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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.

## <sup>1</sup> Summary

- <sup>2</sup>     ● Forecasting the biological impacts of climate change requires understanding how  
<sup>3</sup> species respond to warmer temperatures through inter-annual flexible variation  
<sup>4</sup> vs. through adaptation to local conditions. Yet, we often lack this information  
<sup>5</sup> entirely or find conflicting evidence across previous studies.
- <sup>6</sup>     ● We synthesize common garden studies across Europe and North America that  
<sup>7</sup> reported spring event dates for a mix of angiosperm and gymnosperm tree species  
<sup>8</sup> in the northern hemisphere, capturing data from 384 North American and 101  
<sup>9</sup> European provenances (i.e. populations) with observations from 1962 to 2019,  
<sup>10</sup> alongside fall event data when provided.
- <sup>11</sup>     ● Across continents, we find no evidence of provenance effects (i.e. population  
<sup>12</sup> differences) in spring phenology, but strong clines with latitude and mean annual  
<sup>13</sup> temperature (MAT) in fall. These effects, however, appear to diverge by continent  
<sup>14</sup> and species type (gymnosperm vs. angiosperm), with particularly pronounced  
<sup>15</sup> clines in North America in fall.
- <sup>16</sup>     ● Our results suggest flexible, likely plastic responses, in spring phenology with  
<sup>17</sup> warming, and potential limits—at least in the short term—due to provenance  
<sup>18</sup> effects for fall phenology. They also highlight that, after over 250 years of common  
<sup>19</sup> garden studies on tree phenology, we still lack a holistic predictive model of clines  
<sup>20</sup> across species and phenological events.

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

<sup>23</sup>

## 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.

<sub>107</sub> **2 Materials and Methods**

<sub>108</sub> **2.1 Data collection**

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

<sub>113</sub>           TOPIC = (common garden\* OR provenance\*) AND (leafout\* OR leaf out\*  
<sub>114</sub>           OR budburst OR spring phenolog\*)

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

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

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

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

#### <sup>248</sup> 4.1 Variation across continents and species types

<sup>249</sup> Our results highlight that spring events show much weaker clines than fall events in  
<sup>250</sup> tree species, but suggest important variation between species types in spring events.  
<sup>251</sup> Angiosperms tended to budburst earlier in provenances that were warmer and more  
<sup>252</sup> southerly, while gymnosperms trended in the opposite direction. Such differences could  
<sup>253</sup> be driven by the varying investment strategies, given that all our studied gymnosperms  
<sup>254</sup> were evergreen and all angiosperms were deciduous. As evergreen species photosynthe-  
<sup>255</sup> size without leafout they generally leafout much later than deciduous species, after most  
<sup>256</sup> risk of spring frost (Panchen et al., 2014), and thus may avoid frost risk. In contrast, de-  
<sup>257</sup> ciduous species may tend towards earlier leafout in warmer climates to compete best for  
<sup>258</sup> access to light and other resources (Chamberlain et al., 2019). Testing these hypothe-  
<sup>259</sup> ses would require more information on frost risk and forest community assembly from  
<sup>260</sup> across the provenance locations, but seems an important step towards understanding  
<sup>261</sup> the drivers of this variation. Without a clear mechanism, extrapolating these results  
<sup>262</sup> to other species or across Europe and North America may be difficult, especially given  
<sup>263</sup> biases in the data, and the distinct climatic, geographical, and ecological contexts of  
<sup>264</sup> Europe and North America. Without a clear and universal mechanism driving the ob-  
<sup>265</sup> served phenological responses, the direct applicability of our findings to other contexts  
<sup>266</sup> must be approached with caution.

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

Taken together, these results could explain some of the existing debate on the strength of spring clinal variation, but also highlight how data biases make disentangling the drivers of variation difficult. Angiosperm species showed a weak trend towards earlier budburst in populations from warmer locations. In contrast, fall event clines in Europe were weak, but their fall event type (leaf senescence) is less likely to show clinal variation. Given European studies were biased towards studying angiosperms (3/4 species) that are often canopy-species (e.g., *Fagus*, *Quercus*) these results together could explain a greater focus on clinal variation in spring events across European studies (Basler and Körner, 2012, Gauzere et al., 2020, Sogaard et al., 2008, Deans and Harvey, 1996, Von Wuehlisch et al., 1995). Most North American gardens and provenances included in this study were limited to the Pacific Northwest region, and thus tended to focus on species from forests where gymnosperms are almost always the canopy species (*Pseudotsuga*, *Tsuga*, *Picea*, *Pinus*) and angiosperms are much smaller, more opportunistic species (*Alnus*, *Populus*). This might suggest a far different pattern if gardens included more evenly sampled North American tree species (Fig. 1). Given the tremendous investment required for

295 such gardens, however, it is not surprising they are often limited to one species—  
296 most often those relevant for forestry (e.g., *Pseudotsuga menziesii*, *Tsuja plicata*, *Tsuga*  
297 *heterophylla*, *Picea sitchensis*, *Pinus albicaulis*). Our results, however, highlight the  
298 limited inference we may gain from such an approach to understand trends across  
299 species more broadly, a critical need for climate change forecasting.

