

¹ Changes and trends in budburst and leaf flush

² across Europe and North America

³ A meta-analysis of local adaptation in spring phenology

⁴ studies

⁵ Ziyun Zeng & E. M. Wolkovich

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Abstract

Forecasting the biological impacts of climate change requires understanding how species respond to warmer temperatures through both inter-annual flexible variation versus through adaptation to local conditions. Yet we often lack this information entirely, or find conflicting evidence across studies. This is the case for one of the most reported and consistent impacts of anthropogenic climate change—earlier spring phenology, which is also one of the most critical to forecasting given its role in carbon sequestration. Evidence from some common garden studies suggest important provenance effects, which suggest local adaptation in the underlying cues of spring phenology and supports findings for fall events, while other studies find no evidence. Here we synthesize common garden studies across Europe and North America 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, alongside fall event data when provided. Across continents we find no evidence of provenance effects in spring phenology, but strong clines with latitude and mean annual temperature (MAT) for fall events. These effects, however, appear to diverge by continent and species type (gymnosperm versus angiosperm), especially for fall events where clines with latitude and MAT are much stronger in North America. Our results suggest flexible, likely plastic responses, in spring phenology with warming, and potential limits—at least in the short term—due to provenance effects for fall phenology. They also highlight that, after over 50 years of common garden studies on tree phenology we may still lack a holistic predictive model of clines across species and phenological events.

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, but possibly limiting responses after the limits of plasticity are reached (Chevin and Lande, 2010; Snell-Rood et al., 2018).

Many of the currently observed responses to climate change appear to be mainly 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

38 for many organisms, allowing them to time reproduction and exploit the resources of each growing
39 season (Chuine, 2010; Hänninen and Tanino, 2011; Rytteri et al., 2021; Posledovich et al., 2018). As
40 such, phenology plays a significant role in determining fitness for both plants (Guo et al., 2022; Chuine
41 and Beaubien, 2001) and animals (Wann et al., 2019; Renner and Zohner, 2018; Chuine and Régnière,
42 2017).

43 Shifted phenology in recent decades—with many events moving several days per decade (Vitasse et al.,
44 2021; Kharouba et al., 2018; Menzel et al., 2006)—has led to concerns about fitness consequences, and
45 the limits of possible future shifts. While future phenological shifts will depend on how much phenology
46 is determined by plasticity versus adaptation, our understanding of the balance of these two approaches
47 to variation is limited. This is the case even for species groups that are critical to both forecasting and
48 have been well studied, such as trees.

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

57 Studies of adaptation versus plasticity in tree phenology have been conducted for centuries (Cle-
58 land et al., 2007), through common garden studies. In these studies—conducted often for forestry
59 purposes—researchers grow trees of different geographical origins under the same environmental con-
60 ditions to disentangle the effects of environmental and genetic variation on trees' phenology and phe-
61 notype (Aitken and Bemmels, 2016; Alberto et al., 2013). Such work has established common clines in
62 fall phenology, as source locations with shorter growing seasons (poleward and higher elevations) ex-
63 hibit earlier stopping of growth (such as budset). Research has connected these clines to an underlying
64 proximate mechanism of changing photoperiod cues (i.e., shifts in the photoperiod threshold required
65 to trigger budset), driven by adaptation to the local growing season (Alberto et al., 2013; Savolainen
66 et al., 2007). In contrast, spring phenology appears more plastic (Aitken and Bemmels, 2016) and
67 is determined more strongly by temperature (Flynn and Wolkovich, 2018). Many studies, however,

68 have argued that spring phenology shows levels of adaptation that may be critical to forecasting and
69 mitigation (Vitasse et al., 2009; Basler and Körner, 2012).

70 These contrasting studies highlight how inconsistent evidence for adaptation in tree spring phenology
71 has been. Studies have documented provenance differences of 2-4 days per degree latitude in spring
72 phenology for some species (*Picea abies* in Sogaard et al., 2008 and *Quercus petraea* in Deans and
73 Harvey, 1996) while others have failed to find similar trends along latitudinal gradients (for example,
74 *Picea sitchensis* in Mimura and Aitken, 2007, *Picea glauca* in Li et al., 1997, and *Populus balsamifera*
75 in Farmer, 1993). This has led to debate over the prevalence and importance of adaptation in spring
76 tree phenology. While clines of spring phenology have been found in studies in both Europe (Sogaard
77 et al., 2008; Deans and Harvey, 1996; Von Wuehlisch et al., 1995) and North America (Rossi, 2015;
78 Soolanayakanahally et al., 2013; Hannerz et al., 1999), they may be more studies and debated in
79 Europe (Deans and Harvey, 1996; Vitasse et al., 2009; Basler and Körner, 2012), raising the possibility
80 that they could vary by continent.

