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

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1. Figure 1: Map showing the distribution of common gardens and provenances.
2. Figure 2: Event day of year in relation to provenance latitude and MAT.
3. Figure 3: Effects of latitude on spring and fall event day of year depending on continent and species leaf type.
4. Figure 4: Effects of MAT on spring and fall event day of year depending on continent and species leaf type.

Supporting Information (brief legends):

1. Methods S1: Additional methods.
2. Table S1: Showing all publications included in meta-analysis.

3. Table S2-5: Showing summary of model estimates.

4. Figures S1-3: Supporting figures.

¹ Summary

- ² • Forecasting the biological impacts of climate change requires understanding how
³ species respond to warmer temperatures through inter-annual flexible variation
⁴ ~~versus vs.~~ through adaptation to local conditions. Yet, we often lack this in-
⁵ formation entirely or find conflicting evidence across ~~studies. The latter is the~~
⁶ ~~ease for shifts in spring phenology one of the most reported and consistent~~
⁷ ~~impacts of anthropogenic climate change, and also one of the most critical to~~
⁸ ~~forecasting, given its role in carbon sequestration. Some common garden studies~~
⁹ ~~have found evidence of important provenance effects, which suggest there may be~~
¹⁰ ~~local adaptation in the underlying cues of spring phenology and mirrors findings~~
¹¹ ~~for fall events, while other studies find no evidence. Here, we previous studies.~~
- ¹² • ~~We~~ synthesize common garden studies across Europe and North America that
¹³ reported spring event dates for a mix of angiosperm and gymnosperm tree species
¹⁴ in the northern hemisphere, capturing data from 384 North American ~~provenances~~
¹⁵ and 101 European provenances (*i.e.* populations) with observations from 1962 to
¹⁶ 2019, alongside fall event data when provided.
- ¹⁷ • Across continents, we find no evidence of provenance effects (*i.e.* population
¹⁸ differences) in spring phenology, but strong clines with latitude and mean annual
¹⁹ temperature (MAT) ~~for fall events in fall~~. These effects, however, appear to diverge
²⁰ by continent and species type (gymnosperm ~~versus vs.~~ angiosperm), ~~especially for~~
²¹ ~~fall events where clines with latitude and MAT are much stronger with particularly~~
²² ~~pronounced clines in North America in fall.~~
- ²³ • Our results suggest flexible, likely plastic responses, in spring phenology with
²⁴ warming, and potential limits—at least in the short term—due to provenance
²⁵ effects for fall phenology. They also highlight that, after over 250 years of common
²⁶ garden studies on tree phenology, we still lack a holistic predictive model of clines
²⁷ across species and phenological events.

²⁸ *Keywords:* budburst, budset, climate change, common gardens, ~~forests~~deciduous and
²⁹ evergreen trees, leafout, ~~provenance senescence~~, spring phenology

³⁰

³¹ 1 Introduction

³² Predicting the biological impacts of climate change has made understanding how organ-
³³ isms cope with environmental variation more urgent (Botero et al., 2015). In particu-
³⁴ lar, the relative importance of plasticity versus genetic adaptation is vital for prediction
³⁵ (Chevin et al., 2010), with plasticity expected to allow species to shift more rapidly with
³⁶ climate change than environmental responses based on local adaptation, but possibly
³⁷ stalling responses after the limits of plasticity are reached (Chevin and Lande, 2010,
³⁸ Snell-Rood et al., 2018).

³⁹ Many of the currently observed responses to climate change appear to be mainly plastic
⁴⁰ (Burton et al., 2022, Zettlemoyer and Peterson, 2021, Bonamour et al., 2019, Kingsolver
⁴¹ and Buckley, 2017), including the most reported biological response to climate change—
⁴² shifting phenology. Phenology—the timing of recurring seasonal events—governs the
⁴³ timing of transitions between dormancy and active growth for many organisms, allowing
⁴⁴ them to time reproduction and exploit the resources of each growing season (Chuine,
⁴⁵ 2010, HÄnninen and Tanino, 2011, Rytteri et al., 2021, Posledovich et al., 2018). As
⁴⁶ such, phenology plays a significant role in determining fitness for both plants (Guo
⁴⁷ et al., 2022, Chuine and Beaubien, 2001) and animals (Wann et al., 2019, Renner and
⁴⁸ Zohner, 2018, Chuine and RÄgniÃlre, 2017).

