1 **Title:** Higher sensitivity to warming of flowering than leaf-out is shifting their temporal

2 difference across six temperate woody species in Europe

3 **Running Title: Flowering is more sensitive to warm than leaf-out**

4 **Authors:** Xiaojun Geng[1], Yongshuo H. Fu[1,2]*, Shilong Piao[3,4,5], Fanghua Hao[1], Hans

5 J. De Boeck[2], Xuan Zhang[1], Shouzhi Chen[1], Yahui Guo[1], Janet S. Prevéy[6], Yann

6 Vitasse[7,8], Josep Peñuelas[9,10], Ivan A. Janssens[2], Nils Chr. Stenseth[11]

7 **Affiliations**

8 [1] College of Water Sciences, Beijing Normal University, Beijing 100875, China.

9 [2] Plants and Ecosystems, Department of Biology, University of Antwerp, Antwerp, Belgium.

10 [3] College of Urban and Environmental Sciences, Sino-French Institute for Earth System Science,

11 Peking University, Beijing, China.

12 [4] Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research,

13 Chinese Academy of Sciences, Beijing, China.

14 [5] Center for Excellence in Tibetan Earth Science, Chinese Academy of Sciences, Beijing, China.

15 [6] U.S. Geological Survey, Fort Collins Science Center, Colorado, United States of America.

16 [7] WSL Institute for Snow and Avalanche Research, Davos, Switzerland.

17 [8] Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf,

18 Switzerland.

19 [9] CREAF, Cerdanyola del Vallès, Barcelona 08193, Catalonia, Spain.

20 [10] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, Barcelona 08193, Catalonia,

21 Spain.

22 [11] Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences,

23 University of Oslo, N-0316 Oslo, Norway

24

25 Corresponding author: Yongshuo H. Fu

26 Phone: +86-58802736

27 Email: yfu@bnu.edu.cn

28

29 Competing interest statement: The authors declare no competing interests.

30

31 **Manuscript for *New phytologist***

32   **Abstract**

33   Climatic warming has substantially advanced spring phenology in temperate biomes,

34   but different phenological stages respond differently to temperature, which may affect

35   plant and ecosystem function. We monitored the leaf-out and flowering dates of 6286

36   species–site combinations (1830 sites and 6 European temperate species) during 1980-

37   2016. The sensitivity of flowering to temperature (-5.4 ± 0.04 d K^{-1}, mean ± SE) was

38   higher than the sensitivity of leaf-out (-4.6 ± 0.04 d K^{-1}) across all species. This was

39   observed regardless of whether leaf-out occurred before flowering or not, and was

40   likely caused, apart from differing thermal sensitivities, by the different thermal

41   requirements and photoperiodic controls of flowering and leaf-out. The result was an

42   extended time period between flowering and leaf-out in species that blooming before

43   leaf-out, but a shorter time period between these phenological events in species with

44   the opposite strategy. Further studies on the ecological implications of this phenological

45   shift on resource allocation, fruit maturation, or species competition are needed to

46   improve our understanding of ecosystem responses to climate change.

47

48   **Keywords:** leaf-out time, flowering time, period between phenophases, temperature

49   sensitivity, heat requirement, photoperiod

Introduction

Anthropogenic climate change in recent decades has dramatically advanced spring phenology of plants in temperate and boreal zones (Fu et al., 2015; Menzel et al., 2006; Wolfe et al., 2005). Phenological studies have mostly focused on single phenological events, such as leaf-out or flowering, or on the length of the growing season, defined as the period between leaf-out and foliar senescence (Piao et al., 2019). Differences in responses to temperature between phenological events at the species level, and the ecological consequences of such differences, however, have received considerably less attention (but see references Ettinger, Gee, & Wolkovich, 2018; Gougherty & Gougherty, 2018; Peñuelas & Filella, 2001). Recent studies have reported different responses to warming between phenological events, potentially causing phenological asynchrony (Ettinger et al., 2018; Fu et al., 2014), which could have negative implications such as altered plant-pollinator and flower-parasite interactions (Bock et al., 2014; Duchenne et al., 2020; Memmott, Craze, Waser, & Price, 2007; Renner & Zohner, 2018; Thackeray et al., 2016) and affect resource allocation within plants and interspecies competition, eventually altering terrestrial carbon and water cycling (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Heberling, MacKenzie, Fridley, Kalisz, & Primack, 2019; Li et al., 2016; Peñuelas, Rutishauser, & Filella, 2009). Studying the changes in the periods between phenological events within species in response to global warming is therefore essential to improve our understanding of the response of ecosystems to ongoing climate change.

The timing of leaf-out and flowering determines vegetative and reproductive productivity, respectively. Long-term in situ and remotely sensed observations and temperature-manipulation experiments have all attributed significantly advancing dates of both leaf-out and flowering to climatic warming across temperate and boreal taxa (Menzel et al., 2020; White et al., 2009). Temperature, both chilling and warm spring temperatures, and photoperiod are widely recognized as the dominant environmental factors determining spring phenological events (Cannell & Smith, 1986; Fu et al., 2019; Hänninen, 2016; Jochner & Menzel, 2015). The mechanisms controlling the phenology of leaf-out and flowering may differ among species, and no scientific consensus has yet been reached (Cleland et al., 2007; Meng et al., 2019; Richardson et al., 2013). For example, soil moisture and daylength can affect leaf-out phenology (Körner & Basler, 2010; Peaucelle et al., 2019), but temperature is generally considered the dominant factor controlling spring leaf-out, with warming advancing leaf-out dates of temperate and boreal trees by 3-8 d K^{-1} (Fu et al., 2014; Ge, Wang, Rutishauser, & Dai, 2015; Wolkovich et al., 2012). In contrast, the phenology of flowering may be less dominated by temperature, and instead depend on more complex relationships with physiological and external environmental cues, such as the date of snow-melt in tundra ecosystems (Iler, Hoye, Inouye, & Schmidt, 2013) or water stress in arid grasslands (Moore & Lauenroth, 2017; Zhou et al., 2020). The response of flowering phenology to warming has been reported to be unrelated or even opposite to that of leaf-out phenology (Cook, Wolkovich, & Parmesan, 2012; Hovenden, Wills, Schoor, Williams, & Newton, 2008; Iler et al., 2013; Menzel et al., 2006). These results suggest that the response of leaf-out

4

94   and flowering to temperature vary, so climatic warming will likely affect the period

95   between leaf-out and flowering.

