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2 Deciphering the multiple effects of climate warming on the temporal

3 shift of leaf unfolding

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16 Abstract Changes in winter and spring temperatures have been widely used to explain the diverse responses of spring phenology to climate change. However, few 17 studies have quantified their respective effects. Using 386,320 in-situ observations of 18 leaf unfolding date (LUD) of six tree species in Europe, we show that the accelerated 19 spring thermal accumulation and changes in winter chilling explain, on average, 61% 20 and 39%, respectively, of the advancement of LUD during 1951–2019. We find that 21 winter warming might not have delayed bud dormancy release, but instead it has 22 increased the thermal requirement to reach leaf unfolding. The increase of thermal 23 requirement and the decreased efficiency of spring warming to thermal accumulation 24 partly explain the weakening response of leaf unfolding to warming. Our study 25 26 stresses the need to better assess the antagonistic and heterogeneous effects of winter and spring warming on leaf phenology, which is key to projecting future vegetation-27 climate feedbacks. 28

30 Main

Timing of leaf unfolding influences the onset of the growing season of plants, and, 31 therefore, vegetation productivity, as well as ecosystem water, carbon, and nutrient 32 cycles¹⁻³. Shifts in leaf unfolding date (LUD) may also alter competition between 33 plant species and, thus, community structure at the decadal to centennial timescales, 34 as well as the activities of insects and herbivores⁴⁻⁶. Many studies based on both in 35 situ observations and satellite-derived data have reported a general trend of advancing 36 spring leaf phenology during the past decades, in particular leaf unfolding, in response 37 to climate warming in temperate and boreal regions⁷⁻¹¹. However, although there is 38 now mounting evidence that spring leaf phenology as a whole is shifting earlier in 39 time, both the magnitude and direction of this shift show significant taxonomic, 40 temporal and spatial variations¹²⁻¹⁶. In particular, the sensitivity of LUD to climate 41 warming (S_T , day $^{\circ}C^{-1}$), defined as the shift in LUD per $^{\circ}C$, has significantly declined 42 over the past 30 years in many regions 7,17 . 43

Temperature has been regarded as the most important environmental factor 44 controlling plant phenology in the extratropics¹⁸. Plants in these temperate and boreal 45 46 regions generally require a certain number of cold days to break bud dormancy, and subsequently, a certain number of days with warmer conditions (called forcing 47 temperatures) to trigger cell growth and leaf development¹⁹⁻²². Several studies have 48 argued that changes in winter chilling and thermal accumulation caused by climate 49 change explain the divergent shifts of LUD in response to rising temperature^{7,23-26}. In 50 particular, warming during winter can affect leaf unfolding through two distinct 51 effects: it may delay the timing of bud dormancy release^{27,28}, and may increase the 52 thermal requirement for bud break^{20,29}. Both effects induce a delay in LUD. In 53 54 contrast, spring warming accelerates thermal accumulation and cell growth, which has

| 55 | an advancing effect on leaf unfolding. These opposing effects might explain why the |
|----|--|
| 56 | sensitivity of LUD to warming has significantly declined over the past 30 years ^{7,24} ; |
| 57 | they might also explain why some species have shown scant or no advances in LUD |
| 58 | with climate warming ^{8,23,25} , as they may not be equally sensitive to both effects. |
| 59 | The impacts of climate warming on winter chilling and spring thermal accumulation |
| 60 | and, thus, on shifts in LUD, have not been quantitatively estimated for multiple |
| 61 | species at large spatial scales, particularly when considering the asynchronicity of |
| 62 | winter and spring warming ^{24,30,31} . Moreover, our mechanistic understanding of the |
| 63 | shifts in LUD in response to warming is still far from complete ³² , especially regarding |
| 64 | the reported decline in the sensitivity of LUD to continuously rising temperature ^{7,33} . |
| 65 | This limits our ability to project regional and global changes in LUD under future |
| 66 | climate warming, as well as the resulting changes in ecosystem structure and |
| 67 | functions. |
| 68 | Here, we take a new step to advance our quantitative and mechanistic understanding |
| 69 | of ongoing changes in leaf phenology. Using long-term (1951-2019) in-situ |
| 70 | observation data of LUD for six dominant broadleaved tree species (Aesculus |
| 71 | hippocastanum, Alnus glutinosa, Betula pendula, Fagus sylvatica, Fraxinus excelsior |
| 72 | and Quercus robur, Table S1) collected at 2944 sites in central Europe ³⁴ (see Methods |
| 73 | and Extended Data Fig. 1), this study aims to: 1) quantify the relative contribution of |
| 74 | winter and spring warming to the temporal shifts in LUD in Europe; and 2) explore |
| 75 | the mechanisms that can explain the declining sensitivity of LUD to rising |
| 76 | temperature, as reported over the past decade ⁷ . |
| 77 | To achieve these aims, we applied a process-based phenology model ^{19,28} at each of the |

