

Changes and trends in budburst and leaf flush
across Europe and North America
A meta-analysis of local adaptation in spring phenology
studies

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Abstract

Climate change forecasting plasticity.... adaptation. Spring tree phenology is critical to forecasting ... Despite a long history of study, however, the balance of local adaptation versus plasticity in determining environmental responses is not well understood, especially for spring events. We conducted the first cross-continental meta-analysis of published studies from the peer-reviewed literature that reported spring event dates for a mix of angiosperm and gymnosperm tree species in the northern hemisphere, capturing data from 384 North American provenances and 101 European provenances with observations from 1962 to 2019. We found ... This is important because...

1 Introduction

The increasing need to predict the biological impacts of climate change has made understanding how organisms cope with environmental variation more urgent (Botero et al., 2015). In particular, the relative importance of genetic adaptation versus plasticity is of paramount importance for prediction (Chevin et al., 2010), with plasticity expected to allow species to shift more rapidly with climate change than environmental responses based on local adaptations (Chevin and Lande, 2010; Snell-Rood et al., 2018).

Many of the currently observed responses to climate change appear to be mostly plastic (Burton et al., 2022; Zettlemoyer and Peterson, 2021; Bonamour et al., 2019; Kingsolver and Buckley, 2017), including the most reported biological response to climate change—shifting phenology. Phenology (timing of recurring seasonal events) governs the timing of transitions between dormancy and active growth for many organisms, allowing them to time reproduction and fully exploit the resources of each growing season (Chuine, 2010; Hänninen and Tanino, 2011). Many terrestrial animals time their breeding season to coincide with the availability of food resources. For example, migratory birds arrive at breeding grounds amidst the peaking of insects (Hälfors et al., 2020). Many butterfly species ensure their larvae have an ample food supply by synchronizing their egg-laying with the phenology of their host plants (Rytteri et al., 2021; Posledovich et al., 2018). Similarly, the migration and spawning of many marine organisms are closely tied to water temperature and the availability of planktonic food sources (Genner et al., 2010). Such synchronization enables them to provide optimal food for their young during critical growth stages. Therefore, climate warming and the associated changes in spring phenology timing, such as earlier leafout or insect emergence due to climate change, can disrupt this synchronization and negatively impact animal populations (Wann et al., 2019; Renner and Zohner, 2018; Chuine and Régnière, 2017). As such, phenology plays a significant role in determining fitness (Guo et al., 2022; Chuine and Beaubien, 2001). Shifted phenology in recent decades—with many events moving several days per decade (Vitasse et al., 2021; Kharouba et al., 2018; Menzel et al., 2006)—has thus led to concerns about fitness consequences, and the limits of possible future shifts. Future phenological shifts will depend on how much phenology is determined by adaptation versus plasticity will determine, yet our understanding of the balance of these two approaches to variation is limited, even for species groups that are critical to both forecasting and have been well studied, such as trees.

Tree phenology is critically important to climate change forecasting and has been an area of long-term study of adaptation and plasticity (Cleland et al., 2007). The timing of budburst and senescence can impact plant competition (Fridley, 2012), growth (Myneni et al., 1997), and carbon sequestration (Barichivich et al., 2012)—thus affecting climate change itself. Hundreds of years of study have established common clines in fall phenology, as locations with shorter growing season (poleward, higher elevation) exhibit earlier stopping of growth (e.g., via budset), and connected these to an underlying proximate mechanism of changing photoperiod cues, driven by local adaptation to the local growing season and relevant photoperiod to stop growth (Alberto et al., 2013; Savolainen et al., 2007). In contrast, spring phenology appears far more plastic (Aitken and Bemmels, 2016) and determined more strongly by temperature (Flynn and Wolkovich, 2018). Many studies, however, have argued that spring phenology shows important levels of adaptation.

