Assessing plant phenological changes based on drivers of spring phenology

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ABSTRACT

Understanding plant phenological responses to climate warming is crucial for predicting changes in plant communities and ecosystems but difficult with sensitivity analysis that is not linked to drivers of spring phenology. In this article, we present a new measure *phenological lag* to quantify the overall effect of phenological constraints including insufficient winter chilling, photoperiod, and environmental stresses, based on observed response and that expected from species-specific changes in spring temperatures, i.e., changes in spring forcing (degree days) from warming and average temperature at time of species events. We applied this new analytical framework to a global dataset with 980 species and 1527 responses to synthesize observed changes in spring phenology and investigate the contributions of forcing change, growth temperature, and phenological lag to differential phenological responses reported previously.

Keywords: spring phenology, phenological lag, forcing change, growth temperature, phenological response, meta-analysis

Mechanisms of changes in spring phenology

Plant phenology, particularly in spring, is shifting with warming climate (Fitter and Fitter, 2002; Post et al., 2018; Primack and Gallinat, 2016). Numerous observational studies and controlled experiments, conducted over a range of climatic and phenological conditions (Huang et al., 2020; Parmesan, 2007; Prevéy et al., 2019; Root et al., 2003; Wolkovich et al., 2012), have produced varying results, with observed phenological changes differing by research approach (Wolkovich et al., 2012), climatic region (Parmesan, 2007; Post et al., 2018; Prevéy et al., 2017; Zhang et al., 2015), and functional group (Parmesan, 2007; Root et al., 2003; Willis et al., 2010; Wolkovich et al., 2013; Zettlemoyer et al., 2019). For example, observed changes are often smaller with experimental studies (Wolkovich et al., 2012), native species (Wolkovich et al., 2013), and warmer regions (Prevéy et al., 2017). Understanding these differences (also referred to as discrepancies or mismatches) is crucial for predicting changes in plant communities and ecosystems (Fitter and Fitter, 2002; Polgar et al., 2014; Primack and Gallinat, 2016) but difficult with sensitivity analysis that is not linked to drivers of spring phenology.

Plants in the northern hemisphere require an accumulation of cool winter temperatures (winter chilling) to break dormancy and an accumulation of warm spring temperatures (spring forcing, degree days) to initiate species event (e.g., leafing or flowering) (Piao et al., 2019; Way and Montgomery, 2015). This means that changes in spring phenology result primarily from changes in spring forcing prior to species events if chilling requirements are fully met and other phenological constraints (e.g., photoperiod effect and environmental stresses) remain constant. While the direction of phenological changes (advance or delay) is set by the sign of forcing changes (+ or -), the magnitude of changes depends on quantity of forcing changes, as well as level of growth temperatures at time of species event with a warmer climate, i.e., higher growth

temperatures are associated with smaller observed changes and sensitivity and lower growth temperatures with larger observed changes and sensitivity (Chu et al., 2021, 2023; Prevéy et al., 2017; Shen et al., 2014). As species often differ in timing of spring events, both forcing change and growth temperature are species-specific, reflecting changes in spring temperatures that are relevant to phenological changes of individual species (Chu et al., 2021, 2023). The effects of photoperiod (day length) and environmental stresses (e.g., drought and spring freezing) are similar to those of insufficient winter chilling in constraining the advance of spring phenology (Chen et al., 2011; Huang et al., 2019; Körner and Basler, 2010; Ma et al., 2019; Way and Montgomery, 2015). The difference between observed phenological change and that expected from forcing change and growth temperature represents phenological difference due to effects of phenological constraints and can be thereafter named phenological lag. Separating effects of different constraints is possible if soil moisture/plant water status is monitored (Huang et al., 2019; Post et al., 2022), or species-specific chilling and photoperiod effects (Man et al., 2017a, 2021a; Fu et al., 2019) or cold hardiness (Man et al., 2017b, 2021b) are known from previous research. For example, phenological lag can represent the effect of insufficient chilling when photoperiod effect and environmental stresses are constant (Chen et al., 2011).

The changes in spring phenology are often quantified with sensitivity, a parameter that reflects rates of changes but not uneven warming and responses (Beaubien and Hamann, 2011; Keenan et al., 2020; Post et al., 2018; Rafferty et al., 2020) or magnitude and underlying mechanisms of changes in spring phenology (Chu et al., 2021, 2023). Here, we present a new method to partition observed phenological change into forcing change, growth temperature, and phenological lag, based on changes in spring phenology and temperatures with control (baseline) and warmer climates. We applied this analytical approach to meta-analyze phenological changes

reported in the literature and examined the contributions of forcing change, growth temperature, and phenological lag to differential responses reported previously, i.e., research approach (observational or experimental study), species origin (native or exotic), climatic region (boreal or temperate), and growth form (tree, shrub, herb, or grass).

