, species interactions and community composition are likely to shift in novel and unexpected ways (CaraDonna et al. 2014, Kharouba et al. 2018, Visser and Both 2005). The asynchrony found in Oxbow—advancing leaf-out and flowering, but unresponsive migratory bird arrivals—has the potential to create trophic mismatches and disrupt ecological relationships. Uneven phenological responses to warming across a community may have implications for competition, pollination, trophic interactions, and ultimately community structure and stability (Cahill et al. 2012, Cleland et al. 2007). Site-level comparisons of phenological datasets within the region reveal differences in responsiveness across sites (i.e. Concord plants are shifting faster than Oxbow plants), but also underscore the region-wide pattern that plants are shifting faster than birds.

Limitations of Historical Ecological Data

The "first of spring" observations that Quackenbush recorded and later indexed from his own journals are typical of those commonly noted among amateur naturalists (Primack and Miller-Rushing 2012, Vellend et al. 2013). However, these are extreme phenological events, and shifts in "first" dates may not accurately reflect the phenological behavior of the entire population (CaraDonna et al. 2014, Miller-Rushing, et al. 2008a). Across trophic levels and phenophases, studies have repeatedly shown that mean dates, peak dates, and estimates of duration are better metrics for long-term phenological trends. First arrivals are likely to be affected by migratory cohort size (Miller-Rushing et al. 2008b), while changes in population size confound changes in first flower date (Miller-Rushing et al. 2008a). Although mean, peak, and duration metrics are ideal, historical records often document exclusively first arrival dates (Kolarova et al. 2017) or first flowering dates (Primack and Miller-Rushing 2012), as in the Quackenbush journals.

Our migratory bird analysis may also be limited by differences in the methods behind Quackenbush and Sheehan's observations. Sheehan's annual observations of migratory bird arrivals in Aroostook County cover a much wider geographic area than Quackenbush's notes in Oxbow. The shift toward earlier arrival dates could simply be a product of this expanded search; Sheehan's observations from across the county include a greater range of microclimates and locations that may attract migratory birds before they arrive in Oxbow in any given year. The local mean spring temperatures have not significantly changed since Quackenbush's time; thus, it is possible the birds are tracking temperature, and the shift in arrival dates noted here may be an artifact of the difference in methods between Quackenbush and Sheehan.

Though we know that Quackenbush wrote in his journals almost daily, we do not have a clear understanding of his methods or a measure of his sampling effort. This limitation is common among studies that utilize volunteer or amateur naturalist data (Miller-Rushing et al. 2008c). We assume that Quackenbush's place-based knowledge and extensive recording reflect natural history knowledge. At the very least, Quackenbush's journal provides imperfect observations of migratory bird arrivals, leaf-out, and flowering in a remote location that has been previously excluded from phenology research. Perhaps the Quackenbush journals and their origin story will inspire others to dust off diaries and records from their attics and expand the network of amateur naturalist datasets.

Conclusions

It is unlikely that Quackenbush set out to initiate a study on climate change when he indexed his daily observations in tables of migratory bird arrival, leaf-out, and flowering phenology 70 y ago. His records are a unique historical ecological dataset from an understudied area. Here, we present evidence that the region's migratory birds are not in sync with advancing leaf-out and flowering phenology. We also note that plants in northern New England seem to respond more slowly (in d/°C) to warming spring temperatures when compared to southern New England. If this is the case, data from southern New England may not be used to accurately predict phenological shifts in Maine, even in the case of conspecifics. Underappreciated sources of historical ecological data, including the journals of a hunting guide from a remote, rural county in Maine, allow ecologists to rapidly assess changes in phenology. Identifying new historical ecological data sources and adding contemporary observations to datasets like the Quackenbush journals will improve our understanding of intraspecific variation in phenology and potential asynchronies between migratory birds and the vegetation at their breeding sites.

Acknowledgments

We thank College of the Atlantic, especially J. Anderson and B. Wheeler, for uncovering and sharing and A. Derkacz for digitizing the Quackenbush journals. R. King and K. Pontbriand provided additional support at Acadia National Park's curatorial center. C. McDonough MacKenzie was supported by funding from NSF (DEB-1501266), New England Botanical Club, Waterman Fund, and Schoodic Institute. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Department of Interior or the US Government.

Literature Cited

Augspurger, C.K. 2009. Spring 2007 warmth and frost: Phenology, damage, and refoliation in a temperate deciduous forest. Functional Ecology 23:1031–1039.

Bertin, R.I. 2008. Plant phenology and distribution in relation to recent climate change. The Journal of the Torrey Botanical Society 135:126–146.

Cahill, A.E., M.E. Aiello-Lammens, M.C. Fisher-Reid, X. Hua, C.J. Karanewsky, H. Yeong Ryu, G.C. Sbeglia, F. Spagnolo, J.B. Waldron, O. Warsi, and J.J. Wiens. 2012. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280:20121890–20121890.

CaraDonna, P.J., A.M. Iler, and D.W. Inouye. 2014. Shifts in flowering phenology reshape a subalpine plant community. Proceedings of the National Academy of Sciences of the United States of America 111:4916–4921.