Evidence for local adaptation in spring phenology comes mostly from common garden studies. For more than 250 years, researchers have been comparing populations of trees from different geographical origins under the same environmental conditions through these experiments to disentangle the effects of environmental and genetic variation on trees' phenology and phenotype (Aitken and Bemmels, 2016; Alberto et al., 2013). Studies have documented provenance differences of 2.08-4.17 days per degree latitude for some species (*Picea abies* in Sogaard et al., 2008 and *Quercus petraea* in Deans and Harvey, 1996) while others have not found any trends in budburst along latitudinal gradients (For example, *Picea sitchensis* in Mimura and Aitken, 2007, *Picea glauca* in Li et al., 1997, and *Populus balsamifera* in Farmer, 1993). This has led to some debate over the prevalence and importance of adaptation in spring tree phenology. While clines of spring phenology have been found in studies in both Europe (Sogaard et al., 2008; Deans and Harvey, 1996; Von Wuehlisch et al., 1995) and North America (Rossi, 2015; Soolanayakanahally et al., 2013; Hannerz et al., 1999), they appear potentially more common in European studies.

Continental differences in patterns of adaptation versus plasticity could be driven by climatic differences, as North American springs are more variable across years than European ones (Twardosz et al., 2021; Zohner et al., 2017; Schwartz and Reiter, 2000). Such high temporal variability means that distant sites can effectively experience the same spring climate, but in different years. Studies of spring phenology in arboreta suggest cues for budburst may vary depending on continental climate (Chamberlain and Wolkovich, 2023; Ettinger et al., 2020, 2021), but are poorly controlled compared to traditional provenance trials, making them difficult to use for tests of plasticity versus adaptation (Gauzere et al., 2020). Even for more carefully designed common garden differences in study design—especially studied species—may complicate understanding what underlies potential trends across continents, with European studies focusing more on deciduous angiosperms and North American studies focusing often on evergreen gymnosperms. To test for evidence of adaptation in spring phenology and what factors may underlie differences observed across studies, we comprehensively examined clines for spring and fall events. We test for evidence of adaptation via provenance trends with latitude and climate. Further, to better understand these clines, we also examine the following:

- How different are clines between spring and fall phenology?
- How different are clines between Europe and North America?
- How different are clines between angiosperm and gymnosperm species?

To address these questions, we combined a new meta-analysis of all common garden experiments in temperate tree species across Europe and North America reporting spring phenology with Bayesian hierarchical models.

2 Methods

2.1 Data Collection

To locate common garden studies that reported the timing of spring events of woody plant species we searched and reviewed the peer-reviewed literature. On 14 December 2022 we searched Web of Science (Thompson Reuters, New York, NY) using the following terms:

TOPIC = (common garden* OR provenance*) AND (leafout* OR leaf out* OR budburst
OR spring phenolog*)

which returned 122 publications. We also contacted authors of previous review papers (Aitken and Bemmels, 2016; Alberto et al., 2013), to help further search the literature. We then reviewed the methods and results of all publications to refine to only studies that met the following criteria: (a) focused on woody plants originating from either Europe or North America, (b) had provenance trials/common gardens on the same continent, (c) reported latitude and longitude of provenances and gardens, and

(d) reported spring events in units of calendar days (day of year or DOY) or could be converted into DOY (see Additional Methods in the Supplements).

Based on these criteria we found 19 common gardens distributed throughout North America and Europe, with the majority of data concentrated in North America (Fig. 1 & Supplement Table.1). From each common garden study we extracted phenological data on spring events (budburst and leaf flush) in DOY and, when present in the same paper, fall events (bud set, leaf senescence, growth cessation, and leaf abscission) by species and the geographic information of provenances and gardens. We used ImageJ (version 1.53k; Schneider et al., 2012) to extract values from figures whenever necessary. For studies that reported event dates relative to a reference date other than 1 January (e.g. Rehfeldt, 1994), we converted such dates to DOY using the 'lubridate' package in R (Grolemund and Wickham, 2011).