Partitioning observed changes

Species-specific forcing change (F_C) can be calculated from the difference between degree days (> 0 °C, see Man and Lu, 2010) of baseline (or control) ($\sum_1^i T_{Ci}$) and warmer ($\sum_1^i T_{Wi}$) temperatures at the time of species event (leafing or flowering) with baseline temperatures (O_{Ci}) (see Figure 1).

$$F_C = \sum_1^i T_{Wi} - \sum_1^i T_{Ci}$$

The phenological response expected under the null hypothesis that climate warming does not induce changes in phenological constraints can be determined from forcing change and species phenology with baseline temperatures (Figure 1):

$$N_{Ei} = \min \left| \sum_1^{i-n} T_{Wi} - \sum_1^i T_{Ci} \right|$$

where N_E is the difference in the number of days (n) between baseline $\sum_1^i T_{Ci}$ and warmer $\sum_1^{i-n} T_{Wi}$ temperatures in reaching species forcing needs with baseline temperatures (spring forcing at O_{Ci}). Under this hypothesis, spring phenology is expected to shift from O_{Ci} with baseline temperatures to E_{Wi} with warmer temperatures. N_E is typically positive, meaning earlier leafing and flowering, but can be negative if temperatures decrease over time in observational studies.

Growth temperature (T_N) is the average temperature or rate of forcing accumulation within the window of expected phenological response (between O_{Ci} and E_{Wi}) and can be determined from forcing change and expected response.

$$T_N = F_C/N_E$$

The difference between expected (N_E) and observed (N_O) responses is phenological lag (N_C) reflecting phenological difference due to effects of phenological constraints.

$$N_C = N_E - N_O$$

$N_C > 0$ indicates increasing phenological constraints that may result from increasing chilling deficiency, photoperiod restriction, moisture stress, or risks of spring frosts; $N_C = 0$ indicates no changes; and $N_C < 0$ indicates decreasing constraints with warming climate.

Meta-analysis of global data

Phenological Data

We followed the guidelines of PRISMA (preferred reporting items for systematic reviews and meta-analyses) (O'Dea et al., 2021; Page et al., 2020) to build up the dataset for responses of plant spring phenology to experimental and climatic warming. We used Web of Science and Google Scholar to search experimental and observational studies on warming-induced changes in spring phenology. The following criteria were used to select papers: (a) accessible peer-reviewed articles published in scientific journals for boreal (MAT < 6 °C) and temperate (MAT ≥ 6 °C) regions in the northern hemisphere, (b) studies reporting spring leafing or flowering before Julian day 213 (July 31), (c) studies containing different climatic conditions of baseline (lower temperatures in early period of observations or unwarmed control treatment) and warmer (higher temperatures in later period of observations or warmer treatment) climates, (d) access to local

temperature data (only one study was excluded due to lack of nearby temperature data within 50 km), and (e) reported phenological changes in unique locations, species, and periods of observations/warmer treatments. When publications did not contain sufficient phenological information, we accessed data directly from phenological databases (e.g., China's National Earth System Science Data Center). When results were reported in graphical format, we extracted the required data using the distance measuring tool in Adobe Acrobat Reader DC. In experimental studies with multiple warming treatments, we selected the treatment with the smallest temperature increases to represent a likely scenario of climate change and to maintain data independence. We also excluded studies where the timing of phenological events, total temperature change, or observational time periods were not available.

In total, 66 studies were identified from 87 locations, containing 1,527 phenological responses for 980 species (Tables S1–S3). For studies reporting multiple phenological stages, we only used data for the first occurrence of the event. To account for variation in phenological responses, each study location was characterized by research approach (observation or experiment), climatic region (boreal or temperate), biogeographic origin of species (exotic or native to study area), and growth form (tree, shrub, herb, or grass).

Climate Data

Baseline and warmer temperature data for calculating forcing change, expected response, growth temperature, phenological lag, spring warming (average temperature change from Julian day 1 to 182), and long-term MAT and MAP were obtained from 9 different sources (Table S4). When temperature data were available from multiple sources, we selected the data set with the fewest missing values. For each phenological response, the number of weather stations within 50 km of

