
Version dated: October 29, 2023

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

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1 Introduction

Predicting the biological impacts of climate change has made understanding how organisms cope with environmental variation more urgent (Botero, Weissing, Wright, & Rubenstein, 2015). In particular, the relative importance of plasticity versus genetic adaptation is vital for prediction (Chevin, Lande, & Mace, 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 & Lande, 2010; Snell-Rood, Kobiela, Sikkink, & Shephard, 2018).

32 Many of the currently observed responses to climate change appear to be mainly plastic (Bonamour,
33 Chevin, Charmantier, & Teplicsky, 2019; Burton, Ratikainen, & Einum, 2022; Kingsolver & Buck-
34 ley, 2017; Zettlemoyer & Peterson, 2021), including the most reported biological response to climate
35 change—shifting phenology. Phenology—the timing of recurring seasonal events—governs the tim-
36 ing of transitions between dormancy and active growth for many organisms, allowing them to time
37 reproduction and exploit the resources of each growing season (Chuine, 2010; Hänninen & Tanino,
38 2011; Posledovich et al., 2018; Rytteri, Kuussaari, & Saastamoinen, 2021). As such, phenology plays
39 a significant role in determining fitness for both plants (Chuine & Beaubien, 2001; Guo et al., 2022)
40 and animals (Chuine & Régnière, 2017; Renner & Zohner, 2018; Wann et al., 2019).

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

47 Tree phenology is important to climate change forecasting at both the community and ecosystem levels.
48 The timing of budburst and senescence can impact plant competition, plant invasions, and community
49 assembly (Fridley, 2012). Shifts in phenology can affect tree growth (Myneni, Keeling, Tucker, As-
50 rar, & Nemani, 1997), scaling up to impact ecosystem-level carbon sequestration (Barichivich, Briffa,
51 Osborn, Melvin, & Caesar, 2012), and thus forecasts of climate change. Growing evidence, however,
52 suggests links between growth and phenology are not as consistent as previously predicted—or cur-
53 rently modelled (Dow et al., 2022)—with recent work suggesting how much spring versus fall events
54 shift may determine impacts on tree growth (Zohner et al., 2023).

55 Studies of adaptation versus plasticity in tree phenology have been conducted for centuries (Cleland,
56 Chuine, Menzel, Mooney, & Schwartz, 2007), through common garden studies. In these studies—
57 conducted often for forestry purposes—researchers grow trees of different geographical origins under
58 the same environmental conditions to disentangle the effects of environmental and genetic variation
59 on trees' phenotypes (Aitken & Bemmels, 2016; Alberto et al., 2013). Such work has established
60 common clines in fall phenology, as source locations with shorter growing seasons (poleward and higher
61 elevations) exhibit earlier stopping of growth (such as budset). Research has connected these clines

62 to an underlying proximate mechanism of changing photoperiod cues (i.e., shifts in the photoperiod
63 threshold required to trigger budset), driven by adaptation to the local growing season (Alberto et
64 al., 2013; Savolainen, Pyhajarvi, & Knurr, 2007). In contrast, spring phenology appears more plastic
65 (Aitken & Bemmels, 2016) and determined more strongly by temperature (Flynn & Wolkovich, 2018).
66 Many studies, however, have argued that spring phenology shows levels of adaptation that may be
67 critical to forecasting and mitigation (Basler & Körner, 2012; Vitasse, Delzon, Bresson, Michalet, &
68 Kremer, 2009).

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

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

when possible. We tested for evidence of adaptation via provenance trends with latitude and climate and examined possible factors that underlie these clines, including for differences between: (1) spring and fall phenology, (2) studies in Europe and North America, (3) 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 & 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 (also the locations of most studies), (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, Rasband, & Eliceiri, 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

¹²⁰ (Grolemund & Wickham, 2011).

¹²¹ To understand how climatic differences, in addition to geographical differences, shape local adaptation
¹²² in spring events we extracted several types of climate data using information about provenance latitude,
¹²³ longitude, and elevation from original publications. We estimated each provenance's mean annual
¹²⁴ temperature (MAT) from 1960 to 1991 using the monthly temperature data in the Climate Information
¹²⁵ Tool by Food and Agriculture Organization of the United Nations (FAO, 2022). We verified our
¹²⁶ estimated MAT was similar to MAT calculated using ClimateWNA (Wang, Hamann, Spittlehouse, &
¹²⁷ Carroll, 2016), a source used in previous analyses.

