

HISTORICAL PERSPECTIVE

Comparing fruiting phenology across two historical datasets: Thoreau's observations and herbarium specimens

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• **Background and Aims** Fruiting remains under-represented in long-term phenology records, relative to leaf and flower phenology. Herbarium specimens and historical field notes can fill this gap, but selecting and synthesizing these records for modern-day comparison requires an understanding of whether different historical data sources contain similar information, and whether similar, but not equivalent, fruiting metrics are comparable with one another.

• **Methods** For 67 fleshy-fruited plant species, we compared observations of fruiting phenology made by Henry David Thoreau in Concord, Massachusetts (1850s), with phenology data gathered from herbarium specimens collected across New England (mid-1800s to 2000s). To identify whether fruiting times and the order of fruiting among species are similar between datasets, we compared dates of first, peak and last observed fruiting (recorded by Thoreau), and earliest, mean and latest specimen (collected from herbarium records), as well as fruiting durations.

• **Key Results** On average, earliest herbarium specimen dates were earlier than first fruiting dates observed by Thoreau; mean specimen dates were similar to Thoreau's peak fruiting dates; latest specimen dates were later than Thoreau's last fruiting dates; and durations of fruiting captured by herbarium specimens were longer than durations of fruiting observed by Thoreau. All metrics of fruiting phenology except duration were significantly, positively correlated within (r : 0.69–0.88) and between (r : 0.59–0.85) datasets.

• **Conclusions** Strong correlations in fruiting phenology between Thoreau's observations and data from herbaria suggest that field and herbarium methods capture similar broad-scale phenological information, including relative fruiting times among plant species in New England. Differences in the timing of first, last and duration of fruiting suggest that historical datasets collected with different methods, scales and metrics may not be comparable when exact timing is important. Researchers should strongly consider matching methodology when selecting historical records of fruiting phenology for present-day comparisons.

Key words: Thoreau, herbaria, museum specimen, woody, herbaceous, Weibull, New England, fruit, ripening, plant, phenology.

INTRODUCTION

In contrast to climate-driven changes in leaf-out and flower phenology, which have been well studied (Primack *et al.*, 2004; Menzel *et al.*, 2006; Cleland *et al.*, 2007; Bertin, 2008; Miller-Rushing and Primack, 2008; Panchen *et al.*, 2012; Polgar *et al.*, 2013; Everill *et al.*, 2014; Ellwood *et al.*, 2019), climate-driven changes in fruiting phenology have been relatively neglected in ecological research (Bertin, 2008; Gallinat *et al.*, 2015). Fruiting is vitally important to the reproductive success of plants and to many animals that rely on wild fruits for nutrition (Primack, 1987; Willson and Whelan, 1993; Parrish, 1997; Tiffney, 2004; Smith *et al.*, 2013). Several studies have found that fruiting times are advancing with warmer temperatures (Menzel *et al.*, 2006; Sherry *et al.*, 2007; Gordo and Sanz, 2010; Panchen and Gorelick, 2015), although not in all cases (Menzel *et al.*, 2006; Sherry *et al.*, 2007). Historical phenology records have been instrumental for studying changes in leaf-out

and flowering times, but fewer historical data sources exist to investigate similar patterns for wild fruits.

Herbaria are increasingly being used to study how phenology is changing in the context of climate change (Meineke *et al.*, 2018; Lang *et al.*, 2019). The temporal, spatial and taxonomic breadth of herbarium specimens make them a strong resource in understanding broad trends in phenological change (Heberling and Isaac, 2017; Meineke *et al.*, 2019). Herbarium specimens and historical field notes can fill gaps in our understanding of fruiting phenology by providing historical dates representing the beginning, middle and end of fruiting, but their methodological eccentricities could present challenges for interpreting, comparing and synthesizing the information these different data sets provide.

As researchers increase efforts to understand changes in fruiting phenology, it is important to determine how we can use and compare historical datasets. Historical datasets collected

with different methods, comprising different fruiting metrics, and collected across different geographical scales may reflect different ecological patterns (Pearse *et al.*, 2017). If there are method, metric or scale issues that limit comparison, then researchers need to be careful and deliberate in collecting present-day data with similar methods, metrics and scales for comparison with these historical datasets. For instance, if herbaria and field observations capture different historical patterns, then historical herbarium records would not be an accurate historical basis to compare with present-day observations. Studies have successfully compared field observations and herbarium records of flowering dates (Panchen *et al.*, 2012; Davis *et al.*, 2015); however, there is less certainty that these data sources are comparable for fruiting phenology.

One challenge for synthesizing field observations and herbarium records is that these methods rely on different fruiting metrics (e.g. peak fruiting date versus mean fruiting date), which may or may not be comparable. Potential field observation metrics include first fruiting date (Menzel *et al.*, 2006; Sherry *et al.*, 2007; Gordo and Sanz, 2010; Ettinger *et al.*, 2018; Gallinat *et al.*, 2018b), peak fruiting date (Sherry *et al.*, 2007; Ettinger *et al.*, 2018; Gallinat *et al.*, 2018a, b), last fruiting date (Sherry *et al.*, 2007; Gordo and Sanz, 2010; Gallinat *et al.*, 2018b) and the total duration of fruiting (Sherry *et al.*, 2007). However, there are still gaps in our understanding of community fruiting patterns of plants in the wild and during longer time periods, and historical data from observations in the wild and herbarium specimens collected from wild plants can help to fill those gaps. Herbarium collections are based on methods different from those used to make field observations; for example, collectors are not always gathering specimens with the intention to capture first fruiting dates or other phenophases, whereas field observations are often conducted to do just that. Herbarium specimens are collected more frequently in spring and summer, so they may fail to accurately capture the end of fruiting seasons (Daru *et al.*, 2017). In addition, herbaria contain a range of specimens that can be used to infer different metrics: earliest specimen to be collected in the season among all of the specimens, mean date of collection among all of the specimens, and last specimen collected among all of the specimens, instead of start, peak and end of fruiting over the course of a season at a location. It is not clear whether metrics using herbarium specimens are comparable with field observation metrics, as they do not directly capture the same phenophases. There are few historical datasets on wild fruits available, so it is important for researchers to know how to work with these differences and synthesize or choose between historical datasets.