158 data collection ranged from 1 for studies at a single location to 14 for observational studies
159 across large geographic areas (Table S2).
160
161 **Data analysis**
162 W calculated forcing change, expected response, growth temperature, and phenological lag for
163 each of the 1527 responses compiled. We used linear mixed-effects models to explore the
164 differences in observed responses and phenological lags between research approaches
165 (observations vs. experiments), species origins (native vs. exotic), and climatic regions (boreal
166 vs. temperate), and among growth forms (trees, shrubs, herbs, and grasses). Separate analysis
167 was conducted for each of the four fixed effects and two species events (leafing and flowering).
168 Location and species were treated as random effects.
169 To assess the influences of climatic, phenological, and biological variables, we used a
170 stepwise regression with automated combined forward and backward selection by Akaike
171 information criterion (AIC) (Burnham and Anderson, 2002) to select the best combination of
172 variables for predicting observed responses (N_O).
173 $$N_O \sim A_L + L_A + MAT + MAP + D_T + T_N + F_C + S_W + N_C$$
174 The variables included were altitude (A_L), latitude (L_A), MAT, MAP, spring phenology (D_T),
175 growth temperature (T_N), forcing change (F_C), spring warming (S_W), and phenological lag (N_C).
176
177 **Observed changes in spring phenology**
178 Across 66 studies with 980 species and 1527 responses, observed responses (N_O) ranged from
179 −23.8 to +26.8 days for leafing and −36.3 to +49.9 days for flowering, with an average of +6.0
180 days for both events. These changes differed from expected responses (N_E) which ranged from

−3 to +27 days for leafing and −3 to +26 days for flowering and averaged +7.8 and +9.5 days, respectively. Observed phenological responses were thus smaller than the expected by 1.8 and 3.5 days, on average, for leafing and flowering, respectively.

In experimental studies, observed flowering response was non-significantly smaller than those from observational studies (1.7 days, p=0.232, Figure 2a), while phenological lag was significantly longer for both leafing (3.0 days, p=0.028) and flowering (2.7 days, p=0.027) (Figure 2b). Observed flowering response in exotic species was 2 days greater than in native species (p=0.016), likely due to differences in phenological lag (1.9 days, p=0.019). Observed leafing and flowering responses in boreal region were 4.3 and 1.9 days smaller (p=0.004, p=0.088), respectively, than in temperate region, likely due to smaller forcing changes (equivalent to 2.8 days in leafing and 1.5 days in flowering based on forcing changes and growth temperatures, Table 1 note a). Observed leafing response in grasses was 3.8 days smaller than in trees and shrubs (p=0.033), likely due to differences in forcing changes (6.0 days, Table 1 note b).

Other than phenological lag, forcing change and growth temperature were the most influential variables affecting observed responses (Table 2). The remaining variables combined (altitude, latitude, MAT, and spring warming) explained <2.5% variations in observed leafing and flowering responses.

Differential phenological responses

Observations vs. experiments

By partitioning observed changes based on drivers of spring phenology, we clarified some of the uncertainty regarding the underlying mechanisms of differences in plant phenological response

to climate warming. By synthesizing global data, we found that observed flowering responses in experimental studies were non-significantly smaller than that in observational studies, but this was not the case for leafing responses; these findings differ from those based on temperature sensitivity (Wolkovich et al., 2012). The greater warming in experimental studies did not produce greater observed responses, due to longer phenological lags, which may have resulted in the reduced sensitivity (Wolkovich et al., 2012). First, experimental studies are often conducted at higher altitude sites with lower MAT, later spring phenology, and therefore longer accumulation of winter chilling. The longer phenological lags are therefore unlikely the result of insufficient winter chilling. Second, artificial warming has typically provided higher forcing changes and growth temperatures than natural climate warming (see Table 1). Greater forcing changes produce larger expected responses (observed response + phenological lag), whereas higher growth temperatures reduce expected responses (Chu et al., 2021; Prevéy et al., 2017; Wolkovich et al., 2021). The high temperatures in the artificial warming structures (Marion et al., 1997) can also reduce humidity and soil moisture (Ettinger et al., 2019; Huang et al., 2019), slowing spring development (Ganjurjav et al., 2020; Huang et al., 2019; Moore et al., 2015), particularly in early spring when temperatures in the surrounding environment are low, thus restricting soil water movement. While the different forcing changes adequately accounts for the differences in expected leafing responses (2.5 out of 3.3 days, Table 1 note c), the large differences in forcing changes but similar expected responses in flowering (8.63 and 9.07 days, Figure 2) suggests a strong effect of growth temperature (Table 1 note d) (Chu et al., 2023). Thus, warming-induced moisture stress and high growth temperatures may interact to alter observed phenological responses and temperature sensitivity in experimental studies (Wolkovich et al., 2012). Future experiments should consider humidity, soil moisture, and plant water status