81 Continental differences in patterns of adaptation versus plasticity could be driven by climatic dif-
82 fferences, especially as North American springs are more variable across years than European ones
83 (Twardosz et al., 2021; Zohner et al., 2017; Schwartz and Reiter, 2000). Such high temporal variability
84 means that distant sites can effectively experience the same spring climate, but in different years.
85 Studies of spring phenology in arboreta suggest cues for budburst may vary depending on continen-
86 tal climate (Zohner et al., 2017), but are poorly controlled compared to traditional common garden
87 studies, making them difficult to use for tests of plasticity versus adaptation (Gauzere et al., 2020).
88 Even for more carefully designed common gardens, differences in species studied or other differences
89 in design may complicate understanding what underlies potential trends across continents.

90 To test for evidence of adaptation in spring phenology and what factors may underlie differences
91 observed across studies, we comprehensively examined clines for spring events, including fall events
92 when possible. We tested for evidence of adaptation via provenance trends with latitude and climate
93 and examined possible factors that underlie these clines, asking:

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

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

100 **2 Methods**

101 **2.1 Data Collection**

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

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

107 which returned 122 publications. We also contacted authors of previous review papers (Aitken and
108 Bemmels, 2016; Alberto et al., 2013), to help further search the literature. We then reviewed the meth-
109 ods and results of all publications to refine to only studies that met the following criteria: (a) focused
110 on woody plants originating from either Europe or North America, (b) had provenance trials/common
111 gardens on the same continent, (c) reported latitude and longitude of provenances and gardens, and
112 (d) reported spring events in units of calendar days (day of year or DOY) or could be converted into
113 DOY (see Additional Methods in the Supplements).

114 Based on these criteria we found 19 common gardens distributed throughout North America and
115 Europe, with the majority of data concentrated in North America (Fig. 1 & Supplement Table.1). From
116 each common garden study we extracted phenological data on spring events (budburst and leaf flush) in
117 DOY and, when present in the same paper, fall events (bud set, leaf senescence, growth cessation, and
118 leaf abscission) by species and the geographic information of provenances and gardens. We used ImageJ
119 (version 1.53k; Schneider et al., 2012) to extract values from figures whenever necessary. For studies
120 that reported event dates relative to a reference date other than 1 January (e.g. Rehfeldt, 1994a), we
121 converted such dates to DOY using the ‘lubridate’ package in R (Grolemund and Wickham, 2011).
122 To understand how climatic differences, in addition to geographical differences, shape local adaptation
123 in spring events we extracted several types of climate data using information about provenance latitude,
124 longitude, and elevation from original publications. We estimated the mean annual temperature (MAT)



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. Note: map lines delineate study regions and do not necessarily depict accepted national boundaries

from 1960-1991 for each provenance using the Climate Information Tool by Food and Agriculture Organization of the United Nations (FAO, 2022). We verified our calculated MAT was similar to MAT calculated using ClimateWNA (Wang et al., 2016), a source used in previous analyses.

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.

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

¹⁴⁵ transitions (which required setting `adapt_delta` to 0.99 for some models), \hat{R} values close to 1, and
¹⁴⁶ sufficient effective sample sizes. We present estimates as mean \pm 90% uncertainty intervals given
¹⁴⁷ parenthetically, unless otherwise stated.

¹⁴⁸ 3 Results

¹⁴⁹ Our final dataset included seven deciduous angiosperm and eight evergreen gymnosperm species from
¹⁵⁰ 17 studies and 19 gardens, encompassing 384 North American provenances and 101 European prove-
¹⁵¹ nances, with observations from 1962 to 2019. Seven species (five in North America and two in Europe)
¹⁵² also had fall event information available. Most species in North American gardens were gymnosperms
¹⁵³ (7/11 species) while most species in European gardens were angiosperms (3/4 species).

