

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

Predicting 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 plasticity versus genetic adaptation is vital 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 adaptation (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 (the timing of recurring seasonal events) governs the timing of transitions between dormancy and active growth for many organisms, allowing them to time reproduction and exploit the resources of each growing season (Chuine, 2010; Hänninen and Tanino, 2011; Rytteri et al., 2021; Posledovich et al., 2018). As such, phenology plays a significant role in determining fitness for both plants (Guo et al., 2022; Chuine and Beaubien, 2001) and animals (Wann et al., 2019; Renner and Zohner, 2018; Chuine and Régnière, 2017).

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 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 plasticity versus adaptation; 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 at both the community and ecosystem levels. The timing of budburst and senescence can impact plant competition, plant invasions and community assembly (Fridley, 2012). These effects often occur as phenology affects growth (Myneni et al., 1997), scaling up to impact ecosystem-level carbon sequestration (Barichivich et al., 2012), and thus is integrated into forecasts of climate change itself. Growing evidence, however, suggests links between growth and phenology are not as consistent as previously predicted—or currently modelled (Dow et al., 2022)—with recent work suggesting how much spring versus fall events shift may determine impacts on tree growth (Zohner et al., 2023).

Studies of adaptation versus plasticity in tree phenology have been conducted for centuries (Cleland et al., 2007), through common garden studies (i.e., studies—often for forestry purposes—where researchers grow trees of different geographical origins under the same environmental conditions to disentangle the effects of environmental and genetic variation on trees' phenology and phenotype) (Aitken and Bemmels, 2016; Alberto et al., 2013). This work has established common clines in fall phenology, as source locations with shorter growing season (poleward and higher elevations) exhibit earlier stopping of growth (e.g., budset). Research has connected these clines to an underlying proximate mechanism of changing photoperiod cues (i.e., shifts in the photoperiod threshold that trigger budset), driven by local adaptation to the local growing season (Alberto et al., 2013; Savolainen et al.,

2007). In contrast, spring phenology appears far more plastic (Aitken and Bemmels, 2016) and is determined more strongly by temperature (Flynn and Wolkovich, 2018). Many studies, however, have argued that spring phenology shows high enough levels of adaptation to matter biologically.

Results, however, have not always been consistent. Studies have documented provenance differences of 2-4 days per degree latitude in spring phenology 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 could vary by continent.

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 (Zohner et al., 2017), 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 events, including fall events when possible. We tested for evidence of adaptation via provenance trends with latitude and climate and examined possible factors that underlie these clines, asking:

- 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 Bayesian hierarchical models with a new meta-analysis of all common garden experiments in temperate tree species across Europe and North America reporting spring phenology.

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, 1994a), 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 (12 North American studies versus 5 European studies). See Table.1 in Supplement 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), for each provenance and garden, 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: $GDD = \sum(T_m - 0^\circ\text{C} \text{ for } T_m \geq 0^\circ\text{C}; 0 \text{ for } T_m \leq 0^\circ\text{C})$.

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 confirming no divergent transitions (which required setting `adapt_delta` to 0.99 for some models), \hat{R} values close to 1, and sufficient effective sample sizes. 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 17 studies, 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/ $^{\circ}\text{C}$ [-0.34 - 0.12]) (Fig. 2, Table. 2 & 3 in Supplements), nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09 days/ $^{\circ}\text{C}$ [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT:-0.16 days/ $^{\circ}\text{C}$ [-0.55 - 0.23]) (Fig.3A & 4A). 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).

In contrast, fall events (e.g., 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. 4A).

Clines in fall phenology were stronger and more consistent whereas clines in spring phenology were weaker and somewhat varied in directionality. For fall events, only two field studies found no relationship (Fig. 2): *Fraxinus excelsior* from Garden Q* in the UK (Rosique-Esplugas et al., 2022) and *Fagus sylvatica* from Garden R* in Bulgaria (Petkova et al., 2017). Another study that found no relationship was the only greenhouse experiment included (*Picea engelmannii* from Garden B in the USA, also included in Aitken and Bemmels, 2016), which uniquely used the fall event of ‘the day by which seedling elongation had finished’ (Rehfeldt, 1994b). In contrast, spring event clines were always weak: all species x garden clines included 0 in their 90% intervals.