Researchers have successfully used historical observations to identify how different functional groups have shifted with climate change in relation to one another and to explore the ecological consequences of these shifts (Heberling *et al.*, 2019). This research requires that historical records provide a reliable baseline for comparison, and one way to assess the comparability of observations and herbarium specimens is to determine if they provide similar baseline information, such as historical differences or similarities between fruiting times for woody and herbaceous species. While woody and herbaceous species differ in their leaf-out (Rich *et al.*, 2008; Rollinson and Kaye, 2012) and flowering (Miller-Rushing and Primack, 2008) times, it is unknown whether these functional groups

differ in their fruiting times in temperate ecosystems (but see Giorgetti *et al.*, 2000 for a comparison from a semiarid region). The extent to which these historical records reflect similar or different patterns among groups can indicate the resilience of these patterns to methods of collection, how much these patterns might depend on spatial and temporal scaling, and what methods should be used to compare these groups in the present day to detect true shifts due to climate change or other aspects of a changing environment.

To assess the comparability of different historical datasets for fruiting phenology, we compared observations made by Henry David Thoreau with data collected from herbarium specimens. Observations made by Thoreau in Concord, Massachusetts, in the 1850s have been used to study the effects of climate change on leaf-out, flowering and bird migration (Miller-Rushing and Primack, 2008; Ellwood *et al.*, 2010; Polgar *et al.*, 2013). In 2001, a previously unpublished collection of Thoreau's fruiting observations of wild plants was released (Thoreau, 2001), expanding the opportunities for the use of Thoreau's data to include investigations of fruiting phenology. Herbarium specimens, which contain vast amounts of information on plant species and their phenological life stages (Davis *et al.*, 2015; Willis *et al.*, 2017), can also serve as a source of fruit phenology data (Gallinat *et al.*, 2018a). Specimens are rapidly being digitized for easier access (Soltis, 2017; Daru *et al.*, 2017; Yost *et al.*, 2018; Panchen *et al.*, 2019) and can enable researchers to examine fruiting records from a larger geographical range and longer timespan than is feasible with field studies (Willis *et al.*, 2017).

These two fruit phenology datasets – Thoreau's field observations and data from herbarium specimens – represent an opportunity to compare fruiting patterns and metrics in different historical datasets. Thoreau's observations capture fruiting phenology as first, peak and last fruiting dates; similar, but not equivalent, metrics from herbaria are the earliest, mean and latest specimens of the season among all of the specimens collected of a species. The datasets are similar in that they both assessed large numbers of the same species in New England; however, they differ in geographical and temporal range and collection method. Previous work using herbarium specimens showed that while fruiting times became slightly later (0.1 d per year) over 165 years in New England, geographical location is not a significant predictor of fruiting times (Gallinat *et al.*, 2018a). We therefore focus here on methodological differences between data sources, though we also acknowledge and consider the effects of sampling differences on the results of our comparison.

While the different metrics used in herbarium-based data and field observations could capture different ecological patterns, novel statistical tools have the potential to minimize these differences. The Weibull method developed by Pearse *et al.* (2017) is a technique for estimating true first dates from existing observations, using a Weibull distribution. When collecting data on phenological events, there is a low likelihood of capturing the very first event; for instance, it may occur at an earlier time or in a location different from that where data are collected. The Weibull method uses existing observations to estimate when the true first date may be and has primarily been used to estimate first flowering dates (Pearse *et al.*, 2017). Here, we test this new method with herbarium fruiting data to estimate 'true' earliest

fruiting dates, and test whether these dates are more similar to Thoreau's observed first fruiting dates than are the earliest herbarium specimen dates.

In this study, we address the following questions:

- (1) How does the order of fruiting, for the same species, compare between Thoreau's field observations and herbarium specimens?
- (2) How strongly correlated are the metrics of fruiting phenology within each dataset, and how do similar but not equivalent metrics compare across datasets (e.g. first fruiting versus earliest herbarium specimen date, and peak fruiting versus mean specimen date)?
- (3) Does the Weibull method for estimating true first dates from herbarium data increase the comparability of these data with Thoreau's field observations?
- (4) Are the differences or similarities in fruiting phenology between woody and herbaceous species similar between these two datasets?

Answers to these questions will allow future researchers to optimize the use of historical datasets when studying how fruiting phenology responds to climate change.

MATERIALS AND METHODS

Metrics of fruiting phenology

For herbarium specimens, we use the date of the earliest and latest ripe fruit observation across all seasons, and we calculate mean fruiting date for each species across all specimens in all years. Thoreau provides fruiting observations from Concord in a style that we can readily interpret as first (first observation), peak ('prime') or last ('finished', 'last through') fruiting dates, though he does not provide any description of his methods of observation or reporting. For some species he does not provide the year of observation, whereas for other species he lists one or more years of observation. The duration of fruiting is calculated as the time from first fruiting date to last fruiting date. The progression of fruiting stages provided by both Thoreau's records and herbarium specimens does not reflect measurements of individuals or species within a single fruiting season; instead, these observations are drawn from different individuals across the range of years and locations.

Thoreau's observations

Henry David Thoreau made observations of fruiting phenology in and near Concord, Massachusetts, over an 11-year period from 1850 to 1860. We compiled Thoreau's observations of first fruiting dates from his book *Wild fruits* (Thoreau, 2001) for 72 native plant species that have fleshy fruits. Of these species, he also recorded peak dates for 31 species and last dates for 29 species. Thoreau generally recorded one date per species for each metric of first, peak and last dates. When Thoreau recorded imprecise dates (e.g. 'middle July' or 'end of August'), we assigned dates using a standard rubric (Table 1). Thoreau recorded exact dates for all first dates, 29 of 31 peak dates and 3 of 29 last dates.

