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

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## 1 Summary

### 2 Abstract

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

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

25

## 26 1 Introduction

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

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

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

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

55 Studies of adaptation versus plasticity in tree phenology have been conducted for centuries (Cle-  
56 land et al., 2007), through common garden studies. In these studies—conducted often for forestry  
57 purposes—researchers grow trees of different geographical origins under the same environmental condi-  
58 tions to disentangle the effects of environmental and genetic variation on treesâŽ phenotypes (Aitken  
59 and Bemmels, 2016, Alberto et al., 2013). Such work has established common clines in fall phenol-  
60 ogy, as source locations with shorter growing seasons (poleward and higher elevations) exhibit earlier  
61 stopping of growth (such as budset). Research has connected these clines to an underlying proximate  
62 mechanism of changing photoperiod cues (i.e., shifts in the photoperiod threshold required to trigger  
63 budset), driven by adaptation to the local growing season (Alberto et al., 2013, Savolainen et al., 2007).  
64 In contrast, spring phenology appears more plastic (Aitken and Bemmels, 2016) and determined more  
65 strongly by temperature (Flynn and Wolkovich, 2018). Many studies, however, have argued that spring  
66 phenology shows levels of adaptation that may be critical to forecasting and mitigation (Vitasse et al.,

67 2009, Basler and Körner, 2012).

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

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

88 To test for evidence of adaptation in spring phenology and what factors may underlie differences  
89 observed across studies, we comprehensively examined clines for spring events, including fall events  
90 when possible. We tested for evidence of adaptation via provenance trends with latitude and climate  
91 and examined possible factors that underlie these clines, including for differences between: (1) spring  
92 and fall phenology, (2) studies in Europe and North America, (3) angiosperm and gymnosperm species.  
93 To address these questions, we combined Bayesian hierarchical models with a new meta-analysis of all  
94 common garden experiments in temperate tree species across Europe and North America reporting  
95 spring phenology.

## 96 2 Materials and Methods

### 97 2.1 Data collection

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

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

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

110 Based on these criteria we found 19 common gardens distributed throughout North America and  
111 Europe, with the majority of data concentrated in North America (Fig.1 & Table.S1 in Supporting  
112 Information). From each common garden study we extracted phenological data on spring events (bud-  
113 burst and leaf flush) in DOY and, when present in the same paper, fall events (bud set, leaf senescence,  
114 growth cessation, and leaf abscission) by species and the geographic information of provenances and  
115 gardens. We used ImageJ (version 1.53k; Schneider et al., 2012) to extract values from figures whenever  
116 necessary. For studies that reported event dates relative to a reference date other than 1 January (e.g.  
117 Rehfeldt, 1994a), we converted such dates to DOY using the ‘lubridate’ package in R (Grolemund and  
118 Wickham, 2011).

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

126 To examine climate near spring events more explicitly than MAT allows, we used gridded daily temper-

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

## 2.2 Analyses

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

## 3 Results

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

Overall, spring events were not related to provenance latitude or MAT, neither across continents (latitude: 0.10 days/degree [-0.05 - 0.25]; MAT: -0.11 days/ $^{\circ}\text{C}$  [-0.34 - 0.12]) (Fig.2, Table.S2 & S3 in Supporting Information), nor within North America (latitude: 0.10 days/degree [-0.06 - 0.26]; MAT: -0.09 days/ $^{\circ}\text{C}$  [-0.36 - 0.18]) or Europe (latitude: 0.10 days/degree [-0.23 - 0.42]; MAT: -0.16 days/ $^{\circ}\text{C}$  [-0.55 - 0.23]) (Fig.3A & 4A). Results were similar using other distance metrics in lieu of latitude

158 (see Fig.S1 for results using the difference between provenance and garden latitude, and the spherical  
159 distance between provenance and garden).

160 In contrast, fall events (e.g., budset, leaf senescence, leaf abscission) were earlier at more northern,  
161 cooler MAT sites (that is, they advanced strongly with provenance latitude: 3.16 days/degree [2.87-  
162 3.45], and with decreasing MAT: 4.78 days/°C [4.1 - 5.4], Fig.2, Table.S4 & S5 in Supporting Informa-  
163 tion). This relationship, however, was observed mostly in North America where fall events advanced  
164 4.24 (3.95 - 4.53) days per degree northward, or 6.41 days (5.78 - 7.04) per degree decline in MAT  
165 (°C), whereas in Europe these relationships were weaker: advance of 0.47 (0.21 - 1.17) days per degree  
166 northward, or 0.70 days (1.04 - 2.42) per degree decline in MAT (°C) (Fig.4A).