Effects of provenance latitude on fall events were similar across angiosperms and gymnosperms (Fig.3B). Spring events weakly diverged, delaying at a rate of 0.37 (0.15 - 0.59) days per degree north in angiosperms and advancing 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. Effects of MAT on spring events also weakly diverged (Fig.4B). 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. 4B).

While we expected that coarse metrics, such as latitude and MAT, would generally represent how similar the climates are between the provenances and gardens, we also estimated climate overlap in months much closer to 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 percent 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

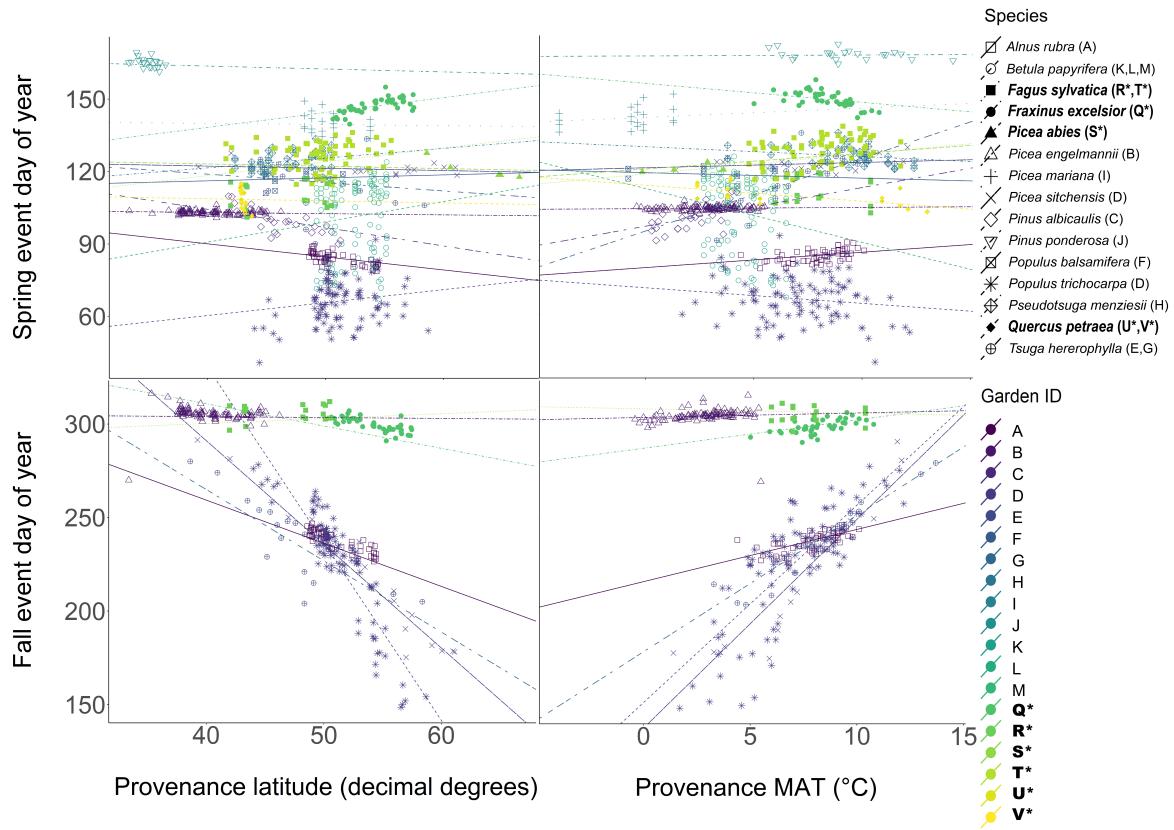


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are bolded and denoted by an asterisk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

gymnosperms (advancing 0.72 [0.51 - 0.92] days per one percent decline in climate overlap) (Fig.3 in Supplements).

