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Weak evidence of provenance effects in spring phenology across Europe and North America

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Running head: Clines in spring phenology

Abstract

Forecasting the biological impacts of climate change requires understanding how species respond to warmer temperatures through inter-annual flexible variation versus through adaptation to local conditions. Yet, we often lack this information entirely or find conflicting evidence across studies. The latter is the case for shifts in spring phenology—one of the most reported and consistent impacts of anthropogenic climate change, and also one of the most critical to forecasting, given its role in carbon sequestration. Some common garden studies have found evidence of important provenance effects, which suggest there may be local adaptation in the underlying cues of spring phenology and mirrors 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 250 years of common garden studies on tree phenology, we still lack a holistic predictive model of clines across species and phenological events.

Keywords: spring phenology, provenance, common gardens, budburst, leafout, budset, forests, climate change

24

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 stalling 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 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. While future phenological shifts will depend on how much phenology is determined by plasticity versus adaptation, our understanding of the balance of these two approaches to variation is limited. This is the case even for species groups that are critical to both forecasting and have been well studied, such as trees.

Tree phenology is 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). Shifts in phenology can affect tree growth (Myneni et al., 1997), scaling up to impact ecosystem-level carbon sequestration (Barichivich et al., 2012), and thus forecasts of climate change. 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. In these studies—conducted often for forestry purposes—researchers grow trees of different geographical origins under the same environmental conditions to disentangle the effects of environmental and genetic variation on trees' phenotypes (Aitken and Bemmels, 2016; Alberto et al., 2013). Such work has established common clines in fall phenology, as source locations with shorter growing seasons (poleward and higher elevations) exhibit earlier stopping of growth (such as budset). Research has connected these clines to an underlying proximate mechanism of changing photoperiod cues (i.e., shifts in the photoperiod threshold required to trigger

62 budget), driven by adaptation to the local growing season (Alberto et al., 2013; Savolainen et al., 2007).
63 In contrast, spring phenology appears more plastic (Aitken and Bemmels, 2016) and determined more
64 strongly by temperature (Flynn and Wolkovich, 2018). Many studies, however, have argued that spring
65 phenology shows levels of adaptation that may be critical to forecasting and mitigation (Vitasse et al.,
66 2009; Basler and Körner, 2012).

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

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

87 To test for evidence of adaptation in spring phenology and what factors may underlie differences
88 observed across studies, we comprehensively examined clines for spring events, including fall events
89 when possible. We tested for evidence of adaptation via provenance trends with latitude and climate
90 and examined possible factors that underlie these clines, including for differences between: (1) spring
91 and fall phenology, (2) studies in Europe and North America, (3) angiosperm and gymnosperm species.

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

95 **2 Methods**

96 **2.1 Data Collection**

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

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

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

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

117 To understand how climatic differences, in addition to geographical differences, shape local adaptation
118 in spring events we extracted several types of climate data using information about provenance latitude,
119 longitude, and elevation from original publications. We estimated each provenance’s mean annual

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

To examine climate near spring events more explicitly than MAT allows, we used gridded daily temperature data for March-May from 2011 to 2020 for all provenances and gardens. We extracted data from E-OBS for European locations and used the ‘daymetr’ in R for North American locations (Cornes et al., 2018; Hufkens et al., 2018). Then, using these data and the ‘overlap’ package in R, we estimated how much the daily temperatures overlapped between each provenance location and their corresponding gardens across the three months for our 10 year period, which we call ‘climate overlap.’ Dataset containing event dates, geographic information, and climatic information of all provenances are archived in Knowledge Network for Biocomplexity (KNB) (Zeng and Wolkovich, 2023).

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 climatic 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 deciduous angiosperm and eight evergreen gymnosperm species from 17 studies and 19 gardens, encompassing 384 North American provenances and 101 European prove-

148 nances, with observations from 1962 to 2019. Seven species (five in North America and two in Europe)
149 also had fall event information available. Most species in North American gardens were gymnosperms
150 (7/11 species) while most species in European gardens were angiosperms (3/4 species).

