Trends in Ecology & Evolution

Review

Old Plants, New Tricks: Phenological Research Using Herbarium Specimens

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The timing of phenological events, such as leaf-out and flowering, strongly influence plant success and their study is vital to understanding how plants will respond to climate change. Phenological research, however, is often limited by the temporal, geographic, or phylogenetic scope of available data. Hundreds of millions of plant specimens in herbaria worldwide offer a potential solution to this problem, especially as digitization efforts drastically improve access to collections. Herbarium specimens represent snapshots of phenological events and have been reliably used to characterize phenological responses to climate. We review the current state of herbarium-based phenological research, identify potential biases and limitations in the collection, digitization, and interpretation of specimen data, and discuss future opportunities for phenological investigations using herbarium specimens.

Trends

Phenology (i.e., the timing of flowering, leaf-out, and other recurring biological events) is an essential component in measuring how species have responded and will continue to respond to climate change.

Herbarium specimens are increasingly being recognized and valued as a reliable source for estimating phenological behavior for a diversity of plant species.

As millions of herbarium specimens become available online through massive digitization efforts, developing efficient methods and standards for the collection of large amounts of specimen-based phenological data is vital to leveraging these data for research purposes.

Through integration with existing phenological datasets such as remote sensing and citizen science observations, herbarium specimens offer the potential to provide novel insights into plant diversity and ecosystem processes under future climate change.

The Potential for Herbarium Specimens to Expand Phenological Research

Plant **phenology** (see Glossary) (i.e., the seasonal timing of life-history events such as flowering and leaf-out) is a key determinant of plant success and ecosystem productivity. Furthermore, as phenological events are often triggered by environmental cues, especially temperature, the study of phenology is essential for predicting how species will respond to climate change. Over the past decade, there has been a concerted effort to incorporate phenological traits, including the onset and duration of individual phenological phases, into evolutionary ecology and climate change biology [1–4]. Despite the importance of phenology to plant success [5–7], however, little is known about the phenological behavior of most species [8]. In particular, the way in which different environmental factors serve as phenological cues across the majority of species remains a mystery [9]. This is mainly due to the difficulty of acquiring the data necessary to identify specific environmental factors that drive phenological transitions for a given species. The collection of these data has traditionally required long-term field observations or manipulative experiments that are difficult to scale up such that they capture entire regions, communities, or plant clades [8,9]. Efforts to collect species-level phenological data, therefore, have been pursued in only a relatively small number of species from a limited geographic distribution and often over short timescales, resulting in a substantial gap in our understanding of phenology [8].

To address this gap, researchers have recently turned to the vast collections of plant **specimens** in the world's herbaria for phenological information [10–14]. Herbarium specimens can be viewed as records of the phenological status of an individual, population, or species at a

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given time and place (Box 1). While the phenological information provided by an individual specimen is limited, many specimens can be used collectively to assemble a long-term picture of the phenological behavior of a region and the species that inhabit it. Expanded phenological information derived from large numbers of specimens can offer insight into two key ecological phenomena: (i) long-term shifts in phenology at a given location over decades or even centuries [10,11,15–17]; and (ii) how seasonal or interannual environmental variation cues phenological transitions (i.e., phenological sensitivity) [14,18,19]. It is now being recognized that herbarium specimens provide a reliable method for estimating phenological sensitivity in plants (Box 2). Furthermore, specimens offer unique attributes that have the potential to greatly expand our understanding of phenology. First, specimens offer a detailed history of phenological change, with many collections dating back centuries [20], before the modern influence of climate change [21]. Second, given their diversity in both phylogenetic and geographic sampling [12], specimens offer the opportunity to study the evolution of phenological traits in a wide range of lineages and biomes as well as how phenological traits may shape patterns of diversity under future climate change.

The pace of herbarium-based phenological research has accelerated rapidly over the past decade (Table 1) facilitated by the increasing availability of online **digitized** herbarium specimens [21–25]. As more of these collections are digitized and climate change research continues to advance, it is now an appropriate time to evaluate the current state of herbarium-based phenological research and discuss potential limitations, areas for improvement, and opportunities for future research.

Historical Uses of Herbarium Specimens to Study Phenology

For hundreds of years, botanists and naturalists have collected and preserved plants as herbarium specimens for taxonomic research, to record the flora of a region [26], to document their economic uses [27], and as a social hobby [28]. Traditionally specimens were not collected with the specific intent to study phenology *per se*. As plant collection became more widespread among professional botanists in the 18th and 19th centuries, however, the ancillary information recorded and retained with each specimen became more detailed and standardized, and thus more amenable to phenological research. Most specimen labels created during the past 150 years provide information on locality, date of collection, and habitat. In addition to label data, physical specimens are rich with information regarding plant health, morphology, and phenological status. From these data researchers can derive descriptive estimates of a species' reproductive season (e.g., flowers in May–June) for inclusion in published floras, species identification, and application in horticulture. The use of such data for more detailed studies of ecological and evolutionary processes, such as phenological sensitivity to temperature, has been limited (Table 1).

Phenology as a field of study dates to the 18th century in Europe and even earlier in Japan and China, where observers recorded the flowering dates of culturally significant plants such as cherry trees [29]. Careful observations of plant phenology and its relationship to meteorological records became common in many European countries, the USA, Japan, South Korea, and China during the 19th century; these observations have a rich tradition in horticulture and agriculture [30] and natural history [31] and in the past couple of decades have been used for climate change and ecological research [32,33]. It is only relatively recently that researchers have begun to use herbarium specimens for plant phenological research.

Modern Uses of Herbarium Specimens to Study Phenology

The recent growth in herbarium-based phenological research is arguably a product of the growing interest in climate change and phenology around the turn of 21st century [34]. Researchers realized that herbarium specimens could potentially be used to detect and

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quantify long-term phenological shifts in response to climate change [10]. This, in turn, led to the use of specimens to estimate phenological sensitivity to various environmental factors, including temperature, day length, and precipitation (Table S1 in the supplemental information online). To date, specimens have been used to estimate the onset of several phenophases, including first flowering, peak flowering, leaf-out, and fruit set, as well as the duration of entire growth phases [19,35–41]. These phenophase estimates have been used to study long-term shifts in phenology and phenological sensitivity to interannual climate variation (Tables 1 and S1).

A literature review focused on the modern use of herbarium specimens to study phenological responses to climate (see the supplemental information online for a full description of our methods) reveals interesting generalities and insights. First, studies that have investigated long-term shifts in phenology have generally found that flowering and leaf-out times have advanced, in some cases dramatically, over the past century (median = 9.5 days, range = 0–97 days) (Table S1; [12,13,17,19,20,42]). These long-term trends are often in agreement with studies that have used alternative sources, such as observational data, to study phenological shifts [43–46]. Second, for most of the studies we reviewed the onset dates of spring flowering and leaf-out tended to be negatively associated with winter or spring temperatures (Table S1; [4,9,16–18]); that is, plants tended to flower and leaf-out earlier in warmer years. However, some species and regions exhibit delayed or mixed phenological responses under warmer temperatures, potentially because they did not experience sufficient winter chilling requirements or because the imprint of past climate conditions has resulted in a response lag [17,47–49]. Third, given the span of time and geographic area that specimens encompass, they almost always capture a greater range of climatic variation experienced by a species than traditional long-term observational data, and thus can provide a more complete estimate of phenological shifts over time as well as phenological sensitivity to interannual or spatial variation in climate (Box 2; [14]).