78 2944 observation sites for each tree species (see Methods). This type of models

| 79 | describe known causal relationships between winter and spring temperatures and bud |
|---|---|
| 80 | development ^{35,36} . Classical phenology models (e.g. Thermal Time, Sequential, |
| 81 | Parallel and Alternating) generally rely on distinct assumptions (see Methods) |
| 82 | regarding the response of bud growth to spring thermal accumulation and/or winter |
| 83 | chilling ^{35,36} . As these models are non-nested, they cannot be used to test the effects of |
| 84 | different assumptions on the response of leaf unfolding to chilling and forcing |
| 85 | temperatures simultaneously ¹⁹ . To circumvent this limitation, we selected the Unified |
| 86 | model as it integrates the different assumptions, and can be simplified by relaxing |
| 87 | some of the hypotheses based on the parameter estimates obtained when the model is |
| 88 | fitted to observed LUDs using inverse modelling and optimisation algorithms (see |
| 89 | Methods and Supplementary Fig. S1). A previous study found more accurate |
| 90 | predictions of LUD in Europe with the Unified model than other commonly used |
| 91 | models ⁷ . We therefore used this model to disentangle the various effects of climate |
| | |
| 92 | warming on leaf unfolding. |
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104 while delays in LUD mostly occurred at sites with temperature declines (e.g. south-

- eastern Germany and Austria) in the period 1951–2019 (Extended Data Figs. 3, 4 &
- 106 Fig. S2). The average advance of LUD to 1° C rise (S_T) in mean annual, mean spring
- and mean winter temperatures in central Europe was 4.4 (\pm 1.8), 3.2 (\pm 1.2) and 1.4
- 108 (± 0.7) days, respectively (Extended Data Fig. 5).
- 109 Overall, the Unified model (see Methods and Table S2) captured the observed LUDs
- of the six tree species included in this study (Extended Data Fig. 6, Figs. S3 & S4).
- 111 The average root mean square error (RMSE) of all simulated LUDs was 5.8 days (Fig.

112 S3), which is shorter than the observation interval (7 days) of the phenological data

used in this study³³, highlighting that uncertainties in simulated LUDs might partly be

due to uncertainties in observed LUDs. The model explained 65–78% of the

spatiotemporal variations in LUD, depending on the species (Extended Data Fig. 6).

116 The RMSE of predicted LUD for each of the six species showed no significant trend

across time series and latitude (Fig. S4). The estimated optimal chilling temperature

118 (T_{op}, °C) mostly varied between 3 and 10°C, with a mean value of 6.5 (\pm 2.1)°C

119 (Extended Data Fig. 7c), which is similar to values obtained with experimental data

120 $(2.5-9.1^{\circ}C)^{37-39}$.

According to the Unified model¹⁹ (see Methods for details), bud dormancy is assumed 121 to be released when chilling accumulation meets plants' critical requirements (CHA₀ 122 in Fig. S1). The forcing stage starts as soon as this chilling requirement is met, and 123 leaf unfolding occurs when the thermal accumulation during the forcing stage exceeds 124 a given threshold. This threshold, denoted by TA₀, declines exponentially with the 125 total amount of chilling received during the whole pre-growing season (CHAtot, Fig. 126 S1b), defined as the period from the onset of chilling accumulation to leaf unfolding. 127 Therefore, the temporal shifts in LUD are determined by the time when bud dormancy 128