227 to better understand disparities between observational and experimental studies and relate plant
228 phenological changes from experimental warming to those from natural climate change
229 (Wolkovich et al., 2012).
230
231 **Native vs. exotic species**
232 Exotic species are often reported with more noticeable observed responses to warming, a trend
233 that is generally based on flowering (Calinger et al., 2013; Willis et al., 2010; Wolkovich et al.,
234 2013). The ecological implications of this response are well described (Polgar et al., 2014;
235 Zettlemoyer et al., 2019), but the underlying mechanisms are not well understood. Lower growth
236 temperatures faced by early-start exotics are likely partially the cause (Chu et al., 2021, 2023), as
237 shown by a reverse trend for late-start exotics (Zohner and Renner, 2014). In this synthesis,
238 phenological lag did not increase from early leafing to late flowering for exotic species, a trend
239 that is consistent with dormancy release commonly reported on leaf and flower buds (Campoy et
240 al., 2013; Gariglio et al., 2006; Hussain et al., 2015; Wall et al., 2008), contrary to that for native
241 species (Figure 2b). The smaller observed response in flowering for native species is associated
242 with longer phenological lags and accumulations of winter chilling (Table 1), indicatingg more
243 stressful environments later in the season or higher stress sensitivity with reproductive events.
244 Comparatively, plants starting growth early in the growing season may be less restricted by soil
245 moisture that often recharges from winter precipitation and is depleted with increased moisture
246 consumption over time (Sherry et al., 2007; Wolkovich et al., 2013; Zettlemoyer et al. 2019),
247 particularly in dry climates (Man and Greenway, 2013). Moisture stress can progressively
248 develop over the season (Piao et al. 2019; Wolkovich et al., 2013; Zettlemoyer et al., 2019) and
249 differentially affect exotic and native species with differing spring phenology (Stuble et al.,

2021; Willis et al., 2010; Wolkovich et al., 2013) The smaller observed responses in flowering of native species suggests reproductive disadvantage (IPCC, 2014; Zettlemoyer et al., 2019). The consistent leafing response, however, does not support suggestions that late-start native species would have relatively shorter active growing seasons and, therefore, a competitive growth disadvantages relative to early-start exotic species with climate warming (Fitter and Fitter, 2002; Morin et al., 2009; Primack and Gallinat, 2016). Total thermal benefits from climate warming do not differ among species with differing spring phenology (Chu et al., 2021). Given the projected increases in temperature and decreases in precipitation for many parts of the world (IPCC, 2014), future studies should assess the differences in drought sensitivity between vegetative and reproductive events and among functional groups and climatic regions.

Boreal vs. temperate region

Spatial variations along altitudinal and latitudinal gradients are often reported but not well understood (Ge et al., 2015; Morin et al., 2009; Parmesan, 2007; Zhang et al., 2015). Our analysis indicates smaller observed responses in boreal region (MAT<6 °C) due to less forcing changes (Tables 1), but not to longer phenological lag or chilling deficiency (Figure 2). The similar spring warming but less forcing changes suggests that the temperature increases in boreal region occur most frequently in the winter (Beaubien and Hamann, 2011; Shen et al., 2015) when temperatures are below freezing and don't contribute to spring forcing (Man and Lu, 2010). The uneven warming has been reported in both natural and experimental settings (Beaubien and Hamann, 2011; Prevéy et al., 2017; Shen et al.; 2015; Slaney et al., 2007; Yang et al., 2020) and supports the claim that average temperature changes do not represent forcing changes (Chu et al., 2021; Keenan et al., 2020; Wolkovich et al.; 2021). When forcing changes

are held constant, however, observed responses increase with altitude and latitude, as shown by the positive regression coefficients in both leafing and flowering models (Table 2). The possible mechanisms behind this may be lower growth temperature and less moisture stress at higher altitude and latitude (Rafferty et al., 2020), as shown by the negative collinearity of altitude and latitude with growth temperature and phenological lag in both leafing and flowering (data not shown). Therefore, boreal region, depending on forcing changes, can have smaller (Ge et al., 2015; Menzel et al., 2006; Rafferty et al., 2020; Shen et al., 2015) or greater (Ge et al., 2015; Parmesan, 2007; Post et al., 2018; Prevéy et al., 2017) phenological responses, spatial trends that may be different from those suggested by phenological sensitivity (Liu et al., 2019; Post et al., 2018). Consequently, climate change may not result in general phenological convergence across altitudes and latitudes (Rafferty et al., 2020; Shen et al., 2015; Tao et al., 2021), contrary to suggestions by others for small scale studies (Prevéy et al., 2017; Vitasse et al., 2018; Ziello et al., 2009).

