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

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

²¹ *Keywords:* budburst, budset, climate change, common gardens, deciduous and evergreen
²² trees, leafout, senescence, spring phenology

²³

24 1 Introduction

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

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

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

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

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

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

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

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

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

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

₁₀₇ **2 Materials and Methods**

₁₀₈ **2.1 Data collection**

₁₀₉ To locate common garden studies that reported the timing of spring events of woody
₁₁₀ plant species we searched and reviewed the peer-reviewed literature. On 14 Decem-
₁₁₁ ber 2022 we searched Web of Science (Thompson Reuters, New York, NY) using the
₁₁₂ following terms:

₁₁₃ TOPIC = (common garden* OR provenance*) AND (leafout* OR leaf out*
₁₁₄ OR budburst OR spring phenolog*)

₁₁₅ which returned 122 publications. We also contacted authors of previous review papers
₁₁₆ (Aitken and Bemmels, 2016, Alberto et al., 2013), to help further search the literature.
₁₁₇ We then reviewed the methods and results of all publications to refine to only studies
₁₁₈ that met the following criteria: (a) focused on woody plants originating from either
₁₁₉ Europe or North America (also the locations of most studies), (b) had provenance
₁₂₀ trials/common gardens on the same continent, (c) reported latitude and longitude of
₁₂₁ provenances and gardens, and (d) reported spring events in units of calendar days (day
₁₂₂ of year or DOY) or could be converted into DOY (see Additional Methods in Supporting
₁₂₃ Information).

₁₂₄ Based on these criteria we found 19 common gardens distributed throughout North
₁₂₅ America and Europe, with the majority of data concentrated in western North America
₁₂₆ (Fig.1 & Table.S1 in Supporting Information). From each common garden study we
₁₂₇ extracted phenological data on spring events (budburst and leaf flush) in DOY and,
₁₂₈ when present in the same paper, fall events (bud set, leaf senescence, growth cessation,
₁₂₉ and leaf abscission) by species and the geographic information of provenances and
₁₃₀ gardens. We used ImageJ (version 1.53k; Schneider et al., 2012) to extract values from
₁₃₁ figures whenever necessary. For studies that reported event dates relative to a reference
₁₃₂ date other than 1 January (e.g. Rehfeldt, 1994a), we converted such dates to DOY

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

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

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

152 2.2 Analyses

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

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

167 3 Results

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

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

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

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

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

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

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

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

222 4 Discussion

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

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

²⁴⁰ species, understanding these diverging results well enough to aid forecasting would take
²⁴¹ significant additional investment in common garden studies.

²⁴² We found the coarse metrics of provenance latitude and MAT were generally good
²⁴³ predictors of phenology, performing better than our more complex and data-rich metric
²⁴⁴ of climate overlap. Latitude and MAT appeared to well represent how similar the
²⁴⁵ climates are between the provenances and gardens in the temperate and boreal forest
²⁴⁶ species we studied, yielding similar results to metrics calculated specifically in the spring
²⁴⁷ with daily climate data.

²⁴⁸ 4.1 Variation across continents and species types

²⁴⁹ Our results highlight that spring events show much weaker clines than fall events in
²⁵⁰ tree species, but suggest important variation between species types in spring events.
²⁵¹ Angiosperms tended to budburst earlier in provenances that were warmer and more
²⁵² southerly, while gymnosperms trended in the opposite direction. Such differences could
²⁵³ be driven by the varying investment strategies, given that all our studied gymnosperms
²⁵⁴ were evergreen and all angiosperms were deciduous. As evergreen species photosynthe-
²⁵⁵ size without leafout they generally leafout much later than deciduous species, after most
²⁵⁶ risk of spring frost (Panchen et al., 2014), and thus may avoid frost risk. In contrast, de-
²⁵⁷ ciduous species may tend towards earlier leafout in warmer climates to compete best for
²⁵⁸ access to light and other resources (Chamberlain et al., 2019). Testing these hypothe-
²⁵⁹ ses would require more information on frost risk and forest community assembly from
²⁶⁰ across the provenance locations, but seems an important step towards understanding
²⁶¹ the drivers of this variation. Without a clear mechanism, extrapolating these results
²⁶² to other species or across Europe and North America may be difficult, especially given
²⁶³ biases in the data, and the distinct climatic, geographical, and ecological contexts of
²⁶⁴ Europe and North America. The direct applicability of our findings to other contexts
²⁶⁵ must be approached with caution.