¹⁵⁴ Overall, spring events were not related to provenance latitude or MAT, neither across continents
¹⁵⁵ (latitude: 0.10 days/degree [-0.05 - 0.25]; MAT: -0.11 days/ $^{\circ}\text{C}$ [-0.34 - 0.12]) (Fig. 2, Table. 2 &
¹⁵⁶ 3 in Supplements), nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09
¹⁵⁷ days/ $^{\circ}\text{C}$ [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT: -0.16 days/ $^{\circ}\text{C}$ [-
¹⁵⁸ 0.55 - 0.23]) (Fig.3A & 4A). Results were similar using other distance metrics in lieu of latitude (see
¹⁵⁹ Supplement Fig.1 for results using the difference between provenance and garden latitude, and the
¹⁶⁰ spherical distance between provenance and garden).

¹⁶¹ In contrast, fall events (e.g., budset, leaf senescence, leaf abscission) were earlier at more northern,
¹⁶² cooler MAT sites (that is, they advanced strongly with provenance latitude: 3.16 days/degree [2.87-
¹⁶³ 3.45], and with decreasing MAT: 4.78 days/ $^{\circ}\text{C}$ [4.1 - 5.4], Fig. 2, Table.4 & 5 in Supplements). This
¹⁶⁴ relationship, however, was observed mostly in North America where fall events advanced 4.24 (3.95 -
¹⁶⁵ 4.53) days per degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT ($^{\circ}\text{C}$), whereas
¹⁶⁶ in Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree northward,
¹⁶⁷ or 0.70 days (1.04 - 2.42) per degree decline in MAT ($^{\circ}\text{C}$) (Fig. 4A).

¹⁶⁸ Clines in fall phenology were stronger and more consistent whereas clines in spring phenology were
¹⁶⁹ weaker and somewhat varied in directionality. For fall events, only two field studies found no rela-
¹⁷⁰ tionship (Fig. 2): *Fraxinus excelsior* from Garden Q* in the UK (Rosique-Esplugas et al., 2022) and
¹⁷¹ *Fagus sylvatica* from Garden R* in Bulgaria (Petkova et al., 2017). Another study that found no
¹⁷² relationship was the only greenhouse experiment included (*Picea engelmannii* from Garden B in the
¹⁷³ USA, also included in Aitken and Bemmels, 2016), which uniquely used the fall event of ‘the day by