Trees, shrubs, herbs, and grasses

Smaller observed responses in herb and grass leafing support findings from some early syntheses (König et al, 2018; Parmesan, 2007), but not those that show a greater response from non-woody plants (Ge et al., 2015; Post and Stenseth, 1999; Root et al., 2003) or no differences (Stuble et al., 2021). Herbs and grasses often leaf out earlier than woody shrubs and trees (Badeck et al., 2004; Heberling et al., 2019) and should have lower growth temperatures and therefore greater phenological responses to climate warming (Chu et al., 2021; Prevéy et al., 2017; Wolkovich et al., 2021). However, different growth forms are often studied separately on sites in different climatic regions, making comparisons challenging. Furthermore, most studies on herb and grass

leafing are conducted in boreal region at high altitudes, low MAT, late spring phenology, low forcing changes, and low spring warming (Table 1); the extremely small forcing changes resulted in small observed responses despite cooler growth temperatures (Figure 2a). The observed responses with herbs and grasses would not be smaller if converted to temperature sensitivity (see Table 1 for large differences in spring warming for leafing). In contrast to leafing, herb and grass flowering studies have greater forcing changes and warmer growth temperatures (Table 1), which lowers both expected and observed responses (Table 1 note d) (Chu et al., 2021; Prevéy et al., 2017; Wolkovich et al., 2021) and potentially induces moisture stress and increases phenological lags (Ganjurjav et al., 2020; Huang et al., 2019; Moore et al., 2015; Post et al., 2022), particularly for grasses (Sherry et al., 2007; Zettlemoyer et al., 2019) that have shallower root systems (Kulmatiski and Beard, 2013; Schenk and Jackson, 2002).

Mechanistic assessment of changes in spring phenology

Averaged across all observational and experimental studies, observed responses and phenological lags are both positive, suggesting that climate warming advances spring phenology but not at rates expected from changes in spring temperatures. The positive lags are likely due to more stressful environments with warmer and drier climate (Huang et al., 2019; Sherry et al., 2007; Zettlemoyer et al., 2019). We quantified phenological lags from changes in spring phenology and temperatures, an approach that does not require species-specific chilling or forcing needs that are often unavailable (Fitter and Fitter, 2002; Morin et al., 2009) or variable in methods of estimation across species and studies (Man and Lu, 2010; Ettinger et al., 2020; Zhang et al., 2018). The relatively early stage of climate warming and association of longer phenological lags with longer accumulation of winter chilling (Table 1) suggest that climate

warming is not likely to induce a general chilling shortage (Chu et al., 2023; Ettinger et al., 2020; Tao et al., 2021; Yang et al., 2020), although incidental effects on individual species or in particular conditions can occur (Fu et al., 2015). Similarly, the variable and minor effects of photoperiod (Basler and Körner, 2012; Chuine et al., 2010; Ettinger et al., 2020; Zohner et al., 2016) (insignificant spring phenology; see Table 2) often reported in studies with extreme warming scenarios (Caffarra and Donnelly, 2011; Fu et al., 2019; Laube et al., 2014) or compounded with that of growth temperatures (Chu et al., 2021), minor effects by nutrient availability (Piao et al., 2019), or incidental spring freezing (Man et al., 2009; 2021b) are not likely to cause the systemic differences in phenological lag between observational and experimental studies or between native and exotic species. Phenological lag indicates the overall lag effect and the need to investigate individual constraints.

Our analysis indicates that both quantity (forcing change) and rate (growth temperature) of spring forcing accumulation strongly influence the magnitude of change in spring phenology, consistent with the findings by Chu et al. (2021) that smaller phenological response with late season species are largely due to their higher growth temperatures. In phenological research, the role of growth temperature is not adequately recognized (Chu et al., 2021, 2023) and can be confounded with progressive increases of phenological lag with greater chilling requirements or insufficient chilling (Asse et al., 2018; Morin et al., 2009; Primack and Gallinat, 2016), photoperiod constraints (Körner and Basler, 2010; Shen et al., 2014; Way and Montgomery, 2015), or moisture stress (Piao et al., 2019; Wolkovich et al., 2013; Zettlemoyer et al., 2019) suggested for late season species. Compared to average spring temperature change that explained <0.5% of the variation in observed responses (Table 2), forcing change quantifies climate warming effect relevant to phenological change of individual species and reduces uneven

warming effects among species with different spring phenology (Chu et al., 2021) and areas in different climatic regions (Post et al., 2018; Yang et al., 2020). Both forcing change and growth temperature can be readily extracted from phenological and temperature data, as demonstrated in this synthesis, but not examined in assessment of plant phenology changes in spring.

Conclusions

Differential phenological responses reported previously are mainly due to different forcing changes, growth temperatures, and environmental stresses from warmer and drier climates. The overall effects of insufficient winter chilling and photoperiod restriction are likely limited but may change with continuous progress of climate warming and advance of spring phenology (IPCC, 2014; Ettinger et al., 2020; Tao et al., 2021). Our method allows for mechanistic partitioning of observed changes by drivers of spring phenology and helps to understand changes in spring phenology and differences in plant phenological responses across different functional groups or climatic regions.