151 Overall, spring events were not related to provenance latitude or MAT, neither across continents
152 (latitude: 0.10 days/degree [-0.05 - 0.25]; MAT: -0.11 days/°C [-0.34 - 0.12]) (Fig. 2, Table. 2 &
153 3 in Supplements), nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09
154 days/°C [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT: -0.16 days/°C [-
155 0.55 - 0.23]) (Fig.3A & 4A). Results were similar using other distance metrics in lieu of latitude (see
156 Supplement Fig.1 for results using the difference between provenance and garden latitude, and the
157 spherical distance between provenance and garden).

158 In contrast, fall events (e.g., budset, leaf senescence, leaf abscission) were earlier at more northern,
159 cooler MAT sites (that is, they advanced strongly with provenance latitude: 3.16 days/degree [2.87-
160 3.45], and with decreasing MAT: 4.78 days/°C [4.1 - 5.4], Fig. 2, Table.4 & 5 in Supplements). This
161 relationship, however, was observed mostly in North America where fall events advanced 4.24 (3.95 -
162 4.53) days per degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT (°C), whereas
163 in Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree northward,
164 or 0.70 days (1.04 - 2.42) per degree decline in MAT (°C) (Fig. 4A).

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

173 Effects of provenance latitude on fall events were similar across angiosperms and gymnosperms (Fig.3B).
174 Spring events weakly diverged, delaying at a rate of 0.37 (0.15 - 0.59) days per degree north in an-
175 giosperms and advancing 0.23 (0.00 - 0.46) days per degree north in gymnosperms. Fall events advanced
176 3.18 (2.76 - 3.62) days per degree north in angiosperms and 3.14 (2.81-3.47) days per degree north in
177 gymnosperms. Effects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced

178 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
179 MAT increased in gymnosperms. Fall events delayed in warmer locations for both species types, but
180 slightly more so for gymnosperms (6.23 days) than angiosperms (3.69 days) (Fig. 4B).

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

191 4 Discussion

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

200 Trends between spring phenology and latitude or MAT were weak, but suggested the possibility of
201 diverging results that could mute an overall trend—albeit a much weaker one than for fall phenology.
202 We found angiosperm versus gymnosperm species diverged in their clines with MAT. Combined with
203 our finding of much stronger clines for fall phenology in North America, these results support the idea
204 of potential variation across continents and/or species type that may underlie the debate in whether
205 spring events show important clinal variation. As clines with spring events were very weak, however,
206 and gardens almost always focus on only one species, understanding these diverging results well enough

207 to aid forecasting would take significant additional investment in common garden studies.

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

213 4.1 Variation across continents and species types

214 Our results highlight that spring events show much weaker clines than fall events in tree species, but
215 suggest important variation between species types in spring events. Angiosperms tended to budburst
216 earlier in provenances that were warmer and more southerly, while gymnosperms trended in the oppo-
217 site direction. Such differences could be driven by their varying investment strategies. As gymnosperms
218 photosynthesize without leafout they generally leafout much later than angiosperms, after most risk
219 of spring frost (Panchen et al., 2014), and thus may avoid frost risk more than angiosperms. In con-
220 trast, angiosperms may tend towards earlier leafout in warmer climates to compete best for access to
221 light and other resources (Chamberlain et al., 2019). Testing these hypotheses would require more
222 information on frost risk and forest community assembly from across the provenance locations.

223 In our dataset, more data on fall events were reported in North America. In Europe, only two gardens
224 reported fall event metrics, one studying *Fagus sylvatica* and one studying *Fraxinus excelsior*. Fall
225 events were earlier in colder, more northern latitudes in both continents, which is consistent with
226 previous literature (Aitken and Bemmels, 2016; Alberto et al., 2013). North American studies of both
227 gymnosperm and angiosperm species reported strong clines, and most often focused on budset, while
228 the two European gardens reported data on ‘leaf senescence’ (Rosique-Esplugas et al., 2022), measured
229 as percentage of tree crown that had changed color (Supplement Table 1). These different metrics
230 could explain the different results. Research has shown that budset is more closely related to growth
231 cessation and thus considered a more robust indicator of when plants stop investing in growth than
232 leaf senescence; it is also more genetically controlled (with different photoperiod thresholds required
233 to trigger budset in different provenances, Alberto et al., 2013).