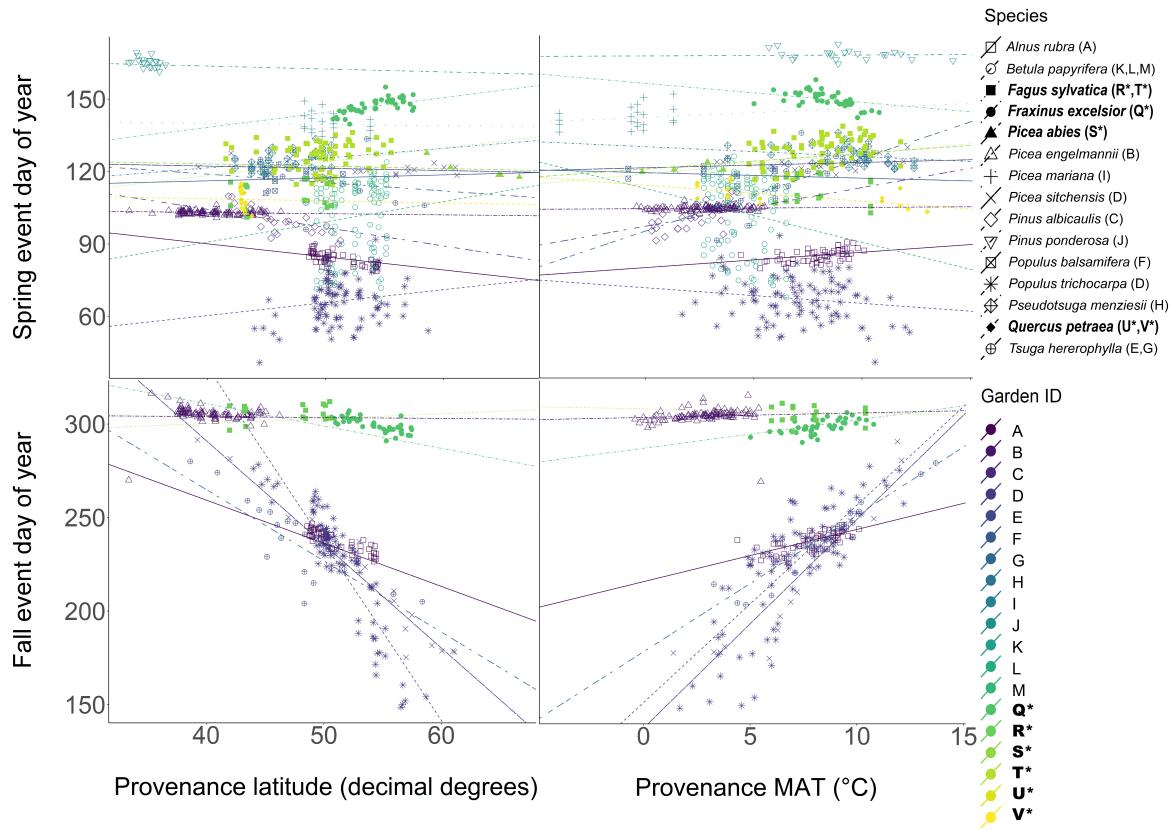


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are bolded and denoted by an asterisk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

174 which seedling elongation had finished' (Rehfeldt, 1994b). In contrast, spring event clines were always
 175 weak: all species x garden clines included 0 in their 90% intervals.

176 Effects of provenance latitude on fall events were similar across angiosperms and gymnosperms (Fig.3B).
 177 Spring events weakly diverged, delaying at a rate of 0.37 (0.15 - 0.59) days per degree north in an-
 178 giosperms and advancing 0.23 (0.00 - 0.46) days per degree north in gymnosperms. Fall events advanced
 179 3.18 (2.76 - 3.62) days per degree north in angiosperms and 3.14 (2.81-3.47) days per degree north in
 180 gymnosperms. Effects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced
 181 0.82 (0.54 - 1.11) days/°C as MAT increased in angiosperms and delayed 0.76 (0.37 - 1.14) days/°C as
 182 MAT increased in gymnosperms. Fall events delayed in warmer locations for both species types, but
 183 slightly more so for gymnosperms (6.23 days) than angiosperms (3.69 days) (Fig. 4B).