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Author Contributions

R.M. and J.T. conceived the general idea of the method; Y.J., X.C., X.Y., R.M., and J.T. compiled data; and Y.J., S.J.M., X.C., X.Y., R.M., J.T., and Q.L.D. contributed to the interpretations of the results and to the writing of the paper.

Supporting Information

Temperature data and R codes for calculating forcing changes, expected responses, growth temperature, spring warming, and phenological lags are deposited at Dryad https://datadryad.org/stash/share/SGMComxqEbUCX1N-1BX1eAOMTSmoZFtN5YR_Mx0PPvE

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Table 1. Mean values of climatic, phenological, and biological variables by species event (leafing and flowering), research approach (observation and experiment), species origin (native and exotic), climatic region (boreal and temperate), and growth form (tree, shrub, herb, and grass). Growth temperature=temperatures at species event with warmer climate, forcing change =warming-induced changes in spring forcing experienced by individual species, spring warming=average spring temperature changes, and phenological lag= phenological difference due to effects of phenological constraints.

Species event	Spring phenology (Julian)	Growth temperature (°C)	Altitude (m)	Latitude (°N)	MAT (°C)	Forcing change (degree days)	Spring warming (°C)	Phenological lag (day)	Sample size (N)
Leafing	111	11.1	687	42.8	7.8	85	1.3	1.8	447
Observation	106	11.0	487	42.6	8.4	79	1.1	1.2	359
Experiment	130	11.2	1500	43.8	5.6	106	1.8	4.1	88
Native	113	11.0	744	43.3	7.4	85	1.3	1.9	379
Exotic	100	11.7	366	40.0	10.2	78	1.2	1.1	68
Boreal	128	10.2	1147	45.7	2.0	65	1.3	2.4	154
Temperate	102	11.5	444	41.3	10.9	94	1.3	1.5	293
Tree	105	11.7	364	41.9	10.1	101	1.4	1.9	246
Shrub	109	10.9	433	43.5	7.8	80	1.4	1.1	107
Herb	131	10.0	1955	43.3	1.8	51	0.8	1.2	54
Grass	123	8.9	1637	45.9	2.1	37	0.7	3.6	40
Flowering	138	13.7	534	45.5	9.0	126	1.3	3.5	1080
Observation	136	13.4	454	46.0	9.2	120	1.2	3.3	956
Experiment	154	16.7	1153	41.8	7.3	174	1.8	4.7	124
Native	142	13.8	617	45.9	8.5	124	1.3	3.7	850
Exotic	125	13.5	229	44.3	10.9	135	1.4	2.4	230
Boreal	167	14.6	1998	42.9	3.3	109	1.4	1.3	175
Temperate	133	13.6	251	46.0	10.1	130	1.3	3.9	905

Tree	114	12.7	289	43.5	10.5	119	1.5	1.4	183
Shrub	125	12.3	446	44.8	8.5	103	1.3	2.9	148
Herb	146	14.2	608	46.1	8.7	129	1.4	3.8	659
Grass	150	15.3	636	46.5	8.9	160	1.4	5.8	90

Note: effects of forcing change and growth temperature illustrated with equation 3 in Materials and Methods

a) the difference in forcing change between boreal and temperate regions for leafing is 29 (94 – 65), equivalent to 2.8 day expected responses under the average growth temperature of boreal region (10.2). Similarly, the difference in flowering is equivalent to 1.5 day expected responses, i.e., 21/14.6.

b) the difference in forcing change between grasses and trees + shrubs for leafing is 53 ((101+80)/2 – 37), equivalent to 6.0 day expected responses under the average growth temperature of grasses (8.9).

c) the difference in forcing change between experimental and observational studies for leafing is 27 (106 –79), equivalent to 2.5 day expected responses under the average growth temperature of observational studies (11.0).

d) different growth temperatures explain 2.6 day difference in flowering between experimental and observational studies, i.e., 174/13.4 – 174/16.7, and 1.8 day difference in flowering between woody (trees and shrubs) and non-woody (herbs and grasses) plants, i.e., (129+160)/(12.7+12.3) – (129+160)/(14.2+15.3).

Table 2. Final stepwise regression coefficients and variable influence on observed phenological responses by Akaike information criterion (AIC).