96

97   Changes in the temporal difference between leaf-out and flowering can affect

98   intraspecific physiological processes such as carbon allocation, because the allocation

99   of resources, e.g. nutrients and nonstructural carbon, to growth or reproduction is

100   mostly affected by the timing of the two phenophases (Gough, Flower, Vogel, & Curtis,

101   2010; Gougherty & Gougherty, 2018; Li et al., 2016). Shifts in phenological temporal

102   differences can also affect interspecific relationships. For example, if flowering is

103   advanced more than leaf-out, plants with wind-borne seed dispersal may be favored

104   within a community because pollen dispersal is more efficient before canopy closure.

105   Such effects could alter community composition in the longer run and alter the nutrient

106   and energy balance of the entire ecosystem (Carter & Rudolf, 2019; Renner & Zohner,

107   2018). Studies of foliar phenology have mainly focused on woody plants, whereas

108   studies of flowering phenology have generally focused on herbaceous species (Renner

109   & Zohner, 2018). The occurrence of divergent changes in leaf-out and flowering dates

110   within species, and whether these divergent patterns differ across species have, to our

111   knowledge, not yet been well investigated at large spatial scales. Studying the changes

112   in the temporal difference between leaf-out and flowering in common temperate woody

113   species is crucial due to the high sensitivity of temperate woody species to climate

114   change and its important impacts on the functions of terrestrial ecosystems.

115

116   Here we analyzed the temporal changes between leaf-out and flowering at the species

117   level for common woody species over a period of rapid climatic warming (1980-2016)

118   in Europe. The temperature sensitivity of leaf-out and flowering was quantified as the

119   change in days per degree warming. Data were collected from 1830 sites in the central

120   Europe, for a total of 6 temperate woody species and 6286 species–site combinations

121   (see Methods and the site distribution in Figure S1). The objectives of this study were

122   to 1) evaluate the temporal changes in leaf-out and flowering and the length of time

123   between these two phenophases and assess whether patterns have diverged within and

124   across species in the last three decades, and 2) associating these changes with potential

125   physiological and environmental drivers to enhance mechanistic insight in these

126   phenomena.

127

128   **Results and discussion**

129   Averaged across all species and sites during 1980-2016, the mean dates of leaf-out (day

130   of the year, DOY: 111 ± 10, mean ± SD) and flowering (DOY: 112 ± 24) were very

131   similar (Figure 1a). However, these averages hide clear differences between species

132   flowering before leaf-out (FL-LO species) as compared to species exhibiting leaf-out

133   prior to flowering (LO-FL species) (Figure 1a; Figure S2). Four species had mean leaf-

134   out dates (DOY: 108 ± 7) earlier than their mean flowering dates (DOY: 124 ± 12) and

135   the two other species had mean flowering dates (DOY: 92 ± 24) prior to mean leaf-out

136   dates (DOY: 117 ± 12). The dates of both leaf-out and flowering were negatively

137   correlated with preseason temperature (see Methods for definition), significant at $P <$

138   0.05 for >78% of the sites, with mean correlation coefficients of -0.54 ± 0.26 for leaf-

139   out and -0.57 ± 0.26 for flowering (Figure S3). Climate warming thus led to significant

140   advances in both leaf-out and flowering after the 1980s, consistently with findings from

141   previous studies (Phillimore, et al., 2016).

142

143   Earlier spring phenological events in temperate ecosystems have been reported to be

144   more sensitive to climatic warming than later phenological events (Menzel et al., 2006;

145   Miller-Rushing & Primack, 2008; Zhang, Yuan, Liu, Dong, & Fu, 2015). However,

146   flowering for all species in our study was more sensitive to warming than leaf-out,

147   regardless of the order of both events (LO-FL or FL-LO, Figure 2). In detail, S_T across

148   all species and sites was -4.6 ± 0.04 d K^{-1} (mean ± SE) for leaf-out and -5.4 ± 0.04 d K^{-1}

149   for flowering, and this difference was statistically significant ($F_{1,10913}$=258.68, P <

150   0.001, Figure 2a). The difference in S_T between leaf-out and flowering was similar for

151   both the LO-FL and FL-LO species. Across the sites and species blooming after leaf-

152   out, the S_T was -4.4 ± 0.04 d K^{-1} for leaf-out and -5.0 ± 0.04 d K^{-1} for flowering

153   ($F_{1,6030.5}$=135.69, P < 0.001); and -4.8 ± 0.07 d K^{-1} for leaf-out and -6.1 ± 0.09 d K^{-1} for

154   flowering ($F_{1,3530.6}$=138.16, P < 0.001) across the LO-FL species and sites (Figure 2a).

155   Additionally, we divided the study area into 0.5°×0.5° pixels, and found no spatial

156   patterns of the differences in S_T between flowering and leaf-out for individual species

157   (Figure S4). Large variations of S_T have been reported for both leaf-out and flowering

158   (Hänninen & Tanino, 2011), but our results indicated a consistently higher S_T for

159   flowering than leaf-out across the six studied species (Figure 2b).

160   This higher temperature sensitivity contributed to an overall rate of advance that was

161   significantly higher for flowering (4.0 ± 0.1 d decade^{-1}, mean $\pm$ SE) than for leaf-out

162   (2.8 ± 0.1 d decade^{-1}) ($F_{1,10646}=247.42$, $P < 0.001$, Figure 1b). With the temperature

163   sensitivity being similar in both groups, flowering advanced more than leaf-out

164   regardless of life strategy. The time period between leaf-out and flowering thus became

165   significantly shorter for the LO-FL species (-2.2 ± 0.4 d decade^{-1}, $F_{1,5696}=405.53$, $P <$

166   0.001, Figure 1c), and tended to be extended, albeit not statistically significantly, for

167   the FL-LO species (0.8 ± 0.7 d decade^{-1}, $F_{1,3487.5}=41.836$, $P < 0.001$). Across all sites

168   and species, the temporal difference between leaf-out and flowering was shortened by

169   1.2 ± 0.5 d decade^{-1} ($P < 0.05$, Figure 1c).

