ORIGINAL PAPER

How consistently do species leaf-out or flower in the same order? Understanding the factors that shape this characteristic of plant communities

Caryn M. Beiter[1] · Theresa M. Crimmins[2]

Abstract

Plant species are frequently reported to undergo leaf-out and flowering in a consistent order from 1 year to the next; however, only a limited number of these findings arise from studies encompassing many species or sites. Here, we evaluate the consistency in the order species leafed out in the northeastern United States using observations contributed to the USA National Phenology Network's *Nature's Notebook* platform. We repeated this analysis for flowering, evaluating a total of 132 species across 84 sites. We documented a relatively high degree of consistency in the order of both events among individual plants, with higher consistency in flowering. A small number of species pairs exhibited very high consistency in phenological order across several sites. The majority of species pairs exhibited variability in how consistently they underwent either leaf-out or flowering from site to site, which could be the result of either plastic or locally adaptive responses. Our investigation revealed that neither functional type nor seasonal position played a major role in shaping how consistently species leafed out or flowered in the same order. Instead, we found the number of days separating the events and interannual variability in timing to be the most influential factors driving the consistency in ordering.

Introduction

Plant species in temperate systems are frequently reported to undergo spring leaf-out and flowering in a predictable sequence, even under variable interannual conditions (Heinrich 1976; Lechowicz 1984; Kramer 1995; Linkosalo 2000; Aizen and Vázquez 2006; Wesolowski and Rowinski 2006; Bennie et al. 2010; Panchen et al. 2014; Cole and Sheldon 2016; Delpierre et al. 2017; Malyshev et al. 2022). Such a predictable ordering in springtime phenological events among species in a community is logical, given that individual species are cued to leaf-out or flower by unique combinations of abiotic conditions (Geng et al. 2020; Buonaiuto and Wolkovich 2021; Chu et al. 2021; Ma et al. 2021). The primary environmental drivers of vegetative and reproductive phenology in temperate systems are thermal accumulation, winter chilling, and day-length (Körner and Basler 2010; Polgar and Primack 2011; Flynn and Wolkovich 2018), though the relative strength of these factors is species-specific (Polgar and Primack 2011; Fu et al. 2014; Laube et al. 2014; Visser and Gienapp 2019).

The unique conditions species require to cue springtime phenological events result in unique responses among species to changing climate conditions. Species that only require warmth to initiate springtime activity tend to demonstrate simple, and often pronounced, advancements in the timing of their activity (Fitter and Fitter 2002; Menzel et al. 2006; Caffarra and Donnelly 2011; Polgar and Primack 2011). In contrast, species with chill requirements have been reported to delay spring activity when chill requirements are not met (Yu et al. 2010; Basler and Körner 2012; Cook et al. 2012; Laube

✉ Caryn M. Beiter
beitercm@miamioh.edu

Theresa M. Crimmins
theresa@usanpn.org

[1] Department of Biology, Miami University, 501 E High St, Oxford, OH 45056, USA

[2] USA National Phenology Network, School of Natural Resources and the Environment University of Arizona, 1311 E. 4Th. St., Suite 325, Tucson, AZ 85721, USA

et al. 2014). Differential changes in species' phenology in response to changing climate conditions have the potential to affect the ordering of leaf-out or flowering among plants in a community; a clear reshuffling of the order species undergo phenological events has been demonstrated through experimental manipulations (Laube et al. 2014). Changes in the order of phenological events could disrupt trophic interactions, with impacts on species fitness or abundance and community structure, ecosystem services such as pollination, gene flow, and competition among species (Rathcke and Lacey 1985; Fitter and Fitter 2002; Cleland et al. 2007; Memmott et al. 2007; Sherry et al. 2007; Thackeray et al. 2010; Polgar et al. 2014; Visser and Gienapp 2019). Our understanding of the order in which species undergo phenological transitions and how this is being affected by changing climate conditions arises from a limited number of studies, many of which report findings from a small number of species and/or a confined geographic region (e.g., Wesolowski and Rowinski 2006; Cole and Sheldon 2016). Only a limited number of studies evaluate multiple species across multiple sites (e.g., Lechowicz 1984; Panchen et al. 2014; Delpierre et al. 2017; Linkosalo 2000). Even fewer investigate patterns among multiple functional groups or phenophases. A more complete understanding of phenological ordering among plants and the underlying factors shaping this property of plant communities supports our ability to anticipate future changes and impacts to ecosystem structure and functioning.

National-scale phenology monitoring networks provide an opportunity to explore patterns in the sequence, or order, in which species undergo phenological transitions among many species and across large regions. In this study, we evaluate how consistently plants at a site leaf-out in the same order each year using observations contributed to *Nature's Notebook*, a plant and animal phenology observing platform maintained by the USA National Phenology Network (Rosemartin et al. 2014). We similarly explore how consistently plants bloom in the same order each year. Since Nature's Notebook launched in 2009, professional and volunteer observers have contributed over 30 M records of phenology at nearly 20,000 sites. Repeated observations are collected on individual plants following status-based protocols (Denny et al. 2014), intended to yield data of sufficient quality and rigor to be used in research and management applications (Crimmins et al. 2022). As in other studies from temperate systems, we expect to see a high level of consistency in the order in which plants leaf-out or flower at the sites observed through *Nature's Notebook*.

Several features of plants may shape the patterns we observe in how consistently plants either leaf-out or flower in the same order at a site. First, the degree of responsiveness of plant phenophases to climate or weather cues, or

phenological sensitivity, has been reported to vary among plant functional types (Fitter and Fitter 2002; Miller-Rushing and Primack 2008; Rollinson and Kaye 2011; Calinger et al. 2013; Way & Montgomery 2015; Munson and Long 2017). As such, we expect greater variability in the timing of leaf-out or flowering among particular groups of plants, and for this to be reflected in the consistency in the order of these events among species pairs. Second, many plant traits, including sensitivity to drivers of phenological events, vary across species' ranges (Savolainen et al. 2007; Leimu and Fischer 2008; Liang 2016). This variable sensitivity can lead to a different order in which species undergo phenological transitions among locations and has been reported in several studies. Waser (1983) reported a consistent order in flowering between *Delphinium nelsonii* and *Ipomopsis aggregata* at individual sites, though which species flowered first varied among locations. Inter-site differences in phenological sequence among species have been reported by others as well (e.g., Heinrich 1976; Wesolowski and Rowinski 2006; Vitasse et al. 2009; Panchen et al. 2014). We expect to see similar variability in the order species either leaf out or flower across sites. Finally, plant species active earlier in the season tend to exhibit greater variability in the timing of their activity than those active later in the season (Geng et al. 2020; Tao et al. 2021; Malyshev et al. 2022). Consequently, we expect to see higher consistency in the order in which species either leaf-out or flower among species active later in the season than those active earlier in the season.