¹²⁸ To examine climate near spring events more explicitly than MAT allows, we used gridded daily temper-
¹²⁹ ature data for March-May from 2011 to 2020 for all provenances and gardens. We extracted data from
¹³⁰ E-OBS for European locations and used the 'daymetr' in R for North American locations (Cornes,
¹³¹ van der Schrier, van den Besselaar, & Jones, 2018; Hufkens, Basler, Milliman, Melaas, & Richardson,
¹³² 2018). Then, using these data and the 'overlap' package in R, we estimated how much the daily
¹³³ temperatures overlapped between each provenance location and their corresponding gardens across
¹³⁴ the three months for our 10 year period, which we call 'climate overlap.' Dataset containing event
¹³⁵ dates, geographic information, and climatic information of all provenances are archived in Knowledge
¹³⁶ Network for Biocomplexity (KNB) (Zeng & Wolkovich, 2023).

¹³⁷ 2.2 Analyses

¹³⁸ To estimate clines in spring and fall phenological events across species we used Bayesian hierarchical
¹³⁹ models. We regressed DOY of events against geographical and climatic predictors with partial pooling
¹⁴⁰ (sometimes called 'random effects') on the intercept and slope for each species within each garden.
¹⁴¹ Because most tree species were present in only one common garden in our dataset, it was impossible to
¹⁴² fit garden and species separately, thus we treat each species within a garden as a unique group. Using
¹⁴³ posterior estimates for each species within a garden, we estimated effects of continent (North America
¹⁴⁴ vs. Europe) and species type (angiosperm vs. gymnosperm). All models were fit in 'rstanarm' package
¹⁴⁵ (version 2.21.3; Goodrich, Gabry, Ali, & Brilleman, 2022) using default priors, with 4 chains and 1000
¹⁴⁶ sampling iterations per chain for a total of 4000 samples. We checked for model fit by confirming no
¹⁴⁷ divergent transitions (which required setting `adapt_delta` to 0.99 for some models), \hat{R} values close
¹⁴⁸ to 1, and sufficient effective sample sizes. We present estimates as mean \pm 90% uncertainty intervals

149 given parenthetically, unless otherwise stated.

150 3 Results

151 Our final dataset included seven deciduous angiosperm and eight evergreen gymnosperm species from
152 17 studies and 19 gardens, encompassing 384 North American provenances and 101 European prove-
153 nances, with observations from 1962 to 2019. Seven species (five in North America and two in Europe)
154 also had fall event information available. Most species in North American gardens were gymnosperms
155 (7/11 species) while most species in European gardens were angiosperms (3/4 species).

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

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

170 Clines in fall phenology were stronger and more consistent whereas clines in spring phenology were
171 weaker and somewhat varied in directionality. For fall events, only two field studies found no rela-
172 tionship (Fig. 2): *Fraxinus excelsior* from Garden Q* in the UK (Rosique-Esplugas, Cottrell, Cavers,
173 Whittet, & Ennos, 2022) and *Fagus sylvatica* from Garden R* in Bulgaria (Petkova, Molle, Huber,
174 Konnert, & Gaviria, 2017). Another study that found no relationship was the only greenhouse exper-
175 iment included (*Picea engelmannii* from Garden B in the USA, also included in Aitken & Bemmels,
176 2016), which uniquely used the fall event of ‘the day by which seedling elongation had finished’ (Re-
177 hfeldt, 1994b). In contrast, spring event clines were always weak: all species x garden clines included

178 0 in their 90% intervals.

179 Effects of provenance latitude on fall events were similar across angiosperms and gymnosperms (Fig.3B).
180 Spring events weakly diverged, delaying at a rate of 0.37 (0.15 - 0.59) days per degree north in an-
181 giosperms and advancing 0.23 (0.00 - 0.46) days per degree north in gymnosperms. Fall events advanced
182 3.18 (2.76 - 3.62) days per degree north in angiosperms and 3.14 (2.81-3.47) days per degree north in
183 gymnosperms. Effects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced
184 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
185 MAT increased in gymnosperms. Fall events delayed in warmer locations for both species types, but
186 slightly more so for gymnosperms (6.23 days) than angiosperms (3.69 days) (Fig. 4B).