⁴⁹ Shifted phenology in recent decades—with many events moving several days per decade
⁵⁰ (Vitasse et al., 2021, Kharouba et al., 2018, Menzel et al., 2006)—has led to concerns
⁵¹ about fitness consequences, and the limits of possible future shifts. While future phe-
⁵² nological shifts will depend on how much phenology is determined by plasticity versus
⁵³ adaptation, our understanding of the balance of these two approaches to variation is

54 limited. This is the case even for species groups that are critical to both forecasting
55 and have been well studied, such as trees.

56 Tree phenology is important to climate change forecasting at both the community and
57 ecosystem levels. The timing of budburst and senescence can impact plant competition,
58 plant invasions, and community assembly (Fridley, 2012). Shifts in phenology can
59 affect tree growth (Myneni et al., 1997), scaling up to impact ecosystem-level carbon
60 sequestration (Barichivich et al., 2012), and thus forecasts of climate change. Growing
61 evidence, however, suggests links between growth and phenology are not as consistent
62 as previously predicted—or currently modelled (Dow et al., 2022)—with recent work
63 suggesting how much spring versus fall events shift may determine impacts on tree
64 growth (Zohner et al., 2023).

65 Studies of adaptation versus plasticity in tree phenology have been conducted for
66 centuries (Cleland et al., 2007), through common garden studies. In these studies—
67 conducted often for forestry purposes—researchers grow trees of different geographical
68 origins ([called ‘provenances’ often in forestry](#)) under the same environmental conditions
69 to disentangle the effects of environmental and genetic variation on trees’
70 phenotypes (Aitken and Bemmels, 2016, Alberto et al., 2013). Such work has established
71 common clines in fall phenology [suggestive of local adaptation](#), as source locations with
72 shorter growing seasons (poleward and higher elevations) exhibit earlier [stopping of](#)
73 [growth cessation](#) (such as budset). Research has connected these clines to an
74 underlying proximate mechanism of changing photoperiod cues (i.e., shifts in the pho-
75 toperiod threshold required to trigger budset), driven by adaptation to the local grow-
76 ing season (Alberto et al., 2013, Savolainen et al., 2007). In contrast, spring phenology
77 appears more plastic (Aitken and Bemmels, 2016) and determined more strongly by
78 temperature (Flynn and Wolkovich, 2018). Many studies, however, have argued that
79 spring phenology shows levels of adaptation that may be critical to forecasting and
80 mitigation (Vitasse et al., 2009, Basler and Körner, 2012).

81 These contrasting studies highlight how inconsistent evidence for adaptation in tree

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

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

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

110 represent a deep evolutionary split in the plant tree of life. To address these questions,
111 we combined Bayesian hierarchical models with a new meta-analysis of all common gar-
112 den experiments in temperate tree species across Europe and North America reporting
113 spring phenology.

114 **2 Materials and Methods**

115 **2.1 Data collection**

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

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

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

131 Based on these criteria we found 19 common gardens distributed throughout North
132 America and Europe, with the majority of data concentrated in western North America
133 (Fig.1 & Table.S1 in Supporting Information). From each common garden study we
134 extracted phenological data on spring events (budburst and leaf flush) in DOY and,

135 when present in the same paper, fall events (bud set, leaf senescence, growth cessation,
136 and leaf abscission) by species and the geographic information of provenances and
137 gardens. We used ImageJ (version 1.53k; Schneider et al., 2012) to extract values from
138 figures whenever necessary. For studies that reported event dates relative to a reference
139 date other than 1 January (e.g. Rehfeldt, 1994a), we converted such dates to DOY
140 using the ‘lubridate’ package in R (Grolemund and Wickham, 2011).

141 To understand how climatic differences, in addition to geographical differences, shape
142 local adaptation in spring events we extracted several types of climate data using infor-
143 mation about provenance latitude, longitude, and elevation from original publications.
144 We estimated each provenance’s mean annual temperature (MAT) from 1960 to 1991
145 using the monthly temperature data in the Climate Information Tool by Food and
146 Agriculture Organization of the United Nations (FAO, 2022). We verified our esti-
147 mated MAT was similar to MAT calculated using ClimateWNA (Wang et al., 2016), a
148 source used in previous analyses.

