

Version dated: February 20, 2024

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

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Running head: Clines in spring phenology

Word count: Summary - 198, Introduction - 1077, Materials and Methods - 821, Results - 1012, Discussion - 1400

Number of figures: 4 (Among these, Figure 1 and 2 should be published in color)

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 vs. through adaptation to local conditions. Yet, we often lack this information
⁵ entirely or find conflicting evidence across studies, which is the case for spring
⁶ phenology.
- ⁷ ● We synthesize common garden studies across Europe and North America that
⁸ reported spring event dates for a mix of angiosperm and gymnosperm tree species
⁹ in the northern hemisphere, capturing data from 384 North American and 101
¹⁰ European provenances (i.e. populations) with observations from 1962 to 2019,
¹¹ alongside fall event data when provided.
- ¹² ● Across continents, we find no evidence of provenance effects in spring phenology,
¹³ but strong clines with latitude and mean annual temperature (MAT) in fall. These
¹⁴ effects, however, appear to diverge by continent and species type (gymnosperm
¹⁵ vs. angiosperm), with particularly pronounced clines in North America in fall
¹⁶ events.
- ¹⁷ ● Our results suggest flexible, likely plastic responses, in spring phenology with
¹⁸ warming, and potential limits—at least in the short term—due to provenance
¹⁹ effects for fall phenology. They also highlight that, after over 250 years of common
²⁰ garden studies on tree phenology, we still lack a holistic predictive model of clines
²¹ across species and phenological events.

²² *Keywords:* budburst, budset, climate change, common gardens, deciduous and evergreen
²³ trees, leafout, senescence, spring phenology

²⁴

25 1 Introduction

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

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

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

50 Tree phenology is important to climate change forecasting at both the community and
51 ecosystem levels. The timing of budburst and senescence can impact plant competition,

52 plant invasions, and community assembly (Fridley, 2012). Shifts in phenology can
53 affect tree growth (Myneni et al., 1997), scaling up to impact ecosystem-level carbon
54 sequestration (Barichivich et al., 2012), and thus forecasts of climate change. Growing
55 evidence, however, suggests links between growth and phenology are not as consistent
56 as previously predicted—or currently modelled (Dow et al., 2022)—with recent work
57 suggesting how much spring versus fall events shift may determine impacts on tree
58 growth (Zohner et al., 2023).

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

75 These contrasting studies highlight how inconsistent evidence for adaptation in tree
76 spring phenology has been. Studies have documented provenance differences of 2-4 days
77 per degree latitude in spring phenology for some species (*Picea abies* in Sogaard et al.,
78 2008 and *Quercus petraea* in Deans and Harvey, 1996) while others have failed to find
79 similar trends along latitudinal gradients (for example, *Picea sitchensis* in Mimura and

80 Aitken, 2007, *Picea glauca* in Li et al., 1997, and *Populus balsamifera* in Farmer, 1993).
81 This has led to debate over the prevalence and importance of adaptation in spring
82 tree phenology. Though clines of spring phenology have been found in both Europe
83 (Sogaard et al., 2008, Deans and Harvey, 1996, Von Wuehlisch et al., 1995) and North
84 America (Rossi, 2015, Soolanayakanahally et al., 2013, Hannerz et al., 1999), there is
85 continuing debate, especially in Europe (Deans and Harvey, 1996, Vitasse et al., 2009,
86 Basler and Körner, 2012), raising the possibility that they could vary by continent.

87 Continental differences in patterns of adaptation versus plasticity could be driven by
88 climatic differences, especially as North American springs are more variable across years
89 than European ones (Twardosz et al., 2021, Zohner et al., 2017, Schwartz and Reiter,
90 2000). Such high temporal variability means that distant sites can effectively experi-
91 ence the same spring climate, but in different years. Studies of spring phenology in
92 arboreta suggest cues for budburst may vary depending on continental climate (Zohner
93 et al., 2017), but are poorly controlled compared to traditional common garden studies,
94 making them difficult to use for inference of plasticity versus adaptation (Gauzere et al.,
95 2020). Even for more carefully designed common gardens, differences in species studied
96 or other differences in design may complicate understanding what underlies potential
97 trends across continents.