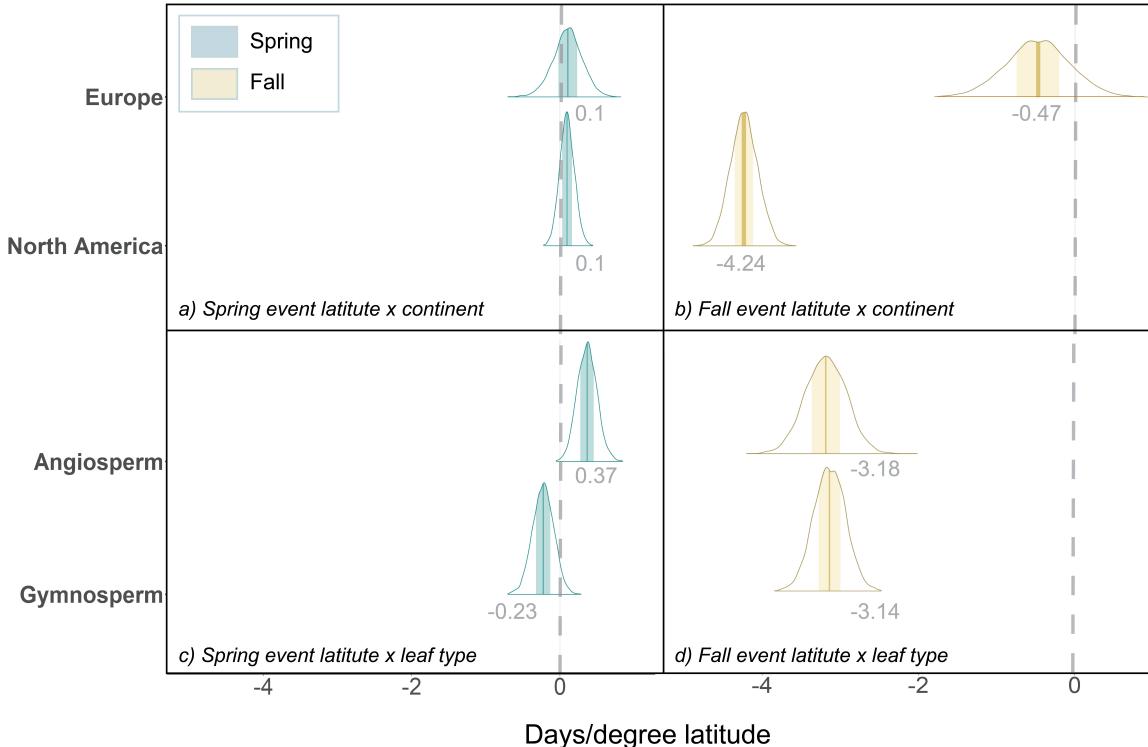


Figure 3: Posterior distributions (99% percentile) for the effect of provenance latitude across different continents and species types. Zero—no effect—is shown with a dashed line. Solid line and shading in posteriors represent mean and 50 percent interval (90% intervals given in text). (a & b) Effect of latitude and continent on spring and fall event date (DOY). Fall events advanced strongly per degree northward, particularly notably in North America. (c & d) 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.

184 While we expected that coarse metrics, such as latitude and MAT, would generally represent how
 185 similar the climates are between the provenances and gardens, we also estimated climate overlap in
 186 months much closer to the events to further test how much climate similarity between provenances and
 187 gardens predicts provenance effects. For spring events, we considered overlap across March to May.
 188 However, results were not qualitatively different than using MAT (See Fig. 2 in Supplements). We
 189 observed very weak effects of climate overlap on spring events (0.01 [0.02 - 0.03] days per one percent
 190 increase in climate overlap), nearly identical across angiosperms (0.02 [0.00 - 0.05]) and gymnosperms
 191 (0.04 [0.00 - 0.09]). Fall events advanced as climate overlap declined, but slightly more strongly for
 192 gymnosperms (advancing 0.72 [0.51 - 0.92] days per one percent decline in climate overlap) (Fig.3 in
 193 Supplements).