In this study, in addition to characterizing overall patterns in the consistency in the order species either leaf-out or flower, we explore how various factors affect this ordering. We ask (1) whether patterns in consistency in the order of either leaf-out or flowering vary by functional type, (2) how well patterns in the consistency in the order of either leaf-out or flowering are preserved across sites, and (3) whether the consistency in the order of leaf-out or flowering varies over the course of the season.

Materials and methods

Over 1600 plant and animal species are available for monitoring in *Nature's Notebook* using vetted standardized phenophase definitions and protocols (Denny et al. 2014). We downloaded all "individual-level phenometrics data" (Rosemartin et al. 2018; USA National Phenology Network 2022) for "breaking leaf buds" and "open flowers" from 2009 to 2022 recorded for plants within 13 temperate zone states (ME, NH, VT, CT, RI, MA, NY, NJ, PA, OH, MI, WI, MN) from the USA-NPN database using the *rnpn* R package. We retained only the first instance of a "yes" report in the calendar year for a phenophase at a site, and records where the first report of "yes" was preceded by a report of

"no" for the phenophase within 7 days. We excluded observations where multiple observers submitted conflicting reports for the same individual plant on the same day. We also excluded sites with only a single species under observation and species*site combinations with fewer than 5 years of observations. After applying these filters, all remaining sites had only one individual per species with observations.

Characterizing overall patterns in consistency

At each site, we determined the consistency with which pairs of species underwent leaf-out or flowering in the same order in the years for which observations were available over the period 2009–2022. At each site, we calculated a measure of the consistency in the rank of phenological events among pairs of species meeting the criteria identified above. This measure, which we refer to as "consistency," reflects the proportion of years when activity in one species precedes that of another. These values range from 0 (timing of activity in species A preceded that of species B in all years) to 1 (timing of activity in species B preceded that of species A in all years). In both of these cases, consistency in phenological ordering is actually 100% (order of phenological events between the two species is the same in every year sampled). Accordingly, we calculated the inverse value for all species pair comparisons where consistency was less than 0.5, so that phenological order consistency values ranged from 0.5 to 1.0. A value of 1.0 indicates that the two species under consideration leafed out or flowered in the same temporal order in every year observed at the site, whereas a value of 0.5 indicates an equal number of years when species A preceded species B and when the inverse occurred. Site*years with the same onset day of year for the two members of the species pair were excluded from consistency calculations.

We explored a potential relationship between the number of days separating events (leaf-out or flowering) in species pairs using logistic regression with a random effect for site. For these tests, consistency values of less than 1.0 were converted to 0. To determine the average number of days separating events at which the probability of consistency = 1.0 switched from less than to 0.5 to greater than 0.5, we solved the logistic regression formula for $y = 0.5$.

Plant functional type comparisons

To determine whether consistency in leaf-out or flowering is higher among certain plant functional types, we assigned each species a label indicating their functional type (deciduous broadleaf, evergreen broadleaf, forb, and graminoid). As some functional types were very rare in the dataset, functional type category membership was very unbalanced. Prior to analyses, we excluded functional type categories with very small sample sizes (more than three standard

deviations from the mean category sample size). For leaf out, we removed the evergreen broadleaf-evergreen broadleaf category ($n = 1$). We then compared consistency values among the remaining groups, which included deciduous broadleaf-deciduous broadleaf, deciduous broadleaf-evergreen broadleaf, and deciduous broadleaf-semi evergreen broadleaf, using a Kruskall-Wallis rank sum test.

For bloom, we removed graminoid-deciduous broadleaf ($n = 7$), evergreen broadleaf-forb ($n = 5$), graminoid-evergreen broadleaf ($n = 4$), evergreen broadleaf-evergreen broadleaf ($n = 3$), and graminoid-forb ($n = 2$). We then compared consistency values among the remaining groups, which included deciduous broadleaf-deciduous broadleaf, deciduous broadleaf-evergreen broadleaf, deciduous broadleaf-forb, and forb-forb, using a Kruskall-Wallis rank sum test.

Among-site comparisons

To evaluate patterns in consistency in leaf-out or bloom ordering among species pairs present at multiple sites, we calculated mean consistency in leaf-out or flowering for these species pairs.

Seasonality comparisons

To determine whether consistency in phenological ordering of leaf-out or flowering is higher among species undergoing transitions later in the season, we assigned each species in a species pair to a tercile (early, mid, or late) based on the day of year of the event (leaf-out or flowering). We assigned species pairs based on these terciles (early-early, early-mid, early-late, mid-mid, mid-late, late-late) and compared the values among the groups using a Kruskall-Wallis rank sum test. We then used the Wilcoxon rank sum test for multiple pairwise comparisons with continuity correction to determine statistically significant pairs of means. Analyses were undertaken separately for leaf-out and flowering.

All analyses were carried out in R v1.4.1106.

Results

What is the consistency in phenological ordering among species pairs for leaf-out and flowering?