Figure 1: Distribution of common gardens (denoted as stars) and provenances (denoted as circles) included in this meta-analysis. The distribution was skewed toward North America (number of studies = 12). See Table.1 in Supplements for information on selected studies.

To understand how climatic differences, in addition to geographical differences, shape local adaptation in spring events we extracted several types of climate data using information about provenance latitude, longitude, and elevation from original publications. We estimated the mean annual temperature (MAT) for each provenance using the Climate Information Tool by Food and Agriculture Organization of the United Nations (FAO, 2022) and ClimateWNA (Wang et al., 2016). To examine more explicitly climate near spring events, we used gridded daily temperature data for 2011 to 2020 for all European and North American provenances and gardens from E-OBS and the 'daymetr' package in R respectively (Cornes et al., 2018; Hufkens et al., 2018). Using these data we estimated how much the daily temperatures overlapped between garden and provenance locations, which we call 'climate overlap.' For this we used the 'overlap' package in R to calculate the percentage overlap of the daily temperature of each provenance and their corresponding gardens in spring months (March to May) from 2011 to 2020. Finally, using the daily temperature data, we also calculated Growing degree days (GDD), a commonly used heat accumulation measure to forecast phenological development in plants (Miller et al., 2001), based on the accumulation of mean daily temperatures (T_m) from 2011 to 2020 above a baseline of 0°C , from January 1 until budburst and leaf flush with the following formula: $\text{GDD} = \sum(T_m - 0^{\circ}\text{C})$ for $T_m \geq 0^{\circ}\text{C}$; 0 for $T_m \leq 0^{\circ}\text{C}$.

2.2 Analyses

To estimate clines in spring and fall phenological events across species we used Bayesian hierarchical models. We regressed DOY of events against geographical and climate predictors with partial pooling (sometimes called 'random effects') on the intercept and slope for each species within each garden. Because most tree species were present in only one common garden in our dataset, it was impossible to fit garden and species separately, thus we treat each species within a garden as a unique group. Using posterior estimates for each species within a garden, we estimated effects of continent (North America vs. Europe) and species type (angiosperm vs. gymnosperm). All models were fit in rstanarm package (version 2.21.3; Goodrich et al., 2022) using default priors, with 4 chains and 1000 sampling

iterations per chain for a total of 4000 samples. We checked for model fit by ... [ADD here]. We present estimates as mean \pm 90% uncertainty intervals given parenthetically, unless otherwise stated.

3 Results

Our final dataset included seven angiosperm and eight gymnosperm species from 19 common gardens, encompassing 384 North American provenances and 101 European provenances, with observations from 1962 to 2019. Seven species also had fall event information available.

Overall, spring events were not related to provenance latitude or MAT, neither across continents (latitude: 0.10 days/degree [-0.05 - 0.25]; MAT: -0.11 days/ $^{\circ}$ C [-0.34 - 0.12]) (Fig. 2, Table. 2 & 3 in Supplements), nor in North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09 days/ $^{\circ}$ C [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT:-0.16 days/ $^{\circ}$ C [-0.55 - 0.23]). Results were similar using other distance metrics in lieu of latitude (see Supplement Fig.1 for results using the difference between provenance and garden latitude, and the spherical distance between provenance and garden).