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

301 **responses**

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

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

322 alongside timing of flowering and fruiting, could help to understand the complex fitness  
323 landscape of spring phenology.

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

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

## 342 5 Acknowledgement

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

<sup>345</sup> **6 Competing interests**

<sup>346</sup> We state that we do not possess any recognized conflicting financial interests or personal  
<sup>347</sup> connections that might have seemed to impact the findings presented in this paper.

<sup>348</sup> **7 Author contributions**

<sup>349</sup> ZAZ collected and cleaned data, performed computations, and analyzed data in an  
<sup>350</sup> iterative process. EMW conceived of the presented idea, designed the computational  
<sup>351</sup> framework, and verified the analytical methods. Both authors discussed results and  
<sup>352</sup> contributed to the final manuscript.

<sup>353</sup> **8 Data availability**

<sup>354</sup> The data that support the findings of this study are openly available in the Knowledge  
<sup>355</sup> Network for Biocomplexity (KNB) repository at <https://knb.ecoinformatics.org>  
<sup>356</sup> /view/urn%3Auuid%3Aa37258b9-23e7-4b0c-a20f-9185cbc27194.

<sup>357</sup> **9 References**

<sup>358</sup> **References**

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**574 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 (\*).

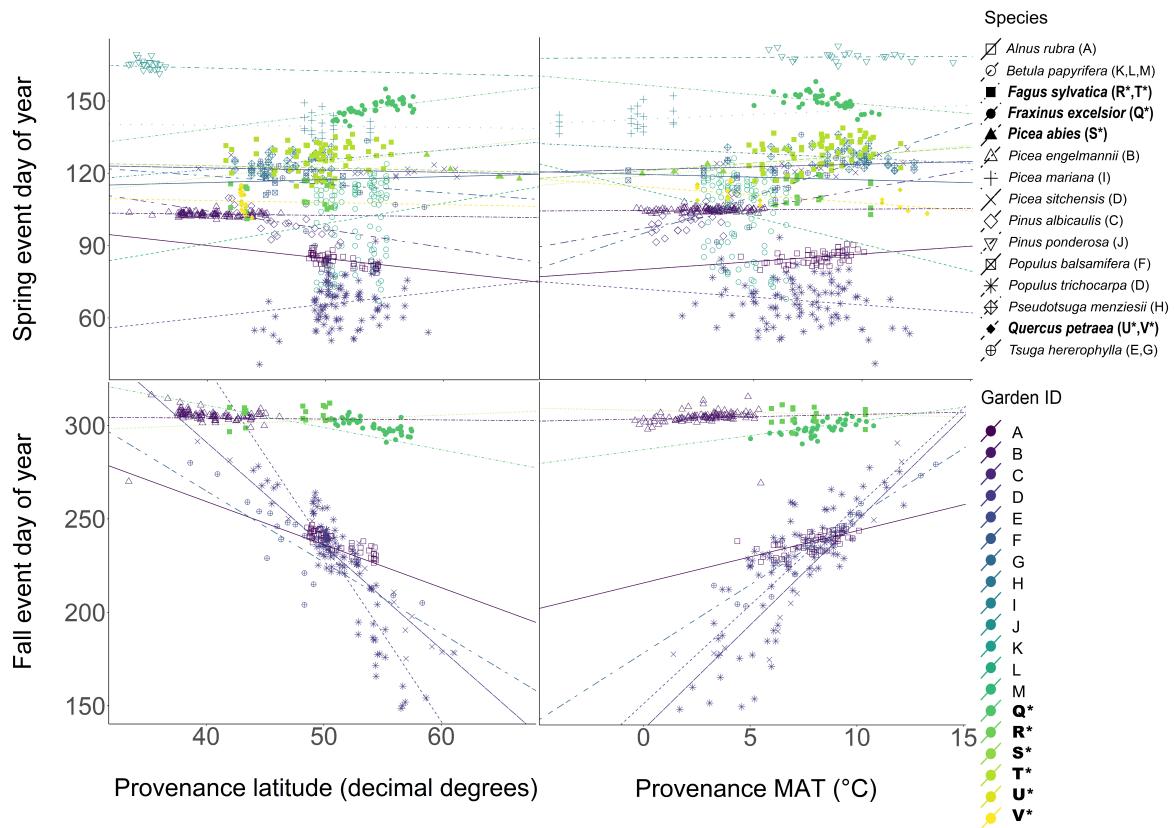


Figure 2: Event day of year (DOY) in relation to provenance latitude and MAT, coded by symbol for species and color for garden with linear fits from hierarchical Bayesian models. Spring events shown on top and fall events at the bottom. European gardens and species are made bold and denoted by an asterisk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