For leaf out, we evaluated 516 distinct site*species pairs encompassing 62 species and 69 sites across the northeastern USA (Table S1, Fig. 1a, c). Of these, 368 (71%) of the species pairs demonstrated a consistency value of 1.0, where leaf-out in one of the species at a site preceded the other in every year observed (Fig. S1). On average, distinct
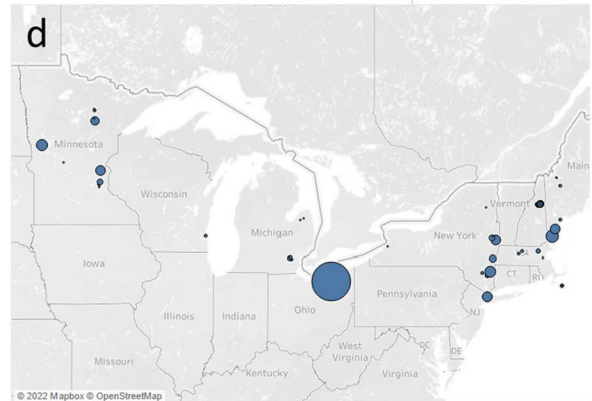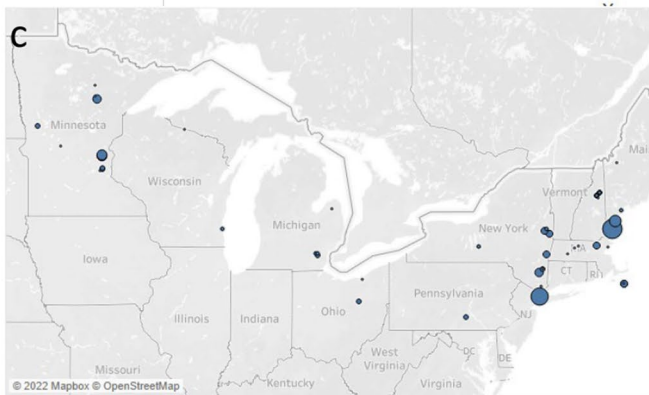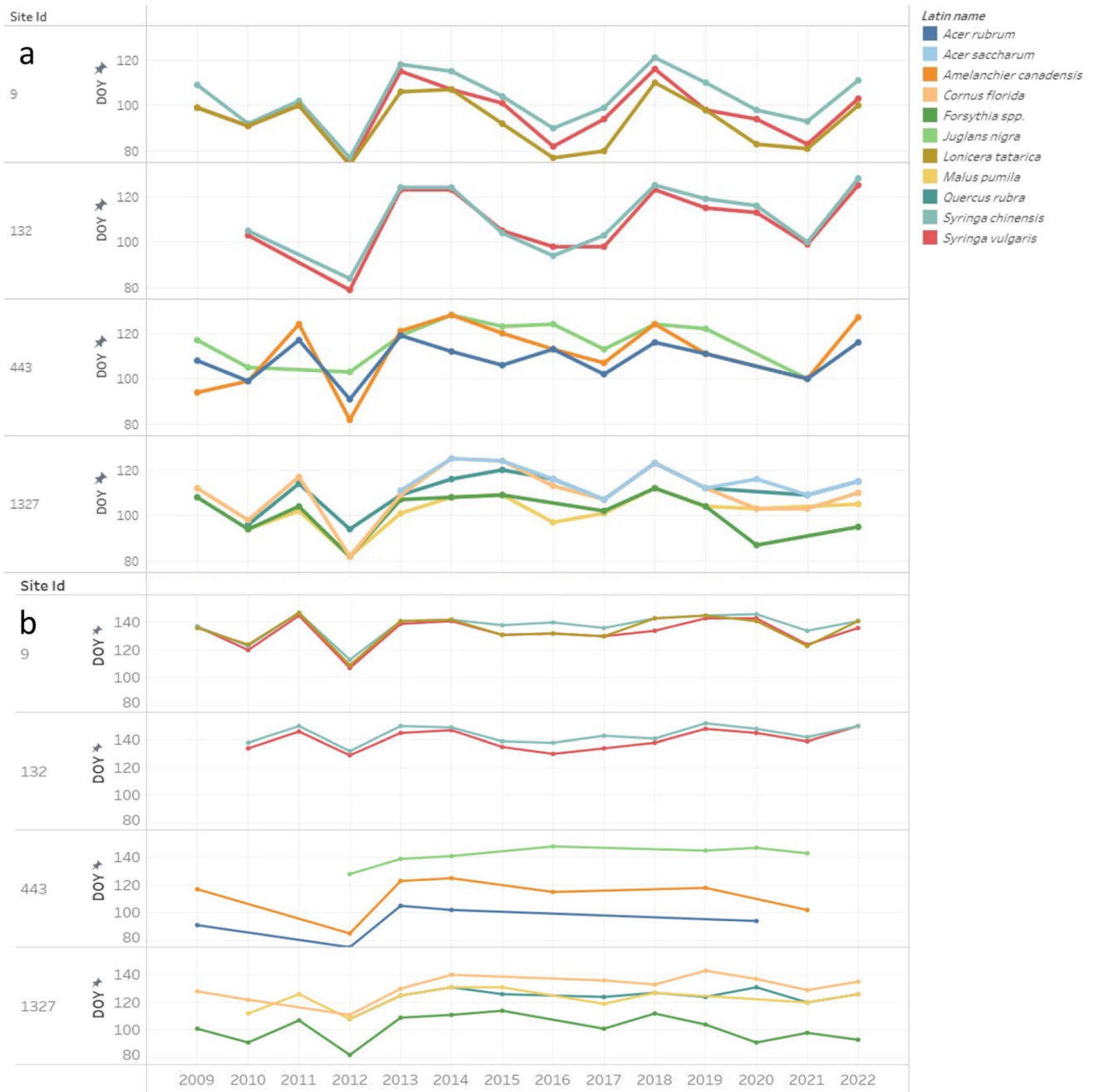
◀**Fig. 1** Representative time-series of **a** leaf-out and **b** flowering day of year (DOY) at distinct sites and sites with at least 5 years of observations of **c** leaf-out and **d** flowering for at least two species in *Nature's Notebook*. Circle size reflects the number of species pairs evaluated at the site. In all, leaf-out was observed at 69 sites and flowering was observed at 79 sites

site*species pairs had observations for 4.1 ± 2.1 years (mean $\pm$ SD).

For flowering, we evaluated 956 species pairs encompassing 95 site*species and 79 sites (Table S1, Fig. 1b, d). Of these, 796 (83%) species pairs exhibited a consistency value of 1.0 (Fig. S2). On average, distinct site*species pairs had observations for 4.6 ± 1.8 years (mean $\pm$ SD).

Understanding consistency in phenological ordering among species

Many species pairs exhibited absolute consistency ($= 1.0$), undergoing leaf-out or flowering in the same order in every year observed at a site. The logistic regression model predicting consistency based on the number of days separating the mean day of year of the event for the two members of a species pair was highly significant for both leaf-out and flowering ($p < 0.001$), indicating that the likelihood of absolute consistency occurring for a species pair increases with the number of days separating them. For leaf-out, the likelihood of a species showing consistency of less than 1.0 was greater when the number of days separating the events in a species pair was less than 1.01. Once the number of days separating the events becomes greater than 1.01, the species pair is more likely to exhibit absolute consistency. The likelihood of the pair exhibiting consistency $= 1.0$ increases by 20% with each additional day separating the two events. Consistency was very rarely < 1.0 once the number of days separating leaf-out among species pairs exceeded 23 days.

For flowering, the likelihood of a species showing consistency of less than 1.0 was greater when the number of days separating the events in a species pair was less than 0.95. Once the number of days separating the events is greater than 0.95, the species pair is more likely to exhibit absolute consistency. The likelihood of the pair exhibiting consistency $= 1.0$ in flowering increases by 12% with each additional day separating the two events. Consistency was very rarely < 1.0 once the number of days separating flowering among species pairs exceeded 35 days.

The variability in the timing of onsets among the members of the species pairs also shapes the consistency with which two species undergo leaf-out or flowering at a site. Reversals in onsets are more likely to occur when one or both species exhibits greater interannual variability in the timing of onset. However, variability in onset has the potential to impact consistency only when the number of days

separating the events is sufficiently small that variable onsets might lead to reversals. Species pairs exhibiting very high interannual variability in onsets can exhibit consistency $= 1.0$ if the number of days separating them is large enough that the events never coincide in time (Fig. 2). As such, the interannual variability in onset dates among species (SD(DOY)) has a smaller impact on consistency than the number of days separating the event. In our leaf-out and flowering pairs, high consistency values are observed among species pairs with both low and high interannual variability in onset dates. The inverse is true as well: low consistency values are observed among species pairs exhibiting all but the extreme lowest measures of interannual variability in onset dates.