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-Espluga 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*, *Tsuja 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

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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>
³⁵⁵ /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 made bold and denoted by an asterisk (*).

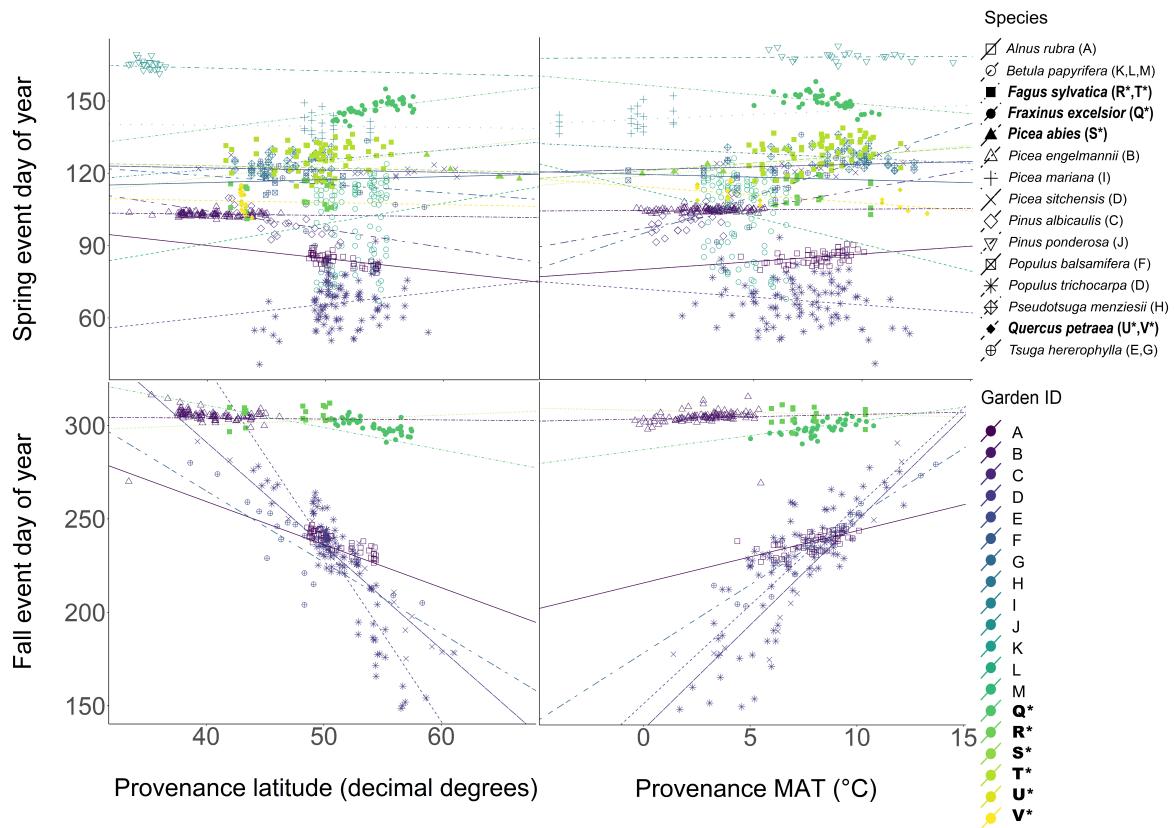


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are made bold and denoted by an asterisk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