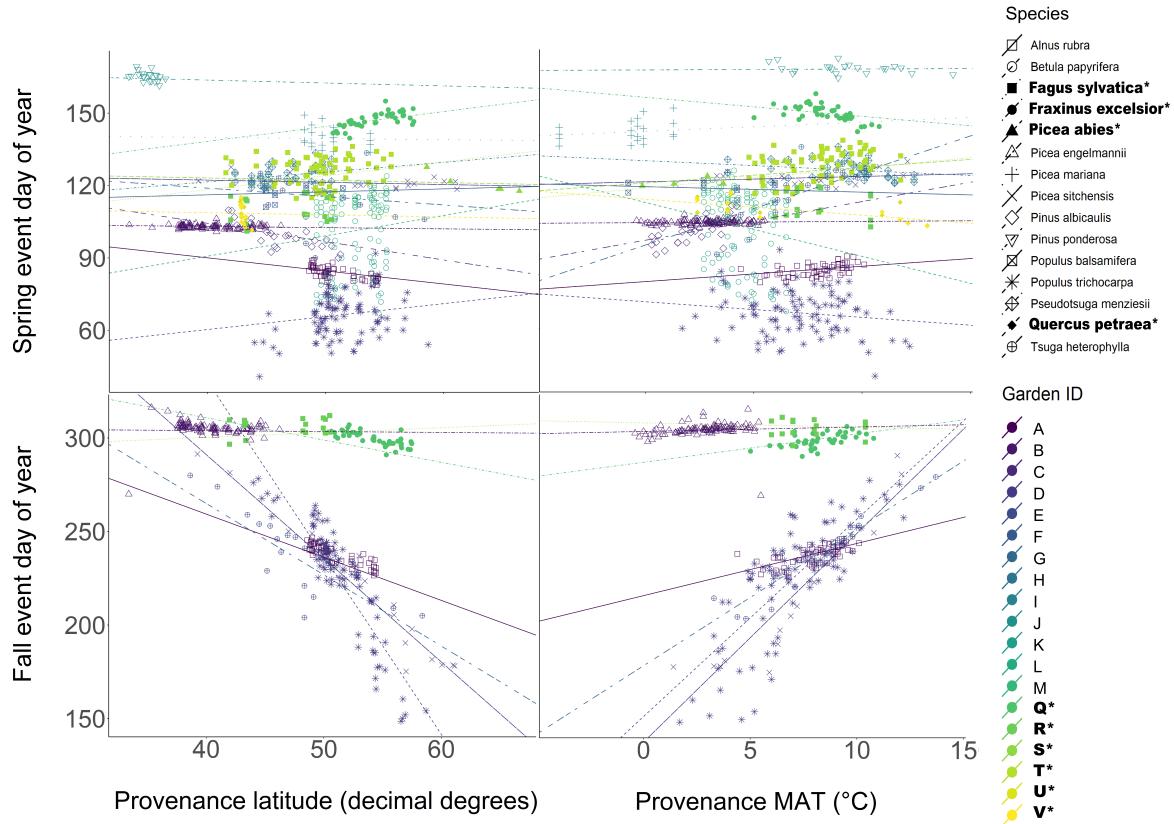


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European Gardens and species are bolded and denoted by an asterisk (*).

In contrast, fall events (budset, leaf senescence, leaf abscission) advanced strongly with provenance

latitude (3.16 days/degree [2.87-3.45]) and the decrease in MAT (4.78 days/ $^{\circ}\text{C}$ [4.1 - 5.4]), meaning fall events were earlier where provenance MAT was lower (Fig. 2, Table 4 & 5 in Supplements). This relationship, however, was observed mostly in North America where fall events advanced 4.24 (3.95 - 4.53) days per degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT ($^{\circ}\text{C}$), whereas in Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree northward, or 0.70 days (1.04 - 2.42) per degree decline in MAT ($^{\circ}\text{C}$) (Fig. 3A).