Consistency among plant functional types

For leaf-out, consistency was not significantly different among the three functional type combinations (deciduous broadleaf-deciduous broadleaf, evergreen broadleaf-deciduous broadleaf, semi-evergreen broadleaf-deciduous broadleaf; $X^2 = 5.63$, $p = 0.06$, df $= 2$, Kruskal–Wallis rank sum test). Similarly, flowering consistency was not significantly different among the four functional type combinations (forb-forb, deciduous broadleaf-deciduous broadleaf, deciduous broadleaf-deciduous broadleaf, evergreen broadleaf-deciduous broadleaf; $X^2 = 5.28$, $p = 0.15$, df $= 3$, Kruskal–Wallis rank sum test).

## Differences in consistency among sites

For leaf-out, 93 species pairs were observed at multiple sites, accounting for 285 of the 516 unique site*species pairs represented in the full leaf-out dataset (Table S2), and 40 species pairs were present at three or more sites. In nearly a third (34) of the species pairs observed at multiple sites, consistency was 1.0 across all sites observed. However, the remaining species pairs had at least one site with a consistency measure of < 1.0.

For flowering, 82 species pairs were observed at multiple sites, accounting for 245 of the 956 unique site*species pairs represented in the full flowering dataset (Table S2), and 24 species pairs were present at three or more sites. Forty-eight (59%) of the species pairs observed at multiple sites exhibited consistency of 1.0 at all sites where the pair was observed. In some cases, this was true for species pairs observed at many sites. The remaining 34 species pairs had at least one site with a consistency measure of < 1.0 (Table S2).

Consistency over the season

Variability in the timing of leaf-out decreases significantly over the course of the season (test of the relationship between mean day of leaf-out for a species at a site and the

Fig. 2 Conceptual model depicting various combinations of variability in the timing of event (variability) and duration between the events (duration) that can occur. Both variability in the timing of the events and the duration between the events factor into the consistency in the sequence of timing in two phenological events
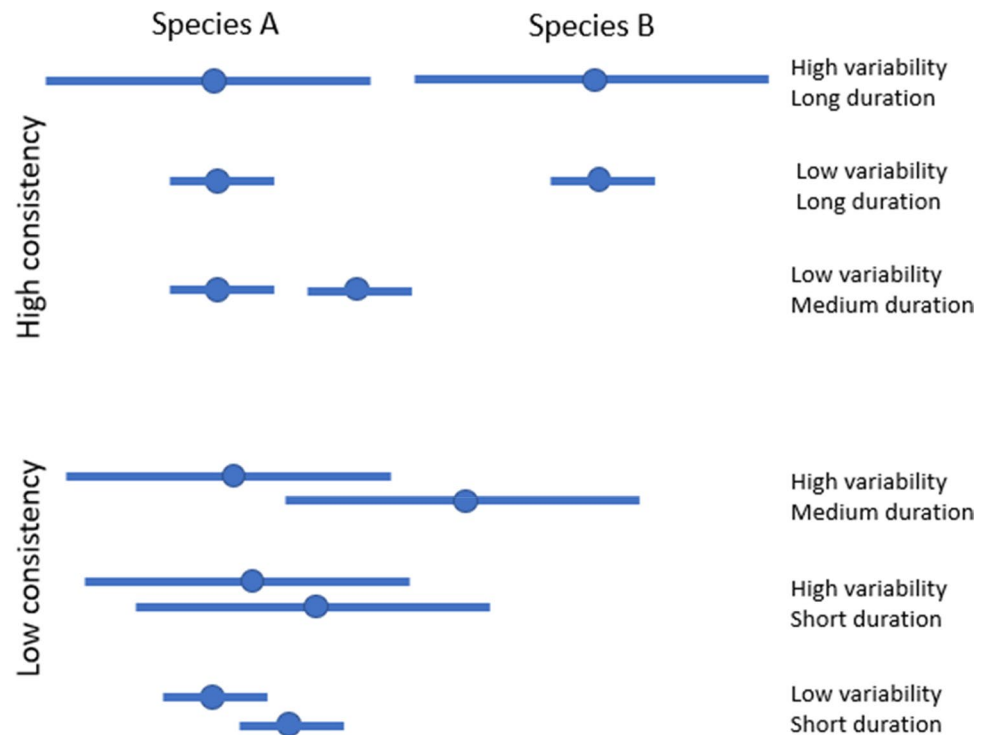
standard deviation of the day of leaf-out for a species at a site via ordinary least squares regression: $y = -0.15 \times + 26.5$; $R^2 = 0.24$, $p < 0.001$). The same is true for flowering (test of the relationship between mean day of open flower for a species at a site and the standard deviation of the day of open flower for a species at a site via ordinary least squares regression: $y = -0.05 \times + 15.21$; $R^2 = 0.08$, $p < 0.001$).

For leaf-out, consistency was significantly different among the six groups of leaf-out timing combinations ($X^2 = 30.64$, $p < 0.001$, df = 5, Kruskal–Wallis rank sum test). Consistency was significantly higher among species pairs originating from different terciles (i.e., early-late, mid-late) than among pairs of species originating from the same tercile (i.e., early-early, mid-mid; Wilcoxon multiple comparisons test, Fig. 3a). Consistency values among early-early species pairs and mid-mid species were not significantly different for leaf-out, though consistency for the late-late species pairs was significantly higher than both early-early and mid-mid pairs. This indicates a tendency for consistency in the order of phenophase transitions among species to be higher for species leafing out in the latest tercile of the season than those leafing out earlier in the season. However, whether the species in a pair originate from the same tercile—that is, leaf-out in the same segment of the season—has a greater influence over the consistency in leaf-out among the pair members.

As with leaf-out, flowering consistency was significantly different among the six groups ($X^2 = 76.81$, $p < 0.001$, df = 5, Kruskal-Wallis rank sum test). Average consistency was lowest among species pairs with both species flowering in the same tercile (i.e., early-early, mid-mid, late-late; Wilcoxon multiple comparisons test, Fig. 3b). Consistency was very high among pairs originating from different terciles (i.e., early-mid, early-late, mid-late). Similar to leaf-out, these results indicate that the average flowering time—the segment of the season in which the species flower—has the greatest influence on the consistency in flowering.

Discussion

Overall, our results revealed a relatively high degree of consistency in the order of leaf-out and flowering, with flowering exhibiting a greater degree of consistency than leaf-out. This finding is generally in agreement with similar studies that reported a predictable but not always perfectly consistent ordering in leaf-out and/or flowering among the species in a community (Heinrich 1976; Lechowicz 1984; Struck 1994; Kramer 1995; Price and Waser 1998; Wesolowski and Rowinski 2006; Panchen et al. 2014).