170

171   To account for the larger advance and higher S_T of flowering, and the smaller temporal

172   difference between leaf-out and flowering when averaged across all species, we

173   propose three mutually nonexclusive hypotheses: (1) a climatic hypothesis, where

174   different warming rates before leaf-out and flowering and a higher warming rate before

175   flowering could lead to larger advances in flowering dates, (2) a heat requirement

176   hypothesis, where a larger heat requirement for leaf-out than flowering could lead to

177   more time for leaf-out to fulfill the heat requirement at the same warming rate before

178   leaf-out and flowering, and to a smaller advance in leaf-out than flowering and (3) a

179   photoperiodic hypothesis, where advances in leaf-out may be more constrained by

180   photoperiod than is flowering, so flowering would be more sensitive to temperature and

181   subsequently lead to a larger advance in flowering dates.

182

We tested the first hypothesis by estimating the changes in spring temperature and heat

accumulation during the preseason (see Methods). The mean annual air temperature

increased by 0.20 °C decade^{-1} over the study area during 1980-2016, and the average

monthly air temperature also tended to increase, except in December (Figure S5a and

b). Warming trends were similar before both leaf-out and flowering across all species

and sites (Figure 2c). We tested the robustness of this climatic hypothesis by estimating

the variation of spring temperature, defined as the standard deviation of temperature

during the preseason (T_{SD}), and found significantly higher T_{SD} before flowering than

leaf-out across all species and site, as well as in groups and for 4/6 individual species

(Figure 3d and Figure S5d). These results suggested that different rates of warming

before leaf-out and flowering could partly explain the larger advance in flowering than

leaf-out for LO-FL species, but could not account for the decreased temporal

differences between leaf-out and flowering for FL-LO species.

196

The second hypothesis involves the physiological processes of plant dormancy. Woody

plants need a specific amount of heat (heat requirement, growing degree days, GDD)

during spring to break dormancy, and a lower heat requirement may lead to earlier

development under climatic warming. We indeed found that the earlier phenological

events required fewer GDD than later events for both the LO-FL and FL-LO species,

but the heat requirement when averaged across all species was significantly higher for

flowering (Figure 3a and b). An alternative interpretation of this observations is that the

204 sensitivity of the heat requirement, i.e. the amount of heat accumulated per degree

205 increase in temperature during the preseason (S_{GDD}), was higher for flowering than leaf-

206 out. A higher sensitivity to heat for flowering may lead to a larger advance than for

207 leaf-out at the same rate of warming before leaf-out and flowering. We indeed found

208 an overall higher S_{GDD} for flowering (37.5 ± 14.3 d) than leaf-out (33.2± 12.6 d,

209 $F_{1,899.21}$=49.97, $P < 0.001$, Figure 3c and d). These results suggested that in addition to

210 S_T, the sensitivity of the heat requirement could also partially account for the reducing

211 temporal difference between leaf-out and flowering, consistent with our heat hypothesis.

212

213 Photoperiod is often considered to codetermine the processes of spring phenology,

214 albeit species-specifically (Flynn & Wolkovich, 2018; Fu et al., 2019; Körner & Basler,

215 2010). A weaker photoperiodic control may be associated with a higher S_T and thus a

216 larger advance in response to global warming (Flynn & Wolkovich, 2018; Way &

217 Montgomery, 2015; Zohner & Renner, 2016). We could not directly estimate the effect

218 of photoperiod, so we applied an alternative indirect estimate. A stronger photoperiodic

219 control of spring phenology would likely be reflected in smaller interannual variation

220 of phenological dates, so we calculated the variation of both leaf-out and flowering

221 (defined as one standard deviation) across all sites and species. The interannual

222 variation was significantly smaller for leaf-out (7.7 ± 0.03 d) than flowering (9.4 ± 0.06

223 d, $F_{1,10948}$=1127.7, $P < 0.001$, Figure 4a), and consistent results were found for each

224 individual species (Figure 4b), suggesting a stronger photoperiodic control of leaf-out

225 than flowering and thus a higher S_T of flowering, consistent with our photoperiodic

226 hypothesis. We further tested this photoperiodic limitation by plotting daylength on the

227 dates of leaf-out and flowering against latitude. Interestingly, the overall trends of

228 daylength with latitude differed significantly between leaf-out and flowering

229 (ANCOVA, F=2.594, $P < 0.001$), as well as for 5/6 species (Figure 4c and d),

230 suggesting that photoperiod likely affected the dates of both leaf-out and flowering, but

231 the effect of photoperiod was larger for leaf-out. These results thus support our

232 hypothesis that photoperiod may partially constrain leaf-out and thereby limit the

233 advance of leaf-out with warming, which could account for the smaller advance in leaf-

234 out than flowering dates.

235

236 Our results demonstrate differences in climatic responses between leaf-out and

237 flowering, with flowering having a higher S_T than leaf-out across temperate woody

238 species. As a result, the temporal difference between these two phenological events has

239 substantially shifted in recent decades. This phenomenon may have substantial

240 ecological implications. The sequences of phenophases play key roles in the allocation

241 of resources by species, because plant growth and reproduction depend on the same

242 internal resource pool, e.g. nutrients and nonstructural carbon, and shifting reproductive

243 phenophases may affect the allocation of resources from growth and survival to

244 fecundity (Gougherty & Gougherty, 2018; Li et al., 2016; Richardson et al., 2013). In

245 addition, the different temperature sensitivity between leaf-out and flowering may also

246 affect interspecies competition. Recent studies have found that FL-LO species are more

247 resistant to freezing (Gougherty & Gougherty, 2018), and a higher S_T and earlier

248 flowering directly affect plant gene flow, indicate an advanced onset of reproduction,

249 which could help seed dispersal, prolong the fruit growing season and improve plant

250 competitiveness, because the seed dispersal may benefit from a longer time period

251 before the canopy fully closed (Carter & Rudolf, 2019; Li et al., 2016; Wang & Ottlé

252 et al., 2014), and subsequently lead to changes in species distribution and composition