98 To test for evidence of adaptation in spring phenology and what factors may under-
99 lies differences observed across studies, we comprehensively examined clines for spring
100 events, including fall events when possible. We tested for evidence of adaptation via
101 provenance trends with latitude and climate and examined possible factors that un-
102 derlie these clines, including for differences between: (1) spring and fall phenology, (2)
103 studies in Europe and North America, (3) angiosperm and gymnosperm species, which
104 represent a deep evolutionary split in the plant tree of life. To address these questions,
105 we combined Bayesian hierarchical models with a new meta-analysis of all common gar-
106 den experiments in temperate tree species across Europe and North America reporting
107 spring phenology.

₁₀₈ **2 Materials and Methods**

₁₀₉ **2.1 Data collection**

₁₁₀ To locate common garden studies that reported the timing of spring events of woody
₁₁₁ plant species we searched and reviewed the peer-reviewed literature. On 14 Decem-
₁₁₂ ber 2022 we searched Web of Science (Thompson Reuters, New York, NY) using the
₁₁₃ following terms:

₁₁₄ TOPIC = (common garden* OR provenance*) AND (leafout* OR leaf out*
₁₁₅ OR budburst OR spring phenolog*)

₁₁₆ which returned 122 publications. We also contacted authors of previous review papers
₁₁₇ (Aitken and Bemmels, 2016, Alberto et al., 2013), to help further search the literature.
₁₁₈ We then reviewed the methods and results of all publications to refine to only studies
₁₁₉ that met the following criteria: (a) focused on woody plants originating from either
₁₂₀ Europe or North America (also the locations of most studies), (b) had provenance
₁₂₁ trials/common gardens on the same continent, (c) reported latitude and longitude of
₁₂₂ provenances and gardens, and (d) reported spring events in units of calendar days (day
₁₂₃ of year or DOY) or could be converted into DOY (see Additional Methods in Supporting
₁₂₄ Information).

₁₂₅ Based on these criteria we found 19 common gardens distributed throughout North
₁₂₆ America and Europe, with the majority of data concentrated in western North America
₁₂₇ (Fig.1 & Table.S1 in Supporting Information). From each common garden study we
₁₂₈ extracted phenological data on spring events (budburst and leaf flush) in DOY and,
₁₂₉ when present in the same paper, fall events (bud set, leaf senescence, growth cessation,
₁₃₀ and leaf abscission) by species and the geographic information of provenances and
₁₃₁ gardens. We used ImageJ (version 1.53k; Schneider et al., 2012) to extract values from
₁₃₂ figures whenever necessary. For studies that reported event dates relative to a reference
₁₃₃ date other than 1 January (e.g. Rehfeldt, 1994a), we converted such dates to DOY

¹³⁴ using the ‘lubridate’ package in R (Grolemund and Wickham, 2011).

¹³⁵ To understand how climatic differences, in addition to geographical differences, shape
¹³⁶ local adaptation in spring events we extracted several types of climate data using infor-
¹³⁷ mation about provenance latitude, longitude, and elevation from original publications.
¹³⁸ We estimated each provenance’s mean annual temperature (MAT) from 1960 to 1991
¹³⁹ using the monthly temperature data in the Climate Information Tool by Food and
¹⁴⁰ Agriculture Organization of the United Nations (FAO, 2022). We verified our esti-
¹⁴¹ mated MAT was similar to MAT calculated using ClimateWNA (Wang et al., 2016), a
¹⁴² source used in previous analyses.