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

159 **2.2 Analyses**

160 To estimate clines in spring and fall phenological events across species we used Bayesian
161 hierarchical models. We regressed DOY of events against geographical and climatic

¹⁶² predictors with partial pooling (sometimes called ‘random effects’) on the intercept and
¹⁶³ slope for each species within each garden. Because most tree species were present in only
¹⁶⁴ one common garden in our dataset, it was impossible to fit garden and species separately,
¹⁶⁵ thus we treat each species within a garden as a unique group. Using posterior estimates
¹⁶⁶ for each species within a garden, we estimated effects of continent (North America
¹⁶⁷ vs. Europe) and species type (angiosperm vs. gymnosperm). All models were fit in
¹⁶⁸ ‘rstanarm’ package (version 2.21.3; Goodrich et al., 2022) using default priors, with 4
¹⁶⁹ chains and 1000 sampling iterations per chain for a total of 4000 samples. We checked for
¹⁷⁰ model fit by confirming no divergent transitions (which required setting `adapt_delta`
¹⁷¹ to 0.99 for some models), \hat{R} values close to 1, and sufficient effective sample sizes. We
¹⁷² present estimates as mean \pm 90% uncertainty intervals given parenthetically, unless
¹⁷³ otherwise stated.

¹⁷⁴ 3 Results

¹⁷⁵ Our final dataset included seven deciduous angiosperm and eight evergreen gymnosperm
¹⁷⁶ species from 17 studies and 19 gardens, encompassing 384 North American provenances
¹⁷⁷ and 101 European provenances, with observations from 1962 to 2019. Seven species (five
¹⁷⁸ in North America and two in Europe) also had fall event information available. Most
¹⁷⁹ species in North American gardens were gymnosperms (7/11 species) while most species
¹⁸⁰ in European gardens were angiosperms (3/4 species).

¹⁸¹ Overall, spring events such as budburst and leaf flush were not related to provenance
¹⁸² latitude or MAT, neither across continents (latitude: 0.10 days/degree [-0.05 - 0.25];
¹⁸³ MAT: -0.11 days/ $^{\circ}\text{C}$ [-0.34 - 0.12]) (Fig.2, Table.S2 & S3 in Supporting Information),
¹⁸⁴ nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09 days/ $^{\circ}\text{C}$
¹⁸⁵ [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT: -0.16 days/ $^{\circ}\text{C}$
¹⁸⁶ [-0.55 - 0.23]) (Fig.3A & 4A). Results were similar using other distance metrics in lieu
¹⁸⁷ of latitude (see Fig.S1 for results using the difference between provenance and garden

188 latitude, and the spherical distance between provenance and garden).

189 In contrast, fall events (e.g., budset, leaf senescence, leaf abscission) were earlier at
190 more northern, cooler MAT sites (that is, they advanced strongly with provenance
191 latitude: 3.16 days/degree [2.87-3.45], and with decreasing MAT: 4.78 days/°C [4.1 -
192 5.4], Fig.2, Table.S4 & S5 in Supporting Information). This relationship, however, was
193 observed mostly in North America where fall events advanced 4.24 (3.95 - 4.53) days per
194 degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT (°C), whereas in
195 Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree
196 northward, or 0.70 days (1.04 - 2.42) per degree decline in MAT (°C) (Fig.4A).

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

206 Effects of provenance latitude on fall events were similar across angiosperms and gym-
207 nosperms (Fig.3B). Spring events weakly diverged, delaying at a rate of 0.37 (0.15 -
208 0.59) days per degree north in angiosperms and advancing 0.23 (0.00 - 0.46) days per
209 degree north in gymnosperms. Fall events advanced 3.18 (2.76 - 3.62) days per degree
210 north in angiosperms and 3.14 (2.81-3.47) days per degree north in gymnosperms. Ef-
211 ffects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced
212 0.82 (0.54 - 1.11) days/°C as MAT increased in angiosperms and delayed 0.76 (0.37 -
213 1.14) days/°C as MAT increased in gymnosperms. Fall events delayed in warmer lo-
214 cations for both species types, but slightly more so for gymnosperms (6.23 days) than
215 angiosperms (3.69 days) (Fig.4B).