234 Taken together, these results could explain some of the existing debate on the strength of spring clinal
235 variation, but also highlight how data biases make disentangling the drivers of variation difficult. An-

236 giosperm species showed a weak trend towards earlier budburst in populations from warmer locations.
237 In contrast fall event clines in Europe were weak, but their fall event type (leaf senescence) is less
238 likely to show clinal variation. Given European studies were biased towards studying angiosperms
239 (3/4 species) that are often canopy-species (e.g., *Fagus*, *Quercus*) these results together could explain
240 a greater focus on clinal variation in spring events across European studies (Basler and Körner, 2012;
241 Gauzere et al., 2020; Sogaard et al., 2008; Deans and Harvey, 1996; Von Wuehlisch et al., 1995).
242 Most North American gardens and provenances included in this study were limited to the Pacific
243 Northwest region, and thus tended to focus on species from forests where gymnosperms are almost
244 always the canopy species (*Pseudotsuga*, *Tsuga*, *Picea*, *Pinus*) and angiosperms are much smaller,
245 more opportunistic species (*Alnus*, *Populus*). This might suggest a far different pattern if gardens in-
246 cluded more evenly sampled North American tree species (Fig. 1). Given the tremendous investment
247 required for such gardens, however, it is not surprising they are often limited to one species—most
248 often those relevant for forestry (e.g., *Pseudotsuga menziesii*, *Tsuga plicata*, *Tsuga heterophylla*, *Picea*
249 *sitchensis*, *Pinus albicaulis*). Our results, however, highlight the limited inference we may gain from
250 such an approach to understand trends across species more broadly, a critical need for climate change
251 forecasting.

252 **4.2 Adaptation in tree phenology: Implications for climate change re-**
253 **sponses**

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

261 Predicting this will require better understanding how different species strategies covary with early-
262 season risks, and how such risks may shift with continued climate change. For temperate zones, many
263 species strategies appear designed to cope with frost, either via avoidance or tolerance (Alberto et al.,
264 2011; Lenz et al., 2016; Allevato et al., 2019), as utilizing the early portion of the growing season can be
265 especially critical for species in colder regions (Morin et al., 2007; Dantec et al., 2015). Climate change

266 at once shifts spring phenology—thus potentially changing each species frost risk—but also appears to
267 reshape the drivers of frost climatically (Chamberlain et al., 2021). Layered onto this are possible shifts
268 in early-season herbivory with warming (Meineke et al., 2019), and trade-offs in early-season risks with
269 access to a long growing season for growth and reproduction, with some species avoiding competition
270 through being very early (Guo et al., 2022). Common garden studies that track and report frost and
271 herbivory damage, alongside timing of flowering and fruiting, could help to understand the complex
272 fitness landscape of spring phenology.

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

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

288 5 Acknowledgement

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290 possible additional common garden studies.

291 6 Data Availability Statement

292 The data that support the findings of this study are openly available in the Knowledge Network for
293 Biocomplexity (KNB) repository at <https://knb.ecoinformatics.org/view/urn%3Auuid%3Aa37258b9-23e7-4b0c-a20f-9185cbc27194>.

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⁴⁹³ **8 Figures**



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 do not necessarily depict accepted national boundaries.