4 Discussion

Overall, our results demonstrated inconsistent and weak clines in spring events across North America and Europe. In contrast, fall events generally showed much stronger clines, especially in North America, and in support of many previous studies (Aitken and Bemmels, 2016; Alberto et al., 2013). While previous studies have suggested spring events are far more plastic compared to fall events (Li et al., 1997; Farmer, 1993; Mimura and Aitken, 2007), our study provides the first major test of this across continents and species and suggests overall no general trend for clines in spring phenology. While not a direct test, our results suggest that spring events are highly plastic; they thus predict that warming springs will continue to be tracked more closely phenologically by trees than warming fall temperatures, in line with most current climate change impact studies (IPCC, 2022).

Trends between spring phenology and latitude or MAT were weak, but suggested the possibility of diverging results that could mute an overall trend (albeit a much weaker one than for fall phenology).

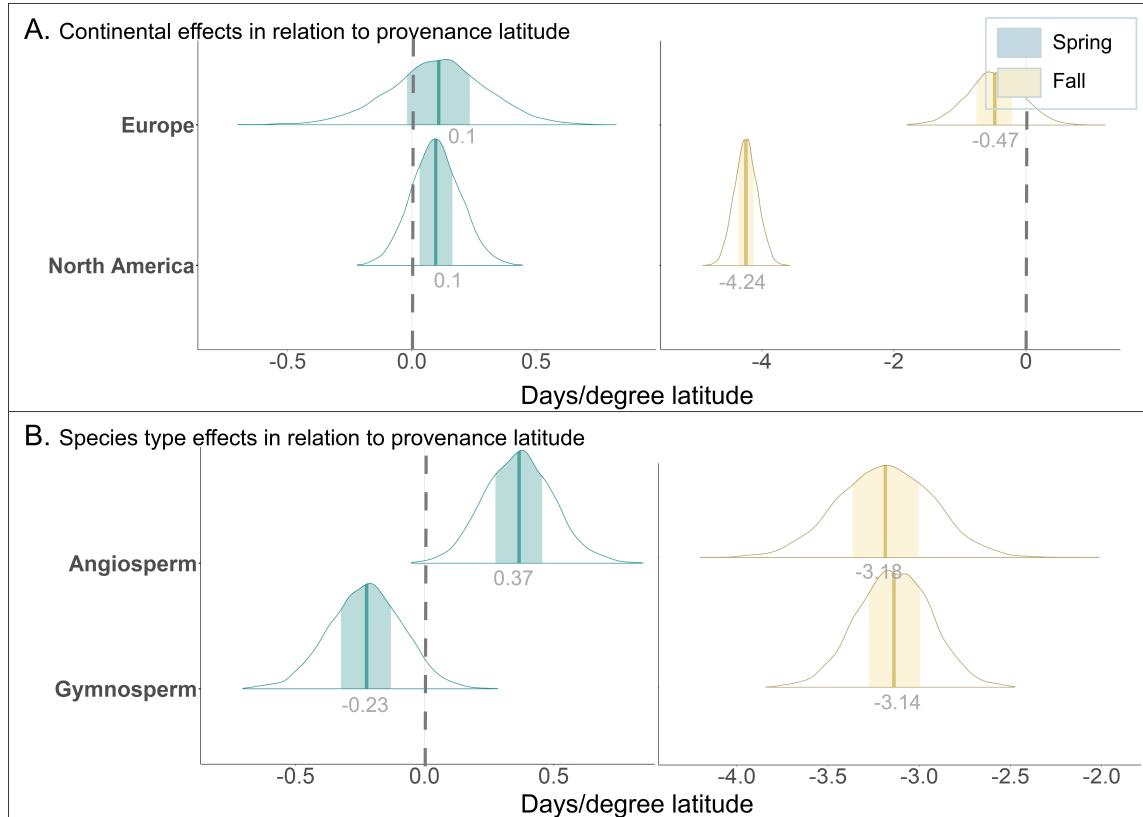


Figure 3: Posterior distributions for the effect of provenance latitude across different continents and species types. Zero—no effect—is shown with a dashed line. Solid line and shading in posteriors represent mean and 50 percent interval (90% intervals given in text). (A) Effect of latitude and continent on spring and fall event date (DOY). Fall events advanced strongly per degree northward, particularly notably in North America. (B) Effect of latitude and leaf type on spring and fall event date (DOY). As we move north, spring events slightly advanced in gymnosperms and delayed in angiosperms. Fall events advanced per degree northward for both species types.

Clines with MAT diverged between angiosperms and gymnosperms. Combined with our finding of stronger clines for fall phenology in North America, our results suggest that data on more species tested across continents could yield important insights into plasticity versus adaptation limits for spring and fall phenology, which would greatly aid forecasting.

We found the coarse metrics of provenance latitude and MAT were generally good predictors of phenology, performing better than climate overlap. Latitude and MAT appeared to well represent how similar the climates are between the provenances and gardens in months close to the events, at least in the narrow range of northern temperature and boreal forests we studied.

4.1 Variation across continents and species groupings

Our results indicated that the effects of provenance latitude and MAT on fall events were similar across angiosperm and gymnosperm species: Fall events delay as MAT increases for both leaf types, slightly more so for gymnosperms, explained by sensitivity to day-length signals. However, the two leaf types exhibited slightly diverging trends in spring events: advancing in angiosperms and delaying in most