¹⁴³ To examine climate near spring events more explicitly than MAT allows, we used grid-
¹⁴⁴ ded daily temperature data for March-May from 2011 to 2020 for all provenances and
¹⁴⁵ gardens. We extracted data from E-OBS for European locations and used the ‘daymetr’
¹⁴⁶ in R for North American locations (Cornes et al., 2018, Hufkens et al., 2018). Then,
¹⁴⁷ using these data and the ‘overlap’ package in R, we estimated how much the daily
¹⁴⁸ temperatures overlapped between each provenance location and their corresponding
¹⁴⁹ gardens across the three months from 2011 to 2020, which we call ‘climate overlap.’
¹⁵⁰ Dataset containing event dates, geographic information, and climatic information of all
¹⁵¹ provenances are archived in Knowledge Network for Biocomplexity (KNB) (Zeng and
¹⁵² Wolkovich, 2023).

¹⁵³ 2.2 Analyses

¹⁵⁴ To estimate clines in spring and fall phenological events across species we used Bayesian
¹⁵⁵ hierarchical models. We regressed DOY of events against geographical and climatic
¹⁵⁶ predictors with partial pooling (sometimes called ‘random effects’) on the intercept and
¹⁵⁷ slope for each species within each garden. Because most tree species were present in only
¹⁵⁸ one common garden in our dataset, it was impossible to fit garden and species separately,
¹⁵⁹ thus we treat each species within a garden as a unique group. Using posterior estimates
¹⁶⁰ for each species within a garden, we estimated effects of continent (North America

161 vs. Europe) and species type (angiosperm vs. gymnosperm). All models were fit in
162 ‘rstanarm’ package (version 2.21.3; Goodrich et al., 2022) using default priors, with 4
163 chains and 1000 sampling iterations per chain for a total of 4000 samples. We checked for
164 model fit by confirming no divergent transitions (which required setting `adapt_delta`
165 to 0.99 for some models), \hat{R} values close to 1, and sufficient effective sample sizes. We
166 present estimates as mean \pm 90% uncertainty intervals given parenthetically, unless
167 otherwise stated.

168 3 Results

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

175 Overall, spring events such as budburst and leaf flush, were not related to provenance
176 latitude or MAT, neither across continents (latitude: 0.10 days/degree [-0.05 - 0.25];
177 MAT: -0.11 days/ $^{\circ}\text{C}$ [-0.34 - 0.12]) (Fig.2, Table.S2 & S3 in Supporting Information),
178 nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09 days/ $^{\circ}\text{C}$
179 [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT: -0.16 days/ $^{\circ}\text{C}$
180 [-0.55 - 0.23]) (Fig.3A & 4A). Results were similar using other distance metrics in lieu
181 of latitude (see Fig.S1 for results using the difference between provenance and garden
182 latitude, and the spherical distance between provenance and garden).

183 In contrast, fall events (e.g., budset, leaf senescence, leaf abscission) were earlier at
184 more northern, cooler MAT sites (that is, they advanced strongly with provenance
185 latitude: 3.16 days/degree [2.87-3.45], and with decreasing MAT: 4.78 days/ $^{\circ}\text{C}$ [4.1 -
186 5.4], Fig.2, Table.S4 & S5 in Supporting Information). This relationship, however, was

187 observed mostly in North America where fall events advanced 4.24 (3.95 - 4.53) days per
188 degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT ($^{\circ}\text{C}$), whereas in
189 Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree
190 northward, or 0.70 days (1.04 - 2.42) per degree decline in MAT ($^{\circ}\text{C}$) (Fig.4A).

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

200 Effects of provenance latitude on fall events were similar across angiosperms and gym-
201 nosperms (Fig.3B). Spring events weakly diverged, delaying at a rate of 0.37 (0.15 -
202 0.59) days per degree north in angiosperms and advancing 0.23 (0.00 - 0.46) days per
203 degree north in gymnosperms. Fall events advanced 3.18 (2.76 - 3.62) days per degree
204 north in angiosperms and 3.14 (2.81-3.47) days per degree north in gymnosperms. Ef-
205 fects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced
206 0.82 (0.54 - 1.11) days/ $^{\circ}\text{C}$ as MAT increased in angiosperms and delayed 0.76 (0.37 -
207 1.14) days/ $^{\circ}\text{C}$ as MAT increased in gymnosperms. Fall events delayed in warmer lo-
208 cations for both species types, but slightly more so for gymnosperms (6.23 days) than
209 angiosperms (3.69 days) (Fig.4B).