Most studies that have used herbarium specimens have focused on a single phenological event, most commonly the date of onset for a single phenophase (Tables 1 and S1). The most frequently studied phenophase in relation to climate change is flowering (39 of 40 studies; Table 1), with a specific focus on either mean flowering date or peak flowering date (Table S1). Only a handful of studies have attempted to quantify different events within a phenophase, such as the onset, peak, and end of flowering date [37,50,51]. Thus, the opportunities for expanded application of comparable and new techniques are abundant. For example, specimens can be used to assess multiple phenological characters at different stages of development (flower buds, open flowers, old flowers, young fruits, and mature fruits), allowing researchers to estimate the sensitivity of different points in a given phenophase as well as determine how different phenophases are related [52]. Additionally, most herbarium-based studies have been limited to northern, temperate biomes (Table 1 and Figure 1), mirroring geographic biases in long-term observational data [8]. The potential to expand phenological investigation into non-temperate biomes using specimens, however, is considerable, as illustrated by the density of tropical and subtropical specimen records in the Integrated Digitized Biocollections (iDigBio) database alone (Figure 1).

Several recent studies have validated herbarium phenological estimates by comparing them with independent estimates of similar phenological phenomena (Table S1). Generally, comparisons with independent phenological data – using photographs (prints, negatives, slides, and digital images) and field observations – show that herbarium-based estimates of both phenological timing [13,25,41,53] and phenological sensitivity to climate are reliable (Box 2). At a broader scale, additional validation of herbarium-based phenological data has come from comparisons with satellite observations of ‘green up’ [17,18,25]. While these studies provide important validation of herbarium-based phenological data, they are nonetheless limited in their

Glossary

Citizen science: the collection of scientific data by members of the public, often without specific scientific training. Citizen scientists are participants in these efforts. They volunteer their time to assist professional scientists in data collection and in return gain skills and knowledge of timely, relevant scientific research. Citizen science is also known, with slight variations in interpretation, as crowdsourced science, public participation in scientific research, and participatory action research.

Digitization: the process of supplementing objects, in this case specimens from natural history collections, with digital data. Digitization of natural history collection specimens usually involves the curation, capturing, and processing of a digital image of the object, transcribing the associated label and ledger text, and geoferencing locality information. Digitized data can then be made available online for researchers, educators, policymakers, and the public.

Herbarium specimen: preserved plant material. A herbarium specimen of a vascular plant is typically created with a representative plant sample that is pressed, dried, mounted on archival paper, labeled, and stored in a herbarium. Some vascular plant organs (e.g., flowers), as well as most nonvascular plants (e.g., marine algae, liverworts, bryophytes), are instead typically stored in either a box or a jar with preserving fluid to retain their 3D forms.

Ontology: a controlled, structured vocabulary that describes and formalizes relationships among related terms. Characteristics of relationships are defined by an established set of hierarchical conditions, such as X (e.g., leaf) is ‘a part of’ another characteristic Y (e.g., plant), which is ‘a member of’ subset or group Z (e.g., organism). See Figure 3Figure I in Box 2 for an illustration of this hierarchical structure.

Phenology: the study of the timing of seasonal biological events as well as, colloquially, the events themselves (Box 1). Plant phenological events include leaf-out, flowering, fruiting, and senescence. Phenology can be determined in a phylogenetic scope and number of regional comparisons. As the use of herbarium-based phenological data grows, so too should efforts to independently validate these data.

binomial context as having occurred or not (e.g., this plant is, or is not, in flower). It can also be described on an ordinal scale that starts at early and progresses through peak, late, and completed or with numeric equivalents of these (i.e., 0–10 for not yet flowering through to completed). Many of these events are evident on herbarium specimens.

Potential Limitations, Errors, and Biases in Herbarium Datasets

Herbarium-based data, like all sources of data, are subject to potential biases and limitations of which researchers must be aware [12,54] (B.H. Daru, unpublished). Such limitations are present from the specimen collection phase, to the digitization and processing of specimens, to the analysis and interpretation of specimen data. By understanding and addressing these challenges, researchers can make full and appropriate use of specimens for phenological research.

Some limitations of using herbarium data for phenology are common to other observational datasets and originate at the time of specimen collection, including accurate species identification and phenological event and phase discrimination. While specimens are often correctly identified by experienced botanists, they may still be misidentified or labeled according to outdated taxonomy. Unlike with observational datasets, however, species and phenophase identifications for herbarium data can easily be confirmed by revisiting anomalous specimens.

Biases Unique to Herbarium Specimens

Herbarium data are known to contain additional, unique biases that stem from the opportunistic nature of their collection. Botanists often collect samples depending on their interests, schedule, and location (e.g., near roadsides, populated areas, or universities) and not to capture the phenological status of the plant *per se* (B.H. Daru, unpublished) [55]. Collection biases relating to plant habit, morphology, and nativity may also occur in herbarium datasets; for example, Schmidt-Lebuhn *et al.* [56] discovered strong biases against very small plants, plants with brown or green inflorescences, and introduced species in a sample of Australian Asteraceae. Rich and Woodruff [57] noted that collections are biased towards common, showy plants that grow in clumps. Additionally, broader taxonomic, spatial, and temporal biases have been identified with Global Biodiversity Information Facility occurrence records, which include herbarium records [54] (B.H. Daru, unpublished).

Specific to phenology, plants may be less likely to be collected at the very beginning or end of a reproductive season, especially if a species is difficult to identify during these stages or is inconspicuous. For example, Davis *et al.* [14] found that first-flowering date estimates from specimens were, on average, 3 days later than first-flowering date estimates from field observations. Botanists may also collect only those individuals exhibiting a certain phenological stage (e.g., mature flowers, fruits) to facilitate identification. However, it is also true that botanists may deliberately collect plants that are flowering or fruiting out of season and are therefore not representative of the overall phenology of the species. Another source of collection bias is the tendency for large numbers of specimens to be collected during single collecting trips, which can result in oversampling and the generation of duplicate specimens distributed to multiple institutions that are subsequently treated as independent samples. Duplication of records is a well-known problem, however, and efforts are currently underway to better account for duplicate records across databases and data portals [58]. Finally, herbarium specimens often represent only a fragment of an entire plant (for woody perennials especially), which makes it important to consider how accurately specimens represent the phenology of the whole plant or local population from which they are sampled.

Biases Due to Digitization

Data quality issues in herbarium data may also arise after collection, during label transcription, or due to digitization. For example, ambiguous handwriting or descriptions can lead to the incorrect transcription of a specimen's location or collection date. In addition to transcription

Box 1. What Is Phenology and How Do We Collect Phenological Information from Herbarium Specimens?