Species event	Intercept	Growth temperature	Altitude	Latitude	MAT	Forcing change	Spring warming	Phenological lag	R-squared Sample (N)
Leafing	2.6439	-0.6075	0.0003	0.0732	0.1480	0.0736	0.9463	-0.9738	0.9453
AIC (%)	449 (27.7)	340 (20.9)	2 (0.1)	15 (0.9)	11 (0.7)	68 (4.2)	7 (0.4)	732 (45.1)	(447)
Flowering	4.521	-0.5917	0.0003	0.0869	0.1466	0.0521	0.7620	-0.9893	0.9653
AIC (%)	785 (18.1)	247 (5.7)	7 (0.2)	20 (0.5)	32 (0.7)	826 (19.1)	5 (0.1)	2409 (55.6)	(1080)

Note: Growth temperature (°C)=temperatures at species event (leafing or flowering) with warmer climate

MAT (°C)=long-term mean annual temperature

Forcing change = warming-induced changes in spring forcing at species events

Spring warming (°C)=average spring temperature change (Julian day 1 to 182)

Phenological lag (days)= phenological difference due to effects of phenological constraints

Spring phenology (date of species event with baseline climate; Julian days) and long-term mean precipitation (MAP, mm) were excluded from final models due to lack of significance

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Forcing change, growth temperature, and phenological lag are calculated from phenological and temperature data for individual species, spring phenology and observed responses are provided in the original studies, and spring warming and long-term MAT and MAP are provided in the original studies, calculated from baseline temperatures, or extracted from Google Maps (www.maps.google.com), FreeMapTools (www.freemaptools.com), or WorldClim Database (Fick and Hijmans, 2017)

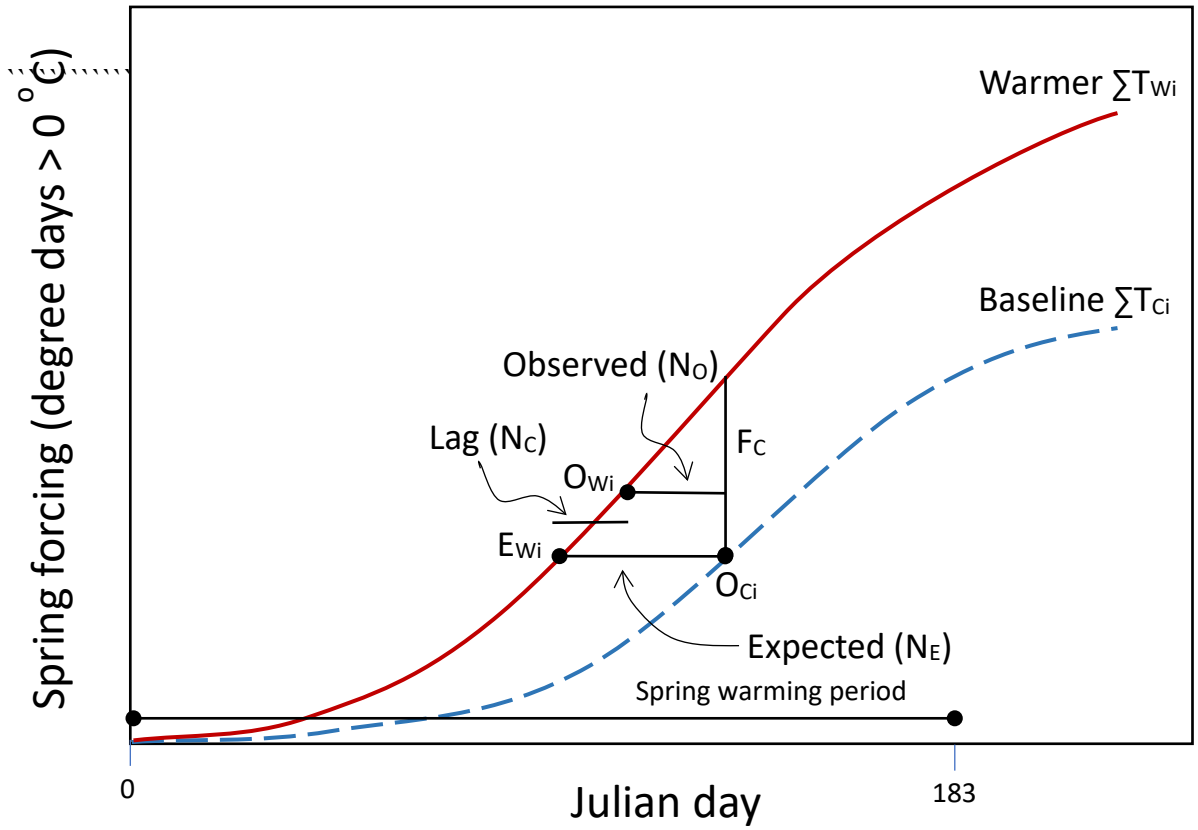

Figure 1. A diagram showing the relationships among forcing change (F_C, difference in spring forcing (degree days) between baseline $\sum_1^i T_{Ci}$ and warmer $\sum_1^i T_{Wi}$ temperatures at species event with baseline temperatures O_{Ci}), expected response (N_E, difference between climatic conditions of baseline and warmer temperatures in reaching species forcing needs with baseline temperatures, i.e., spring forcing at O_{Ci}), growth temperature (F_C/N_E, average temperature at species event with warmer temperatures), and phenological lag (N_C, difference between expected N_E and observed N_O responses with warmer temperatures).