253 in terrestrial ecosystems (Post, 2019; Vitasse et al., 2011). The effect of changes in the

254 temporal difference between leaf-out and flowering on carbon allocation and

255 interspecies competition, however, needs to be investigated further. In summary, we

256 found significant changes in the temporal difference between leaf-out and flowering

257 across temperate species, with likely substantial ecological implications going from

258 altered plant allocation of resources to changed interspecific relationships.
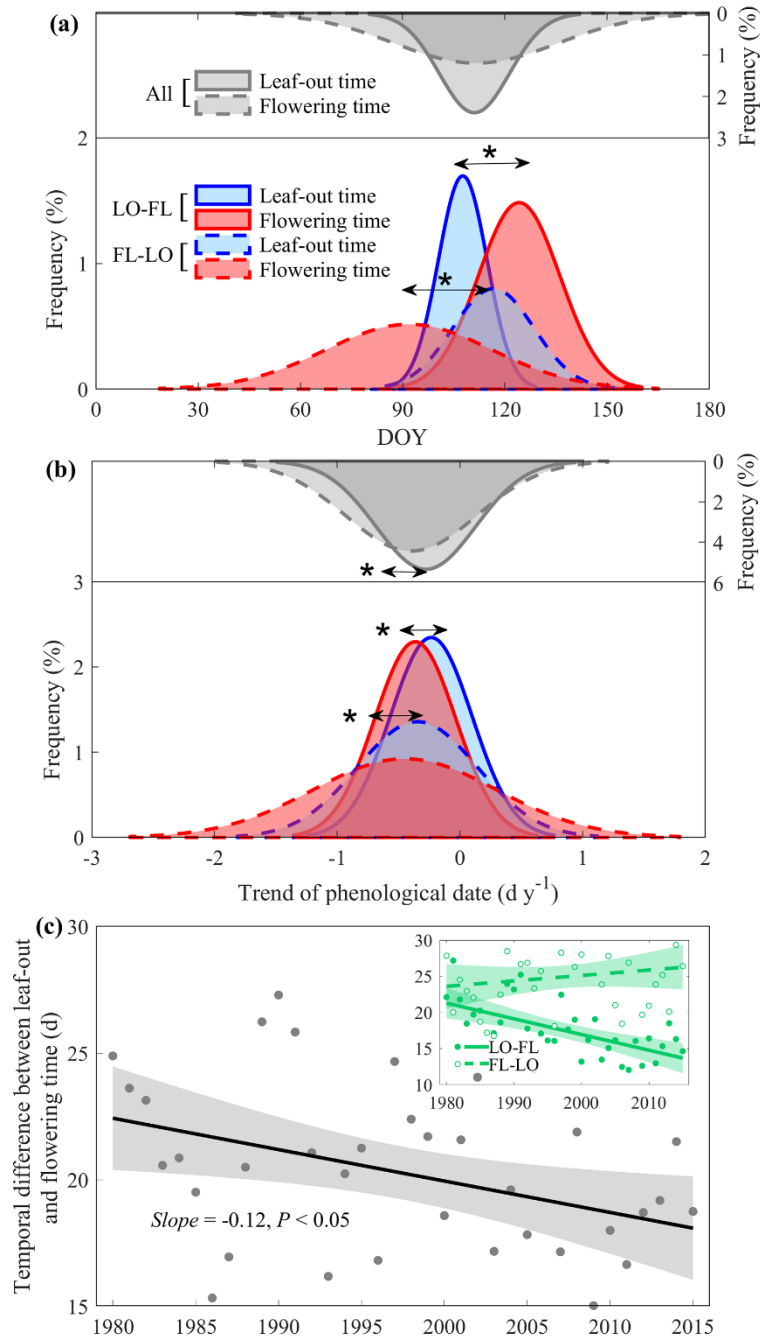
Figure 1 Dates and trends of spring phenology, and the temporal difference between leaf-out and flowering time during 1980-2016. (a) Frequency distribution of phenological dates across sites and species. **(b)** Frequency distribution of trends of phenological dates across sites and species. The asterisks in (a) and (b) indicate significant differences between leaf-out and flowering times in the same group at $P < 0.05$ (paired t-test). **(c)** Temporal trend of the difference between leaf-out and flowering.

265   The dots represent averages of multiple sites in a year, and the shadings represent 95%

266   confidence intervals. The subpanel is the trend of temporal difference between leaf-out

267   and flowering by group. "All" indicates all species across sites and species, "LO-FL"

268   indicates species bloom after leaf-out, and "FL-LO" indicates species bloom before
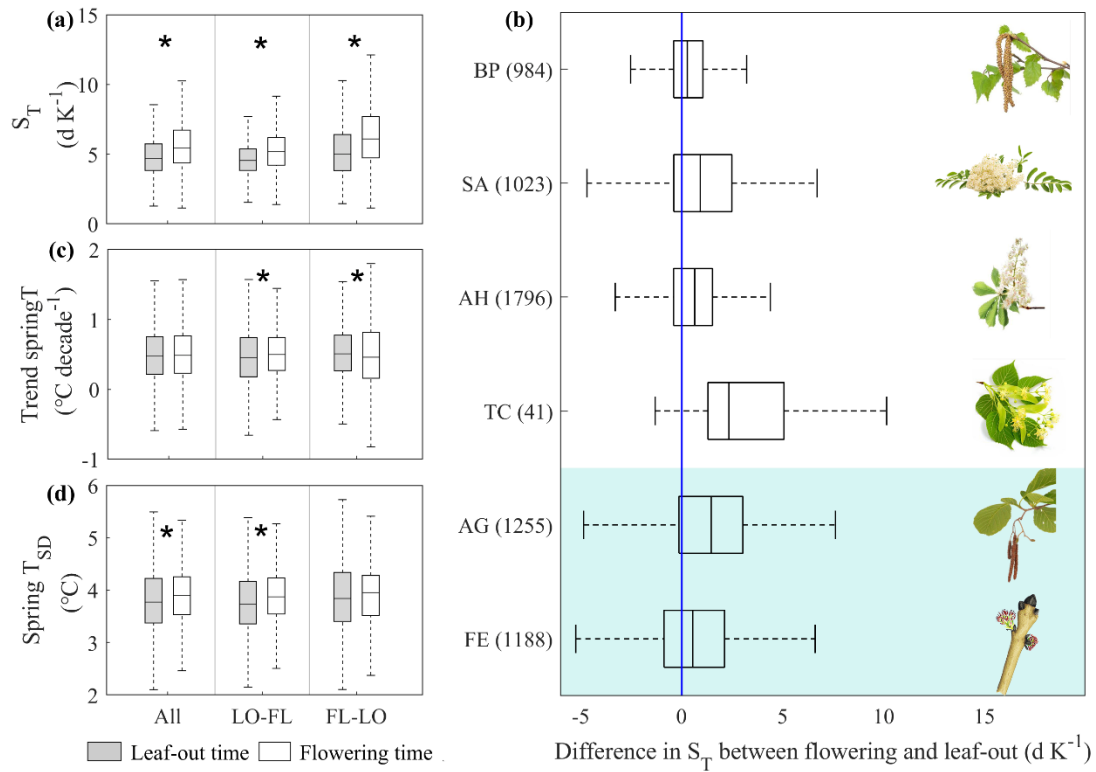
269   leaf-out.