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

175 Effects of provenance latitude on fall events were similar across angiosperms and gymnosperms (Fig.3B).  
176 Spring events weakly diverged, delaying at a rate of 0.37 (0.15 - 0.59) days per degree north in an-  
177 giosperms and advancing 0.23 (0.00 - 0.46) days per degree north in gymnosperms. Fall events advanced  
178 3.18 (2.76 - 3.62) days per degree north in angiosperms and 3.14 (2.81-3.47) days per degree north in  
179 gymnosperms. Effects of MAT on spring events also weakly diverged (Fig.4B). Spring events advanced  
180 0.82 (0.54 - 1.11) days/°C as MAT increased in angiosperms and delayed 0.76 (0.37 - 1.14) days/°C as  
181 MAT increased in gymnosperms. Fall events delayed in warmer locations for both species types, but  
182 slightly more so for gymnosperms (6.23 days) than angiosperms (3.69 days) (Fig.4B).

183 While we expected that coarse metrics, such as latitude and MAT, would generally represent how  
184 similar the climates are between the provenances and gardens, we also estimated climate overlap in  
185 months much closer to the events to further test how much climate similarity between provenances  
186 and gardens predicts provenance effects. For spring events, we considered overlap across March to  
187 May. However, results were not qualitatively different than using MAT (See Fig.S2 in Supporting  
188 Information). We observed very weak effects of climate overlap on spring events (0.01 [0.02 - 0.03]  
189 days per one percent increase in climate overlap), nearly identical across angiosperms (0.02 [0.00 -  
190 0.05]) and gymnosperms (0.04 [0.00 - 0.09]). Fall events advanced as climate overlap declined, but

<sup>191</sup> slightly more strongly for gymnosperms (advancing 0.72 [0.51 - 0.92] days per one percent decline in  
<sup>192</sup> climate overlap) (Fig.S3 in Supporting Information).

## <sup>193</sup> 4 Discussion

<sup>194</sup> Overall, our results demonstrated inconsistent and weak clines in spring events across North America  
<sup>195</sup> and Europe. In contrast, fall events generally showed much stronger clines, especially in North America,  
<sup>196</sup> and in support of many previous studies (Aitken and Bemmels, 2016, Alberto et al., 2013). While  
<sup>197</sup> previous studies have suggested spring events are far more plastic compared to fall events (Li et al.,  
<sup>198</sup> 1997, Farmer, 1993, Mimura and Aitken, 2007), our study provides the first major test of this across  
<sup>199</sup> continents and species and suggests no general trend for clines in spring phenology. Our results thus  
<sup>200</sup> predict that warming springs will continue to be tracked more closely phenologically by trees than  
<sup>201</sup> warming fall temperatures (IPCC, 2022)

<sup>202</sup> Trends between spring phenology and latitude or MAT were weak, but suggested the possibility of  
<sup>203</sup> diverging results that could mute an overall trend—albeit a much weaker one than for fall phenology.  
<sup>204</sup> We found angiosperm versus gymnosperm species diverged in their clines with MAT. Combined with  
<sup>205</sup> our finding of much stronger clines for fall phenology in North America, these results support the idea  
<sup>206</sup> of potential variation across continents and/or species type that may underlie the debate in whether  
<sup>207</sup> spring events show important clinal variation. As clines with spring events were very weak, however,  
<sup>208</sup> and gardens almost always focus on only one species, understanding these diverging results well enough  
<sup>209</sup> to aid forecasting would take significant additional investment in common garden studies.

<sup>210</sup> We found the coarse metrics of provenance latitude and MAT were generally good predictors of phenol-  
<sup>211</sup> ogy, performing better than our more complex and data-rich metric of climate overlap. Latitude and  
<sup>212</sup> MAT appeared to well represent how similar the climates are between the provenances and gardens  
<sup>213</sup> in the temperate and boreal forest species we studied, yielding similar results to metrics calculated  
<sup>214</sup> specifically in the spring with daily climate data.