Influence of functional type and seasonality on consistency

In contrast to our expectations, our evaluation revealed that functional type has little to no impact on the consistency in which plants underwent either leaf out or flowering. We had expected to see different degrees of consistency among

Fig. 3 Consistency in pheno-
logical ordering of **a** leaf-out
and **b** flowering among pairs
of species undergoing transi-
tions in the early, middle, or late
spring-season terciles. Levels
not connected by the same letter
are significantly different
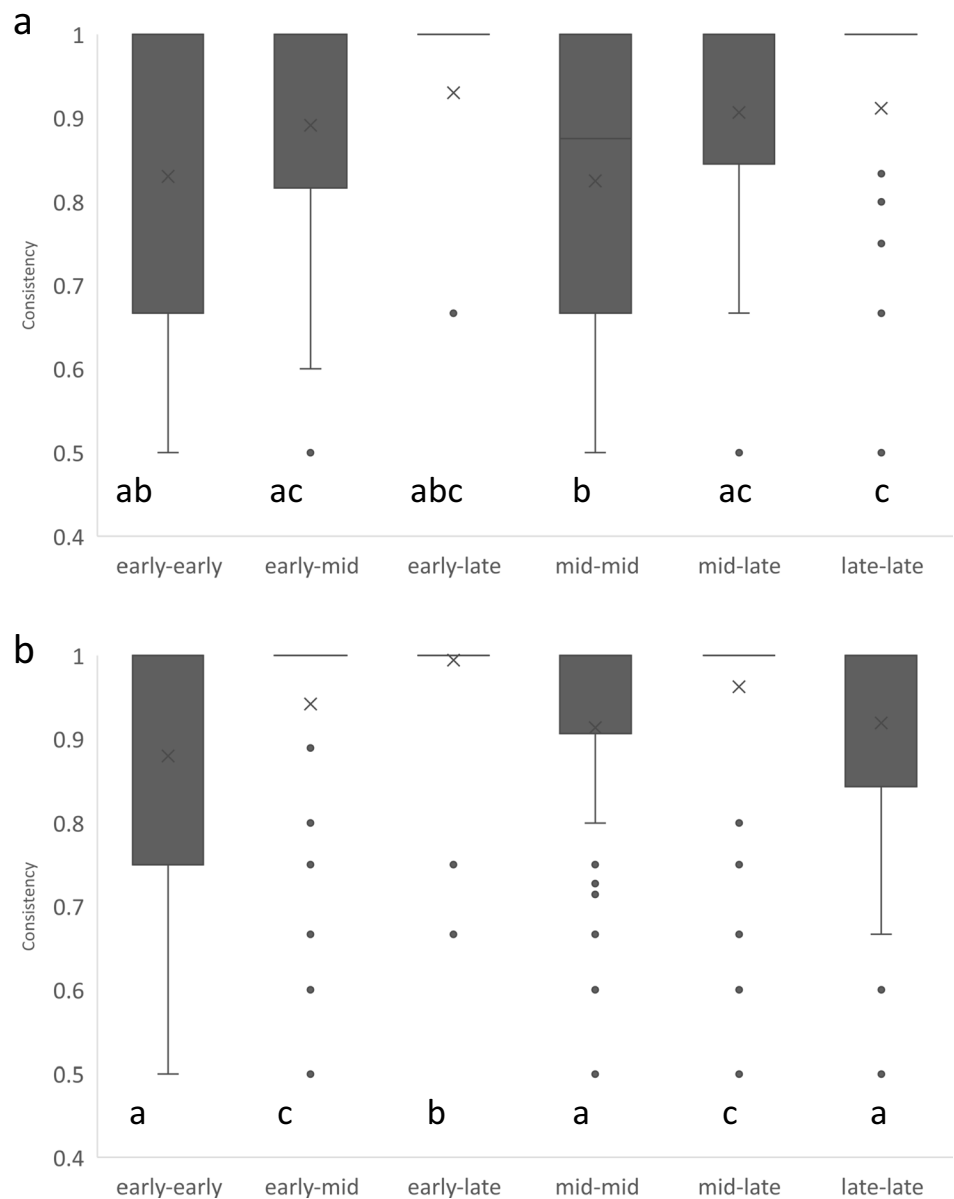
functional type groups as a consequence of the different
levels of pheonological sensitivity reported in other studies
(e.g., Fitter & Fitter 2002; Calinger et al. 2013; Way and
Montgomery 2015). However, given the composition of our
dataset, functional types such as graminoids were not well
represented and excluded from comparisons. Subsequent
analyses incorporating these functional types are merited.

Our exploration also revealed that for the most part, season-
ality does not play a major role in shaping the consistency in
which species undergo either leaf-out or flowering. Our expec-
tation was that the greater variability in the timing of leaf-out
and flowering typically observed earlier in the season (Abu-
Asab et al. 2001; Fitter and Fitter 2002; Sparks and Menzel
2002; Menzel et al. 2006; Sherry et al. 2007; Ma et al. 2021;

Tao et al. 2021) could drive lower consistency values for spe-
cies undergoing these events earlier in the season. The only
evidence we saw to support this prediction was significantly
higher consistency among plants leafing-out late in the season
compared to those leafing out earlier in the season (Fig. 3a).
This finding suggests that as climate conditions change in the
future, we may not see greater disruptions in the order species
undergo leaf-out (or flowering) within particular segments of
the spring season. Relatedly, greater variability earlier in the
season may also explain differences in consistency observed
between leaf-out and flowering. It seems likely that the higher
rates of consistency observed in flowering compared to leaf-
out are the result of flowering events typically occurring later
in the year than leaf-out in many of the species evaluated.

In our analysis, the most influential factor driving the consistency in the order of leaf-out or flowering among species pairs was the span of time separating the two events (Fig. 2). In our study, species undergoing leaf-out or flowering separated by more than three days on average were more likely than not to exhibit consistency in the sequence of leaf-out between two species. Furthermore, species pairs leafing out on average more than 23 days apart did not show reversals. For flowering, species pairs ceased to exhibit reversals once the duration separating their events exceeded 35 days. As climate conditions continue to change and species respond independently by shifting their phenology, both the span of days separating phenological events in pairs of species and the variability in the timing of the two events are likely to be affected. When species shift their phenology sufficiently that they are separated by less than a day, on average, reversals in sequence among the members of the pair will become increasingly more likely.

Among-site patterns in consistency

A notable strength and unique feature of the dataset evaluated in this study is the large number of species observed at a large number of sites. These features enable us to explore patterns in the consistency in the order of various phenophases in a novel way, including evaluating the degree to which ordering in leaf-out or flowering among pairs of species is preserved across large regions.