TABLE 1. Standard rubric for assigning dates for Thoreau's descriptions of fruiting timing. All dates from January and February of the following year were characterized as 31 December (day of year 365) to indicate in the analyses that these fruiting events were late in the season, not extremely early in the season

Thoreau's description	Assigned date	Day of year
'Middle July'	15 July	196
'Late July'	30 July	211
'Through July'	30 July	211
'August'	15 August	227
'Middle August'	15 August	227
'End of August'	30 August	242
'Till September'	1 September	244
'Early September'	5 September	248
'Into September'	10 September	253
'Middle September'	15 September	258
'Through September'	30 September	273
'Early October'	5 October	278
'Through October'	30 October	303
'November'	15 November	319

Herbarium specimens

For the same species that Thoreau observed, we inspected herbarium specimens in person and online for most woody species and exclusively online for herbaceous species and the remaining woody species (Fig. 1). We accessed digitized versions of specimens from the Consortium of Northeastern Herbaria (<http://portal.neherbaria.org>), Harvard University Herbarium (<http://huh.harvard.edu>), University of Connecticut Herbarium (<http://bgbaseserver.eeb.uconn.edu>) and iDigBio portal (<https://www.idigbio.org/portal>). Thirty-one of the study species had already been evaluated for phenology and included in a recent study (Gallinat *et al.*, 2018a), and for an additional 41 species we evaluated the presence of fruits using the same protocols: fruits were determined to be ripe based on a combination of colour, size and apparent texture when the specimen was pressed. If the specimen had ripe fruits, we recorded the date, location, collector and herbarium. We collected data from specimens across New England (Massachusetts, Rhode Island, Connecticut, Vermont, New Hampshire and Maine) (Fig. 2) and across the timespan of available specimens (mid-1800s to early 2000s) (Fig. 3).

We excluded specimens that were collected at the same location on the same day in order to not over-represent areas with high sampling effort. We excluded three species that Thoreau monitored which have fruit year-round and for which it is difficult to determine if the fruits on the specimens are from the previous year or the current year: *Gaultheria procumbens*, *Juniperus virginiana* and *Mitchella repens*. We also excluded two species for which it is difficult to distinguish ripe from unripe fruits: *Peltandra virginica* and *Symplocarpus foetidus*.

For the final analyses, we used 67 species, of which 65 were native species and 2 were non-native species, with data collected from 3432 herbarium specimens of these same species (Supplementary Data Table 1). Of the specimens, 2264 were from woody plants and 1168 were from herbaceous plants. Species' herbarium specimen sample sizes ranged from 20 (*Sassafras albidum*) to 181 (*Vaccinium angustifolium*). For comparisons with Thoreau's observations, we included 67



FIG. 1. Image of a digitized *Clintonia borealis* herbarium specimen with ripe fruits, accessed online through the Consortium of Northeast Herbaria (<http://portal.neherbaria.org/portal>). The specimen was collected on 5 August 1931 in Cornwall, Connecticut (catalogue number CONN00123819). Fruits were determined to be ripe using a combination of colour, size and apparent texture when the specimen was pressed.

species in analyses of first fruiting, 31 species in analyses of peak fruiting, and 29 species in analyses of last fruiting and duration.

Data analysis

All analyses were conducted using R statistical software, version 3.5.1 (R Core Team, 2018). We conducted Shapiro-Wilk normality tests of the data. All data were normal except

for Thoreau's observations of peak dates, last dates and durations; when we analysed these data using non-parametric Wilcoxon signed-rank tests, results were identical to those of paired *t*-tests. Here, for simplicity of interpretation, we present results from paired *t*-tests for all analyses.

We conducted paired *t*-tests to compare the differences between Thoreau's observations of first date, peak date, last date and duration, the date of the earliest specimen, mean and latest specimen, and the duration of herbarium specimens for each species (the duration of herbarium specimens