Plant phenology refers to seasonally recurring phases in a plant's life history. These phases can broadly be classified into either vegetative phases (e.g., bud break, presence of full-sized leaves) or reproductive phases (e.g., flowering). Within these broad phases, there is often a distinct set of sequential subphases, or phenophases, that are identified by the presence of organs at a specific stage of development (e.g., flower buds, open flowers, wilted or spent flowers, ripe fruits). While there is no formal definition of what constitutes a phenophase, a given phenophase can be characterized by an onset date, a date of peak abundance, and a termination date. These points are referred to as phenological events. Composite metrics can be derived from these events, such as the duration of a phenophase estimated as the number of days between its onset and termination dates. Successive phenophases and phenological events need not be mutually exclusive as sequential phenophases may overlap. For example, the flowering phenophase need not be complete before the fruiting phenophase begins.

Herbarium-based phenological research has primarily focused on a key subset of phenological events partly because of their ecological importance and partly because of the limitations of measuring phenology from specimens. These events mainly include first flowering date, peak flowering date, and, to a lesser extent, fruit set date and leaf-out date (Table 1).

The collection of phenological data from herbarium specimens is fundamentally based on the presence and absence of key reproductive or vegetative traits. Most often, the presence – and occasionally the quantity – of these traits is then used to score the specimen as being in a particular phenophase and representative of a particular phenological event. For example, in the specimen featured in this box (Figure I) a small number of flower buds in combination with a large number of open flowers indicate that the specimen is in the flowering phenophase and most likely represents a specimen at peak flowering.

While the collection of phenological data from herbarium specimens has proliferated, standardization of methodologies for doing so has lagged. Studies range from quantitative definitions of specific phenological events (e.g. [19]) to coarse categorizations such as 'flowering time' (e.g. [17]) averaged across all specimens with any number of flowers present. Furthermore, consideration will need to be given to anatomical differences across taxonomic groups (e.g., grasses with numerous, diminutive flowers versus orchids with few, large flowers [96]). The absence of standardized measures of the flowering status of herbarium specimens makes comparisons and inferences across studies challenging, although not impossible.

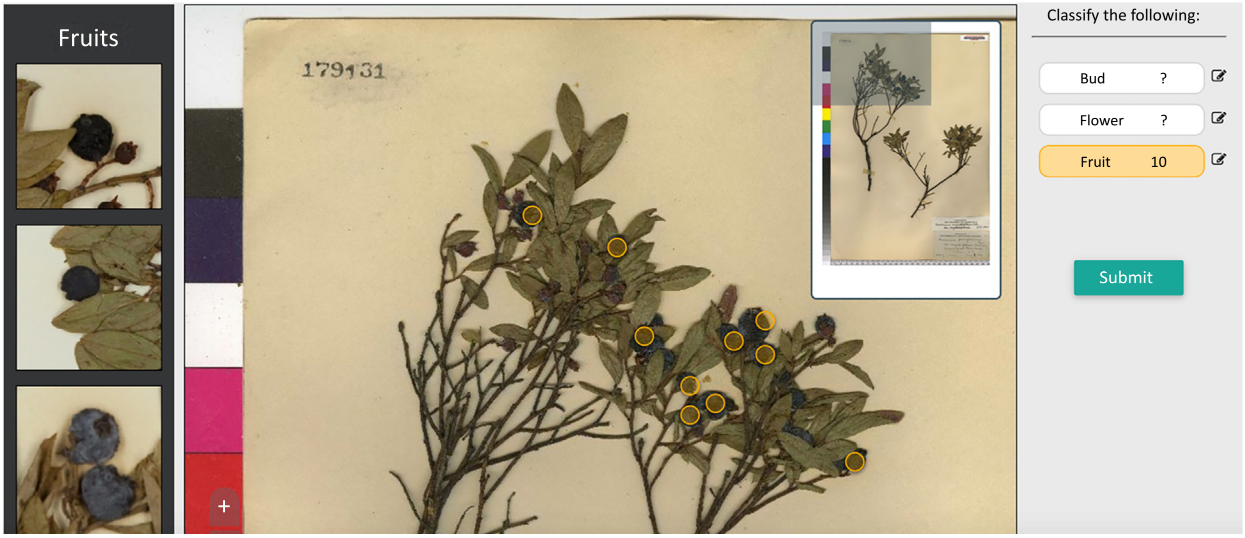

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Figure I. Herbarium Specimen of *Vaccinium angustifolium* Aiton (Lowbush Blueberry). The specimen is presented through the interface of CrowdCurio, a web-based platform for the annotation of phenological information on digitized herbarium specimens [52]. Here the phenological information being collected includes counts of flower buds, flowers, and fruits. Citizen scientists count each phenological trait by clicking on the presence of corresponding objects on the image (orange dots). As a reference, examples of each phenological trait are provided on the left.

errors, discriminating among phenophases can be even more difficult if observers are assessing digital images rather than the physical specimens themselves. While these problems can often be resolved from other contextual clues (e.g., when the collector was alive, whether the label is typed or handwritten), each of these aspects of data quality must be assessed and managed when studying phenology. Moreover, different countries and individuals have developed separate methods for recording specimen information, which presents a challenge for data aggregation. This topic has recently received renewed attention and methods to improve the standardization and integration of these data are currently being developed (Box 3).

Clearly, herbarium records are subject to error, as are all sources of data, and may contain geographic, phylogenetic, temporal, or other biases because they were not assembled to answer phenological questions. Nevertheless, one of the strengths of herbarium data is that their biases can be minimized by careful selection of species and phenological phases for assessment, rigorous training of observers, high-quality imaging, and the continued development of statistical methods to test and correct for biases.

Future Directions

Given the potential illustrated by previous studies and the vast number of digital herbarium specimens coming online, the capacity of herbarium-based phenological research is immense. The use of these virtual collections, however, will require a more rigorous effort to standardize methodology as well as the development of new tools for large-scale data collection and analysis.

The Future of Herbarium Specimen Data Integration

The first major undertaking for herbarium-based phenological research is simply the mining of available data. In the USA as of 26 February 2017, over 1 811 365 imaged and georeferenced vascular plant (Tracheophyta) specimens are digitally archived in the iDigBio portal (http://www.idigbio.org; Figure 1), a nationally funded and primary aggregator of museum specimen data. This number will only increase as it represents a fraction of the total number of specimens housed in US herbaria [~57 million specimens in the top 100 herbaria according to the Global Registry of Biodiversity Repositories (biocol.org)]. In addition to the USA, large-scale digitization efforts are under way or near complete in Australia (http://avh.chah.org.au), Austria (http://herbarium.univie.ac.at), Brazil (http://inct.florabrasil.net), Canada (http://www.canadensys.net), China (http://www.cvh.org.cn), France (http://science.mnhn.fr), South Africa (http://www.sanbi.org/), and elsewhere. In total there are estimated to be ~350 million specimens in over 3000 herbaria in 165 countries (http://sweetgum.nybg.org/science/ih/). However, digitization efforts have not typically included information on a specimen's phenological status, largely because of the challenge of having expert botanists annotate so many specimens. The question then becomes: what kinds of data should be recorded from these specimens and in what detail?