### <sup>215</sup> 4.1 Variation across continents and species types

<sup>216</sup> Our results highlight that spring events show much weaker clines than fall events in tree species, but  
<sup>217</sup> suggest important variation between species types in spring events. Angiosperms tended to budburst  
<sup>218</sup> earlier in provenances that were warmer and more southerly, while gymnosperms trended in the oppo-  
<sup>219</sup> site direction. Such differences could be driven by their varying investment strategies. As gymnosperms  
<sup>220</sup> photosynthesize without leafout they generally leafout much later than angiosperms, after most risk  
<sup>221</sup> of spring frost (Panchen et al., 2014), and thus may avoid frost risk more than angiosperms. In con-

222 trast, angiosperms may tend towards earlier leafout in warmer climates to compete best for access to  
223 light and other resources (Chamberlain et al., 2019). Testing these hypotheses would require more  
224 information on frost risk and forest community assembly from across the provenance locations.

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

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

254 **4.2 Adaptation in tree phenology: Implications for climate change re-**  
255 **sponses**

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

263 Predicting this will require better understanding how different species strategies covary with early-  
264 season risks, and how such risks may shift with continued climate change. For temperate zones, many  
265 species strategies appear designed to cope with frost, either via avoidance or tolerance (Alberto et al.,  
266 2011, Lenz et al., 2016, Allevato et al., 2019), as utilizing the early portion of the growing season can be  
267 especially critical for species in colder regions (Morin et al., 2007, Dantec et al., 2015). Climate change  
268 at once shifts spring phenology—thus potentially changing each species frost risk—but also appears to  
269 reshape the drivers of frost climatically (Chamberlain et al., 2021). Layered onto this are possible shifts  
270 in early-season herbivory with warming (Meineke et al., 2019), and trade-offs in early-season risks with  
271 access to a long growing season for growth and reproduction, with some species avoiding competition  
272 through being very early (Guo et al., 2022). Common garden studies that track and report frost and  
273 herbivory damage, alongside timing of flowering and fruiting, could help to understand the complex  
274 fitness landscape of spring phenology.

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

282 Understanding environmental clines in phenology will ultimately be critical to predicting how species  
283 shift their ranges as well. Implications of small differences in spring phenology could mean different  
284 levels of gene flow, while co- and counter-gradient variation have important implications for gene glow  
285 over larger geographical regions (Bachmann et al., 2020), and thus could shape future range shifts.  
286 Much like frost risk, climate change likely shifts multiple factors at once, as climate change shifts

<sup>287</sup> pollinators and wind patterns (Kling and Ackerly, 2021). With the anticipated escalation of global  
<sup>288</sup> temperatures in the forthcoming century, these mechanisms are poised to play a pivotal role in shaping  
<sup>289</sup> the dynamics of plant communities and the overall carbon balance of ecosystems.

## <sup>290</sup> 5 Acknowledgement

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<sup>292</sup> possible additional common garden studies.

## <sup>293</sup> 6 Competing interests

<sup>294</sup> We state that we do not possess any recognized conflicting financial interests or personal connections  
<sup>295</sup> that might have seemed to impact the findings presented in this paper.

## <sup>296</sup> 7 Author contributions

<sup>297</sup> ZAZ collected and cleaned data, performed computations, and analyzed data in an iterative process.  
<sup>298</sup> EMW conceived of the presented idea, designed the computational framework, and verified the ana-  
<sup>299</sup> lytical methods. Both authors discussed results and contributed to the final manuscript.

## <sup>300</sup> 8 Data availability

<sup>301</sup> The data that support the findings of this study are openly available in the Knowledge Network for  
<sup>302</sup> Biocomplexity (KNB) repository at <https://knb.ecoinformatics.org/view/urn%3Auuid%3Aa37258b9-23e7-4b0c-a20f-9185cbc27194>.

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<sup>496</sup> the Advancement of Science)* **381**(6653), eadf5098–eadf5098.

<sup>497</sup> **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.