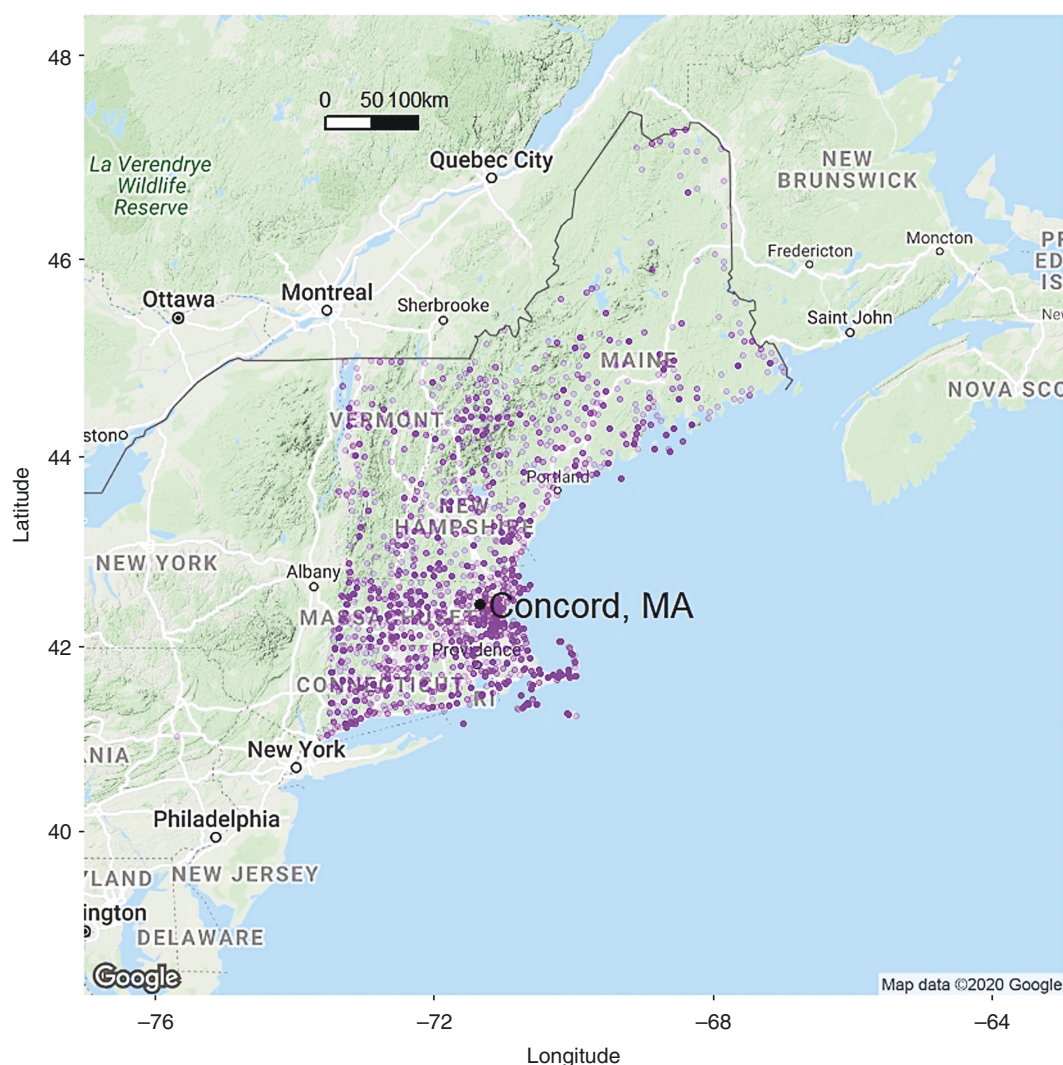


FIG. 2. Map of the locations of the herbarium specimens in New England. Darker colour indicates that points are overlapping and more specimens are found in that area. The black dot labelled 'Concord, MA' indicates where Thoreau recorded his observations. Base map from Google Maps ©2020.

is the time from the earliest to the latest specimen). To understand if any differences in variance may affect differences in fruiting times, we ran F -tests to test for equal variance in these four fruiting metrics between the two datasets. To determine the correlations for each metric of fruiting phenology between the two datasets, we calculated Pearson's correlation coefficients for all species together. We also calculated the correlations between first, peak and last dates for Thoreau's observations, and earliest, mean and latest specimens for the herbarium specimens, for all species together within each dataset.

To test whether geographical and temporal biases of these historical datasets affected the ecological patterns they captured, we conducted additional analyses with data restricted to similar geography and years. Due to the longer timespan and larger geographical area encompassed by the herbarium specimens, we conducted analyses comparing the differences between fruiting times and correlations between Thoreau's observations and the herbarium specimens using (1) only herbarium specimens collected before 1950 (Supplementary Data

Tables 2–4) and (2) only herbarium specimens collected in Massachusetts, Connecticut and Rhode Island (Supplementary Data Tables 5–7). These analyses did not produce different results from the full dataset, as the geographical differences and the differences over time were relatively minor in comparison with the differences among species. As a result, we used the full herbarium dataset for all analyses and interpretation.

To test whether Weibull 'true' first dates were more similar to Thoreau's observations than were earliest specimen dates, we used the *phst* package (Pearse et al., 2017) to calculate Weibull first-date estimates from the herbarium specimens. The Weibull method uses existing observations to produce an estimate of the first date with 95 % confidence intervals. The estimate is affected by the distribution and number of observations underlying the estimate. For example, a greater number of observations clustered closer to the observed first date will result in an estimate that is closer to the observed first date and smaller confidence intervals. As confidence intervals could not be calculated for *Vaccinium corymbosum*, this species was excluded from analyses using confidence intervals. To identify

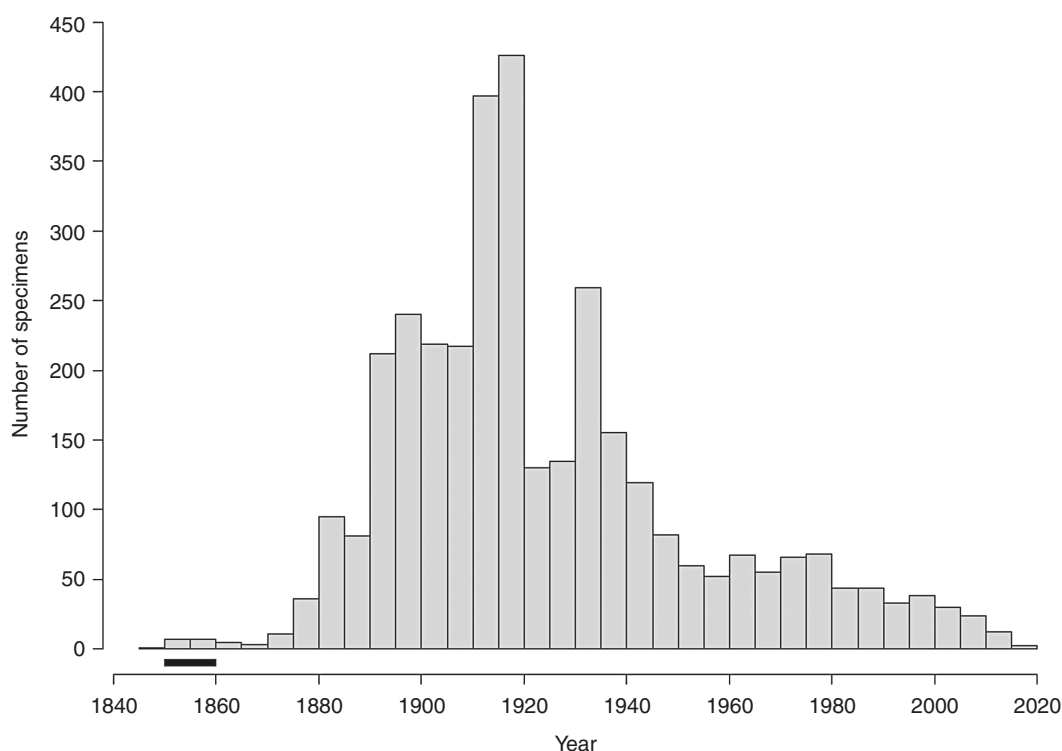


FIG. 3. Histogram of the number of herbarium specimens collected ($n = 3432$) by year, from 1849 to 2016. The black bar represents the timespan (1850–60) when Thoreau recorded his observations.

how different the herbarium-based Weibull estimates were from earliest specimen dates, we calculated correlations. To test whether Weibull estimates or earliest specimen dates have a stronger relationship with Thoreau's dates, we compared the correlations between (1) Thoreau's observed first dates and the Weibull first dates and (2) Thoreau's observed first dates and the herbarium earliest specimen dates.