Figure 2 Temperature variations and the temperature sensitivity across sites and differences between flowering and leaf-out time. (a) Temperature sensitivity (S_T) across sites and species. The S_T was defined as the number of advanced days for one unit increase in Kelvin temperature, determined by reduced major-axis (RMA) regression between spring phenology (leaf-out and flowering dates) and mean air temperature during the preseason. **(b)** Differences in S_T between flowering and leaf-out by species. Positive values in (b) indicate flowering is more sensitive to temperature variation than leaf-out. **(c)** Temporal changes of mean air temperature during the preseason during 1980-2016 across sites and species. **(d)** Variation in spring temperature (T_{SD}) across sites and species. T_{SD} was calculated as the standard deviation of mean spring temperature during the preseason. The asterisks in (a), (c) and (d) indicate significant differences at $P < 0.05$ (paired t-test), and the blue line in (b) indicates no difference. The inserted images in (b) show the leaf and flower morphology

283   of each species. "All" indicates all sites and species, "LO-FL" indicates species bloom

284   after leaf-out, and "FL-LO" indicates species bloom before leaf-out. BP, *Betula*

285   *pendula*; SA, *Sorbus aucuparia*; AH, *Aesculus hippocastanum*; TC, *Tilia cordata*; AG,

286   *Alnus glutinosa*; FE, *Fraxinus excelsior*. The values in bracket after the species names
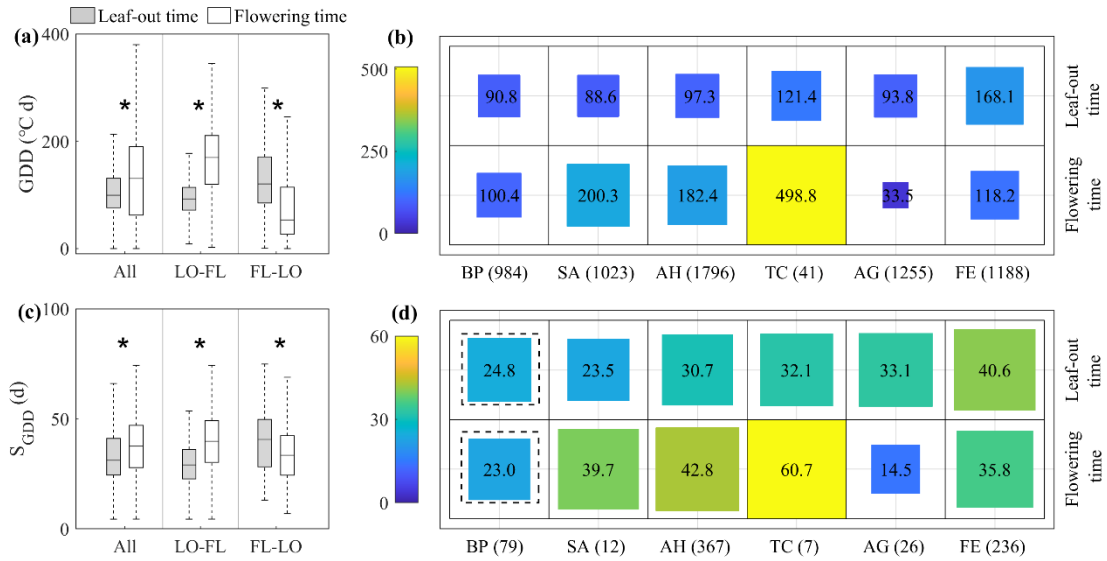
287   are the number of sites in study.