In our analysis, species pairs observed at multiple sites revealed high consistency in the ordering of events across multiple sites in approximately a third of species pairs for leaf out and in approximately half of species pairs for flowering. Said another way, for many species pairs, consistency in the order of activity between the two species varied from site to site, or across regions. Such variability could reflect plastic responses among species to different conditions at individual sites in a single year. Alternatively, differences in the consistency across sites could indicate local adaptation among individual plants. Phenology and sensitivity to drivers of phenological events have been documented to vary across a species' range as a result of local adaptation (Savolainen et al. 2007; Leimu and Fischer 2008; Liang 2016). Experimental approaches are necessary to further disentangle whether among-site differences are driven by plasticity, local adaptation, or a combination of these factors.

A small number of species pairs exhibited very high consistency in the order of either leaf-out or flowering across several sites. For example, hobblebush (*Viburnum lantanoides*) and Canada mayflower (*Maianthemum canadense*) exhibited the same order of flowering across 11 sites in every year observed. High consistency values such as this are best be explained by the amount of time separating the events. Hobblebush is active very early in the season and Canada

mayflower is active later in the spring season; accordingly, conditions cueing flowering in these two species would need to change dramatically to cause them to reorder their flowering sequence.

Strengths and limitations of the phenology dataset evaluated

The phenology observations evaluated in this study originate from participants in the USA-NPN's *Nature's Notebook* program, who are both professionals and volunteers. The quality of observations contributed by volunteers is frequently questioned (Aceves-Bueno et al. 2017). Volunteer-contributed data may suffer from a variety of errors that could affect our estimates of consistency, including species misidentifications, phenophase misidentifications, and infrequent or inconsistent observations.

Volunteers' ability to properly identify species is variable; volunteer observers tend to generate more accurate data when presented with concrete tasks such as taking measurements or making categorial assessments as opposed to the more open-ended tasks of species identification (McDonough MacKenzie et al. 2017). When participating in *Nature's Notebook*, observers are required to identify and register plants and then to collect periodic observations on the plants following a protocol comprised of binary and categorical choices. As such, species identifications may be the step most vulnerable to error in the phenology observation process. Errors in species identification would not affect the site-specific pairwise comparisons. However, misidentified species could impact inter-site comparisons by pooling observations from incorrectly identified species with individuals of the intended species.

Observers' assessments of phenophase status may also include errors, though since these assessments are categorical in nature (yes/no/unsure), they are less likely than species identifications to be in error. Fuccillo et al. (2015) demonstrated that on average, participants in *Nature's Notebook* correctly assess the phenophase status of plants 91% of the time. Volunteers' ability to correctly assess phenophase status is poorest when evaluating the first phenological events of the season, which is often breaking leaf buds. Accordingly, the observations of leaf-out could exhibit a higher error rate than those of flowering, contributing to the lower consistency measures observed in leaf-out than in flowering. However, we see similar variability among observations for leaf-out contributed by professionals and volunteer observers. For example, the observations originating from site #2 were contributed by a USA-NPN staff member and are therefore expected to be of high quality. The observations of leaf-out at this site show a similar degree of variability to those contributed at other sites. Furthermore, variability in observations at site #2 is greater for leaf-out than

for flowering. As such, we qualitatively conclude that the variability observed in onset dates is more likely to reflect the true activity of the plants under observation than due to observer error. Plants observed erratically or infrequently were likely excluded from our analyses; we required the date of onset for a leaf-out or flowering for an individual plant (a report of "yes" to leaves or open flowers) to be preceded by a report of no leaves or flowers within the preceding week. As such, the tendency for infrequent observations within the *Nature's Notebook* dataset does not impact our results.

In the dataset evaluated, only a single individual of a species was observed at a site, by nature of the sites that were retained in the analysis. As such, we assume that the phenology of this individual reflects that of the local population. The phenology of individual plants at a site may vary as a result of local conditions such as soil moisture, social status, age, or shade status (Capdevielle-Vargas et al. 2015; Gressler et al. 2015; Delpierre et al. 2017), and volunteer observers may preferentially chose to observe individual plants that are more accessible or that are not representative of the local population (Daru et al. 2018). Observations collected on individual plants not representative of the population would not likely have a major impact on our estimates of consistency but could affect inter-site comparisons of species pairs and by extension, our identification of species possibly exhibiting local adaptation. A more robust evaluation of the potential of local adaptation across a species' range should incorporate observations of more individuals at distinct sites across the range.

In this study, we evaluated phenology observations of nearly 1500 species pairs contributed from close to 100 sites across the northeastern United States. The spatial extent and taxonomic breadth of this dataset enabled a robust evaluation of the consistency with which species undergo springtime phenological activity. In addition, this dataset enabled a novel investigation of phenological behavior across species ranges. The rapidly growing phenology data maintained by the USA-NPN hold the potential to support investigations of this nature to an increasing extent.

Implications

Our findings suggest that if changing climate conditions cause species to shift their timing such that the amount of days separating them decreases, the likelihood of disruptions in their phenological ordering becomes increasingly greater. This may be especially true for species pairs cued by different drivers. Species highly sensitive to temperature to trigger leaf bud break advance their phenological activity under warmer spring temperatures, while those with stronger winter chill or photoperiod requirements often delay activity when exposed to anomalous springtime warmth (Körner and Baser 2010; Way and Montgomery 2015). Changes in temperature

driving these events could lead to either temporal compression or divergence in the timing of activity among species pairs, with an impact on the consistency of their sequencing (Fitter and Fitter 2002; Sherry et al. 2007; CaraDonna et al. 2014; Laube et al. 2014; Zohner et al. 2016, 2018). Disruptions in phenological sequence can reduce synchrony among species (Montgomery et al. 2020) with impacts on both community structure and function. Shifts in the timing or sequence of leaf-out phenology have implications for large-scale cycles like carbon and water, as well as folivorous insect populations which in turn affect insect outbreak and soil nutrient dynamics and higher trophic levels (Visser et al. 1998; Chapman et al. 2006; Richardson et al. 2009; Kim et al. 2018; Ekholm et al. 2020). Similarly, shifts in flowering phenology can lead to shifts in floral density and co-flowering patterns, with consequences for plant fitness, gene flow, and pollinators (Rathcke and Lacey 1985; Fitter and Fitter 2002; Memmott et al. 2007; Sherry et al. 2007).

Conclusions

In this study, we documented relatively high consistency in the sequence of leaf-out and flowering among individual plants collected across a large region, with higher consistency in flowering than in leaf-out. While our analysis indicated that plant functional type and position within the season (e.g., early leaf-out vs later season leaf-out) do not play much of a role, it revealed that consistency in the order of phenological events is shaped primarily by the number of days separating the events as well as by interannual variability in timing. Increased understanding of the complex nature of phenological sequencing provides important insight into the dynamic behavior of and interactions between species as well as trophic disruptions due to climate change. The multiple-site, pairwise analysis of phenological ordering presented here demonstrates a novel approach to evaluating and understanding the primary factors shaping interspecific consistency and may provide new ways to uncover plastic or locally adaptive responses in individuals or species. This approach merits further investigation with the suggestion to include observations from an increased number of sites and plant functional types gathered across a larger region over longer time periods. In addition, this work illustrates the opportunity that national-scale phenology monitoring network platforms provide to explore patterns in the order of phenological events among many species and across broad geographic scales.