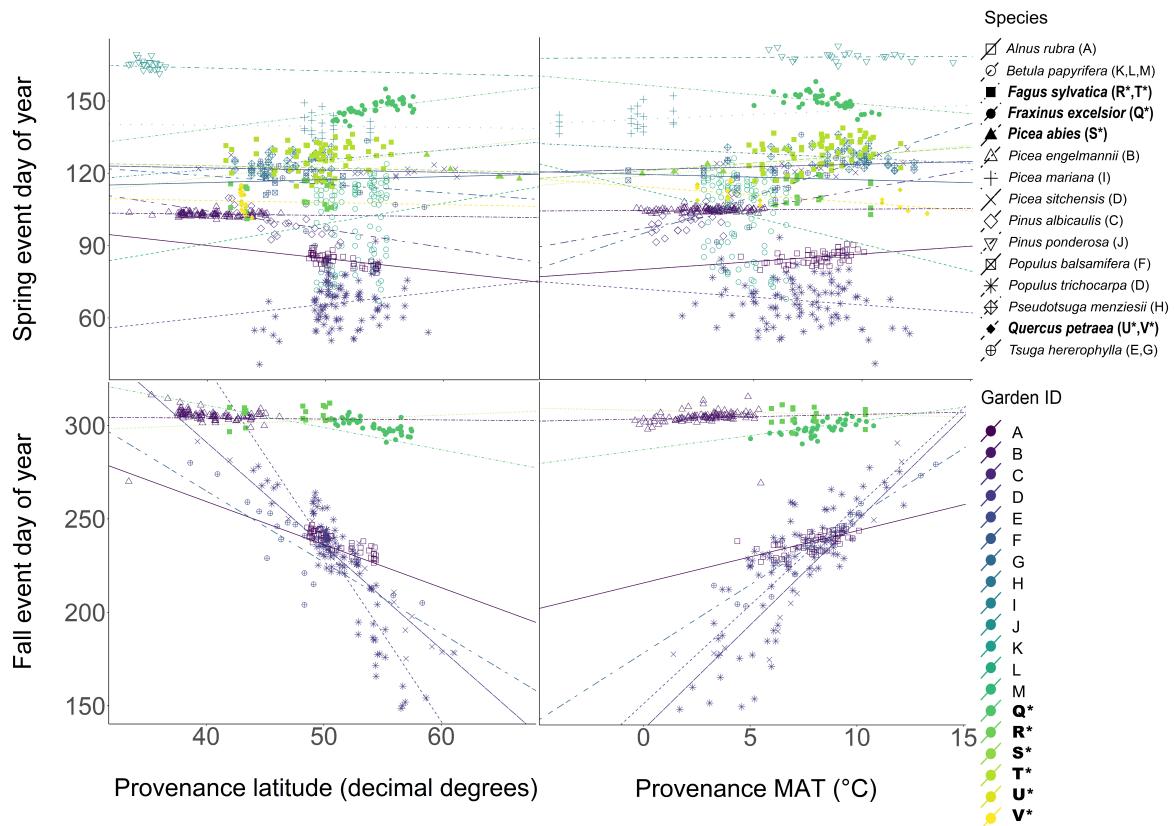


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are bolded and denoted by an asterisk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