Figure 3 Differences in growing degree days and its sensitivity to spring temperature. (a) The heat accumulation (growing degree days, GDD) during preseason. **(b)** The GDD during preseason for each species. **(c)** The sensitivity of the GDD requirement to spring temperature (S_{GDD}); sites with significant changes of both spring temperature and GDD at $P < 0.1$ were selected, which accounting for 32% of the total. (d) The S_{GDD} for each species on the selected sites. The asterisks in (a) and (c) indicate significant differences at $P < 0.05$ (paired t-test), and the values marked with dotted square in (d) indicate insignificant difference between leaf-out and flowering time. "All" indicates all sites and species, "LO-FL" indicates species bloom after leaf-out, and "FL-LO" indicates species bloom before leaf-out. BP, *Betula pendula*; SA, *Sorbus aucuparia*; AH, *Aesculus hippocastanum*; TC, *Tilia cordata*; AG, *Alnus glutinosa*; FE, *Fraxinus excelsior*. The values in bracket after the species names are the number of sites in study.
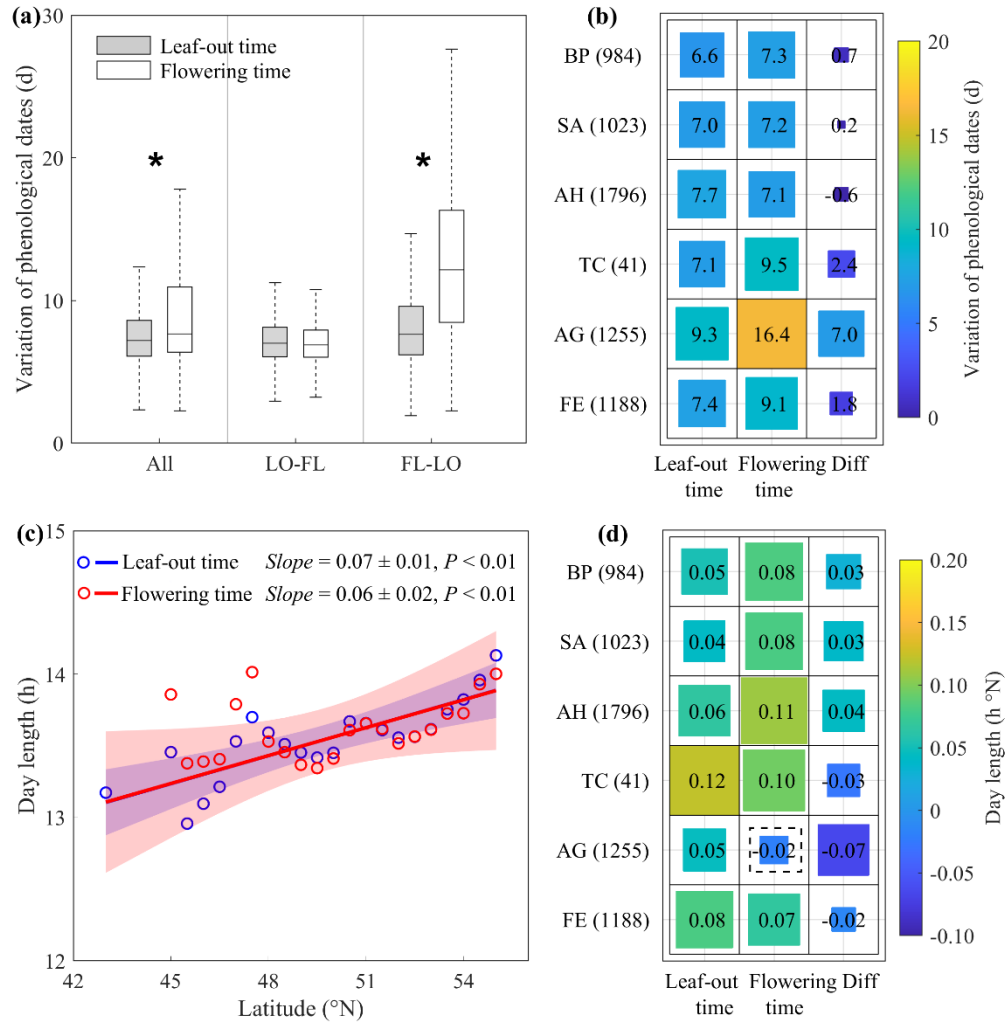
Figure 4 Variation of spring phenology and the spatial distribution of the daylength between leaf-out and flowering time. (a) The variation of spring phenology dates, calculated as one standard deviation of leaf-out date or flowering dates across sites and species. **(b)** The variation of spring phenology for each species. **(c)** The latitudinal variation of the daylength on the mean leaf-out and flowering dates. All sites were averaged every 0.5° along the latitudinal gradient. The shadings represent 95% confidence intervals. **(d)** The latitudinal variation of the daylength on the leaf-out and flowering dates and their difference for each species. The asterisks in (a) and (c) indicate significant differences at $P < 0.05$ (paired t-test), and the values marked with dotted square in (d) indicate insignificant trends. "All" indicates all sites and species,

311   "LO-FL" indicates species bloom after leaf-out, and "FL-LO" indicates species bloom

312   before leaf-out. BP, *Betula pendula*; SA, *Sorbus aucuparia*; AH, *Aesculus*

313   *hippocastanum*; TC, *Tilia cordata*; AG, *Alnus glutinosa*; FE, *Fraxinus excelsior*. The

314   values in bracket after the species names are the number of sites in study.

315 **Material and Methods**

316 **Phenological data set.** We used in situ observations of both leaf-out and first flowering

317 from the open-access European phenological data sets: the Pan European Phenology

318 Network (PEPXX), http://www.pep725.eu/ (Templ et al., 2018). We used BBCH codes

319 11 (i.e. first visible leaf stalk) and 60 (i.e. beginning of flowering) for 6 species at 1830

320 sites, mainly in central Europe (Figure S1). For each species and site, phenological

321 dates had been recorded for at least 15 years during 1980-2016, with both leaf-out and

322 flowering records in any year.

323 **Climatic data set.** The climatic data including daily average air temperature (°C),

324 precipitation (mm) and solar radiation (W m^{-2}), for each site were derived from a bias-

325 corrected reanalysis dataset at a spatial resolution of 0.25° (approximately 25 km),

326 which was specifically described in ref (Beer et al., 2014).

327 **Preseason** was defined as the period before the average leaf-out or flowering date for

328 each species at each site, ranging from 15 to 120 d (with 15-d steps), using the highest

329 absolute partial correlation coefficient between phenological dates and the mean air

330 temperature to remove the confounding effects of precipitation and radiation, defined

331 as the sum of precipitation and radiation during the preseason (Figure S3).

332 **Temperature sensitivity (S_T)** was defined as the number of advanced days per degree

333 increase in air temperature, determined by reduced major-axis regression (RMA)

334 (Keenan, Richardson, & Hufkens, 2019; Fu et al., 2015) between leaf-out or flowering

335 date and mean air temperature during the preseason.

336 **Growing degree days (GDD)** were used to measure the heat requirements for the onset

337   of leaf-out and flowering, calculated as the sum of mean daily air temperature above a

338   5 °C temperature threshold, following previous studies (Wang & Ottle et al., 2014; Fu

339   et al., 2015), during the preseason:

340
$$GDD = \sum_{t_0}^{t_i} (T_t - 5) \qquad if \quad T_t \geq 5$$

341   where t_0 is the start of the preseason, t_i is the date of leaf-out or flowering for each site

342   and T_t is mean daily air temperature.

343   **Sensitivity of GDD to spring temperature (S_{GDD})** was estimated using the slope of

344   the linear regression for the time series of GDD to average spring temperature during

345   the preseason, as previously described (Fu et al., 2019).