To compare fruiting phenology between woody and herbaceous species, we ran non-paired t -tests comparing the two groups for each phenophase, within each dataset. We compared between woody and herbaceous species for first date, peak date, last date and duration for Thoreau's observations, and earliest specimen, mean specimen date, latest specimen and duration for the herbarium specimens. We excluded *Rubus pubescens* from this analysis, as it is a subshrub or herbaceous perennial and does not fall easily into either group.

RESULTS

Comparing fruiting sequence between Thoreau's observations and the herbarium specimens

Three of the four comparable metrics of fruiting time are significantly positively correlated between Thoreau's observations and the herbarium specimens. We found that the most highly correlated metric of fruiting between the two datasets is last fruiting date/latest herbarium specimen ($r = 0.85$, $P < 0.001$) (Table 2). The next most correlated is peak fruiting date/mean herbarium specimen ($r = 0.78$, $P < 0.001$), followed by first fruiting date/earliest herbarium specimen ($r = 0.59$, $P < 0.001$).

TABLE 2. Pearson's correlations between Thoreau and herbarium data for different metrics of fruiting

Metric of fruiting	r	n	Significance
First/earliest	0.59	67	***
Peak/mean	0.78	31	***
Last/latest	0.85	29	***
Duration	0.34	29	n.s.

n , number of species included.

*** $P < 0.001$; n.s., not significant

Duration is not significantly correlated between the two datasets ($P > 0.05$).

These correlations demonstrate strong consistency in the sequence of fruiting. Species like *Fragaria virginiana*, *Amelanchier* sp. and *Vaccinium angustifolium* consistently fruit early in the season (first fruit in June), while *Aralia racemosa*, *Ilex verticillata* and *Nyssa sylvatica* start fruiting late in the season (first fruit in August or September) in both datasets (Fig. 4).

Differences in fruiting times between Thoreau's observations and the herbarium specimens

In comparing Thoreau's observations and data from herbarium specimens for the different metrics of fruiting, we found that, on average, the earliest herbarium specimens are 28 d

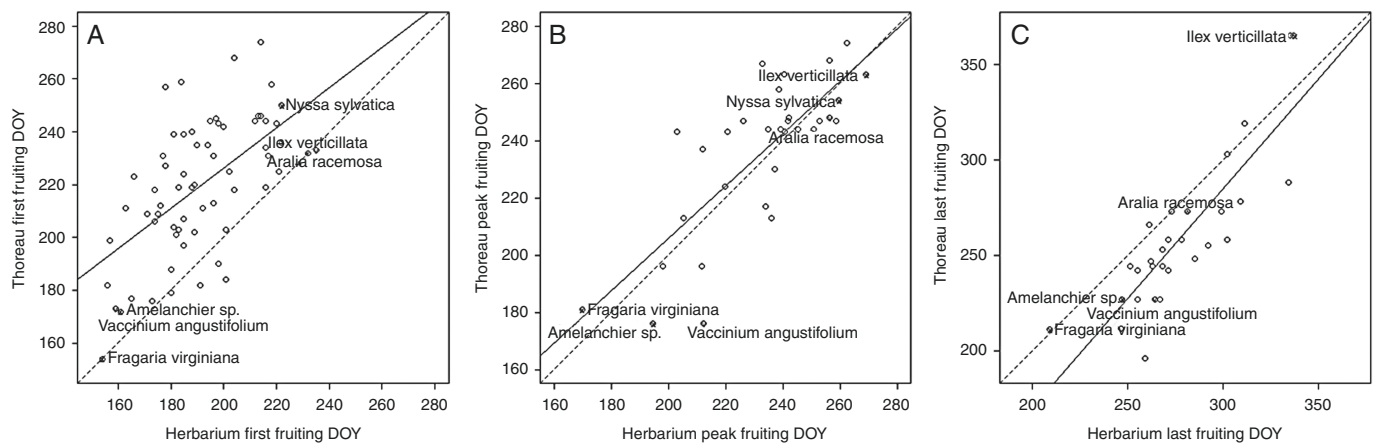


FIG. 4. Linear regressions comparing Thoreau's observations and the herbarium specimens for (A) first fruiting dates ($y = 0.76x + 73.9$, $P < 0.001$, $R^2 = 0.34$), (B) peak fruiting dates ($y = 0.91x + 23.1$, $P < 0.001$, $R^2 = 0.59$) and (C) last fruiting dates ($y = 1.15x - 60.2$, $P < 0.001$, $R^2 = 0.71$). DOY, day of year. Three typically early-fruiting species (*Amelanchier* sp., *Fragaria virginiana* and *Vaccinium angustifolium*) and three late-fruiting species (*Aralia racemosa*, *Ilex verticillata* and *Nyssa sylvatica*) are labelled. The dashed lines are 1:1 lines and the solid lines are linear regression lines.

TABLE 3. Differences between Thoreau and herbarium fruiting metrics. Differences are mean herbarium dates minus Thoreau dates. Negative values indicate earlier herbarium dates and positive values indicate later dates or longer durations for the herbarium data

Metric of fruiting	Difference in means (95% CI)	n	Significance
First/earliest	-28.2 (-23.0 to -33.3)	67	***
Peak/mean	-3.0 (-9.2 to 3.3)	31	n.s.
Last/latest	18.4 (10.3 to 26.6)	29	***
Duration	39.1 (28.1 to 50.1)	29	***

n, number of species included.

*** $P < 0.001$; n.s., not significant.

TABLE 4. F-values from tests of equal variance between the Thoreau and herbarium data for different metrics of fruiting. F-values are ratios of the Thoreau variance/herbarium variance. Values >1 indicate that the variance is greater in the Thoreau dataset

Metric of fruiting	F-value (95% CI)	n	Significance
First/earliest	1.64 (1.01–2.67)	67	*
Peak/mean	1.38 (0.66–2.85)	31	n.s.
Last/latest	1.84 (0.86–3.91)	29	n.s.
Duration	1.40 (0.66–2.99)	29	n.s.

n, number of species included.