210 While we expected that coarse metrics, such as latitude and MAT, would generally
211 represent how similar the climates are between the provenances and gardens, we also
212 estimated climate overlap in months much closer to the events to further test how
213 much climate similarity between provenances and gardens predicts provenance effects
214 (i.e. differential responses observed among plant populations from different geographi-

215 cal origins). For spring events, we considered overlap across March to May. However,
216 results were not qualitatively different than using MAT (See Fig.S2 in Supporting In-
217 formation). We observed very weak effects of climate overlap on spring events (0.01
218 [0.02 - 0.03] days per one percent increase in climate overlap), nearly identical across
219 angiosperms (0.02 [0.00 - 0.05]) and gymnosperms (0.04 [0.00 - 0.09]). Fall events
220 advanced as climate overlap declined, but slightly more strongly for gymnosperms (ad-
221 vancing 0.72 [0.51 - 0.92] days per one percent decline in climate overlap) (Fig.S3 in
222 Supporting Information).

223 4 Discussion

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

233 Trends between spring phenology and latitude or MAT were weak, but suggested the
234 possibility of diverging results that could mute an overall trend—albeit a much weaker
235 one than for fall phenology. We found angiosperm (all deciduous) versus gymnosperm
236 (all evergreen) species diverged in their clines with MAT. Combined with our finding
237 of much stronger clines for fall phenology in North America, these results support the
238 idea of potential variation across continents and/or species type that may underlie
239 the debate in whether spring events show important clinal variation. As clines with
240 spring events were very weak, however, and gardens almost always focus on only one

²⁴¹ species, understanding these diverging results well enough to aid forecasting would take
²⁴² significant additional investment in common garden studies.

²⁴³ We found the coarse metrics of provenance latitude and MAT were generally good pre-
²⁴⁴ dictors of phenology, performing better than our more complex, data-rich, and season-
²⁴⁵ specific metric of climate overlap. Latitude and MAT appeared to well represent how
²⁴⁶ similar the climates are between the provenances and gardens in the temperate and bo-
²⁴⁷ real forest species we studied, yielding similar results to metrics calculated specifically
²⁴⁸ in the spring with daily climate data.

²⁴⁹ 4.1 Variation across continents and species types

²⁵⁰ Our results highlight that spring events show much weaker clines than fall events in
²⁵¹ tree species, but suggest important variation between species types in spring events.
²⁵² Angiosperms tended to budburst earlier in provenances that were warmer and more
²⁵³ southerly, while gymnosperms trended in the opposite direction. Such differences could
²⁵⁴ be driven by the varying investment strategies, given that all our studied gymnosperms
²⁵⁵ were evergreen and all angiosperms were deciduous. As evergreen species photosynthe-
²⁵⁶ size without leafout they generally leafout much later than deciduous species, after most
²⁵⁷ risk of spring frost (Panchen et al., 2014), and thus may avoid frost risk. In contrast, de-
²⁵⁸ ciduous species may tend towards earlier leafout in warmer climates to compete best for
²⁵⁹ access to light and other resources (Chamberlain et al., 2019). Testing these hypothe-
²⁶⁰ ses would require more information on frost risk and forest community assembly from
²⁶¹ across the provenance locations, but seems an important step towards understanding
²⁶² the drivers of this variation. Without a clear mechanism, extrapolating these results
²⁶³ to other species or across Europe and North America may be difficult, especially given
²⁶⁴ biases in the data, and the distinct climatic, geographical, and ecological contexts of
²⁶⁵ Europe and North America.