346   **Daylength** was calculated as a function of latitude and phenological date (day of the

347   year, DOY):

348
$$Daylength = 24 - \frac{24}{\pi} cos^{-1} \left[\frac{sin\frac{0.8333\pi}{180} + sin\frac{L\pi}{180} sin\varphi}{cos\frac{L\pi}{180} \times cos\varphi} \right]$$

349
$$\varphi = sin^{-1}(0.29795 \times cos\theta)$$

350
$$\theta = 0.2163108 + 2 \times tan^{-1}\left(0.9671396 \times tan(0.0086 \times (DOY - 186))\right)$$

351   where L is the latitude of the phenological site (Fu et al., 2019).

352   **Statistical analysis.** We determined the frequency distributions of the variables (i.e. the

353   timing and temporal trends of phenological dates) and plotted them in histograms. The

354   differences between leaf-out and flowering were tested using paired t-tests for each

355   group and across species. To test the spatial patterns of the major variables (i.e. S_T), we

356   divided the study area into pixels of 0.5°×0.5° resolution, and calculated the average S_T

357   at sites within pixels. To adequately model the structure in the data (e.g. site and year)

358 and to further test the robustness of the results, we adopted mixed-effect models using

359 the lmerTest package in R3.5.2, with site and year as random factors (Phillimore, Leech,

360 Pearce-Higgins, & Hadfield, 2016).

361

References

Beer, C., Weber, U., Tomelleri, E., Carvalhais, N., Mahecha, M., ... Reichstein, M. (2014). Harmonized European long-term climate data for assessing the effect of changing temporal variability on land-atmosphere CO_2 fluxes. *Journal of Climate*, 27(13), 4815-4834. doi: 10.1175/JCLI-D-13-00543.1

Bock, A., Sparks, T. H., Estrella, N., Jee, N., Casebow, A., Schunk, C., ... Menzel, A. (2014). Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology*, 20(11), 3508-3519. doi: 10.1111/gcb.12579

Cannell, M., & Smith, R. I. (1986). Climate warming, spring budburst and frost damage on trees. *Journal of Applied Ecology*, 23(1), 177-191. doi: 10.2307/2403090

Carter, S. K., & Rudolf, V. H. W. (2019). Shifts in phenological mean and synchrony interact to shape competitive outcomes. *Ecology*, 100(11), e2826. doi: 10.1002/ecy.2826

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, 7(22), 357-365

Cook, B. I., Wolkovich, E. M., & Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences*, 109(23), 9000-9005. doi: 10.1073/pnas.1118364109

Duchenne, F., Thébault, E., Michez, D., Elias, M., Drake, M., Persson, M., ... Fontaine, C. (2020). Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nature Ecology & Evolution*, 4(1), 115-121. doi: 10.1038/s41559-019-1062-4

Ettinger, A. K., Gee, S., & Wolkovich, E. M. (2018). Phenological sequences: how early-season events define those that follow. *American Journal of Botany*, 105(10), 1771-1780. doi: 10.1002/ajb2.1174

Flynn, D. F. B., & Wolkovich, E. M. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*, 219(4), 1353-1362. doi: 10.1111/nph.15232

Fu, Y. H., Piao, S., Op De Beeck, M., Cong, N., Zhao, H., Zhang, Y., ... Janssens, I. A. (2014). Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecology and Biogeography*, 23(11), 1255-1263. doi: 10.1111/geb.12210

Fu, Y. H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitasse, Y., ... Janssens, I. A. (2019). Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology*, 25, 2410-2418. doi: 10.1111/gcb.14633

Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., ... Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, 526(7571), 104. doi: 10.1038/nature15402

Fu, Y. H., Campioli, M., Vitasse, Y., De Boeck, H. J., Van den Berge, J., AbdElgawad, H., ... Janssens, I. A. (2014). Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences*, 111(20), 7355-7360. doi: 10.1073/pnas.1321727111

Ge, Q., Wang, H., Rutishauser, T., & Dai, J. (2015). Phenological response to climate change in China: a meta-analysis. *Global Change Biology*, 21(1), 265-274. doi: 10.1111/gcb.12648

Gough, C. M., Flower, C. E., Vogel, C. S., & Curtis, P. S. (2010). Phenological and temperature controls on the temporal non-structural carbohydrate dynamics of *Populus grandidentata* and *Quercus rubra*. *Forests*, 1(1), 65-81. doi: 10.3390/f1010065

Gougherty, A. V., & Gougherty, S. W. (2018). Sequence of flower and leaf emergence in deciduous trees

is linked to ecological traits, phylogenetics, and climate. *New Phytologist*, 220(1), 121-131. doi: 10.1111/nph.15270

Hänninen, H. (2016). *Boreal and Temperate Trees in a Changing Climate*. Dordrecht, Netherlands: Springer Business Media.

Hänninen, H., & Tanino, K. (2011). Tree seasonality in a warming climate. *Trends in Plant Science*, 16(8), 412-416. doi: 10.1016/j.tplants.2011.05.001

Heberling, J. M., MacKenzie, M.D., Fridley, J. D., Kalisz, S., & Primack, R. B. (2019). Phenological mismatch with trees reduces wildflower carbon budgets. *Ecology Letters*, 22(4), 616-623. doi: 10.1111/ele.13224

Hovenden, M. J., Wills, K. E., Schoor, J. K. V., Williams, A. L., & Newton, P. C. D. (2008). Flowering phenology in a species-rich temperate grassland is sensitive to warming but not elevated CO_2. *New Phytologist*, 178(4), 815-822. doi: 10.1111/j.1469-8137.2008.02419.x

Iler, A. M., Hoye, T. T., Inouye, D. W., & Schmidt, N. M. (2013). Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1624), 20120489. doi: 10.1098/rstb.2012.0489

Jochner, S., & Menzel, A. (2015). Does flower phenology mirror the slowdown of global warming? *Ecology and Evolution*, 5(11), 2284-2295. doi: 10.1002/ece3.1503

Keenan, T. F., Richardson, A. D., & Hufkens, K. (2019). On quantifying the apparent temperature sensitivity of plant phenology. *New Phytologist*, 225(2), 1033-1040. doi: 10.1111/nph.16114

Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, 327, 1461-1462. doi: 10.1126/science.1186473

Li, X., Jiang, L., Meng, F., Wang, S., Niu, H., Iler, A. M., ... Wang, G. (2016). Responses of sequential and hierarchical phenological events to warming and cooling in alpine meadows. *Nature Communications*, 7(1), 12489. doi: 10.1038/ncomms12489

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, 10(8), 710-717. doi: 10.1111/j.1461-0248.2007.01061.x

Meng, F., Zhang, L., Niu, H., Suonan, J., Zhang, Z., Wang, Q., ... Du, M. (2019). Divergent responses of community reproductive and vegetative phenology to warming and cooling: asymmetry versus symmetry. *Frontiers in Plant Science*, 10. doi: 10.3389/fpls.2019.01310

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), 1969-1976. doi: 10.1111/j.1365-2486.2006.01193.x

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., ... Estrella, N. (2020). Climate change fingerprints in recent European plant phenology. *Global Change Biology*, 26(4), 2599-2612. doi: 10.1111/gcb.15000

Miller-Rushing, A. J., & Primack, R. B. (2008). Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology*, 89(2), 332-341. doi: 10.1890/07-0068.1

Moore, L. M., & Lauenroth, W. K. (2017). Differential effects of temperature and precipitation on early- vs. late-flowering species. *Ecosphere*, 8(5), e1819. doi: 10.1002/ecs2.1819

Peaucelle, M., Janssens, I. A., Stocker, B. D., Descals Ferrando, A., Fu, Y. H., Molowny-Horas, R., ... Peñuelas, J. (2019). Spatial variance of spring phenology in temperate deciduous forests is constrained by background climatic conditions. *Nature Communications*, 10(1). doi: 10.1038/s41467-019-13365-1

460 Peñuelas, J., Rutishauser, T., & Filella, I. (2009). Phenology feedbacks on climate change. *Science*,
461   324(5929), 887-888. doi: 10.1126/science.1173004
462 Peñuelas, J., & Filella, I. (2001). Responses to a warming world (Perspectives: Phenology). *Science*,
463   294(5543), 793. doi: 10.1126/science.1066860
464 Phillimore, A. B., Leech, D. I., Pearce-Higgins, J. W., & Hadfield, J. D. (2016). Passerines may be
465   sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global Change*
466   *Biology*, 22(10), 3259-3272. doi: 10.1111/gcb.13302
467 Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y. H., Dai, J., ... Zhu, X. (2019). Plant phenology and
468   global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922-
469   1940. doi: 10.1111/gcb.14619
470 Post, E. (2019). *Time in Ecology: A Theoretical Framework*: Princeton University Press.
471 Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions
472   among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*,
473   49(1), 165-182. doi: 10.1146/annurev-ecolsys-110617-062535
474 Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., ... Toomey, M. (2013).
475   Climate change, phenology, and phenological control of vegetation feedbacks to the climate system.
476   *Agricultural and Forest Meteorology*, 169, 156-173. doi: 10.1016/j.agrformet.2012.09.012
477 Templ, B., Koch, E., Bolmgren, K., Ungersboeck, M., Paul, A., Scheifinger, H., ... Zust, A. (2018). Pan
478   European Phenological database (PEP725): a single point of access for European data.
479   *International Journal of Biometeorology*, 62(6), 1109-1113. doi: 10.1007/s00484-018-1512-8
480 Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... Wanless, S.
481   (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241-
482   294. doi: 10.1038/nature18608
483 Vitasse, Y., François, C., Delpierre N., Dufrêne, E., Kremer, A., … Delzon, S. (2011). Assessing the
484   effects of climate change on the phenology of European temperate trees. *Agricultural and Forest*
485   *Meteorology*, (151), 969-980
486 Wang, T., Ottle, C., Peng, S., Janssens, I. A., Lin, X., Poulter, B., ... Ciais, P. (2014). The influence of
487   local spring temperature variance on temperature sensitivity of spring phenology. *Global Change*
488   *Biology*, 20(5), 1473-1480. doi: 10.1111/gcb.12509
489 Way, D. A., & Montgomery, R. A. (2015). Photoperiod constraints on tree phenology, performance and
490   migration in a warming world. *Plant Cell and Environment*, 38, 1725-1736. doi: 10.1111/pce.12431
491 White, M. A., Beurs, D. K. M., Didan, K., Inouye, D. W., Richardson, A. D., Jensen, O. P., ... Lauenroth,
492   W. K. (2009). Intercomparison, interpretation, and assessment of spring phenology in North
493   America estimated from remote sensing for 1982-2006. *Global Change Biology*, 15(10), 2335-2359.
494   doi: 10.1111/j.1365-2486.2009.01910.x
495 Wolfe, D. W., Schwartz, M. D., Lakso, A. N., Otsuki, Y., Pool, R. M., ... Shaulis, N. J. (2005). Climate
496   change and shifts in spring phenology of three horticultural woody perennials in northeastern USA.
497   *International Journal of Biometeorology*, 49(5), 303-309. doi: 10.1007/s00484-004-0248-9
498 Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., ... Cleland,
499   E. E. (2012). Warming experiments underpredict plant phenological responses to climate change.
500   *Nature*, 485(7399), 494-497. doi: 10.1038/nature11014
501 Zhang, H., Yuan, W., Liu, S., Dong, W., & Fu, Y (2015). Sensitivity of flowering phenology to changing
502   temperature in China. *Journal of Geophysical Research: Biogeosciences*, 120(8), 1658-1665. doi:
503   10.1002/2015JG003112

504   Zhou, X., Geng, X., Yin, G., Hänninen, H., Hao, F., Zhang, X., ... Fu, Y. H. (2020). Legacy effect of
505   spring phenology on vegetation growth in temperate China. *Agricultural and Forest Meteorology*,
506   281, 107845. doi: 10.1016/j.agrformet.2019.107845
507   Zohner, C. M., & Renner, S. S. (2016). Day length unlikely to constrain climate-driven shifts in leaf-out
508   times of northern woody plants. *Nature Climate Change*, 6, 1120-1123