* $P < 0.05$; n.s., not significant.

earlier than Thoreau's observed first fruiting dates ($t = 10.96$, d.f. = 66, $P < 0.001$), and the latest herbarium specimens are 18 d later than Thoreau's observed last fruiting dates ($t = 4.63$, d.f. = 28, $P < 0.001$; Table 3). Peak fruiting dates and mean herbarium specimens are not significantly different between the two datasets ($t = 0.97$, d.f. = 30, $P = 0.34$). Thus, average

duration of fruiting is 39 d longer for the herbarium specimens ($t = 7.29$, d.f. = 28, $P < 0.001$).

Some species, like *Rubus occidentalis* and *Sambucus canadensis*, have similar first fruiting dates and earliest herbarium specimens in both datasets. Other species show large differences between the two datasets. The earliest specimen of *Solanum ptychanthum* is 79 d earlier than Thoreau's first fruiting date for this species; the earliest *Lindera benzoin* specimen is 75 d earlier, and the earliest *Myrica pensylvanica* specimen is 64 d earlier. Although the earliest herbarium specimens are earlier on average, there are a few species with earlier dates in Thoreau's observations. For example, *Gaylussacia baccata* has a first fruiting date 17 d earlier in Thoreau's observations. There are similar differences for last fruiting dates and latest herbarium specimens. *Sassafras albidum* and *Crataegus macrosperma* have similar last fruiting dates and latest herbarium specimens in each dataset. On the other hand, the latest *Rubus pubescens* specimen is 63 d later than Thoreau's observed last fruiting date, and the latest *Myrica pensylvanica* specimen is 46 d later. Meanwhile, *Smilax rotundifolia* has a last fruiting date 30 d later in Thoreau's observations.

By testing for equal variance in first fruiting date versus earliest herbarium specimen, peak fruiting date versus mean herbarium specimen, last fruiting date versus latest herbarium specimen, and fruiting duration across the two datasets, we found that the only metric for which variances are statistically different is first fruiting date/earliest specimen ($F = 1.64$, d.f. = 66, $P = 0.046$; Table 4), with Thoreau's observations having greater variance.

Comparing fruiting metrics within Thoreau's observations and the herbarium specimens

Within datasets, different fruiting metrics (e.g. Thoreau's observations of first, peak and last fruiting dates) are significantly positively correlated to one another, and relationships among

metrics are stronger in Thoreau's observations than the herbarium specimens (Table 5). For both datasets, the highest correlation is between first date or earliest specimen and peak date or mean specimen (Thoreau, $r = 0.88$, $P < 0.001$; herbarium, $r = 0.77$, $P < 0.001$). The next highest correlation is between peak or mean and last date or latest specimen (Thoreau, $r = 0.77$, $P < 0.001$; herbarium, $r = 0.69$, $P < 0.001$). The lowest correlation, though still highly significant, is between first date or earliest specimen and last date or latest specimen, with the herbarium specimens having a much lower correlation than Thoreau's observations (Thoreau, $r = 0.74$, $P < 0.001$; herbarium, $r = 0.40$, $P < 0.001$).

Weibull first fruiting dates

Applying the Weibull method to the herbarium data results in first fruiting date estimates that are 4 d earlier, on average, than the herbarium earliest specimen dates ($t = 8.90$, d.f. = 66, $P < 0.001$; Table 6), and the two are strongly correlated ($r = 0.98$, $P < 0.001$; Table 6). For most species, Weibull dates are only a few days earlier than earliest specimen dates; however, there are some exceptions: the Weibull first fruiting date is 23 d earlier for *Myrica pensylvanica* and 19 d earlier for *Sassafras albidum*. The first dates Thoreau observed are more strongly correlated with the earliest herbarium specimens ($r = 0.59$, $P < 0.001$) than with the Weibull-estimated first dates ($r = 0.48$, $P < 0.001$). Most of Thoreau's first dates (92%) occur later and fall outside the 95 % confidence intervals for the Weibull-estimated first dates.

Differences in fruiting times between woody and herbaceous species

In comparing the fruiting times of woody and herbaceous species, we find largely the same results when using Thoreau's

observations and the herbarium specimens. With Thoreau's observations, there are no significant differences between woody and herbaceous species' fruiting times for first date ($t = 0.10$, d.f. = 32, $P = 0.921$), peak date ($t = 1.20$, d.f. = 22, $P = 0.244$), last date ($t = 1.06$, d.f. = 13, $P = 0.303$) and fruiting duration ($t = 2.00$, d.f. = 26, $P = 0.057$; Table 7). Similarly, with the herbarium specimens there are no significant differences between woody and herbaceous species' fruiting times for earliest specimen date ($t = 0.21$, d.f. = 28, $P = 0.837$), mean specimen date ($t = 0.29$, d.f. = 14, $P = 0.778$) and latest specimen date ($t = 1.78$, d.f. = 10, $P = 0.107$). In contrast to Thoreau's observations, the herbarium specimens indicate that woody species do have significantly longer fruiting durations ($t = 2.61$, d.f. = 13, $P = 0.022$).

DISCUSSION

Historical records can be invaluable to understanding changes in phenology over time and in relation to climate change. Historical records of wild fruiting times are particularly rare, and, as with all historical records, should be selected and synthesized for phenology research with an understanding of how their methodological qualities and sampling issues might affect the ecological patterns they capture. Here, we find that two historical datasets of fruiting phenology – herbarium specimens collected from 1849 to 2016 and observations made by Henry David Thoreau from 1850 to 60 – reflect broadly similar patterns in the order of fruiting times and differences between herbaceous and woody plant species in New England. However, we find that the exact timing of different fruiting stages (defined with similar, but not equivalent, metrics) differs for some species between the two datasets, in some cases widely. We find that Weibull estimates of first 'true' fruiting dates calculated from herbarium specimens do not increase comparability between the two data sets. Given the differences between these datasets, we recommend researchers consider, as much as possible, matching methodology, including the data source, phenophase metrics and scaling, when selecting historical records of fruiting phenology for present-day comparisons. Where this is not possible, researchers should be aware of these issues and how they might affect the outcome of their study.

Consistency of fruiting sequence and duration between datasets

First date and earliest specimen, peak date and mean specimen, and last date and latest specimen are highly correlated

TABLE 5. Pearson's correlations between metrics of fruiting within the Thoreau and herbarium datasets

Metric of fruiting	Dataset	r	n	Significance
First and peak	Thoreau	0.88	31	***
Earliest and mean	Herbarium	0.77	67	***
Peak and last	Thoreau	0.77	16	***
Mean and latest	Herbarium	0.69	67	***
First and last	Thoreau	0.74	29	***
Earliest and latest	Herbarium	0.40	67	***

n , number of species included.