Standardization of Herbarium-Based Data

In the phenological studies that have been completed to date (Table 1), researchers often evaluated phenological stages differently according to their research priorities and rarely made

Box 2. Validity and Expanded Potential of Herbarium-Based Phenological Data

Despite the recent increase in published studies, the suitability of herbarium specimens for generating accurate measures of phenological responses to climate conditions has seldom been assessed [14,15,48,51,84,85] despite the potential for geographic and temporal biases in these collections [54,55] (B.H. Daru, unpublished).

In a recent effort to validate the use of herbarium specimens for assessment of plant responses to climate change, Davis *et al.* [14] compared flowering phenology from field observational records from 1852–1858, 1878, 1888–1902, and 2004–2013 with flowering times obtained from herbarium specimens. Twenty common species from New England, USA were selected for their ease of scoring, for the existence of several decades of field observational records spanning the years 1852–2013, and for the abundance of herbarium specimens. Results from this study demonstrated that the date of first flowering was 3 days earlier in field observations than in herbarium records. However, both field observations and herbarium observations showed the same tendency to flower earlier in more recent years over this 160-year period. Both datasets demonstrate that plants flower earlier in response to warmer temperatures. These results support the conclusion that herbarium records are likely to be a reliable source of climate change response.

The study by Davis *et al.* also detected that the herbarium records spanned variation in climate (climatic space) much more effectively than observational records alone, mainly due to the larger number of years represented (33 years using field observations versus 122 years using herbarium specimens; Figure I). During the study period (1852–2013), mean spring temperatures varied widely, ranging from <1°C to >8°C. Similarly, mean annual temperatures ranged from <6°C to >11°C. During this interval herbarium data covered a much larger percentage of the climatic space than observational data (91% versus 76%, respectively) due to the inclusion of herbarium records collected during exceptionally warm years and cold years. By contrast, observational data were notably lacking in years with unusually cool springs. These results collectively demonstrate that herbarium specimens can greatly expand our knowledge of how phenology varies with temperature from one year to the next.

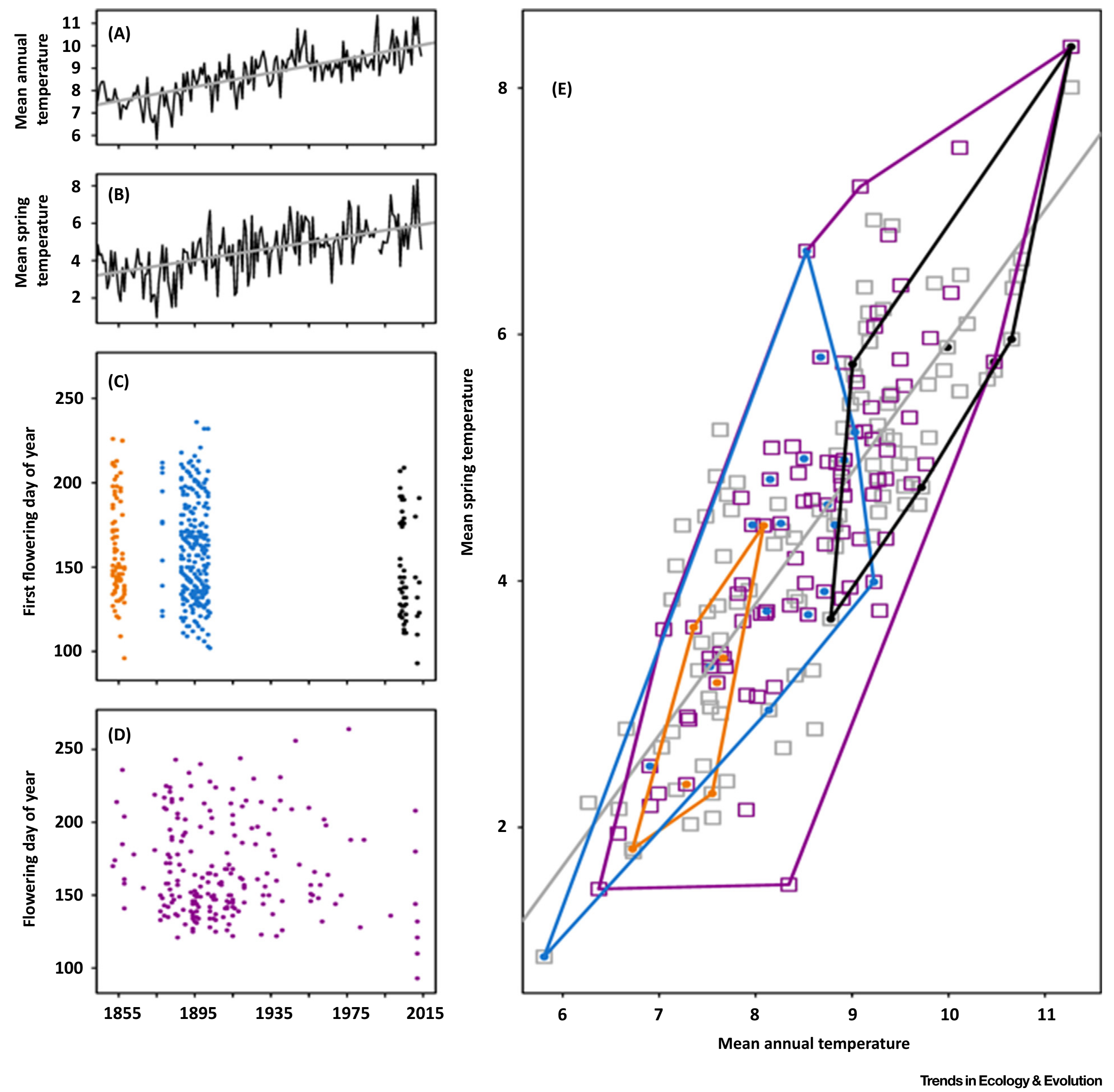

Figure I. Climatic and Phenological Data. (A) Mean annual temperatures (°C) and (B) mean monthly temperatures are increasing over time at the Blue Hill Meteorological Observatory, Boston, MA, USA (1852–2015). (C) Observed first flowering dates of 20 wildflower species in Concord, MA, USA have been recorded at only three distinct time periods (1852–1858, 1878 and 1888–1902, and 2003–2013) whereas (D) earliest flowering dates recorded from herbarium sheets of the same 20 species from the same county have been recorded for larger numbers of years and are more evenly spaced over time. (E) Consequently, herbarium data (magenta boxes and magenta convex hull) cover a larger area of the total climatic space of mean annual temperatures and spring temperatures (1852–2013; all boxes) than do the field observations from 1852–1858 (orange dots and convex hull), 1878 and 1888–1902 (blue dots and convex hull), or 2004–2013 (black dots and convex hull). Empty grey boxes indicate years in the climate space with no corresponding phenological data. Convex hulls encompass the outer boundaries of the climate space defined by the most extreme observations. The gray line is the best-fit regression line relating mean spring temperature to mean annual temperature. Reproduced, with permission, from [14].