²⁶⁶ In our dataset, more data on fall events were reported in North America. In Europe,
²⁶⁷ only two gardens reported fall event metrics, one studying *Fagus sylvatica* and one

268 studying *Fraxinus excelsior*. Fall events were earlier in colder, more northern latitudes
269 in both continents, which is consistent with previous literature (Aitken and Bemmels,
270 2016, Alberto et al., 2013). North American studies of both gymnosperm and an-
271 giosperm species reported strong clines, and most often focused on budset, while the
272 two European gardens reported data on ‘leaf senescence’ (Rosique-Esplugas et al., 2022),
273 measured as percentage of tree crown that had changed color (Table.S1 in Supporting
274 Information). These different metrics could explain the different results. Research has
275 shown that budset is more closely related to growth cessation and thus considered a
276 more robust indicator of when plants stop investing in growth than leaf senescence; it
277 is also more genetically controlled (with different photoperiod thresholds required to
278 trigger budset in different provenances, Alberto et al., 2013).

279 Taken together, these results could explain some of the existing debate on the strength of
280 spring clinal variation, but also highlight how data biases make disentangling the drivers
281 of variation difficult. Angiosperm species showed a weak trend towards earlier budburst
282 in populations from warmer locations. In contrast, fall event clines in Europe were weak,
283 but their fall event type (leaf senescence) is less likely to show clinal variation. Given
284 European studies were biased towards studying angiosperms (3/4 species) that are often
285 canopy-species (e.g., *Fagus*, *Quercus*) these results together could explain a greater
286 focus on clinal variation in spring events across European studies (Basler and Körner,
287 2012, Gauzere et al., 2020, Sogaard et al., 2008, Deans and Harvey, 1996, Von Wuehlisch
288 et al., 1995). Most North American gardens and provenances included in this study were
289 limited to the Pacific Northwest region, and thus tended to focus on species from forests
290 where gymnosperms are almost always the canopy species (*Pseudotsuga*, *Tsuga*, *Picea*,
291 *Pinus*) and angiosperms are much smaller, more opportunistic species (*Alnus*, *Populus*).
292 This might suggest a far different pattern if gardens included more evenly sampled
293 North American tree species (Fig.1). Given the tremendous investment required for
294 such gardens, however, it is not surprising they are often limited to one species—
295 most often those relevant for forestry (e.g., *Pseudotsuga menziesii*, *Tsuga plicata*, *Tsuga*

296 *heterophylla*, *Picea sitchensis*, *Pinus albicaulis*). Our results, however, highlight the
297 limited inference we may gain from such an approach to understand trends across
298 species more broadly, a critical need for climate change forecasting.

299 **4.2 Adaptation in tree phenology: Implications for climate change
300 responses**

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

309 Predicting this will require better understanding how different species strategies covary
310 with early-season risks, and how such risks may shift with continued climate change.
311 For temperate zones, many species strategies appear designed to cope with frost, either
312 via avoidance or tolerance (Alberto et al., 2011, Lenz et al., 2016, Allevato et al., 2019),
313 as utilizing the early portion of the growing season can be especially critical for species
314 in colder regions (Morin et al., 2007, Dantec et al., 2015). Climate change at once shifts
315 spring phenology—thus potentially changing each species frost risk—but also appears
316 to reshape the drivers of frost climatically (Chamberlain et al., 2021). Layered onto
317 this are possible shifts in early-season herbivory with warming (Meineke et al., 2019),
318 and trade-offs in early-season risks with access to a long growing season for growth and
319 reproduction, with some species avoiding competition through being very early (Guo
320 et al., 2022). Common garden studies that track and report frost and herbivory damage,
321 alongside timing of flowering and fruiting, could help to understand the complex fitness
322 landscape of spring phenology.

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

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

341 5 Acknowledgement

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

344 6 Competing interests

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

347 7 Author contributions

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

352 8 Data availability

353 The data that support the findings of this study are openly available in the Knowledge
354 Network for Biocomplexity (KNB) repository at [https://knb.ecoinformatics.org](https://knb.ecoinformatics.org/view/urn%3Auuid%3Aa37258b9-23e7-4b0c-a20f-9185cbc27194)
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⁵⁷³ **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 shown in bold and denoted by an asterisk (*).