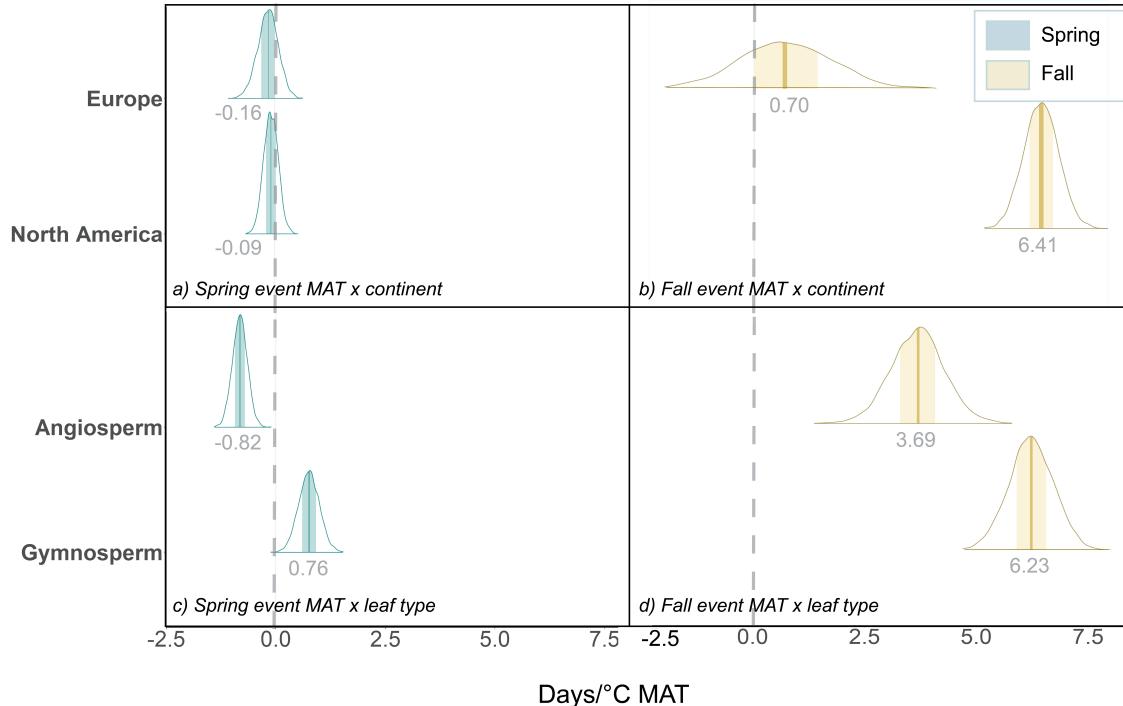


Figure 4: Posterior distributions (99% percentile) for the effect of MAT across different continents and species types. Zero—no effect—is shown with a dashed line. Solid line and shading in posteriors represent mean and 50 percent interval (90% intervals given in text). (a & b) Effect of MAT and continent on spring and fall event date (DOY). Fall events advanced strongly with decreasing MAT, particularly notably in North America. (c & d) 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.

194 4 Discussion

195 Overall, our results demonstrated inconsistent and weak clines in spring events across North America
 196 and Europe. In contrast, fall events generally showed much stronger clines, especially in North America,
 197 and in support of many previous studies (Aitken and Bemmels, 2016; Alberto et al., 2013). While
 198 previous studies have suggested spring events are far more plastic compared to fall events (Li et al.,
 199 1997; Farmer, 1993; Mimura and Aitken, 2007), our study provides the first major test of this across
 200 continents and species and suggests no general trend for clines in spring phenology. Our results thus
 201 predict that warming springs will continue to be tracked more closely phenologically by trees than
 202 warming fall temperatures (IPCC, 2022)

203 Trends between spring phenology and latitude or MAT were weak, but suggested the possibility of

204 diverging results that could mute an overall trend—albeit a much weaker one than for fall phenology.
205 We found angiosperm versus gymnosperm species diverged in their clines with MAT. Combined with
206 our finding of much stronger clines for fall phenology in North America, these results support the idea
207 of potential variation across continents and/or species type that may underlie the debate in whether
208 spring events show important clinal variation. As clines with spring events were very weak, however,
209 and gardens almost always focus on only one species, understanding these diverging results well enough
210 to aid forecasting would take significant additional investment in common garden studies.

211 We found the coarse metrics of provenance latitude and MAT were generally good predictors of phe-
212 nology, performing better than our more complex and data-rich metric of climate overlap. Latitude
213 and MAT appeared to well represent how similar the climates are between the provenances and gar-
214 dens in the temperate and boreal forest species we studied, yielding similar results metrics calculated
215 specifically in the spring with daily climate data.

216 4.1 Variation across continents and species types

217 Our results highlight that spring events show much weaker clines than fall events in tree species, but
218 suggest important variation between species types in spring events. Angiosperms tended to budburst
219 earlier in provenances that were warmer and more southerly, while gymnosperms trended in the oppo-
220 site direction. Such differences could be driven by their varying investment strategies. As gymnosperms
221 photosynthesize without leafout they generally leafout much later than angiosperms, after most risk of
222 spring frost (Panchen et al., 2014), and thus may avoid frost risk more than angiosperms. In contrast,
223 angiosperms may tend towards earlier leafout in warmer climates to compete best for access to light
224 and other resources (?). Testing these hypotheses would require More information on frost risk and
225 forest community assembly from across the provenance locations.

226 In our dataset, more data on fall events were reported in North America. In Europe, only two gardens
227 reported fall event metrics, one studying *Fagus sylvatica* and one studying *Fraxinus excelsior*. Fall
228 events were earlier in colder, more northern latitudes in both continents, which is consistent with
229 previous literature (Aitken and Bemmels, 2016; Alberto et al., 2013). North American studies of both
230 gymnosperm and angiosperm species reported strong clines, and most often focused on budset, while
231 the two European gardens reported data on ‘leaf senescence’ (Supplement Table.1). Leaf senescence
232 was visually inspected based on the percentage of the tree crown that had changed color when the

assessor stood on the south-facing side of each tree (Rosique-Esplugas et al., 2022). We note that budset is most closely related to growth cessation and tied to photoperiod signals, making it generally considered a more robust indicator of when plants stop investing in growth and more genetically controlled than leaf senescence (Alberto et al., 2013).