Cleland, E., I. Chuine, A. Menzel, H. Mooney, and M. Schwarts. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

Daru, B.H., D.S. Park, R.B. Primack, C.G. Willis, D.S. Barrington, T.J.S. Whitfeld, T.G. Seidler, P.W. Sweeney, D.R. Foster, A.M. Ellison, and C.C. Davis. 2017. Widespread sampling biases in herbaria revealed from large-scale digitization. New Phytologist 217:939–955.

Ellwood, E.R., R.B. Primack, and M.L. Talmadge. 2010. Effects of climate change on spring arrival times of birds in Thoreau's Concord from 1851 to 2007. The Condor 112:754–762.

Ellwood, E.R., S.A. Temple, R.B. Primack, N.L. Bradley, and C.C. Davis. 2013. Record-breaking early flowering in the eastern United States. PloS one 8:e53788.

Ettinger, A.K., S. Gee, and E.M. Wolkovich. 2018. Phenological sequences: How early-season events define those that follow. American Journal of Botany 105:1–10.

Everill, P.H., R.B. Primack, and E.R. Ellwood. 2014. Determining past leaf-out times of New England's deciduous forests from herbarium specimens. American Journal of Botany 101:1293–1300.

Fernandez, I.J., C.V. Schmitt, S.D. Birkel, E. Stancioff, A.J. Pershing, J.T. Kelley, J.A. Runge, G.L. Jacobson, and P.A. Mayewski. 2015. Maine's Climate Future: 2015 Update. University of Maine, Orono, ME. 24 pp.

Fitter, A.H., and R.S.R. Fitter. 2002. Rapid changes in flowering time in British plants. Science 296:1689–1691.

Gallinat, A.S., R.B. Primack, C.G. Willis, B. Nordt, A.D. Stevens, R. Fahey, A.T. Whittemore, Y. Du, and Z.A. Panchen. 2018. Patterns and predictors of fleshy fruit phenology at five international botanical gardens. American Journal of Botany 105:1824–1834.

Heberling, J.M., C. McDonough MacKenzie, J.D. Fridley, S. Kalisz, and R.B. Primack. 2019. Phenological mismatch with trees reduces wildflower carbon budgets. Ecology Letters 22:616–623. DOI:10.111/ele.13224.

Inouye, D.W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Judd, R.W. 1984. Lumbering and the farming frontier in Aroostook County, Maine, 1840–1880. Journal of Forest History 28:56–67.

Karmalkar, A.V., and R.S. Bradley. 2017. Consequences of global warming of 1.5 °C and 2 °C for regional temperature and precipitation changes in the contiguous United States. PloS one 12:e0168697–17.

Kharouba, H.M., J. Ehrlén, A. Gelman, K. Bolmgren, J.M. Allen, S.E. Travers, and E.M. Wolkovich. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences 124:201714511–201714516.

Kolarova, E., M. Matiu, and A. Menzel. 2017. Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries. International Journal of Biometeorology 61:1279–1289.

Korner, C., and D. Basler. 2010. Response: Warming, photoperiods, and tree phenology. Science 329:278–278.

Ledneva, A., A.J. Miller-Rushing, R.B. Primack, and C. Imbres. 2004. Climate change as reflected in a naturalist's diary, Middleborough, Massachusetts. The Wilson Bulletin 116:224–231.

Marra, P.P., C.M. Francis, R.S. Mulvihill, and F.R. Moore. 2004. The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315.

McDonough MacKenzie, C., R.B. Primack, and A.J. Miller-Rushing. 2018. Local environment, not local adaptation, drives leaf-out phenology in common gardens along an elevational gradient in Acadia National Park, Maine. American Journal of Botany 105:986–995.

McDonough MacKenie, C., G. Mittelhauser, A.J. Miller-Rushing, and R.B. Primack. 2019a. Floristic change in New England and New York: regional patterns of plant species loss and decline. Rhodora 121(985):1–36.

McDonough MacKenzie, C., R.B. Primack, and A.J. Miller-Rushing. 2019b. Trails-as-transects: Phenology monitoring across heterogeneous microclimates in Acadia National Park, Maine. Ecosphere 10(3):e02626.

Miller-Rushing, A.J., and R.B. Primack. 2008. Global warming and flowering times in Thoreau's Concord: A community perspective. Ecology 89:332–341.

Miller-Rushing, A.J., R.B. Primack, D. Primack, and S. Mukunda. 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. American Journal of Botany 93:1667–1674.

Miller-Rushing, A.J., D.W. Inouye, and R.B. Primack. 2008a. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. Journal of Ecology 96:1289–1296.

Miller-Rushing, A.J., T. Lloyd Evans, R.B. Primack, and P. Satzinger. 2008b. Bird migration times, climate change, and changing population sizes. Global Change Biology 14:1959–1972.

Miller-Rushing, A.J., R.B. Primack, and R. Stymeist. 2008c. Interpreting variation in bird migration times as observed by volunteers. The Auk 125:565–573.