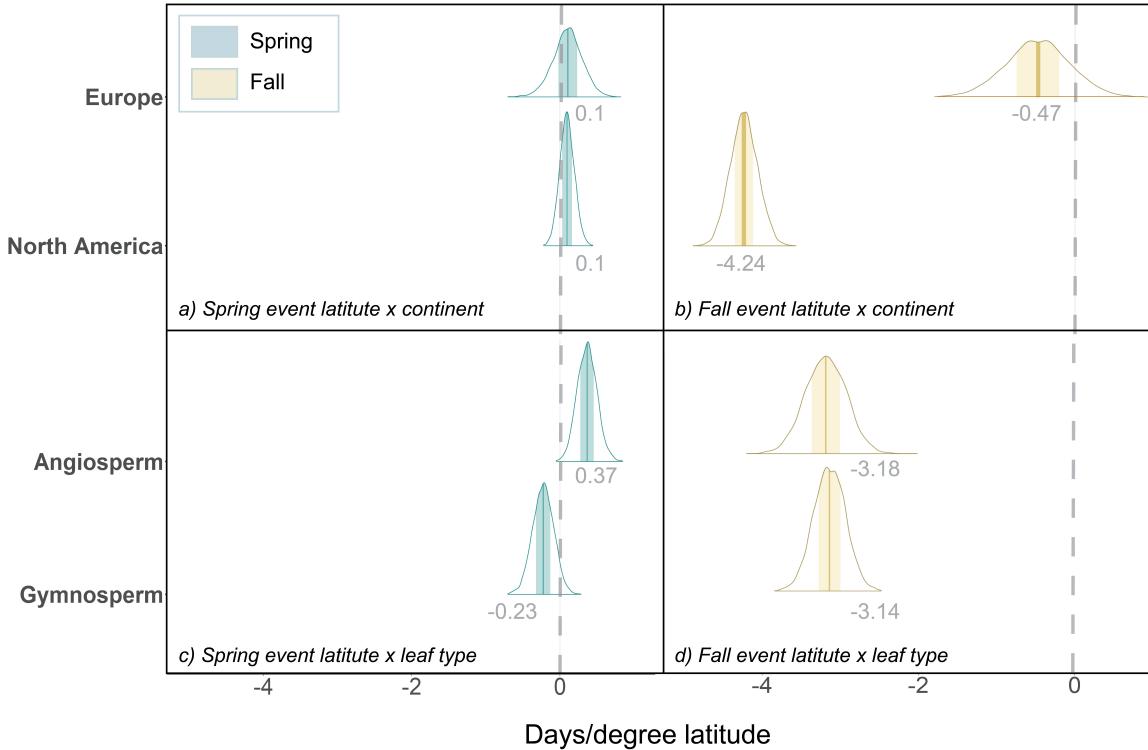


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given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

## 498 11 Supporting Information (brief legends)

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

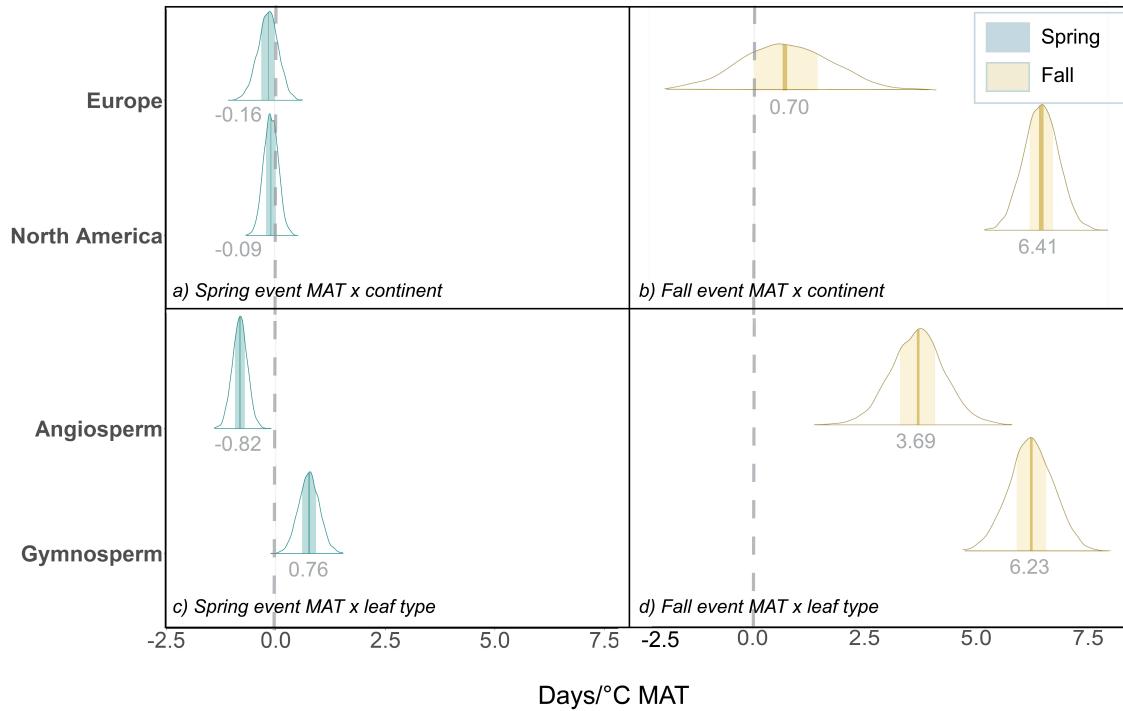


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in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