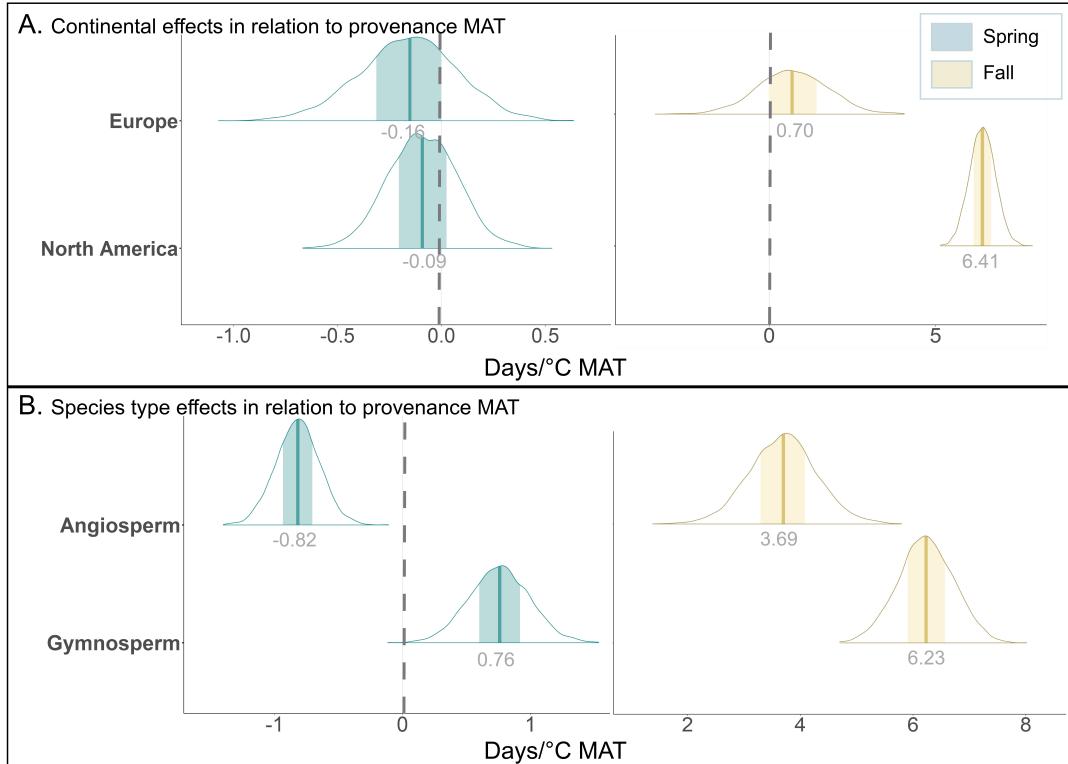


Figure 3: Posterior distributions for the effect of MAT across different continents and species types. Zero – no effect – is shown with a dashed line. Solid line and shading in posteriors represent mean and 50 percent interval. (A) Effect of MAT and continent on spring and fall event date (DOY). Fall events advanced strongly with decreasing MAT, particularly notably in North America. Effect of MAT and leaf type on spring and fall event date (DOY) weakly diverged. (B) Effect of MAT and leaf type on spring and fall event date (DOY). As MAT increased, spring events slightly advanced in angiosperms and delayed in gymnosperms. Fall events delayed in warmer locations for both species types.

Effects of provenance latitude on both spring and fall events were similar across angiosperms and gymnosperms. Spring events slightly delayed 0.37 (0.15 - 0.59) days per degree north in angiosperms and 0.23 (0.00 - 0.46) days per degree north in gymnosperms. Fall events advanced 3.18 (2.76 - 3.62) days per degree north in angiosperms and 3.14 (2.81-3.47) days per degree north in gymnosperms. However, effects of MAT on spring events weakly diverged (Fig. 3B). Spring events advanced 0.82 (0.54 - 1.11) days/ $^{\circ}\text{C}$ as MAT increased in angiosperms and delayed 0.76 (0.37 - 1.14) days/ $^{\circ}\text{C}$ as MAT increased in gymnosperms. Fall events delayed in warmer locations for both species types, but slightly more so for gymnosperms (6.23 days) than angiosperms (3.69 days) (Fig. 3B).

While we believe that coarse metrics such as latitude and MAT would ultimately represent how similar the climates are between the provenances and gardens, we also estimated climate overlap in months

that matter for the events to further test how much climate similarity between provenances and gardens predicts local adaptation. For spring events, we considered overlap across March to May. However, results were not qualitatively different than using MAT (See Fig. 2 in Supplements). We observed very weak effects of climate overlap on spring events (0.01 [0.02 - 0.03] days per one per cent increase in climate overlap), nearly identical across angiosperms (0.02 [0.00 - 0.05]) and gymnosperms (0.04 [0.00 - 0.09]). Fall events advanced as climate overlap declined, but slightly more strongly for gymnosperms (advancing 0.72 [0.51 - 0.92] days per one per cent decline in climate overlap) (Fig.3 in Supplements).