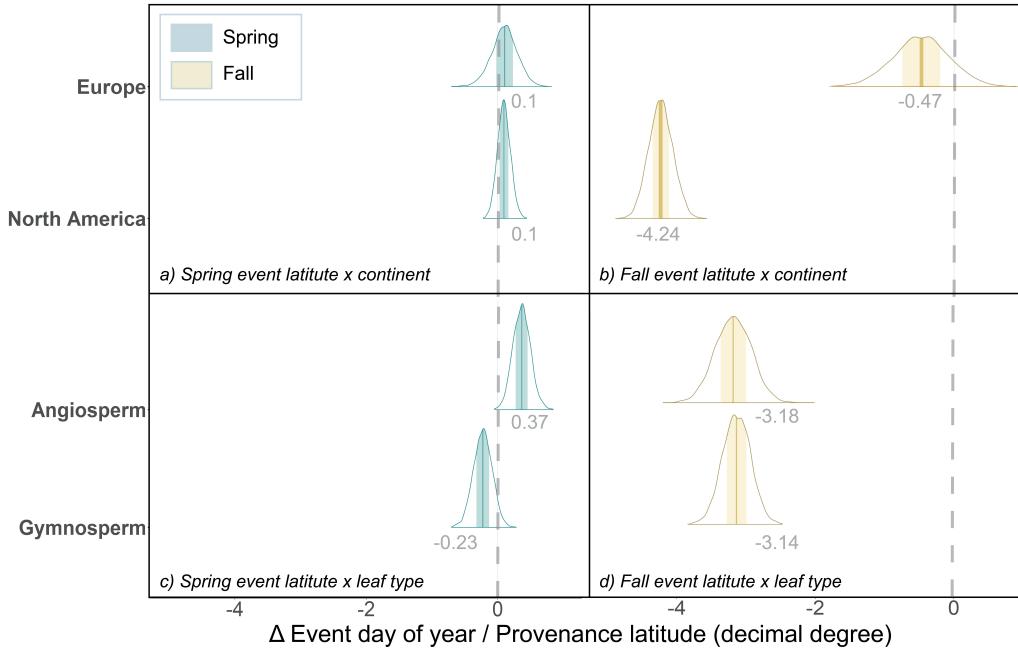


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given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

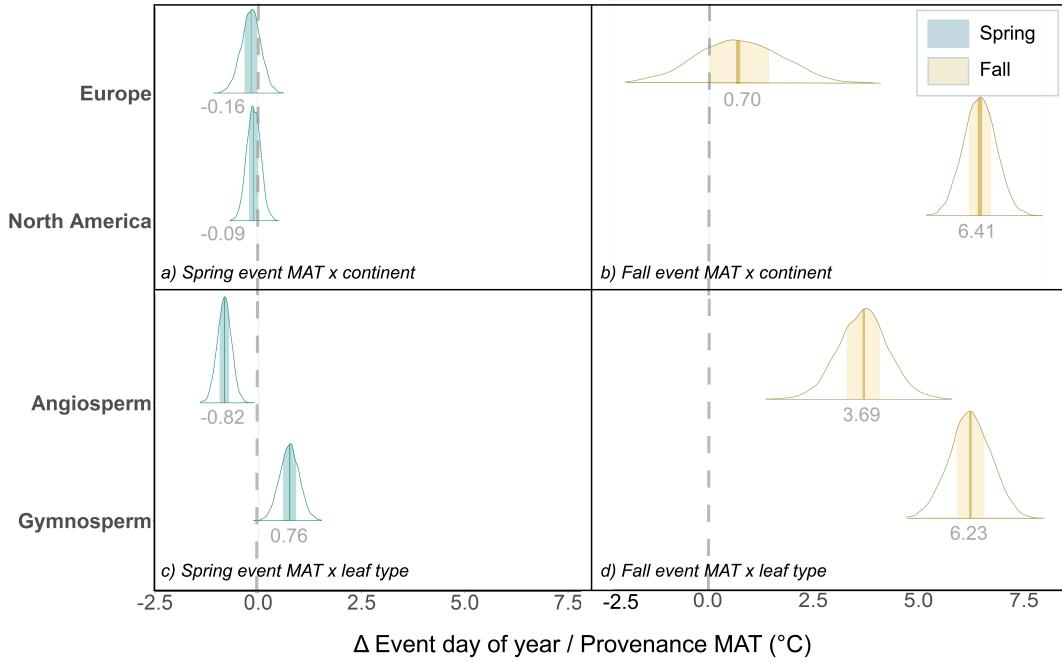


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in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