Table 1. Summary of Published Studies That Have Used Herbarium Specimens to Study Phenological Responses to Climate Change, Including Long-Term Phenological Shifts and Phenological Sensitivity (i.e., the Relationship between the Timing of a Phenological Event and Seasonal Environmental Variation)

Refs	Publication year	Region	Biome	Time span	Specimen records	Number of herbaria	Number of taxa	Phenophase
[53]	1996	Central and South America	Tropical	NA	1673	1	18	Flowering
[73]	1996	North America	Tropical	NA	690	NA	178	Flowering
[74]	2001	Americas	Tropical	NA	NA	2	12	Flowering
[10]	2004	North America	Temperate	1885–2002	372	1	66	Flowering
[75]	2005	North America	Desert	1900–1999	NA	2	27	Flowering
[76]	2006	Australia	Tropical	>100 years	36 774	2	1371	Flowering
[16]	2006	North America	Temperate	1918–2003	216	7	1	Flowering
[15]	2006	North America	Temperate	1881–2002	177	1	42	Flowering
[77]	2007	North America	Desert	1900–1999	1499	715	100	Flowering
[78]	2007	North America	Temperate	1902–2000	2073	7	18	Flowering
[79]	2009	Americas	Tropical	NA	374	1+	39	Flowering
[35]	2009	Australia	Alpine	1950–2007	371	3	20	Flowering
[80]	2009	Europe	Mediterranean, alpine	30 years	>200	1	1	Flowering/fruiting/ leaf lifespan
[81]	2010	North America	Desert	1902–2006	NA	1	87	Flowering
[82]	2010	Australia	Temperate	1910–2006	NA	3	101	Flowering/fruiting
[83]	2011	Asia	Alpine, subalpine	1848–2003	76	4	1	Flowering
[84]	2011	Europe	Temperate	1848–1958	77	2	1	Flowering
[85]	2011	Central and South America	Tropical, tropical alpine	1950–2000	3382	7	35	Flowering/fruiting
[37]	2012	Europe	Temperate	1852–2007	600	1	5	Flowering/fruiting
[86]	2012	Europe	Temperate	1837–2011	5424	NA	39	Flowering
[11]	2012	North America	Temperate	1840–2010	1587	5	28	Flowering
[19]	2013	North America	Temperate	1848–1958	NA	1	141	Flowering
[87]	2013	Asia	Palearctic	1960–2000	909	3	41	Flowering
[18]	2014	North America	Temperate	1834–2008	1599	7	27	Leaf-out
[42]	2014	Asia	Subtropical	1893–2003	NA	3	1	Flowering
[47]	2014	Asia	Subtropical	1884–2009	1147	10	36	Flowering
[88]	2014	North America	Desert, temperature	1890–2010	823 033	8	24 105	Flowering
[89]	2014	Europe	Temperate	1879–2014	46	1	3	Leaf-out
[90]	2015	North America	Temperate	1950–2012	>30 000	9	280	Flowering
[14]	2015	North America	Temperate	1852–2013	1108	4	20	Flowering
[48]	2015	Asia	Temperate, subalpine	1913–2011	134	1	3	Flowering
[91]	2015	North America	Temperate	1872–2009	277	20	12	Flowering/fruiting
[17]	2015	North America	Temperate, subtropical	1951–2009	19 328	3	>1700	Flowering
[92]	2015	Asia	Subtropical	1920–2007	5258	1	2059	Flowering
[38]	2015	Australia	Temperate, chaparral	2003–2011	158	1	5	Flowering
[39]	2016	North America	Temperate	1888–2009	289	11	1	Flowering
[93]	2016	North America	Temperate	1890–2014	88 531	49	17 962	Flowering
[51]	2016	North America	Arctic, taiga, temperate	NA	2111	8	3	Flowering/fruiting
[94]	2017	North America	Temperate, montane, desert	1895–2013	27 234	NA	16	Flowering
[95]	2017	North America	Arctic	1896–2015	3795	4+	23	Flowering/fruiting

See Table S1 for additional information on each study as well as additional recent studies that have used herbarium species to estimate phenological data but not in the context of climate change.