Declarations

Competing interests The authors declare no competing interests.

References

Abu-Asab MS, Peterson PM, Shetler SG, Orli SS (2001) Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodivers Conserv 10:597–612. https://doi.org/10.1023/A:1016667125469

Aceves-Bueno E, Adeleye AS, Feraud M, Huang Y, Tao M, Yang Y, Anderson SE (2017) The accuracy of citizen science data: a qualitative review. Bullet Ecol Soc America 98(4):278–290. https://doi.org/10.1002/bes2.1336

Aizen MA, Vázquez DP (2006) Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement? Ecography 29(3):357–366. https://doi.org/10.1111/j.2006.0906-7590.04552.x

Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agric Forest Meteorol 165:73–81. https://doi.org/10.1016/j.agrformet.2012.06.001

Bennie J, Kubin E, Wiltshire A, Huntley B, Baxter R (2010) Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. Glob Change Biol 16:1503–1514. https://doi.org/10.1111/j.1365-2486.2009.02095.x

Buonaiuto DM, Wolkovich EM (2021) Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. J Ecol 109:2922–2933. https://doi.org/10.1111/1365-2745.13708

Caffarra A, Donnelly A (2011) The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. Int J Biometeorol 55:711–721. https://doi.org/10.1007/s00484-010-0386-1

Calinger KM, Queenborough S, Curtis PS (2013) Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. Ecol Lett 16(8):1037–1044. https://doi.org/10.1111/ele.12135

Capdevielle-Vargas R, Estrella N, Menzel A (2015) Multiple-year assessment of phenological plasticity within a beech (*Fagus sylvatica L.*) stand in southern Germany. Agric For Meteorol 211–212:13–22. https://doi.org/10.1016/j.agrformet.2015.03.019

CaraDonna PJ, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. Proc Natl Acad Sci USA 111:4916–4921. https://doi.org/10.1073/pnas.1323073111

Chapman SK, Whitham TG, Powell M (2006) Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees. Oikos 14(3):566–574

Chu X, Man R, Zhang H, Yuan W, Tao J, Dang QL (2021) Does climate warming favor early season species? Front Plant Sci 18:2617. https://doi.org/10.3389/fpls.2021.765351

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–365. https://doi.org/10.1016/j.tree.2007.04.003

Cole EF, Sheldon BC (2016) The shifting phenological landscape: within- and between-species variation in leaf emergence in a mixed-deciduous woodland. Ecol Evol 7:1135–1147. https://doi.org/10.1002/ece3.2718

Cook BI, Wolkovich EM, Parmesan C (2012) Divergent responses to spring and winter warming drive community level flowering trends. PNAS 109(23):9000–9005. https://doi.org/10.1073/pnas.111836410

Crimmins T, Denny E, Posthumus E, Rosemartin A, Croll R, Montano M, Panci H (2022) Science and management advancement made possible by the USA National Phenology Network's Nature's Notebook Platform. Bioscience 72(9):908–920. https://doi.org/10.1093/biosci/biac061

Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfield TJS, Seidler TG, Sweeney PW, Foster DR, Ellison AM, Davis CC (2018) Widespread sampling biases in herbaria revealed from large-scale digitization. New Phytol 217:939–955. https://doi.org/10.1111/nph.14855

Delpierre N, Guillemot J, Dufrêne E, Cecchini S, Nicolas M (2017) Tree phenological ranks repeat from year to year and correlate with growth in temperate deciduous forests. Agric For Meteorol 234–235:1–10. https://doi.org/10.1016/j.agrformet.2016.12.008

Denny E, Gerst KL, Miller-Rushing A, Tierney G, Crimmins TM, Enquist CAF, Guertin P, Rosemartin A, Schwartz MD, Thomas K, Weltzin JF (2014) Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. Int J Biometeorol 58:591–660. https://doi.org/10.1007/s00484-014-0789-5

Ekholm A, Tack AJ, Pulkkinen P, Roslin T (2020) Host plant phenology, insect outbreaks and herbivore communities–The importance of timing. J Anim Ecol 89(3):829–841. https://doi.org/10.1111/1365-2656.13151

Fitter A, Fitter R (2002) Rapid changes in flowering time in British plants. Science 296:1689–1691. https://doi.org/10.1126/science.1071617

Flynn DFB, Wolkovich EM (2018) Temperature and photoperiod drive spring phenology in all species in a temperate forest community. New Phytol 219:1353–1362. https://doi.org/10.1111/nph.15232

Fu YSH, Piao S, Zhao H, Jeong SJ, Wang X, Vitasse Y, Ciais P, Janssens IA (2014) Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. Glob Change Biol 20:3743–3755. https://doi.org/10.1111/gcb.12610

Fuccillo KK, Crimmins TM, de Rivera CE, Elder TS (2015) Assessing accuracy in citizen science-based plant phenology monitoring. Int J Biometeorol 59:917–926. https://doi.org/10.1007/s00484-014-0892-7

Geng X, Fu YH, Hao F, Zhou X, Zhang X, Yin G, Vitasse Y, Piao S, Niu K, de Boeck HJ (2020) Climate warming increases spring phenological differences among temperate trees. Glob Change Biol 26:5979–5987. https://doi.org/10.1111/gcb.15301

Gressler E, Jochner S, Capdevielle-Vargas RM, Morellato PCM, Menzel A (2015) Vertical variation in autumn leaf phenology of Fagus sylvatica L. in southern Germany. Agric For Meteorol 201:176–186. https://doi.org/10.1016/j.agrformet.2014.10.013

Heinrich B (1976) Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57(5):890–899. https://doi.org/10.2307/1941055

Kim JH, Hwang T, Yang Y, Schaaf CL, Boose E, Munger JW (2018) Warming-induced earlier greenup leads to reduced stream

discharge in a temperate mixed forest catchment. J Geophys Res Biogeosci 123(6):1960–1975. https://doi.org/10.1029/2018J G004438

Körner C, Basler D (2010) Phenology under global warming. Science 327:1461–1462. https://doi.org/10.1126/science.1186473

Kramer K (1995) Phenotypic plasticity of the phenology of 7 European tree species in relation to climatic warming. Plant, Cell Environ 18:93–104. https://doi.org/10.1111/j.1365-3040.1995.tb00356.x

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A (2014) Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biol 20:170–182. https://doi.org/10.1111/gcb.12360

Lechowicz M (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. Am Nat 124:821–842. https://doi.org/10.1086/284319