*** $P < 0.001$.

TABLE 6. Differences in mean first dates and correlations of first dates between the Weibull method, Thoreau dataset and herbarium dataset. The difference subtracts the second dataset listed from the first. A positive number means that the second dataset listed has earlier first dates

Dataset comparison	Difference in means (95 % CI)	Significance (means)	n	r	Significance (r)
Herbarium–Weibull	4.4 (3.4–5.4)	***	67	0.98	***
Thoreau–Weibull	32.6 (26.9–38.3)	***	67	0.48	***
Thoreau–Herbarium	28.2 (23.0–33.3)	***	67	0.59	***

n , number of species included.

*** $P < 0.001$.

TABLE 7. Differences between woody and herbaceous species fruiting metrics in the Thoreau and herbarium datasets. Differences are mean dates for woody species minus mean dates for herbaceous species. Negative values indicate earlier dates or shorter durations for woody species and positive values indicate later dates or longer durations for woody species

Metric of fruiting	Dataset	Difference in means (95 % CI)	Significance	Woody <i>n</i>	Herbaceous <i>n</i>
First	Thoreau	0.7 (–13.2 to 14.5)	n.s.	48	18
Earliest	Herbarium	1.2 (–10.7 to 13.2)	n.s.	48	18
Peak	Thoreau	–11.5 (–31.4 to 8.4)	n.s.	21	10
Mean	Herbarium	–2.9 (–24.5 to 18.7)	n.s.	21	10
Last	Thoreau	13.4 (–13.1 to 39.9)	n.s.	21	7
Latest	Herbarium	23.1 (–6.0 to 52.2)	n.s.	21	7
Duration	Thoreau	14.3 (–0.4 to 29.0)	n.s.	21	7
Duration	Herbarium	22.0 (3.7 to 40.3)	*	21	7

n, number of species included.

**P* < 0.05; n.s., not significant.

between Thoreau's observations and the herbarium specimens. These relationships indicate that there is a very consistent order of fruiting across species, and that this pattern is robust to differences in collection method and phenophase metric. Both historical datasets appear to be capturing a real biological trend in fruiting patterns: the sequence of fruiting for these 67 species is relatively consistent across New England. A consistent trend in the order of fruiting times in woody plants across states in New England was also found by Gallinat *et al.* (2018a) for many of the same species. Other studies in this region have similarly found that there is a consistent order to when species leaf out (Polgar *et al.*, 2013; Everill *et al.*, 2014; Panchen *et al.*, 2012) and flower (Miller-Rushing and Primack, 2008; Ellwood *et al.*, 2013). Our study builds on previous results by additionally including herbaceous species, using two different methods, and demonstrating that the order of fruiting across species remains consistent when herbaceous species are considered.

Surprisingly, we found that between the two datasets the last fruiting dates and latest specimens were more strongly correlated than were first and earliest, or peak and mean fruiting dates. We expected peak or mean dates to be the most consistent because mean phenological values tend to be less affected by sample size or variability (Miller-Rushing *et al.*, 2008). In addition, peak flowering dates have been shown to be more comparable between field observations and herbarium specimens than first dates (Davis *et al.*, 2015). Furthermore, Gallinat *et al.* (2018b) found a stronger correlation between first fruiting and start of peak fruiting than between end of peak and last fruiting, when comparing across recent years and locations of botanical gardens in the USA, Germany and China.

It is possible that the stronger correlation between last dates and latest specimens in our study reflects a consistent order in which fruits are consumed by wildlife. Last dates may combine information on both fruiting order and frugivore feeding preferences. For example, fruits with higher antioxidant contents, like arrowwood (*Viburnum dentatum*), may reliably be eaten first, whereas less desirable fruits, like winterberries (*Ilex verticillata*), may consistently be left until later in the season (Bolser *et al.*, 2013), which could be reflected in later field observations and specimen collections. Other studies support this trend of preference for certain fruits, indicating for example

that birds select fruits with higher lipid content (Stiles, 1980; Greenberg and Walter, 2010).

A future study could determine if this correlation between last fruiting dates and latest herbarium specimens is driven by frugivore feeding preference, phenology or the abundance and nutritional quality of fruits of different species. Studies should also compare fruiting data with bird migration and feeding data to understand how the timing of fruiting coincides with the timing of bird migration, and the impacts any potential mismatches could have on plant and bird populations.

Duration of fruiting is not significantly correlated between the two datasets. This may be due to differences in the frequency and duration of sampling, which should be considered when interpreting historical data on fruiting times. Collectors of herbarium specimens are not looking for the very first and last fruit, whereas Thoreau was.

Differences in fruiting times between Thoreau's observations and the herbarium specimens

The exact timing of fruiting frequently differed between the two datasets. The herbarium specimens have consistently earlier earliest specimens, later latest specimens, and longer durations than Thoreau's observations. The herbarium specimens represent a greater number of years and a greater geographical range; however, our analyses suggest that this is not the main reason for the difference in fruiting times. When we compare Thoreau's observation with herbarium specimens temporally restricted to before 1850 or geographically restricted to southern New England, the results are nearly the same as when comparing all of the herbarium specimens. Further, the results of our equal variance tests indicate that these differences are not due to the herbarium data having greater variance in fruiting dates. On the other hand, the herbarium specimens and Thoreau's observations have peak dates that are not significantly different. In contrast to our findings, Davis *et al.* (2015) found that field studies captured first flowering dates 3 d earlier on average than herbarium specimens. The difference in first and last fruiting dates may be attributable to differences in the frequency and duration of sampling, which should be considered when interpreting

historical data on fruiting times. These metrics may not be equivalent when comparing the timing of the start and end of fruiting.