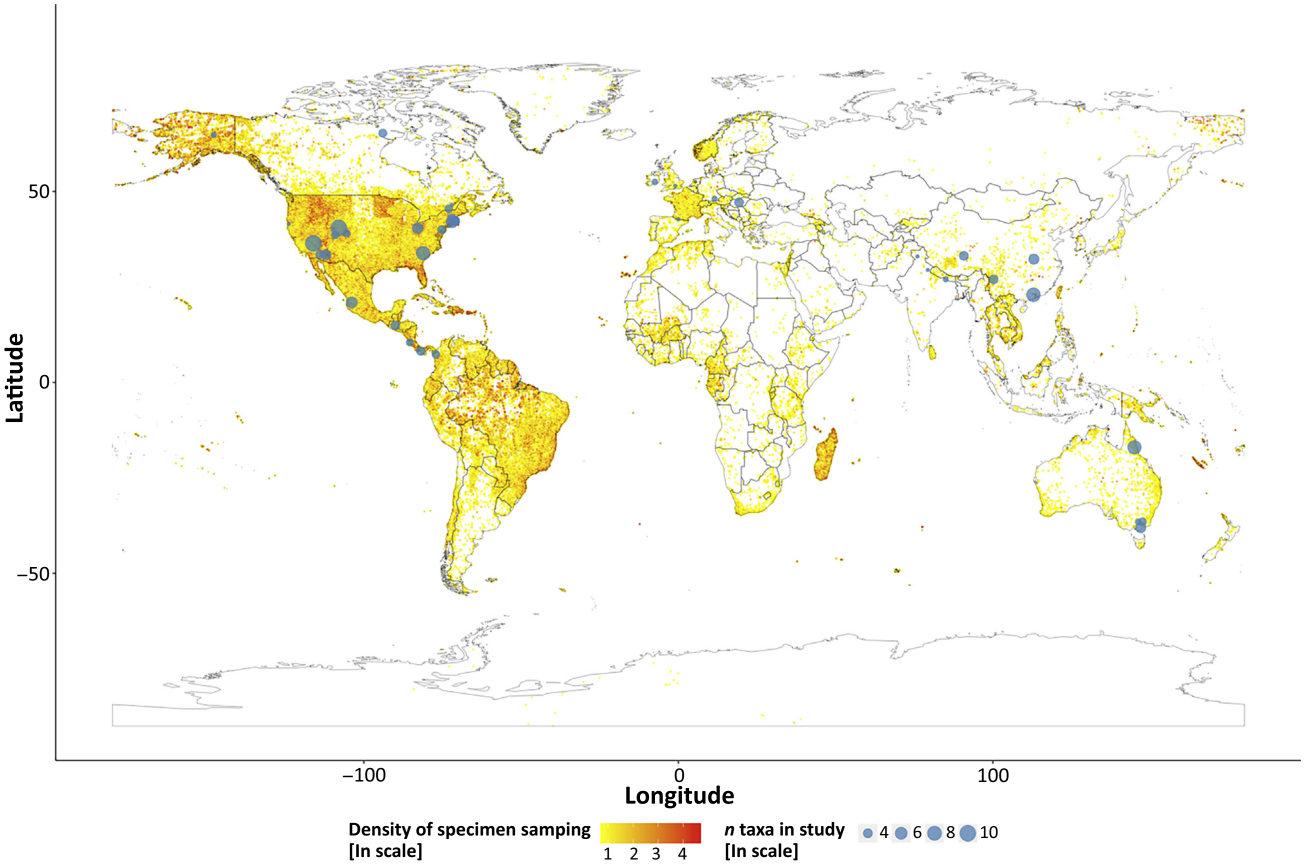

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Figure 1. Geographic Distribution of Published Herbarium-Based Phenological Studies. Studies are indicated as circles. Circles are scaled to represent the relative size of each study in terms of species analyzed. The distribution of studies is overlaid on a heat map of digitized specimen images of vascular plants (Tracheophyta) available via the Integrated Digitized Biocollections (iDigBio) portal (1 811 365 specimens as of 26 February 2017).

data publicly available, thus limiting the utility of those data beyond the life of the individual projects. The most serious challenge for the future of herbarium-based phenological research is the standardization of phenological terms and methods for scoring phenophases and phenological events. Such standardization is important not only to ensure that herbarium-based studies are comparable but also to facilitate effective integration with other types of phenological data such as **citizen science** observations [51], satellite imagery [25], and stationary camera images (i.e., PhenoCam) [59].

Biodiversity data standards for the biocollections community have already been established in the Darwin Core Data Standards [60]. Most digitizing institutions generate data conforming to the Darwin Core, which comprises defined metadata properties and a small set of classes; however, phenological terms are not currently defined by the Darwin Core and instead are captured in unrelated fields such as ‘occurrenceRemarks’, ‘organismRemarks’, ‘dynamicProperties’, or ‘fieldNotes’. Many institutions capture flowering information in the ‘reproductiveCondition’ field, but this field lacks a standardized vocabulary. For example, we discovered 3900 unique terms to describe reproductive status in a search of the ‘reproductiveCondition’ field of 5.7 million specimens in SEINet, a portal of digitized specimens for Arizona and New Mexico, USA. Lack of standardization complicates data integration and presents a huge obstacle to the mobilization and consolidation of herbarium data from multiple institutions

Box 3. Current Developments in Communication and Data Standardization across the Phenological Research Community

As phenological data acquisition rapidly expands with increased digitization of specimen data, remote sensing, citizen science, and other efforts, the need for integration of data from disparate sources and among different types of data is growing. Fortunately, efforts are under way to foster communication and develop standards across the phenological research community.

iDigBio – the US National Science Foundation's designated national center for the coordination of biodiversity specimen digitization under the Advancing the Digitization of Biodiversity Collections (ADBC) initiative – has greatly increased communication among data-collecting communities by supporting collaborative workshops and working groups involving members of research, cyberinfrastructure, and other stakeholder communities. One such working group is currently drafting data standards targeting the phenological status of herbarium specimens. These new standards will be integrated into APPLE Core – an herbarium-specific set of standards – and the working group is also exploring how to integrate these standards into the Darwin Core. Next steps for this working group include determining how data housed in the 'reproductiveCondition' field can be integrated into standardized fields and how to integrate the herbarium-based phenology standards with another developing standardization initiative, the Plant Phenology Ontology (PPO).

The PPO working group aims to rigorously define plant phenological terms and formally specify the relationships of these terms to each other and to terms from other **ontologies** such as the Plant Ontology and Phenotypic Quality Ontology [97]. Ontologies provide highly structured, controlled vocabularies for data annotation and are particularly useful for standardization because they not only establish a common terminology but also formalize logical relationships between terms such that they can be analyzed using computerized reasoning [98]. For example, queries of unstructured data often rely on matching search terms to identical terms in a database. Structuring data with ontologies allows computers to match search terms with both identical terms and those that are logically related. This capability enables integration among a wide range of study types, including: (i) studies addressing similar phenophases but using different methodologies; (ii) studies involving different phenophases; and (iii) studies not specifically addressing phenology but producing other types of data – for instance, trait or climatic data (Figure I). Thus, the PPO will empower researchers to aggregate larger datasets and address broader questions involving the interplay of phenology and other factors.

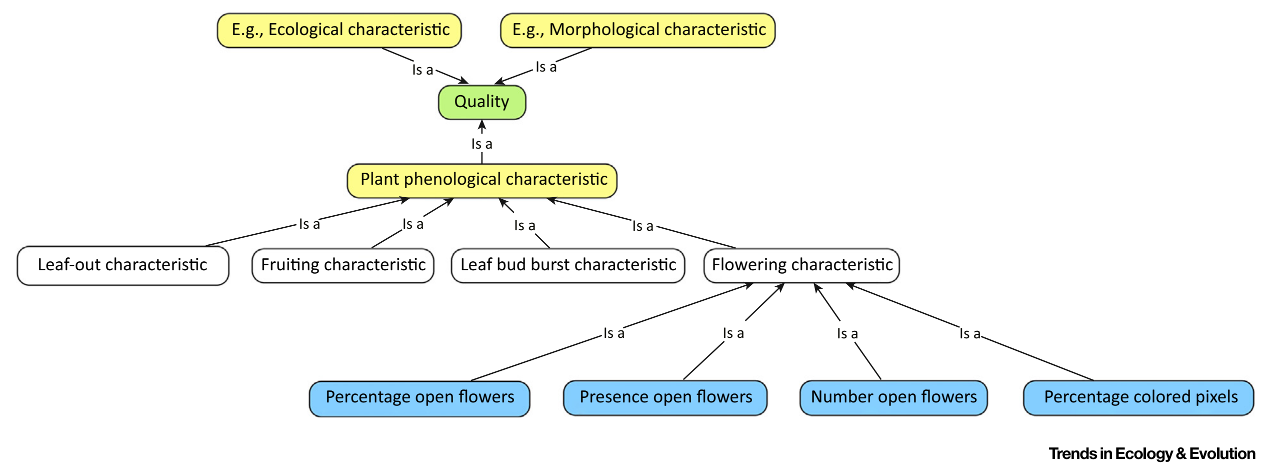


Figure I. Simplified Representation of Ontological Classes and Logical Structure. In a complete ontology, each term or 'class' has a specific definition and is linked to any and all related classes via 'relation terms' such as 'is_a' or 'part_of'. These structured linkages between classes allow integration among different methods of measuring a class (represented in blue), different subclasses within a class (white), and other types of data (yellow), which are subclasses of the general term 'quality' currently defined by the Phenotypic Quality Ontology.

for phenological research. The development of standards and ontologies (Box 3) is a vital step toward unlocking the research potential of digitized specimens.