187 While we expected that coarse metrics, such as latitude and MAT, would generally represent how
188 similar the climates are between the provenances and gardens, we also estimated climate overlap in
189 months much closer to the events to further test how much climate similarity between provenances and
190 gardens predicts provenance effects. For spring events, we considered overlap across March to May.
191 However, results were not qualitatively different than using MAT (See Fig. 2 in Supplements). We
192 observed very weak effects of climate overlap on spring events (0.01 [0.02 - 0.03] days per one percent
193 increase in climate overlap), nearly identical across angiosperms (0.02 [0.00 - 0.05]) and gymnosperms
194 (0.04 [0.00 - 0.09]). Fall events advanced as climate overlap declined, but slightly more strongly for
195 gymnosperms (advancing 0.72 [0.51 - 0.92] days per one percent decline in climate overlap) (Fig.3 in
196 Supplements).

197 4 Discussion

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

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

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

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

219 **4.1 Variation across continents and species types**

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

230 In our dataset, more data on fall events were reported in North America. In Europe, only two gardens
231 reported fall event metrics, one studying *Fagus sylvatica* and one studying *Fraxinus excelsior*. Fall
232 events were earlier in colder, more northern latitudes in both continents, which is consistent with
233 previous literature (Aitken & Bemmels, 2016; Alberto et al., 2013). North American studies of both
234 gymnosperm and angiosperm species reported strong clines, and most often focused on budset, while
235 the two European gardens reported data on ‘leaf senescence’ (Rosique-Esplugas et al., 2022), measured

236 as percentage of tree crown that had changed color (Supplement Table.1). These different metrics
237 could explain the different results. Research has shown that budset is more closely related to growth
238 cessation and thus considered a more robust indicator of when plants stop investing in growth than
239 leaf senescence; it is also more genetically controlled (with different photoperiod thresholds required
240 to trigger budset in different provenances, Alberto et al., 2013).

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

258 **4.2 Adaptation in tree phenology: Implications for climate change re-**
259 **sponses**

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

266 (Gauzere et al., 2020).

267 Predicting this will require better understanding how different species strategies covary with early-
268 season risks, and how such risks may shift with continued climate change. For temperate zones, many
269 species strategies appear designed to cope with frost, either via avoidance or tolerance (Alberto et
270 al., 2011; Allevato et al., 2019; Lenz, Hoch, Körner, & Vitasse, 2016), as utilizing the early portion of
271 the growing season can be especially critical for species in colder regions (Dantec et al., 2015; Morin,
272 Augspurger, & Chuine, 2007). Climate change at once shifts spring phenology—thus potentially chang-
273 ing each species frost risk—but also appears to reshape the drivers of frost climatically (Chamberlain,
274 Cook, Morales-Castilla, & Wolkovich, 2021). Layered onto this are possible shifts in early-season
275 herbivory with warming (Meineke, Classen, Sanders, Jonathan Davies, & Iler, 2019), and trade-offs
276 in early-season risks with access to a long growing season for growth and reproduction, with some
277 species avoiding competition through being very early (Guo et al., 2022). Common garden studies
278 that track and report frost and herbivory damage, alongside timing of flowering and fruiting, could
279 help to understand the complex fitness landscape of spring phenology.

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

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

296 5 Acknowledgement

297 We thank S. Aitken, I. Chuine, R. Guy, C Körner and Y. Vitasse for reviewing our list of papers for
298 possible additional common garden studies.

299 6 Data Availability Statement

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

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⁴⁸⁶ **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.