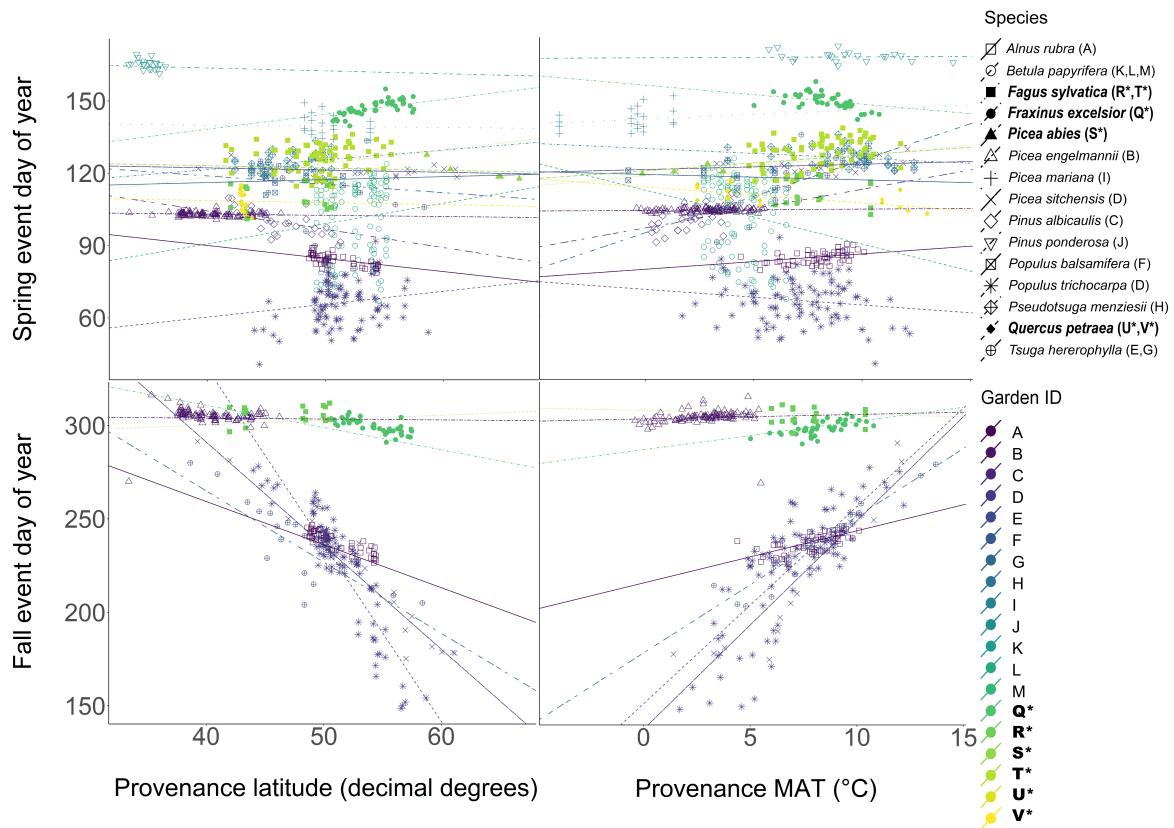


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are shown in bold and denoted by an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