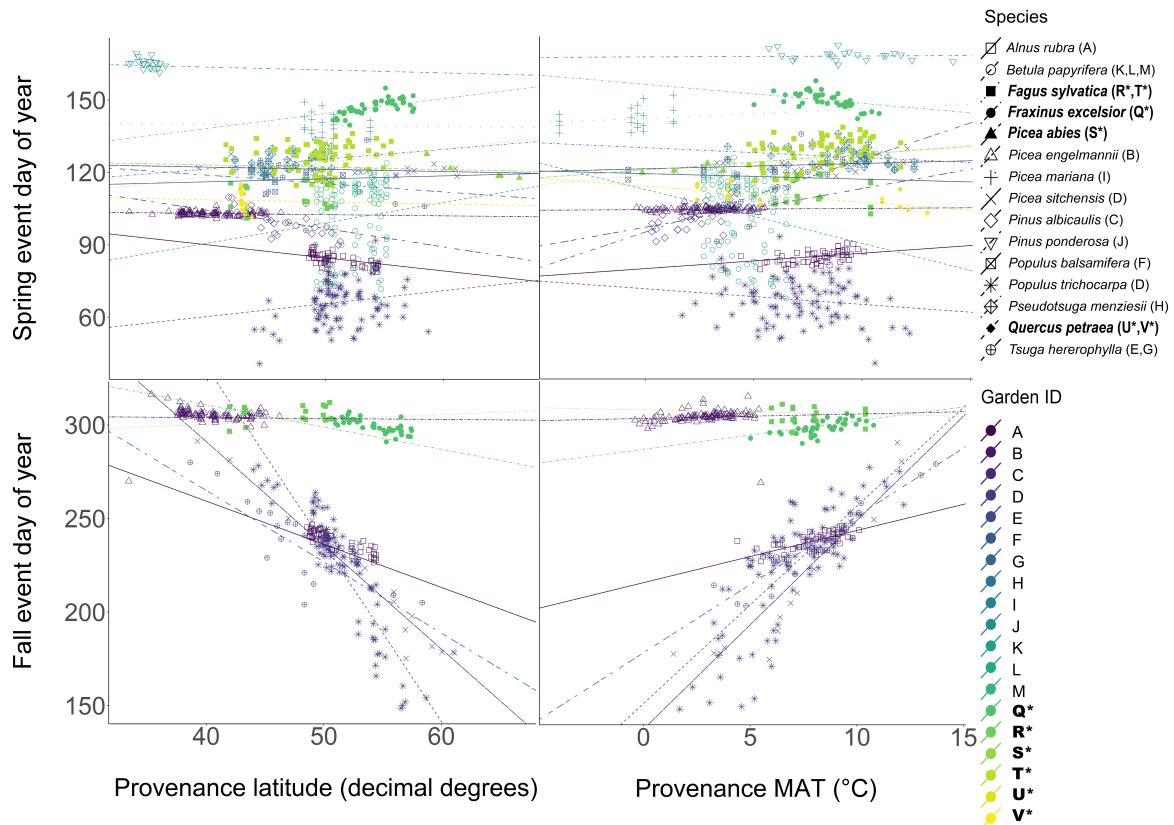


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are bolded and denoted by an asterisk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