Taken together, these results could explain some of the existing debate on the strength of spring clinal variation, but also highlight how data biases make disentangling the drivers of variation difficult. Angiosperm species showed a weak trend towards earlier budburst in populations from warmer locations. In contrast fall event clines in Europe were weak, but their fall event type (leaf senescence) is less likely to show clinal variation. Given European studies were biased towards studying angiosperms (3/4 species) that are often canopy-species (e.g., *Fagus*, *Quercus*) these results together could explain a greater focus on clinal variation in spring events across European studies (Basler and Körner, 2012; Gauzere et al., 2020; Sogaard et al., 2008; Deans and Harvey, 1996; Von Wuehlisch et al., 1995). Most North American gardens and provenances included in this study were limited to the Pacific Northwest region, and thus tended to focus on species from forests where gymnosperms are almost always the canopy species (*Pseudotsuga*, *Tsuga*, *Picea*, *Pinus*) and angiosperms are much smaller, more opportunistic species (*Alnus*, *Populus*). This might suggest a far different pattern if gardens included more evenly sampled North American tree species (Fig. 1). Given the tremendous investment required for such gardens, however, it is not surprising they are often limited to one species—most often those relevant for forestry (e.g., *Pseudotsuga menziesii*, *Tsuga plicata*, *Tsuga heterophylla*, *Picea sitchensis*, *Pinus albicaulis*). Our results, however, highlight the limited inference we may gain from such an approach to understand trends across species more broadly.

4.2 Adaptation in tree phenology: Implications for climate change responses

Our results suggest that current advances in spring phenology will likely continue, but predicting any shifts due to provenance effects will require new data across more species. Plastic responses to warming, as our results suggest for spring events, mean species can adjust to the shifting environments of climate change—up to some point. Beyond that point theory suggests plastic traits may limit adaptation to climate change (Chevin et al., 2010). This may mean species will be replaced when their plastic spring phenological responses are no longer adequate, or shifting reaction norms could lead to adaptation (Gauzere et al., 2020).

263 Predicting this will require better understanding how different species strategies covary with early-
264 season risks, and how such risks may shift with continued climate change. For temperate zones, many
265 species strategies appear designed to cope with frost, either via avoidance or tolerance (Alberto et al.,
266 2011; Lenz et al., 2016; Allevato et al., 2019), as utilizing the early portion of the growing season can be
267 especially critical for species in colder regions (Morin et al., 2007; Dantec et al., 2015). Climate change
268 at once shifts spring phenology—thus potentially changing each species frost risk—but also appears
269 to reshape the drivers of frost climatically (?). Layered onto this are possible shifts in early-season
270 herbivory with warming (?), and trade-offs in early-season risks with access to a long growing season
271 for growth and reproduction, with some species avoiding competition through being very early (Guo
272 et al., 2022). Common garden studies that track and report frost and herbivory damage, alongside
273 timing of flowering and fruiting, could help to understand the complex fitness landscape of spring
274 phenology.

275 In contrast to spring events which were weak and variable, fall events exhibited strong clines, which
276 appeared co-gradient with the environment (i.e. late-season events advanced earlier with northward
277 latitudes). This supports previous results and the general theory that fall events are consistently
278 designed to avoid tissue loss at the end of the season, when the cost of such losses could be particularly
279 high (Aitken and Bemmels, 2016; Alberto et al., 2013). Spring events showed no clear trends, but
280 Increasing research into counter-gradient variation for flowering events could be relevant when spring
281 vegetative and flowering events are linked (Buonaiuto et al., 2021).

282 Understanding environmental clines in phenology will ultimately be critical to predicting how species
283 shift their ranges as well. Implications of small differences in spring phenology could mean different
284 levels of gene flow, while co- and counter-gradient variation have important implications for gene glow
285 over larger geographical regions (Bachmann et al., 2020), and thus could shape future range shifts.
286 Much like frost risk, climate change likely shifts multiple factors at once, as climate change shifts
287 pollinators and wind patterns (Kling and Ackerly, 2021). With the anticipated escalation of global
288 temperatures in the forthcoming century, these mechanisms are poised to play a pivotal role in shaping
289 the dynamics of plant communities and the overall carbon balance of ecosystems.

290 **5 Figures**

291 **6 References**

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