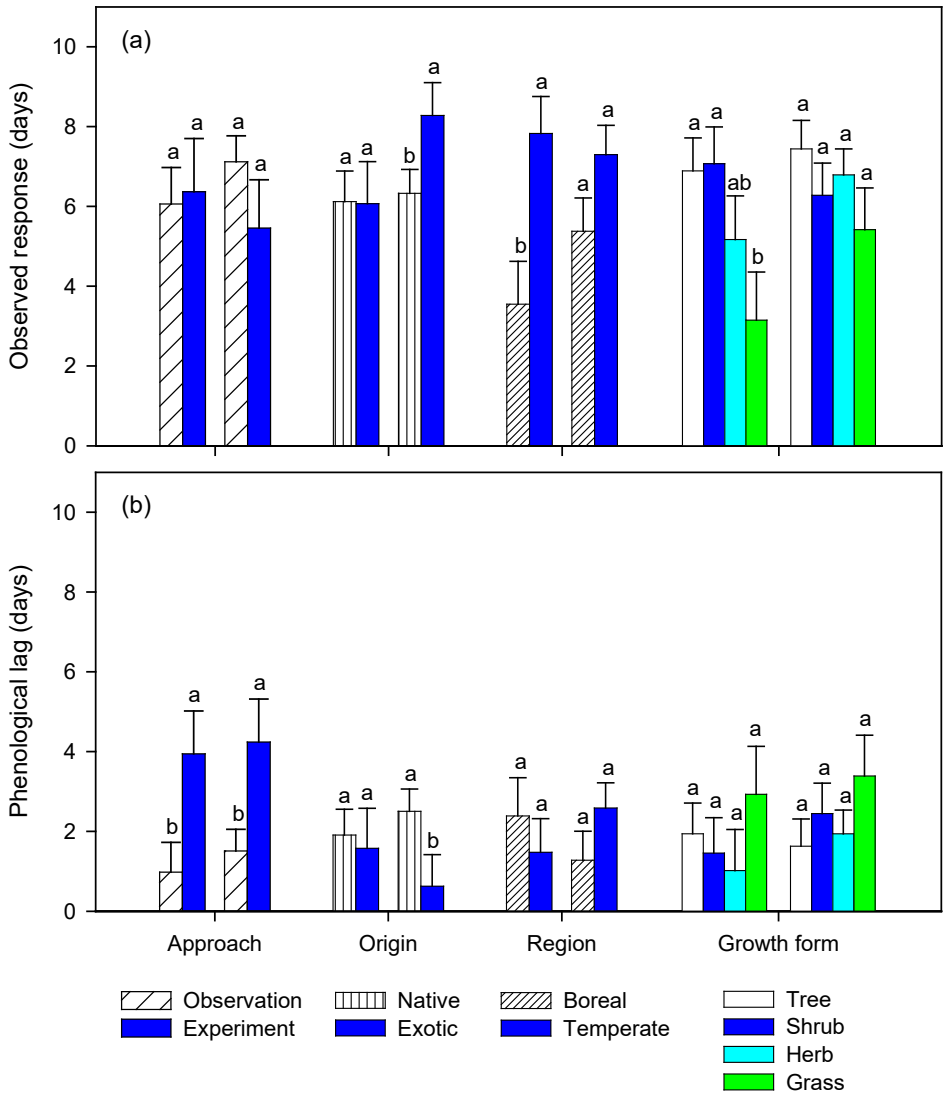

Figure 2. Observed responses and phenological lags (least square means ± standard errors) in leafing and flowering (left and right set of bars in each pair, respectively) by research approach (observation and experiment), species origin (native and exotic), climatic region (boreal and temperate), and growth form (tree, shrub, herb, and grass) extracted from reported plant phenological changes in spring. Phenological lags are calculated from the differences between observed responses and those expected from species-specific changes in spring temperatures. Different letters indicate means differ significantly (p<0.05).

Supplementary data

Table S1 | A list of references for all studies included

Table S2 | A summary of study information

Table S3 | MetaData containing all information used in the analysis

Table S4 | Sources of weather data