Comparison of fruiting metrics within datasets

We found that, within datasets, the different fruiting metrics – first date, peak date and last date for Thoreau's observations and earliest specimen, mean specimen and latest specimen for the herbarium specimens – are mostly highly correlated with one another (r : 0.69–0.88, except herbarium earliest and latest fruiting r = 0.40). This finding echoes previous findings of relationships among fruiting stages at botanical gardens (Gallinat *et al.*, 2018b) and other studies which have found that the timings of plant phenophases are correlated (Schwartz and Reiter, 2000; Ettinger *et al.*, 2018). These correlations indicate that the three metrics of fruiting phenology within each dataset capture some redundant information. However, Miller-Rushing *et al.* (2008) caution that first flowering dates are more variable than peak dates. First dates are dependent on population size, sample size and sampling frequency. In our analysis, we found that the herbarium specimens have consistently earlier earliest specimens and later latest specimens than Thoreau's observed first and last dates, whether we use the whole data set or only the herbarium specimens collected before 1950. Similarly, the results hold when we only use specimens from southern New England. These consistent results further support the conclusion that the beginning and end of a phenophase are more influenced by differences in frequency and duration of sampling. Therefore, we recommend comparing peak or mean fruiting dates when investigating the timing of a phenophase, particularly if a study is merging data from different breadths of space and time. However, peak and mean fruiting metrics were not the most strongly correlated across datasets (particularly compared with end of fruiting metrics), indicating that the peak and mean probably do not capture identical information. When choosing datasets, the most accurate and useful comparisons will still likely be between datasets with similar methods, metrics and scaling.

Evaluating the Weibull method

We found that estimates of first fruiting dates calculated from the herbarium data using the Weibull method were, on average, 4 d earlier than corresponding earliest specimen dates, but the order of fruiting remained the same. Small windows of time may have important biological implications for some species. For example, in *Frangula alnus* later fruits were more likely to be dispersed by birds (Bolmgren and Eriksson, 2014).

There were a few species for which the Weibull first fruiting date was more than a week earlier (10–20 d) than the earliest specimen date. These larger shifts may be due to a smaller sample size and greater variation in the spread of the samples for these species. For example, *Myrica pensylvanica*'s first date shifts 23 d earlier and it has a sample size of 30 herbarium specimens; *Sassafras albidum*'s first date shifts 19 d earlier and it

has a sample size of 20. In contrast, some of the other species are represented by >100 samples.

We also compared first fruiting dates observed by Thoreau with the earliest specimens gathered from herbarium specimens and with those generated using a Weibull approach on the herbarium dates. If Thoreau's observations were more strongly correlated with the Weibull first fruiting dates, it could suggest that applying this tool improves the proximity of herbarium-based estimates to field-based estimates. However, we found that Thoreau's first dates were more strongly correlated with the herbarium earliest specimens than with the Weibull first dates. Future research should clarify if the small differences in first fruiting dates found when comparing the herbarium specimens and Weibull method estimates are biologically important.

Comparing fruiting times of woody and herbaceous species

Thoreau's observations and the herbarium specimens produced similar results for whether woody and herbaceous species differ in their fruiting phenology. Using each dataset, we found that woody and herbaceous species did not differ significantly in fruiting timing for any of the metrics, except duration using the herbarium specimens, which indicated that woody species fruited for longer periods. Herbaceous and woody species started fruiting at about the same time. Woody species fruited later, but not significantly so, than herbaceous species, on average (13 d for Thoreau's observations and 23 d for the herbarium specimens). Using Thoreau's observations, fruiting duration was 14 d longer for woody species, although this difference was not significant. On the other hand, using the herbarium specimens, woody species' fruiting duration was 22 d longer, and this difference was significant. Differences in statistical results may be due to the small number (seven) of herbaceous species included in these analyses of end of season metrics. Overall, these two historical datasets appear to be comparable when comparing woody and herbaceous species, and future studies should be able to use these historical data as baselines for comparison to identify whether these groups have shifted their fruiting times in relation to one another.

Conclusions

Historical records of wild fruiting times are rare and valuable resources for understanding how fruiting times are changing; they should be selected and synthesized for phenology research with an understanding of how their methodological qualities might affect the ecological patterns they capture. This study demonstrates that two different historical datasets – Thoreau's observations and herbarium specimens – capture very similar information about the order in which woody and herbaceous species fruit in New England. The high correlations of metrics within datasets confirm findings from previous studies and help validate these historical datasets. The high correlations between the metrics of fruiting in Thoreau's observations and the herbarium specimens suggest that we may successfully use and compare different methodologies for studying the order in which species fruit. Differences among

species are large and consistent enough to clearly emerge regardless of the two methods used here. On the other hand, these datasets do not reflect consistent fruiting timing for the same species, with the earlier earliest and later latest herbarium specimens. Therefore, different historical datasets with similar, but not equivalent, methods may not provide the same information about the timing of the beginning and end of the fruiting season. We find that Weibull estimates of first ‘true’ fruiting dates calculated from herbarium specimens do not increase comparability between the two datasets. Nonetheless, we find that the datasets do identify similar patterns between the fruiting phenology of herbaceous and woody species. Given that the results from these datasets are not altogether consistent, we recommend researchers strongly consider matching methodology, including the data source, phenophase metrics and scaling, when selecting historical records of fruiting phenology for present-day comparisons.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: list of species, fruiting dates and sample sizes. Table S2: differences between Thoreau and herbarium fruiting metrics, using only herbarium specimens collected before 1950. Table S3: *F*-values from tests of equal variance between the Thoreau and herbarium data for different metrics of fruiting, using only herbarium specimens collected before 1950. Table S4: Pearson’s correlations between Thoreau and herbarium data for different metrics of fruiting, using only herbarium specimens collected before 1950. Table S5: differences between Thoreau and herbarium fruiting metrics, using only herbarium specimens collected in Massachusetts, Connecticut and Rhode Island. Table S6: *F*-values from tests of equal variance between the Thoreau and herbarium data for different metrics of fruiting, using only herbarium specimens collected in Massachusetts, Connecticut and Rhode Island. Table S7: Pearson’s correlations between Thoreau and herbarium data for different metrics of fruiting, using only herbarium specimens collected in Massachusetts, Connecticut and Rhode Island.

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L.C.S. and R.B.P. All data recorded from fruiting herbarium specimens, including species, date, location of collection, museum and collector will be available on the Open Science Framework.

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