216 While we expected that coarse metrics, such as latitude and MAT, would generally
217 represent how similar the climates are between the provenances and gardens, we also
218 estimated climate overlap in months much closer to the events to further test how much
219 climate similarity between provenances and gardens predicts provenance effects (*i.e.*
220 differential responses observed among plant populations from different geographical
221 origins). For spring events, we considered overlap across March to May. However,
222 results were not qualitatively different than using MAT (See Fig.S2 in Supporting In-
223 formation). We observed very weak effects of climate overlap on spring events (0.01
224 [0.02 - 0.03] days per one percent increase in climate overlap), nearly identical across
225 angiosperms (0.02 [0.00 - 0.05]) and gymnosperms (0.04 [0.00 - 0.09]). Fall events
226 advanced as climate overlap declined, but slightly more strongly for gymnosperms (ad-
227 vancing 0.72 [0.51 - 0.92] days per one percent decline in climate overlap) (Fig.S3 in
228 Supporting Information).

229 **4 Discussion**

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

239 Trends between spring phenology and latitude or MAT were weak, but suggested the
240 possibility of diverging results that could mute an overall trend—albeit a much weaker
241 one than for fall phenology. We found angiosperm ~~versus~~-gymnosperm (all deciduous)

242 versus gymnosperm (all evergreen) species diverged in their clines with MAT. Combined
243 with our finding of much stronger clines for fall phenology in North America, these
244 results support the idea of potential variation across continents and/or species type
245 that may underlie the debate in whether spring events show important clinal variation.
246 As clines with spring events were very weak, however, and gardens almost always focus
247 on only one species, understanding these diverging results well enough to aid forecasting
248 would take significant additional investment in common garden studies.

249 We found the coarse metrics of provenance latitude and MAT were generally good
250 predictors of phenology, performing better than our more complex and data-rich metric
251 of climate overlap. Latitude and MAT appeared to well represent how similar the
252 climates are between the provenances and gardens in the temperate and boreal forest
253 species we studied, yielding similar results to metrics calculated specifically in the spring
254 with daily climate data.

255 4.1 Variation across continents and species types

256 Our results highlight that spring events show much weaker clines than fall events in
257 tree species, but suggest important variation between species types in spring events.
258 Angiosperms tended to budburst earlier in provenances that were warmer and more
259 southerly, while gymnosperms trended in the opposite direction. Such differences could
260 be driven by their the varying investment strategies. As gymnosperms , given that
261 all our studied gymnosperms were evergreen and all angiosperms were deciduous. As
262 evergreen species photosynthesize without leafout they generally leafout much later than
263 angiosperms deciduous species, after most risk of spring frost (Panchen et al., 2014), and
264 thus may avoid frost riskmore than angiosperms. In contrast, angiosperms deciduous
265 species may tend towards earlier leafout in warmer climates to compete best for access
266 to light and other resources (Chamberlain et al., 2019). Testing these hypotheses would
267 require more information on frost risk and forest community assembly from across the
268 provenance locations. , but seems an important step towards understanding the drivers

269 of this variation. Without a clear mechanism, extrapolating these results to other
270 species or across Europe and North America may be difficult, especially given biases
271 in the data, and the distinct climatic, geographical, and ecological contexts of Europe
272 and North America. The direct applicability of our findings to other contexts must be
273 approached with caution.

274 In our dataset, more data on fall events were reported in North America. In Europe,
275 only two gardens reported fall event metrics, one studying *Fagus sylvatica* and one
276 studying *Fraxinus excelsior*. Fall events were earlier in colder, more northern latitudes
277 in both continents, which is consistent with previous literature (Aitken and Bemmels,
278 2016, Alberto et al., 2013). North American studies of both gymnosperm and an-
279 giosperm species reported strong clines, and most often focused on budset, while the
280 two European gardens reported data on ‘leaf senescence’ (Rosique-Esplugas et al., 2022),
281 measured as percentage of tree crown that had changed color (Table S1 in Supporting
282 Information). These different metrics could explain the different results. Research has
283 shown that budset is more closely related to growth cessation and thus considered a
284 more robust indicator of when plants stop investing in growth than leaf senescence; it
285 is also more genetically controlled (with different photoperiod thresholds required to
286 trigger budset in different provenances, Alberto et al., 2013).