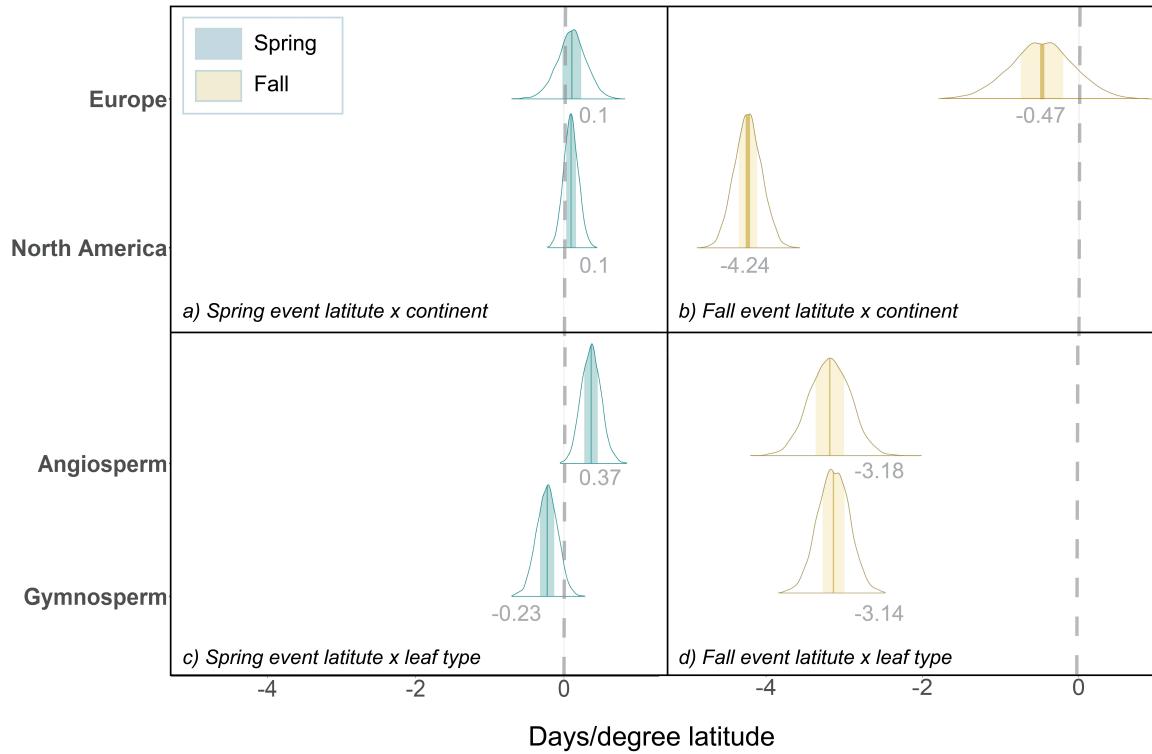


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in text). Zero—no effect—is shown with a dashed line. Spring events did not shift with latitude by continent, but fall events advanced strongly per degree northward, particularly in North America. Spring events slightly advanced in gymnosperms and delayed in angiosperms per degree northward. Fall events advanced per degree northward for both species types.

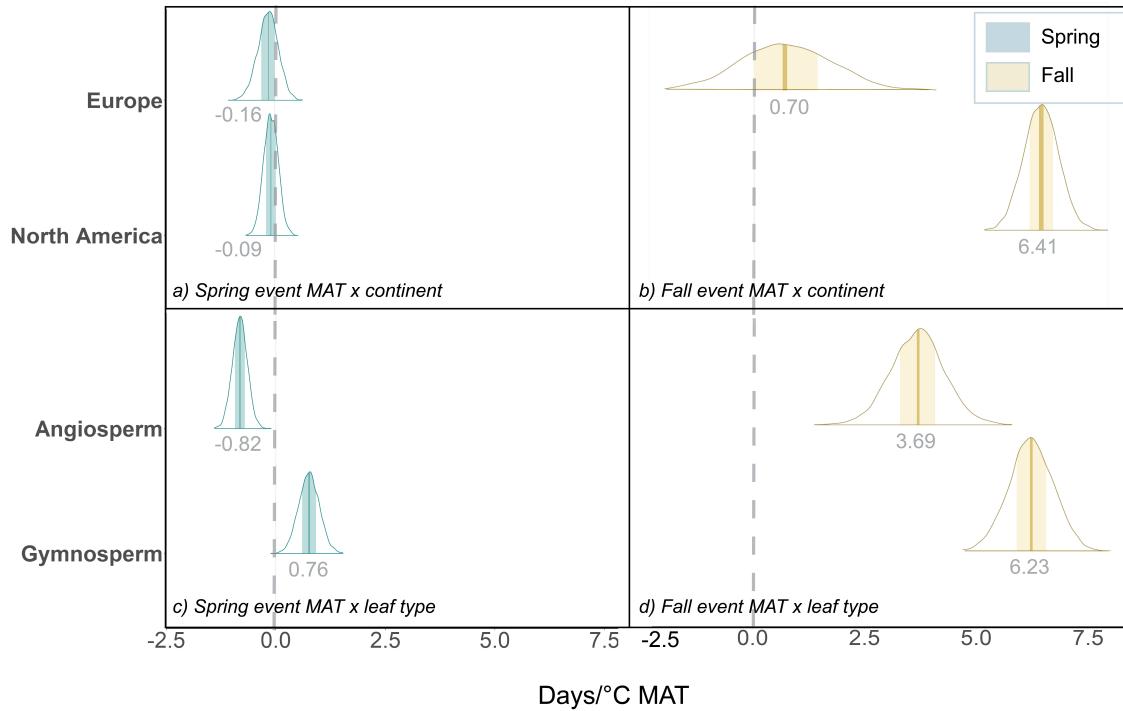


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in text). Zero—no effect—is shown with a dashed line. Spring events did not shift with MAT by continent, but fall events advanced strongly with decreasing MAT, particularly notably in North America. Spring events slightly advanced in angiosperms and delayed in gymnosperms with increasing MAT. Fall events delayed with increasing MAT for both species types.