Standardization of herbarium specimen data, in combination with the availability of new data-management tools, will facilitate the large-scale collection and use of phenological data from specimens. The task of scoring phenological data from millions of digitized specimens, however, is a monumental task. As noted above, herbarium-based phenological studies to date have typically focused on only a single phenophase and classified specimens in binary terms (e.g., flowering/not flowering). This limited approach is due in no small part to the challenge of scoring phenology for a large number of specimens. Standardization can facilitate the collection of these data in two ways: (i) by providing a template for scoring phenology that can be easily incorporated into the digitization or post-digitization workflow; and (ii) by providing guidelines for the conversion of raw count data (e.g., number of flowers) collected via citizen science crowdsourcing into predefined phenophases.

New Tools to Collect Herbarium-Based Data at Large Scales

Efforts to scale up the collection of phenological data using new tools are already under way and would only benefit from the incorporation of a standardized ontology and data structure. The New England Vascular Plant (NEVP) project, for instance, has developed an extension of the specimen management system Symbiota [23] that provides an interactive online platform to score a range of predefined phenophases based on coarse estimates of different phenological characteristics (e.g., 'early flowering' with ≤25% flowers open). This approach has the advantage of speed and efficiency and can be easily incorporated into an existing digitization pipeline where, along with transcribing the label information, technicians input phenological scores. Another tool, similarly meant to be implemented within an existing collection database, is the Phenological Predictability Index (PPI) module in the Botanical Research and Herbarium Management System (BRAHMS) [41]. The PPI module, however, is geared more toward standardizing estimates of phenological activity as opposed to scaling the collection of the data itself.

Another avenue for scaling phenological data collection is the use of citizen science crowdsourcing. The popular citizen science platform Zooniverse [61] has utilized crowdsourcing in the collection of data from digital specimens including label transcription [Notes from Nature (http://www.notesfromnature.org)] and even phenological data [Orchid Observers (www.orchidobservers.org)]. Another crowdsourcing tool that has been developed to collect phenological data from specimens is CrowdCurio (http://www.crowdcurio.com) [52]. Preliminary results from CrowdCurio have demonstrated that phenological data collected from non-expert users are comparable to those compiled by expert users, suggesting that it has the potential to be a powerful tool for the collection of detailed, accurate phenological data [52]. In addition to crowdsourcing, machine learning – the ability of computers to learn a task without being specifically programmed – offers an exciting new tool for the collection of large amounts of phenological data from specimens. Several recent studies have demonstrated that machine learning can be used to identify species with a high degree of accuracy based on leaf shape and venation [62]. In either case data collected with these new and powerful tools should be made to conform to standardization efforts so that they can be easily incorporated into existing herbarium databases.

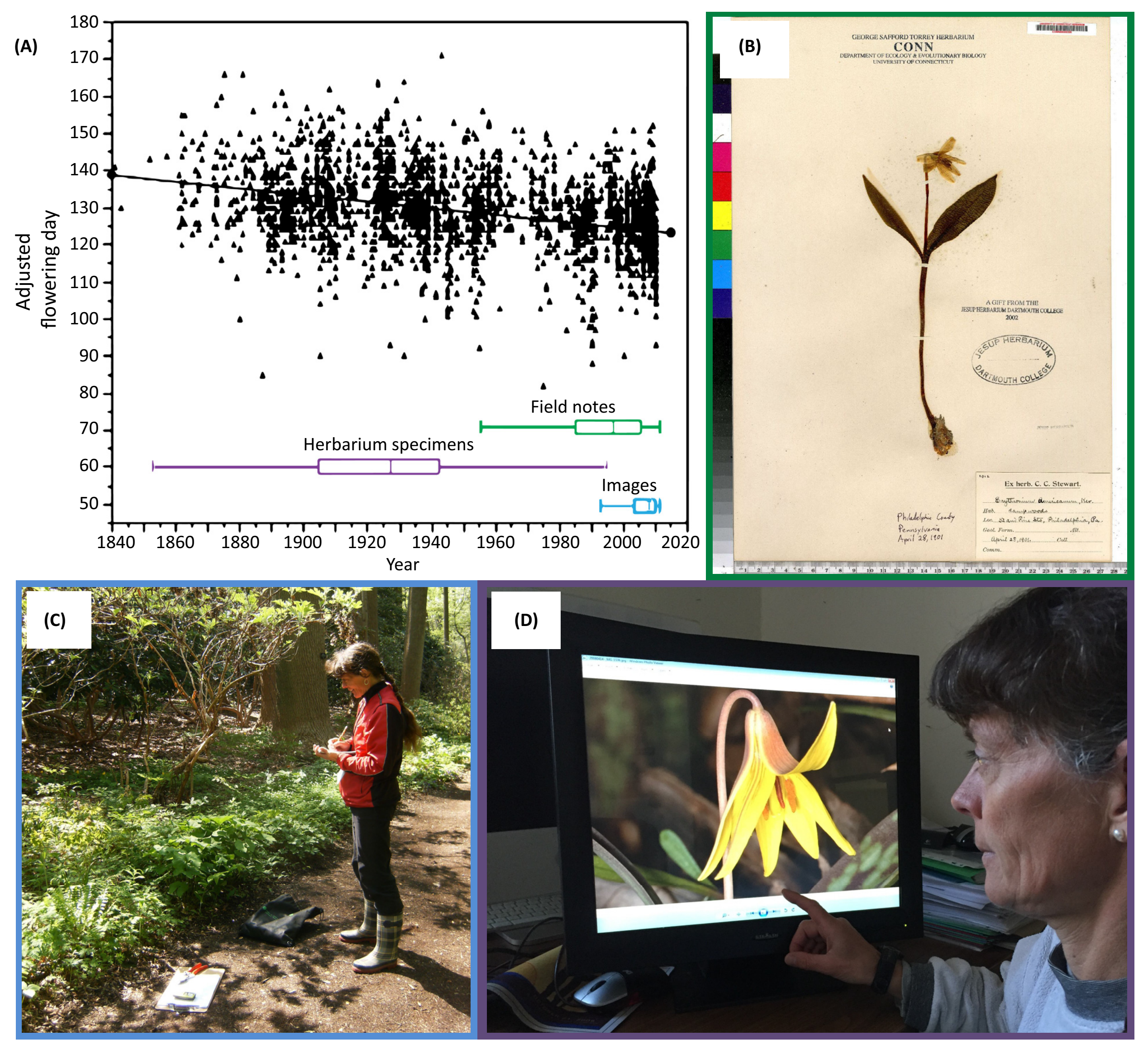
The Future of Herbarium-Based Phenological Research

One of the most promising aspects of herbarium-based phenological data is the potential to expand our taxonomic and geographic sampling of phenological research. For example, the

Box 4. Integrating Herbarium Records with Other Data Sources

Many herbarium specimens were collected half a century or more ago, so how can they be used to study the rapidly changing climate over the past few decades? One approach is to combine herbarium record data with other types of phenological observations. In the Philadelphia region of the northeastern USA, researchers demonstrated the effectiveness of combining the dates of full flowering of 28 spring-flowering species obtained from herbarium specimens (mostly from 1889–1959) with recent field observations of peak flowering (mostly from 1955–2010) and dated photographs of plants in flower (mostly from 1998–2010) (Figure I) [11]. Analyses of the combined dataset showed stronger flowering responses to temperature and greater changes over time and explained more of the variation than using data from herbarium specimens alone. Data from photographs (11% of records) and field observations (26%) were less abundant than herbarium specimens (63%) but were crucial for showing the effects of climate change on flowering phenology during recent decades. These seemingly disparate data are compatible because field studies, herbarium specimens, and photographs each commonly record flowering phenology and, most often, peak flowering. Further, the phenological stage of herbarium specimens and the flowers in photographs can be evaluated at any time.