4 Discussion

While coarse metrics such as latitude and MAT may represent how similar the climates are between the provenances and gardens in times that matter for the events. If climates are very similar, then we would expect similar timings [add more here].

We pooled the timing of budburst and leaf flush into a single category of ‘spring events’ and the timing of bud set, leaf senescence, growth cessation, and leaf abscission into ‘fall events.’ Such pooling is justified because of the shared pressures from natural selection that govern these events (Gill et al., 2015).

The weak relationship between spring event dates and provenance latitude and MAT that we find in European studies might be explained by the higher extent of climate overlap in those studies. The more similar the climate is between provenances and gardens, the less difference between spring event dates.

The inconsistent and weak clines in spring events that we found suggest high plasticity in spring phenology across continents and species. Fall events, on the other hand, exhibit stronger clines which suggest more local adaptation, especially in North America. Overall, our results predict that warming springs will continue to be tracked more closely phenologically by trees than warming fall temperatures.

In contrast to spring events, we found strong latitudinal clines in fall events across both continents, with local adaptation appearing much stronger in North America than in Europe. Our results show that spring events are highly plastic, and thus may shift with warming, but data on more species and greater information on important factors, such as their geographic location in relation to their origins and elevation, are needed for forecasting.

1. Opening: 1-2 paragraph overview of our findings (spring phenology show no real clines, some variation by continent and gymnosperm/angiosperm but hard to fully disentangle). Suggests some small clines of spring phenology in some studies, but no consistent effects
2. Subheader: Adaptation in spring vs fall phenology: Implications for climate change responses
 - (a) Mostly unorganized list of things we may want to say in this section
 - i. Current advances in spring phenology may continue, but delays in fall phenology will depend on speed of adaptation
 - ii. If current advances in spring phenology continues it could mean shifts in spring frost etc.
 - iii. Spring phenology, specifically the timing of budburst and leaf flush, plays a significant role in determining plant fitness and has been widely adopted as a useful tool to investigate plant adaptation mechanisms (Guo et al., 2022; Chuine and Beaubien, 2001). In temperate and boreal environments, the optimal timing for spring growth initiation is determined by a balance of avoiding late spring frost and having a long growing season (Alberto et al., 2011; Lenz et al., 2016; Allevato et al., 2019). Utilizing the early portion of the growing season can be especially critical for species in colder regions

- (Morin et al., 2007; Dantec et al., 2015) and the ones with suboptimal shade tolerance (Richardson and O'Keefe, 2009). Plants that budburst earlier can take advantage of a longer growing season and avoid competition (Guo et al., 2022).
- iv. Clines in fall phenology are stronger and more consistent while clines in spring phenology are weaker and can go either way (highlight that some studies and we should include WHICH ones do show clines by XX days).
 - v. Mention some of the co and counter-gradient studies here
 - vi. An accurate understanding of how environmental conditions might influence species distribution at a continental scale is critical for future range shift prediction.
 - vii. Implications of small differences in spring phenology could mean different gene flow etc.
 - viii. the degree of adaptation dictated by climate change differs across different geographical areas (Loarie et al., 2009).
 - ix. Need to cite elevation studies and discuss them somewhere here.
 - x. Somewhere mention results from chamber studies and local adaptation (which are hard to interpret given issues with chilling)
 - xi. What else?
3. Subheader: Variation across continents and species groupings
- (a) Unorganized list of things we may want to say in this section
 - i. No strong evidence of continental differences, could make sense based on long-term climate history perhaps ...
 - ii. discuss xylem (ring versus diffuse porous spp) and embolism but might be too in the weeds (see Salk article)

5 Figures

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