287 Taken together, these results could explain some of the existing debate on the strength of
288 spring clinal variation, but also highlight how data biases make disentangling the drivers
289 of variation difficult. Angiosperm species showed a weak trend towards earlier budburst
290 in populations from warmer locations. In contrast, fall event clines in Europe were weak,
291 but their fall event type (leaf senescence) is less likely to show clinal variation. Given
292 European studies were biased towards studying angiosperms (3/4 species) that are often
293 canopy-species (e.g., *Fagus*, *Quercus*) these results together could explain a greater
294 focus on clinal variation in spring events across European studies (Basler and Körner,
295 2012, Gauzere et al., 2020, Sogaard et al., 2008, Deans and Harvey, 1996, Von Wuehlisch
296 et al., 1995). Most North American gardens and provenances included in this study were

297 limited to the Pacific Northwest region, and thus tended to focus on species from forests
298 where gymnosperms are almost always the canopy species (*Pseudotsuga*, *Tsuga*, *Picea*,
299 *Pinus*) and angiosperms are much smaller, more opportunistic species (*Alnus*, *Populus*).
300 This might suggest a far different pattern if gardens included more evenly sampled
301 North American tree species (Fig.1). Given the tremendous investment required for
302 such gardens, however, it is not surprising they are often limited to one species—
303 most often those relevant for forestry (e.g., *Pseudotsuga menziesii*, *Tsuga plicata*, *Tsuga*
304 *heterophylla*, *Picea sitchensis*, *Pinus albicaulis*). Our results, however, highlight the
305 limited inference we may gain from such an approach to understand trends across
306 species more broadly, a critical need for climate change forecasting.

307 **4.2 Adaptation in tree phenology: Implications for climate change
308 responses**

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

317 Predicting this will require better understanding how different species strategies covary
318 with early-season risks, and how such risks may shift with continued climate change.
319 For temperate zones, many species strategies appear designed to cope with frost, either
320 via avoidance or tolerance (Alberto et al., 2011, Lenz et al., 2016, Allevato et al., 2019),
321 as utilizing the early portion of the growing season can be especially critical for species
322 in colder regions (Morin et al., 2007, Dantec et al., 2015). Climate change at once shifts
323 spring phenology—thus potentially changing each species frost risk—but also appears

324 to reshape the drivers of frost climatically (Chamberlain et al., 2021). Layered onto
325 this are possible shifts in early-season herbivory with warming (Meineke et al., 2019),
326 and trade-offs in early-season risks with access to a long growing season for growth and
327 reproduction, with some species avoiding competition through being very early (Guo
328 et al., 2022). Common garden studies that track and report frost and herbivory damage,
329 alongside timing of flowering and fruiting, could help to understand the complex fitness
330 landscape of spring phenology.

331 In contrast to spring events which were weak and variable, fall events exhibited strong
332 clines, which appeared co-gradient with the environment (i.e. late-season events ad-
333 vanced earlier with northward latitudes). This supports previous results and the gen-
334 eral theory that fall events are consistently designed to avoid tissue loss at the end of
335 the season, when the cost of such losses could be particularly high (Aitken and Bem-
336 mels, 2016, Alberto et al., 2013). Spring events showed no clear trends, but increasing
337 research into counter-gradient variation for flowering events could be relevant when
338 spring vegetative and flowering events are linked (Buonaiuto et al., 2021).

339 Understanding environmental clines in phenology will ultimately be critical to predict-
340 ing how species shift their ranges as well. Implications of small differences in spring
341 phenology could mean different levels of gene flow, while co- and counter-gradient vari-
342 ation have important implications for gene glow over larger geographical regions (Bach-
343 mann et al., 2020), and thus could shape future range shifts. Much like frost risk,
344 climate change likely shifts multiple factors at once, as climate change shifts pollinators
345 and wind patterns (Kling and Ackerly, 2021). With the anticipated escalation of global
346 temperatures in the forthcoming century, these mechanisms are poised to play a pivotal
347 role in shaping the dynamics of plant communities and the overall carbon balance of
348 ecosystems.

³⁴⁹ **5 Acknowledgement**

³⁵⁰ We thank S. Aitken, I. Chuine, R. Guy, C Körner and Y. Vitasse for reviewing our list
³⁵¹ of papers for possible additional common garden studies.

³⁵² **6 Competing interests**

³⁵³ We state that we do not possess any recognized conflicting financial interests or personal
³⁵⁴ connections that might have seemed to impact the findings presented in this paper.

³⁵⁵ **7 Author contributions**

³⁵⁶ ZAZ collected and cleaned data, performed computations, and analyzed data in an
³⁵⁷ iterative process. EMW conceived of the presented idea, designed the computational
³⁵⁸ framework, and verified the analytical methods. Both authors discussed results and
³⁵⁹ contributed to the final manuscript.