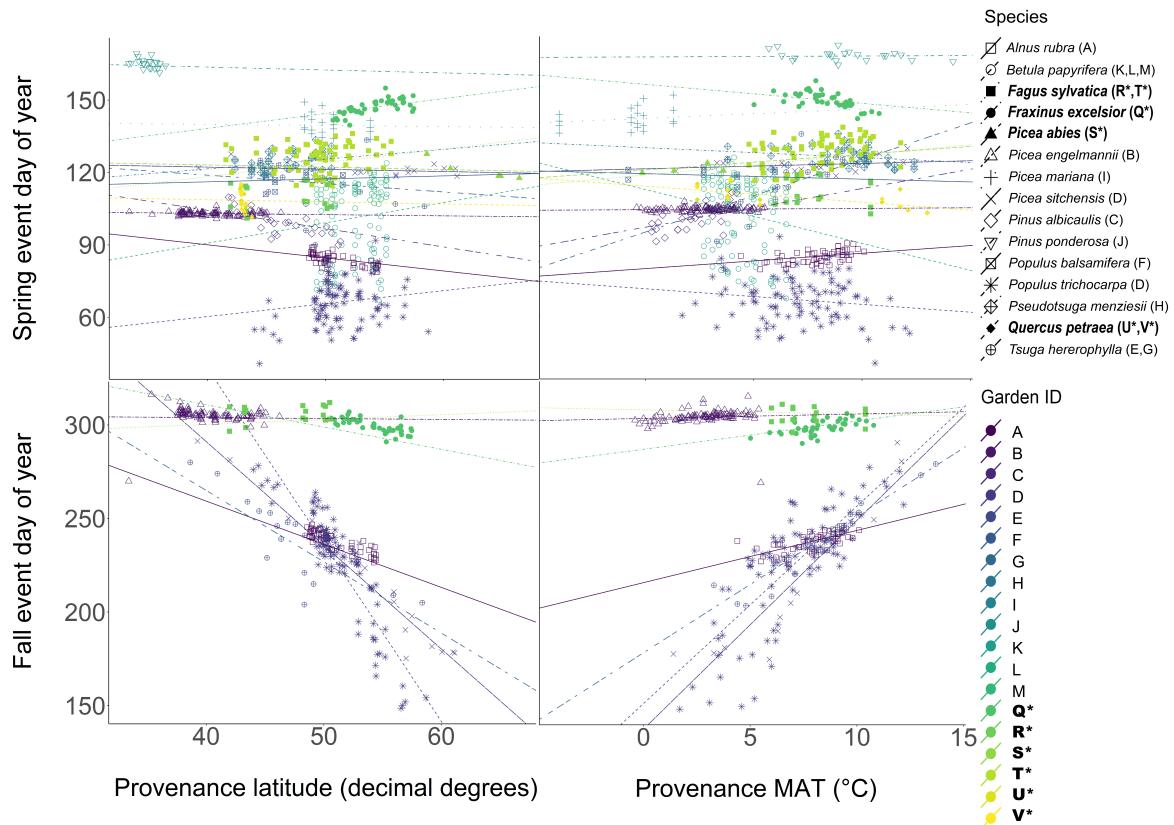


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are bolded and denoted by an asterisk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