Leaf-out dates, a major component of ecosystem processes, can also be determined from herbarium specimens for many plant species, especially temperate trees that leaf-out when they flower, such as many species of maple, oak, birch, and poplar. For example, in a study of 27 common tree species in New England, 1599 herbarium specimens in a stage of early leaf-out demonstrated that trees now leaf-out earlier than a century ago and leaf-out earlier in warm years [18]. A surprising finding was that annual variation in temperature was far greater in determining leaf-out dates than geographical variation in temperature and that differences among species in leaf-out times were not significant. Further, the geographic variation in leaf-out dates determined using herbarium specimens was significantly correlated with geographic variation in leaf-out dates determined using remote sensing data provided by satellites. This correlation provides independent confirmation that remote sensing, a rapidly growing tool in climate change research, is accurately measuring leaf-out times over large geographic areas. The study also showed that, on average, herbarium specimens show later leaf-out dates than remote sensing dates, perhaps because remote sensing instruments are sensitive to ground cover, the shrub layer, and the very first tree leaves.



Trends in Ecology & Evolution

Figure I. Example of Integrated Historical Data Sources. (A) Plot of flowering day over time for 28 species in the Philadelphia area based on a combination of estimates from herbarium specimens (63% of data points; 1841–2010), field notes (26% of data points; 1841–2010), and photographic images (11% of data points; 1977–2010) [42]. Box plots show the means and upper and lower quartiles of years for each data type. (B) Example herbarium specimen of *Erythronium americanum* (dogtooth violet) used to estimate flowering day. Specimen image provided by George Safford Torrey Herbarium (CONN), University of Connecticut; accessed through the Consortium of Northeastern Herbaria website (http://www.neherbaria.org). (C) Photograph of Z. Panchen, the lead author of [11], collecting phenological data in the field. (D) Photograph of Z. Panchen assessing a dated photograph of *E. americanum* acquired from a local botanical club for phenological data. (A) reproduced, with permission, from [11]. (C,D) used with permission from Z. Panchen.

vast collections of specimens from species-rich tropical and subtropical biomes (Table 1 and Figure 1) could be used to greatly enhance phenological research in these regions where field-based phenological data, especially on the timescale of recent climate change, are often limited [40,63,64].

Herbarium data could also be used to investigate the extent to which species may no longer be phenologically responding to a warming climate. Most of the planet has experienced record-breaking temperatures in recent years and plants have largely responded with advanced phenology [31]. However, it is possible that winter temperatures may become too warm for plant species to meet their winter chilling requirements [65], causing a delay in leafing out and flowering. This hypothesis could be tested using specimens collected in especially warm versus cold years.

Another exciting area of future research is the integration of herbarium data with other sources of phenological data (Box 4). Besides herbarium specimens, historical phenological data are limited [8,15]. Data can sometimes be discovered through historical records and photographic collections but these are often limited in geographic and temporal coverage [11,15]. For contemporary phenological data, researchers are turning to expanding citizen science networks to provide enormous numbers of phenological observations over huge geographic areas (USA-National Phenology Network, iNaturalist, Project Budburst). These datasets could be combined to greatly increase the spatial density of observations as well as to validate the results of herbarium-based phenological data [51]. In addition, the continued development of remote sensing technology offers another source of phenological data that can be integrated with herbarium-based data. For example, ecosystem models based on remote sensing data are often limited in their predictive ability because of a lack of long-term, species-level phenological data [66]. Herbarium-based phenological estimates, which have been found to agree with broader phenological estimates based on Landsat and MODIS satellite data [17,18,25], could provide the necessary species-specific data to improve these models.

Herbarium specimen data combined with data concerning other, associated species may help answer another pressing phenological question: is climate change leading to ecological mismatches among organisms at different trophic levels? Due to large annual variations in climate and organismal phenology, robust evidence for ecological mismatches has been notoriously difficult to identify [67]. As an example of a potential way forward, Bertin [50] used herbarium specimens to compare peak flowering phenology with ruby-throated hummingbird migrations. Herbarium specimens may also be examined for other traits that contribute to fitness and interact with phenology, such as herbivory, frost damage, flower size, or fruit set. Finally, herbarium specimens can be used to estimate changes in abundance and distribution, allowing researchers to estimate the influence of phenological sensitivity on local or regional species loss [68].

Despite the potential for herbarium specimens to vastly expand our understanding of plant phenology – as well as other fundamental aspects of plant biology [12] – the value of collections remains threatened by declines in institutional investment, basic research funding [69,70], and the intensity of collection of new specimens in recent decades [20,71,72]. It is vital that these trends be reversed to preserve the value of herbarium collections as unique records of phenological change. To this end, digitization is not a means to replace physical specimens but rather an opportunity to expand access to and interest in these important collections. Physical specimens will continue to play an important role in herbarium-based phenological research and, perhaps more importantly, may contribute to research opportunities we have not yet imagined.

Concluding Remarks

The estimated 350 million herbarium specimens around the world were not collected with phenological research in mind; however, specimen data are becoming widely recognized for their potential to contribute to this rapidly growing field and to enable us to detect and predict the effects of climate change on the seasonal cycles of plants. Herbarium specimens provide a window into the past that increases our temporal, geographic – and taxonomic vision of how phenology – and potentially plant success and ecosystem processes, have changed and will continue to be affected as the climate changes. With a thorough and growing understanding of the potential and limitations of this rich historical data source, combined with the modern tools of digitization, data sharing, and integration, researchers will increasingly be able to address critical questions about plant biology, community and ecosystem ecology, and how climate change impacts the rhythm of the natural world.

Outstanding Questions

How reliable are herbarium specimens as measures of phenological behavior outside temperate North America, particularly in biomes that experience distinctly different or minimal seasonal transitions such as savannas or tropical rainforests?

What is the potential for the use of herbarium specimens to measure phenological events besides flowering and leaf-out (e.g., fruiting time, leaf senescence time)?

Does the reliability of herbarium specimens for phenological research depend on other key characteristics of the plant such as growth form, lifespan, or mating system?

What are the most efficient ways of scaling up the collection of phenological data from herbarium specimens – particularly with crowdsourcing and citizen science methods – that will ensure the most accurate and useful results?

Can the expanded geographic range and annual variation provided by herbarium specimens be used to quantify the relative importance of alternative environmental cues for spring leafing out and flowering such as winter chilling requirements, spring warming, and photoperiod?

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Supplemental Information

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