³⁶⁰ **8 Data availability**

³⁶¹ The data that support the findings of this study are openly available in the Knowledge
³⁶² Network for Biocomplexity (KNB) repository at <https://knb.ecoinformatics.org>
³⁶³ /view/urn%3Auuid%3Aa37258b9-23e7-4b0c-a20f-9185cbc27194.

³⁶⁴ **9 References**

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581 **10 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.S1 in Supporting Information for sourcing information on selected studies. Note: map lines do not necessarily depict accepted national boundaries. [European sites are made bold and denoted by an asterisk \(*\)](#).

582 **11 Supporting Information (brief legends)**

- 583 1. Additional methods on exact procedures we followed for meta-analysis and reasons
 584 for the exclusion of a small number of studies. 2. Table S1: showing all publications
 585 included in meta-analysis. 3. Tables S2-5: showing model estimates. 4. Figures S1-3:
 586 supporting figures.

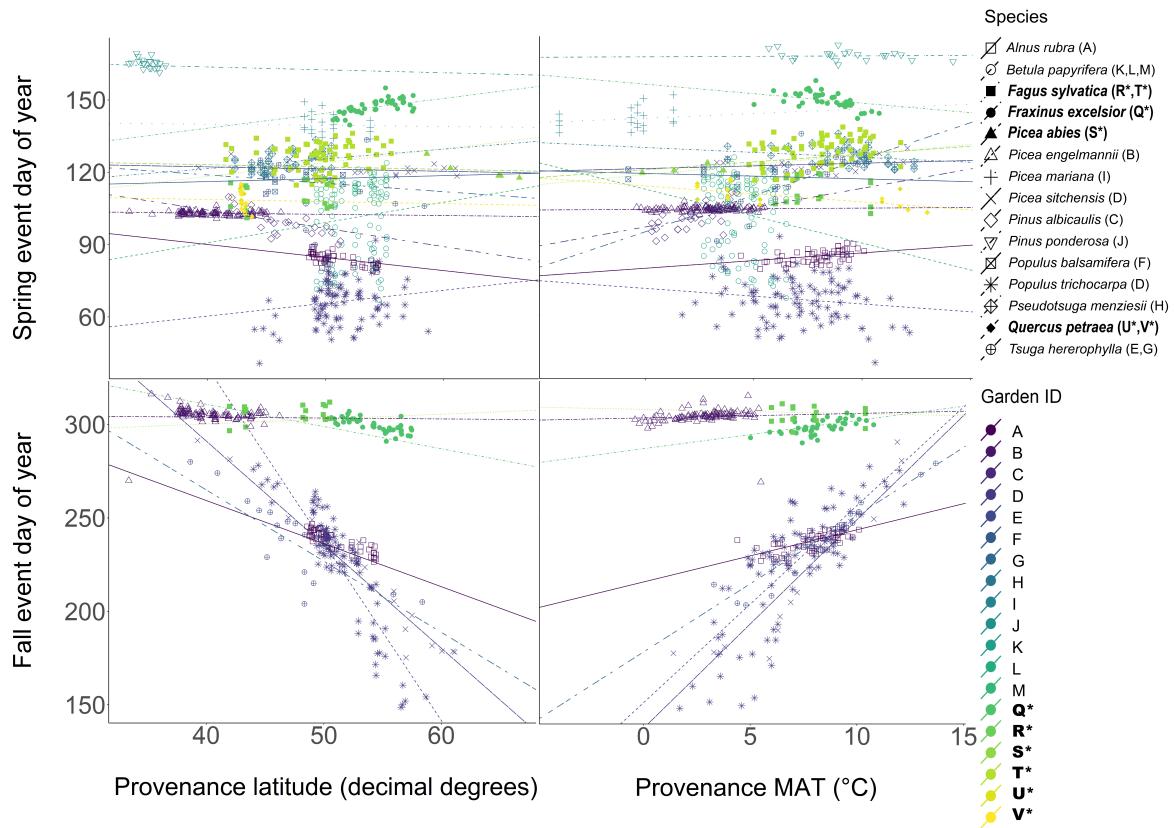


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are ~~bolded~~made bold and denoted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