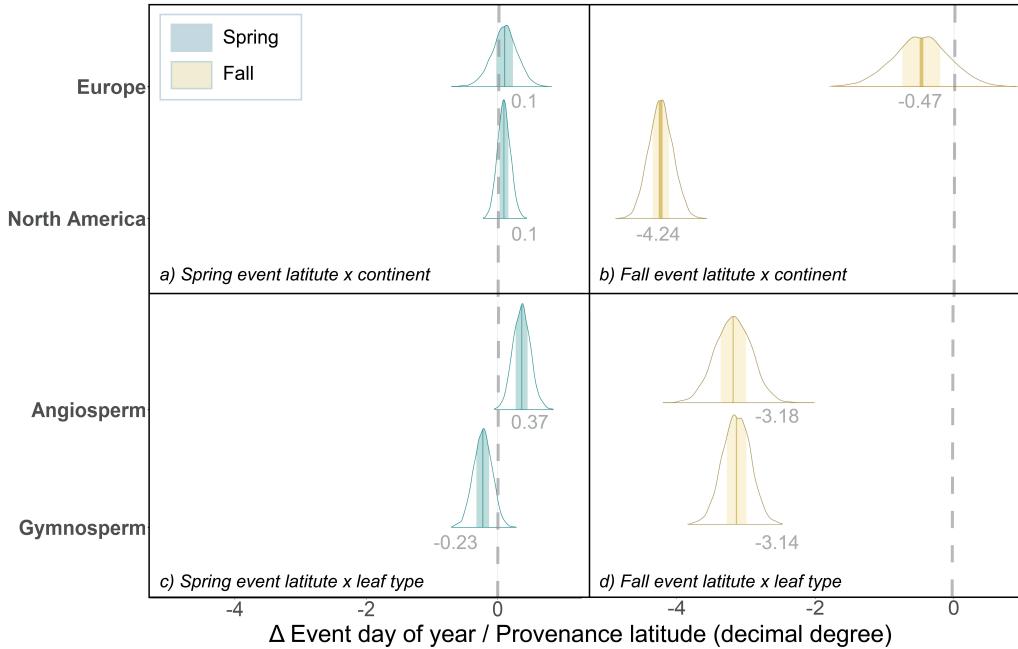


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given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

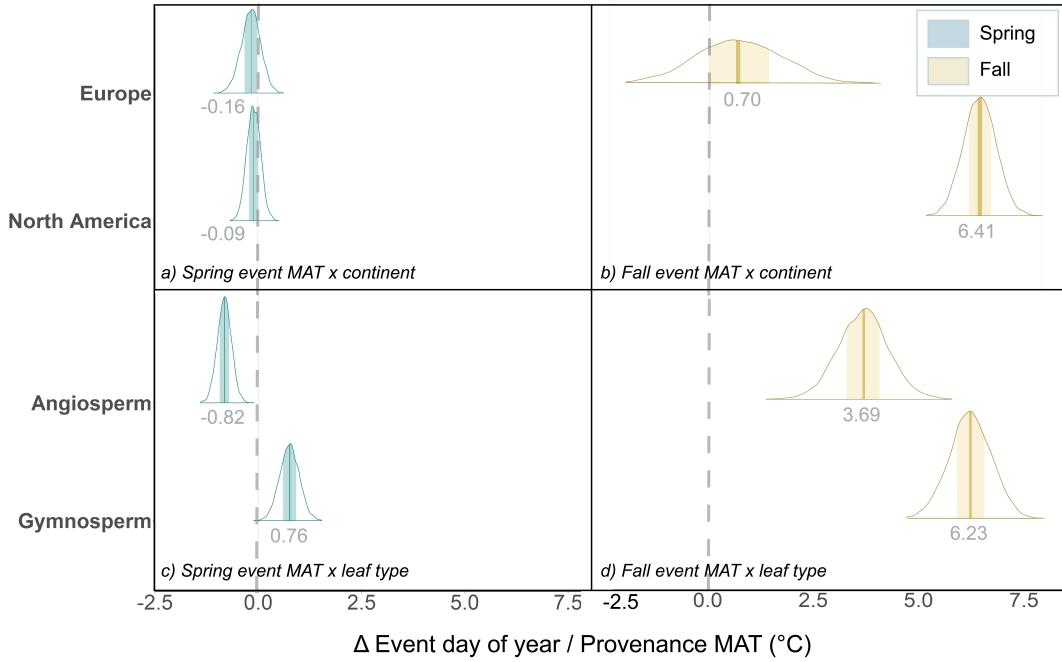


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in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