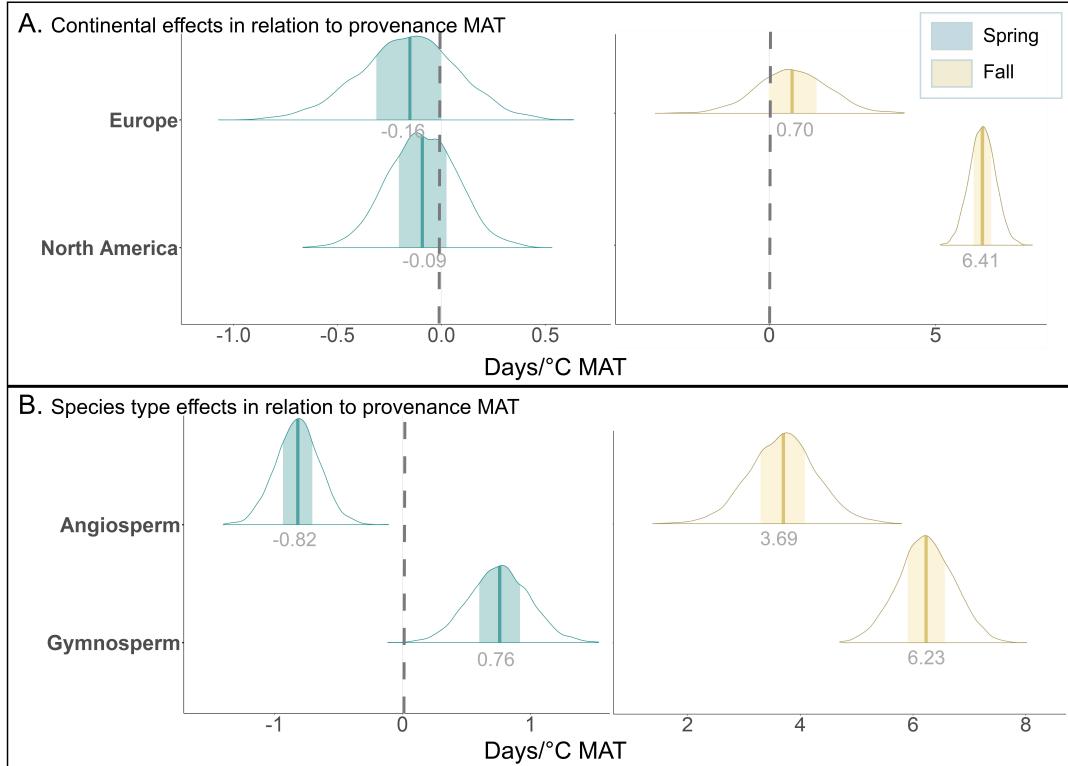


Figure 4: Posterior distributions for the effect of MAT across different continents and species types. Zero—no effect—is shown with a dashed line. Solid line and shading in posteriors represent mean and 50 percent interval (90% intervals given in text). (A) Effect of MAT and continent on spring and fall event date (DOY). Fall events advanced strongly with decreasing MAT, particularly notably in North America. (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.

gymnosperms as MAT increases. Such differences make sense as timing of budburst and leafout varies by leaf type. Gymnosperms photosynthesize without leafout and thus generally leafout later than angiosperms, after much risk of spring frost (Panchen et al., 2014). Meanwhile, xylem anatomy also plays a part in determining spring timing due to the importance of vessel diameter to embolism risks induced by frost in spring. According to Salk and lantbruksuniversitet (2020), species with narrow xylem such as coniferous gymnosperms and diffuse-porous angiosperms did not exhibit the consistent phenological trends shown in ring-porous species. Therefore, there might be additional differences if we have more species and more information on leafout timing and frost risk approach.

While we noticed more prominent clines in fall events in North America, there was no strong evidence of overall continental differences in spring events, which might again suggest a higher degree of plasticity in spring events. Meanwhile, most North American gardens and provenances included in this study were limited to the Pacific Northwest region, which might mask the kind of climate pattern we were hoping to see from the entirety of North America (Fig. 1).

4.2 Adaptation in spring vs fall phenology: Implications for climate change responses

Our results suggest that current advances in spring phenology may continue, but delays in fall phenology could depend on the speed of adaptation. While some previous chamber studies have found potential adaptation, these could have been influenced by chilling at the provenance site (Ettinger et al., 2020). However, field studies and common garden experiences do not have this effect. Spring events from the studies we looked at appeared to exhibit high plasticity, while fall events showed strong clines, which is consistent with previous work (Aitken and Bemmels, 2016; Alberto et al., 2013). These findings have important implications for growing discussion of how shifting phenology and tree growth relate as our results suggest there are strong limits on shifts in fall phenology (Zohner et al., 2023; Zani et al., 2020).