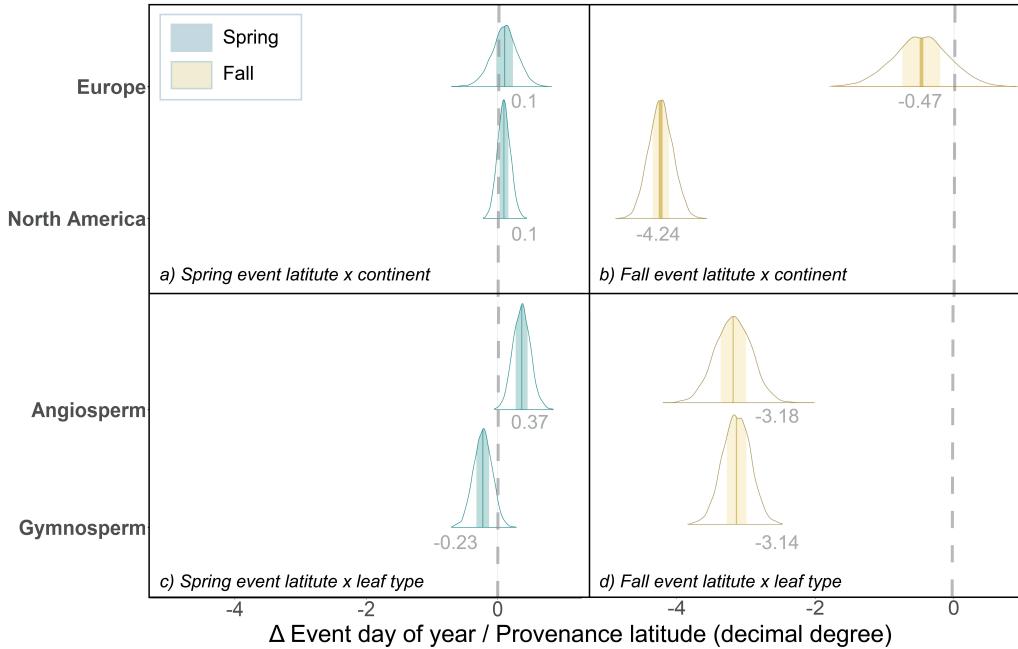


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given 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 ([all evergreen species](#)) and delayed in angiosperms ([all deciduous species](#)) per degree northward. Fall events advanced per degree northward for both species types.

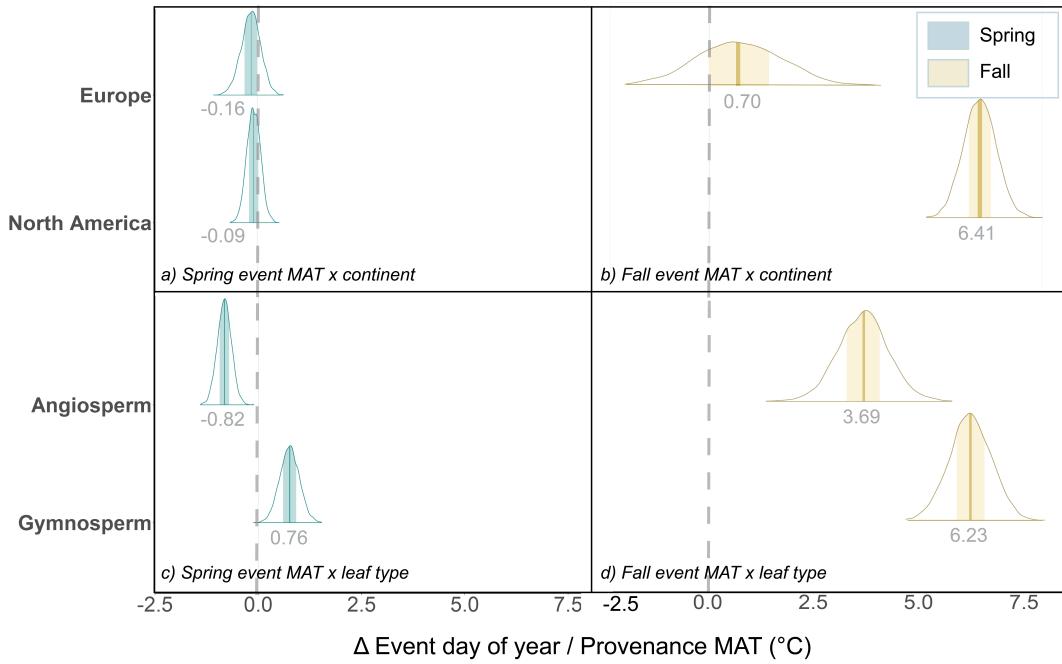


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in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