Leimu R, Fischer M (2008) A meta-analysis of local adaptation in plants. PLoS One 3(12):e4010. https://doi.org/10.1371/journal.pone.0004010

Liang L (2016) Beyond the bioclimatic law: geographic adaptation patterns of temperate plant phenology. Progress Phys Geogr Earth Environ 40:811–834. https://doi.org/10.1177/0309133316656558

Linkosalo T (2000) Mutual regularity of spring phenology of some boreal tree species: predicting with other species and phenological models. Can J for Res 30:667–673

Ma Q, Huang J-G, Hänninen H, Li X, Berninger F (2021) Climate warming prolongs the time interval between leaf-out and flowering in temperate trees: effects of chilling, forcing and photoperiod. J Ecol 109(3):1319–1330. https://doi.org/10.1111/1365-2745.13558

Malyshev AV, van der Maaten E, Garthen A, Ma D, Schwabe M, Kreyling J (2022) Inter-individual budburst variation in *Fagus sylvatica* is driven by warming rate. Front Plant Sci 13:853521. https://doi.org/10.3389/fpls.2022.853521

McDonough MacKenzie C, Murray G, Primack R, Weihrauch D (2017) Lessons from citizen science: assessing volunteer-collected plant phenology data with Mountain Watch. Biol Conserv 208:121–126. https://doi.org/10.1016/j.biocon.2016.07.027

Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant–pollinator interactions. Ecol Lett 10:710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Almkübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatczak K, Måge F, Zust A (2006) European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969–1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Miller-Rushing AJ, Primack RB (2008) Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology 89:332–341. https://doi.org/10.1890/07-0068.1

Montgomery RA, Rice KE, Stefanski A, Rich RL, Reich PB (2020) Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit and geographic range. PNAS 117:10397–10405. https://doi.org/10.1073/pnas.1917508117

Munson SM, Long AL (2017) Climate drives shifts in grass reproductive phenology across the western USA. New Phytol 213(4):1945–1955. https://doi.org/10.1111/nph.14327

Panchen ZA, Primack RB, Nordt B, Ellwood ER, Stevens AD, Renner SS, Willis CG, Fahey R, Whittemore A, Du Y, Davis CC (2014) Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. New Phytol 203(4):1208–1219. https://doi.org/10.1111/nph.12892

Polgar C, Primack R (2011) Leaf-phenology of temperate woody plants: from trees to ecosystems. New Phytol 191:926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x

Polgar C, Gallinat A, Primack RB (2014) Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. New Phytol 202(1):106–115. https://doi.org/10.1111/nph.12647

Price MV, Waser NM (1998) Effects of experimental warming on plant reproductive phenology in a subalpine meadow. Ecology 79(4):1261–1271. https://doi.org/10.1890/0012-9658(1998)079[1261:EOEWOP]2.0.CO;2

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Ann Rev Ecol Syst 16:179–214. https://doi.org/10.1146/annurev.es.16.110185.001143

Richardson AD, Hollinger DY, Dail DB, Lee JT, Munger JW, O'keefe J (2009) Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. Tree Physiol 29(3):321–331. https://doi.org/10.1093/treephys/tpn040

Rollinson CR, Kaye MW (2011) Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. Glob Change Biol 18(3):1108–1116. https://doi.org/10.1111/j.1365-2486.2011.02612.x

Rosemartin AH, Crimmins TM, Enquist CAF, Gerst KL, Kellermann JL, Posthumus EE, Denny EG, Guertin P, Marsh L, Weltzin JF (2014) Organizing phenological data resources to inform natural resource conservation. Biol Cons 173:90–601. https://doi.org/10.1016/j.biocon.2013.07.003

Rosemartin A, Denny EG, Gerst KL, Marsh RL, Posthumus EE, Crimmins TMd, Weltzin JF (2018) USA Phenology Network observational data documentation. US Geol Surv Open-File Rep 24:2018–1060. https://doi.org/10.3133/ofr20181060

Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. Annu Rev Ecol Evol Cyst 38:595–619. https://doi.org/10.1146/annurev.ecolsys.38.091206.095646

Sherry RA, Zhou X, Gu S, Arnone JA, Schimel DS, Verburg PS, Wallace LL, Luo Y (2007) Divergence of reproductive phenology under climate warming. Proceed Natl Acad Sci USA 104:198–202. https://doi.org/10.1073/pnas.0605642104

Sparks TH, Menzel A (2002) Observed changes in seasons: an overview. Int J Climatol 22(14):1715–1725. https://doi.org/10.1002/joc.821

Struck M (1994) Flowering phenology in the arid winter rainfall region of southern Africa. Bothalia 24(1):77–90. https://doi.org/10.4102/abc.v24i1.754

Tao J, Man R, Dang QL (2021) Earlier and more variable spring phenology projected for eastern Canadian boreal and temperate forests with climate warming. Trees For People 6:100127. https://doi.org/10.1016/j.tfp.2021.100127

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield ID, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16(12):3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

USA National Phenology Network. 2022. Plant individual phenometrics data, 2009–2022. USA-NPN, Tucson, Arizona, USA. https://doi.org/10.5066/F78S4N1V Accessed Jul 28, 2022

Visser ME, Noordwijk AV, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). Proceedings of the Royal Society of London. Series B: Biol Sci 265(1408):1867-1870

Visser ME, Gienapp P (2019) Evolutionary and demographic consequences of phenological mismatches. Nat Ecol Evol 3(6):879–885. https://doi.org/10.1038/s41559-019-0880-8

Vitasse Y, Delzon S, Bresson CC, Michalet R, Kremer A (2009) Altitudinal differentiation in growth and phenology among populations

of temperate-zone tree species growing in a common garden. Can J for Res 39:1259–1269

Waser NM (1983) Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In: Jones CE, Little RJ (eds) Handbook of Experimental Pollination Biology. Van Nostrand, New York, pp 277–293

Way DA, Montgomery RA (2015) Photoperiod constraints on tree phenology performance and migration in a warming world. Plant, Cell Environ 38:1725–1736. https://doi.org/10.1111/pce.12431

Wesolowski T, Rowinski P (2006) Timing of bud burst and tree-leaf development in a multispecies temperate forest. For Ecol Manage 237:387–393. https://doi.org/10.1016/j.foreco.2006.09.061

Yu H, Luedeling E, Xu J (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proc Natl Acad Sci 107(51):22151–22156. https://doi.org/10.1073/pnas.1012490107

Zohner CM, Benito BM, Svenning J-C, Renner SS (2016) Day Length Unlikely to Constrain Climate-Driven Shifts in Leaf-out times of Northern Woody Plants. Nat Clim Chang 6:1120–1123. https://doi.org/10.1038/NCLIMATE3138

Zohner CM, Lidong M, Renner SS (2018) Global warming reduces leaf-out and flowering synchrony among individuals. eLife 7:e40214. https://doi.org/10.7554/eLife.40214