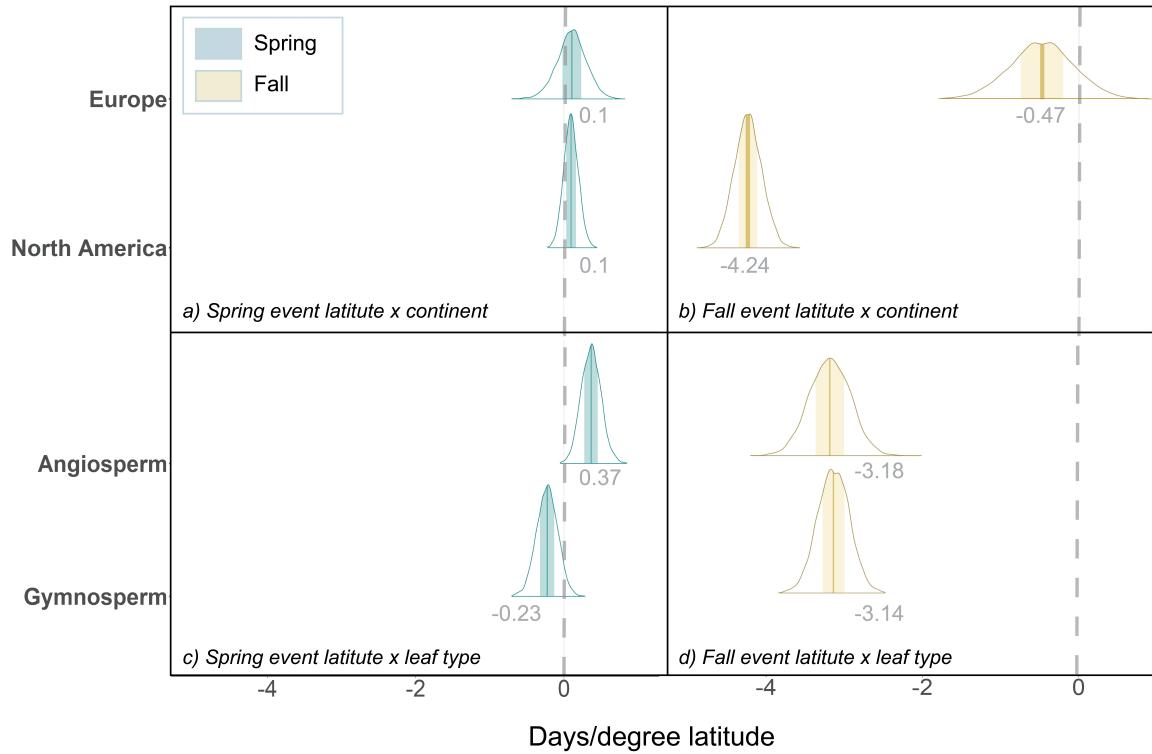


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given 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.

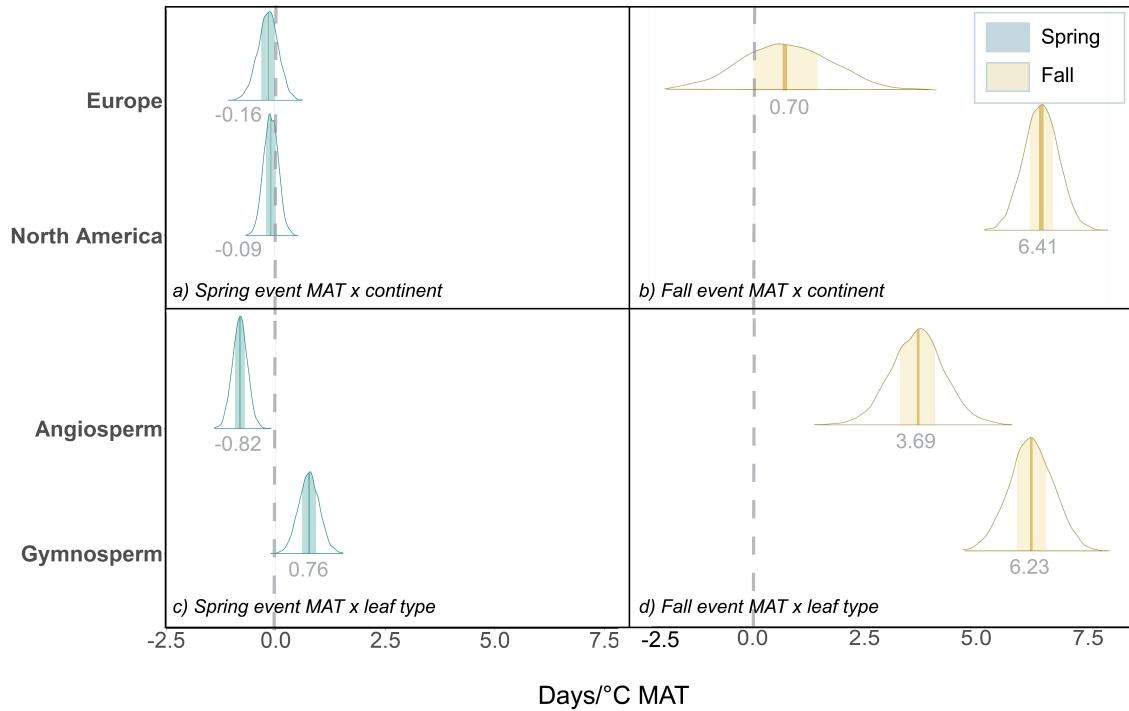


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in 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.