Muffler, L., C. Beierkuhnlein, G. Aas, A. Jentsch, A.H. Schweiger, C. Zohner, and J. Kreyling. 2016. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the Northern Hemisphere. Global Ecology and Biogeography 25:1061–1071.

Panchen, Z.A., R.B. Primack, T. Aniśko, and R.E. Lyons. 2012. Herbarium specimens, photographs, and field observations show Philadelphia area plants are responding to climate change. American Journal of Botany 99:751–756.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860–1872.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Parry, M.L., J.P. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson (Eds.). 2007. Climate Change 2007. Intergovernmental Panel on Climate Change, Cambrige, UK. 987 pp.

Polgar, C.A., and R.B. Primack. 2011. Leaf-out phenology of temperate woody plants: From trees to ecosystems. New Phytologist 191:926–941.

Polgar, C., A. Gallinat, and R.B. Primack. 2014. Drivers of leaf-out phenology and their implications for species invasions: Insights from Thoreau's Concord. New Phytologist 202:106–115.

Prevéy, J., M. Vellend, N. Rüger, R.D. Hollister, A.D. Bjorkman, I.H. Myers-Smith, S.C. Elmendorf, K. Clark, E.J. Cooper, B. Elberling, A.M. Fosaa, G.H.R. Henry, T.T. Høye, I.S. Jónsdóttir, K. Klanderud, E. Lévesque, M. Mauritz, U. Molau, S.M. Natali, S.F. Oberbauer, Z.A. Panchen, E. Post, S.B. Rumpf, N.M. Schmidt, E.A.G. Schuur, P.R. Semenchuk, T. Troxler, J.M. Welker, and C. Rixen. 2017. Greater temperature sensitivity of plant phenology at colder sites: Implications for convergence across northern latitudes. Global Change Biology 23:2660–2671.

Primack, R.B., and A.J. Miller-Rushing. 2012. Uncovering, collecting, and analyzing records to investigate the ecological impacts of climate change: A template from Thoreau's Concord. BioScience 62:170–181.

Primack, D., C. Imbres, R.B. Primack, A.J. Miller-Rushing, and P. Del Tredici. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. American Journal of Botany 91:1260–1264.

Primack, R., A. Miller-Rushing, and K. Dharaneeswaran. 2009. Changes in the flora of Thoreau's Concord. Biological Conservation 142:500–508.

Polgar, C.A., R.B. Primack, J.S. Dukes, C. Schaaf, Z. Wang, and S.S. Hoeppner. 2014. Tree leaf-out response to temperature: Comparing field observations, remote sensing, and a warming experiment. International Journal of Biometeorology 58(6):1251–1257.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, K.E., R.A. Montgomery, A. Stefanski, R.L. Rich, and P.B. Reich. 2018. Experimental warming advances phenology of groundlayer plants at the boreal–temperate forest ecotone. American Journal of Botany 69:491–11.

Richardson, A.D., B.H. Braswell, D.Y. Hollinger, J.P. Jenkins, and S.V. Ollinger. 2009. Near-surface remote sensing of spatial and temporal variation in canopy phenology. Ecological Applications 19:1417–1428.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

US Census Bureau. 2010. Geographic identifiers: 2010 demographic profile data (G001): Oxbow Plantation, Aroostook County, Maine. Available online at https://factfinder.census.gov/faces/tableservices/jsf/pages/productview.xhtml?src=bkmk. Accessed October 2016.

Vellend, M., C.D. Brown, H.M. Kharouba, J.L. McCune, and I.H. Myers-Smith. 2013. Historical ecology: Using unconventional data sources to test for effects of global environmental change. American Journal of Botany 100:1294–1305.

Visser, M.E. 2016. Phenology: Interactions of climate change and species. Nature 535:236.

Visser, M.E., and C. Both. 2005. Shifts in phenology due to global climate change: The need for a yardstick. The Royal Society 272:2561–2569.

Vitasse, Y., C. Signarbieux, and Y.H. Fu. 2017. Global warming leads to more uniform spring phenology across elevations. Proceedings of the National Academy of Sciences 9:201717342–201717345.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wilson, W., Jr. 2017. The Dynamics of Arrivals of Maine migratory breeding birds: Results from a 24-year study. Biology 6:38–17.

Wilson, W.H.J. 2007. Spring arrival dates of migratory breeding birds in Maine: Sensitivity to climate change. 119:665–677.

Wilson, W.H.J., D. Kipervaser, and S. Lilley. 2000. Spring arrival dates of Maine migratory breeding birds: 1994–1997 vs. 1899–1911. Northeastern Naturalist 7:1–7.

Wolkovich, E.M., B.I. Cook, J.M. Allen, T.M. Crimmins, J.L. Betancourt, S.E. Travers, S. Pau, J. Regetz, T.J. Davies, N.J.B. Kraft, T.R. Ault, K. Bolmgren, S.J. Mazer, G.J. McCabe, B.J. McGill, C. Parmesan, N. Salamin, M.D. Schwartz, and E.E. Cleland. 2012. Warming experiments underpredict plant phenological responses to climate change. Nature 485:494–497.