It is worth noting that these trends likely vary by species and depend on frost tolerance strategy. If current advances in spring phenology continues, it could suggest shifts in spring frost. 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). Further, plants that budburst earlier can take advantage of a longer growing season and avoid competition (Guo et al., 2022). However, differences across species means that this will not impact all species the same. While fall event always exhibited co-gradient relationships (i.e. events advanced as we moved northward or up in elevation), spring events were more varied among species. The implication of such variations could be that spring leafout sets up flowering, and thus, some counter-gradient could better aid gene flow over larger geographical regions.

All of above are critical to predicting not just phenological change, but range expansions with climate change: An accurate understanding of how environmental conditions might influence species distribution at a continental scale is critical for future range shift prediction. Implications of small differences in spring phenology could mean different levels of gene flow.

Our observations reveal that although temperature by itself could serve as a reasonable indicator for predicting when fall events occur across various locations, it's crucial to acknowledge that the degree of adaptation dictated by climate change differs across different geographical areas (Loarie et al., 2009). High-latitude sites, for example, are likely restricted by the impact of photoperiod (Gill et al., 2015). Diverse mechanisms that govern the timing of leaf senescence at the ecosystem level hold the potential to exert significant influence over not only the interactions occurring within plant communities but also the intricate process of carbon storage within ecosystems. With the anticipated escalation of global temperatures in the forthcoming century, these mechanisms are poised to play a pivotal role in shaping the dynamics of plant communities and the overall carbon balance of ecosystems.

5 Figures

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