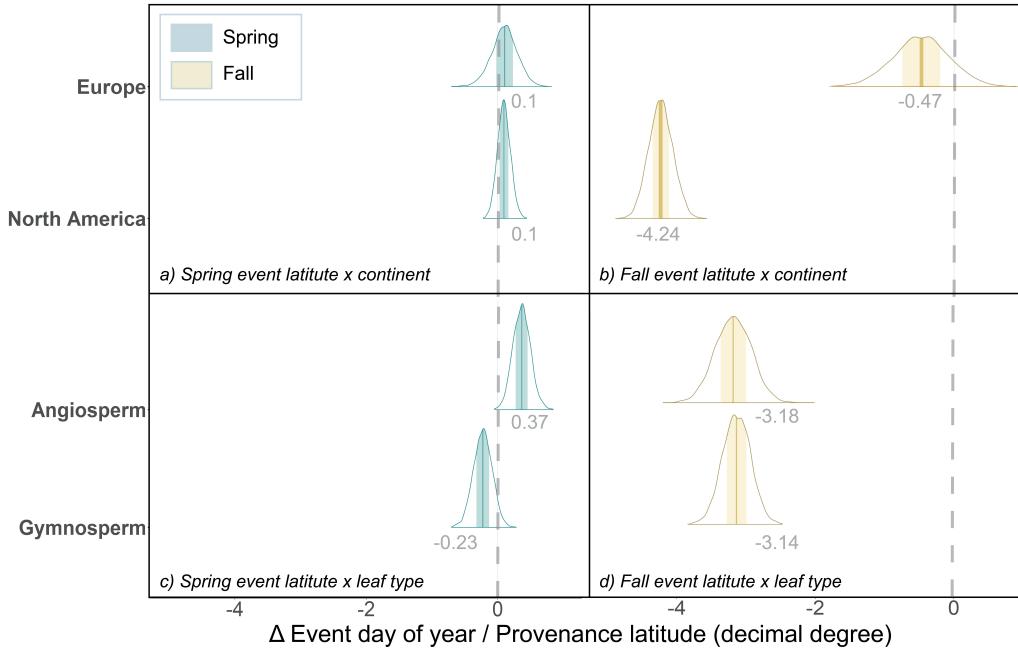


Figure 3: Effects of latitude on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given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

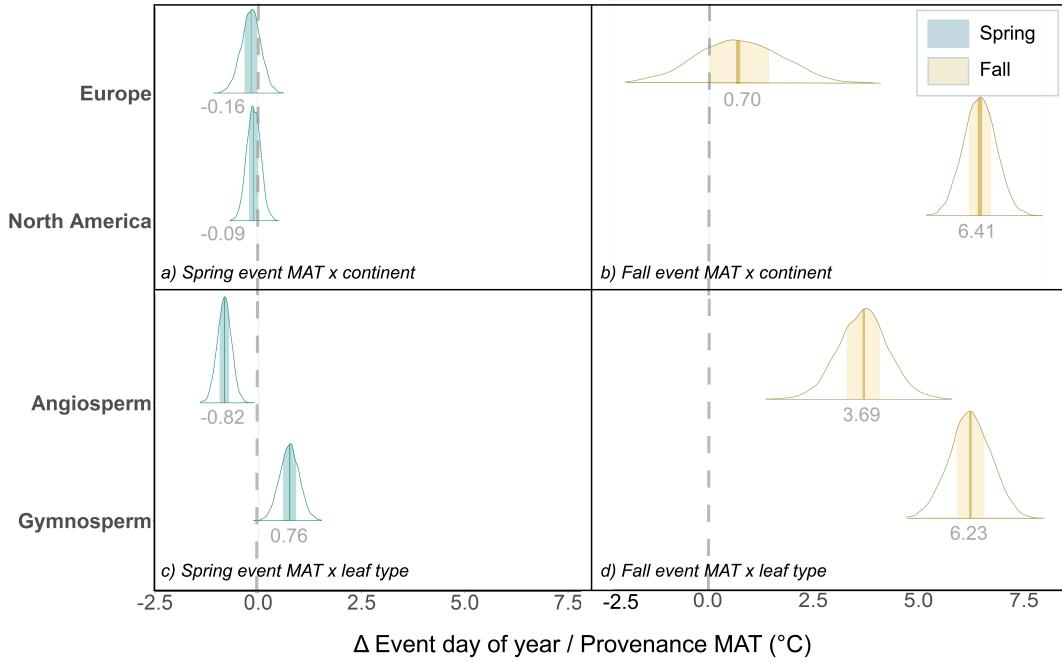


Figure 4: Effects of MAT on spring and fall event date (DOY) depending on (a & b) continent, and (c & d) species leaf type shown as posterior distributions (full distribution represents 99% percentile, solid line and shading in posteriors represent mean and 50 percent interval, 90% intervals given in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