| 129 | is released (d_{f0}), which in turn depends on the chilling accumulation rate (CH _r , Eq. 1), |
|-----|---|
| 130 | the thermal accumulation rate (Fr, Eq. 2), and the required amount of thermal |
| 131 | accumulation (TA ₀ , Eq. 3), the latter being contingent on CHA_{tot} (Eq. 4) before leaf |
| 132 | unfolding (Fig. S1). |
| 133 | Our results show that advances in LUD were mainly caused by the acceleration in |
| 134 | thermal accumulation induced by the spring warming (ΔD_{Fr} , Figs. 1a & Extended |
| 135 | Data Fig. 8). For the periods 1980–1999 and 2000–2019, the forcing stage duration |
| 136 | was, respectively, 4.0 (\pm 3.8) and 8.7 (\pm 7.0) days shorter than in the reference period |
| 137 | (1951–1979). In contrast, the increase TA_0 induced by the decline in CHA_{tot} delayed |
| 138 | LUD by 1.2 (±1.6) and 2.3 (±2.0) days in 1981–2000 and 2000–2019, respectively, |
| 139 | compared to the earlier period (ΔD_{TA0} , Fig. 1a). Changes in dormancy release day |
| 140 | (ΔD_{df0}), which is also the onset of the forcing stage, contributed less to the shifts in |
| 141 | LUD, generally by less than 2 days. From the period 1951–1979 to 1980–1999 and |
| 142 | 2000–2019, the dormancy release day advanced, on average, by 0.3 (\pm 2.1) and 1.7 |
| 143 | (±3.9) days, respectively (Fig. 1a). Temporal shifts in dormancy release day differed |
| 144 | significantly across species and were overall greater for Fraxinus excelsior (Fe) and |
| 145 | Quercus robur (Qr) , which have comparatively later LUDs (Fig. S5) than other |
| 146 | species (Fig. 1 & Extended Data Fig. 2). Overall, ΔD_{Fr} , ΔD_{TA0} and ΔD_{df0} explained |
| 147 | 61%, 22%, and 17% (Eqs. 12–14) of the total advance in LUD between the reference |
| 148 | period (1951–1979) and the most recent period (2000–2019) (Fig. 1b). In other words, |
| 149 | the acceleration in thermal accumulation caused by climate warming (ΔD_{Fr}) explained |
| 150 | 61% of the temporal shift in LUD, while changes in chilling accumulation |
| 151 | $(\Delta D_{df0} + \Delta D_{TA0})$ explained the remaining 39% through their influence on plants' |
| 152 | thermal requirement and dormancy release date (Fig. 1b). |
| | |

153 Revealing the antagonistic effects of temperature on LUD

154 The warming-induced change in the dormancy release day has been widely invoked to explain why the LUDs of some plants show a weak or even delayed shift with climate 155 warming^{7,8,16}. A common hypothesis relies on the premise that warm temperatures in 156 winter delay the timing at which the chilling requirement for dormancy release is met, 157 thus postponing the start of the forcing stage and mitigating the advancement of the 158 159 LUD. However, our results suggest that the winter warming only marginally changed the timing of dormancy release, especially from 1951–1979 to 1980–1999 (Fig. 1). At 160 most of the observation sites, the optimized response functions to chilling temperature 161 162 showed an optimum (see the pattern plotted in Fig. S6b), in contrast to the widely used index-chilling days^{20,36} (Fig. S6a), which assumes a uniform effect of chilling 163 temperatures as long as they remain below a certain threshold. Winter temperatures 164 165 recorded at the observation sites were mostly 3-12°C lower than the local optimal chilling temperature (T_{op} , °C) in the period 1951–1979, and then gradually increased 166 towards T_{op} with time (Fig. 2a). This decreasing difference between winter 167 168 temperature and optimal chilling temperatures translated into an important increase in the chilling rates during winter (e.g. between days d_{c1} and d_{c2} in Fig. 3). On the 169 contrary, in late autumn and early spring, chilling tended to decrease because the 170 temperature tended to be higher than T_{op} (e.g. before d_{c1} and after d_{c2} in Fig. 3). 171 172 However, the increased chilling rate during winter partly or sometimes even fully, 173 offset the decreased chilling rates in late autumn. This explains why the dormancy release days (ΔD_{df0}) were not substantially postponed and mostly occurred slightly 174 earlier for the six species investigated (Fig. 1). 175 176 The decrease in chilling accumulation rate in early spring between 1951–1979 and

177 2000–2019 (due to spring warming which caused the temperature to increase above

178 T_{op}, Figs. 2b & 3) resulted in an overall decrease in the total amount of chilling

| 179 | accumulated before bud break (Fig. 2c). As a result, while dormancy could be |
|-----|---|
| 180 | released earlier, due to more efficient winter chilling during the most recent decades, |
| 181 | total chilling accumulation nonetheless declined by 0.8 (\pm 0.9)%, on average, from |
| 182 | 1951–1979 to 1980–1999, and by 2.0 (±1.2)% from 1951–1979 to 2000–2019 (Fig. |
| 183 | 2c). This decline translates into a slight but significant increase in the critical forcing |
| 184 | accumulation required for leaf unfolding (TA0), by $0.5(\pm 0.5)$ and $1.2(\pm 0.8)$ % between |
| 185 | the reference period and 1981–2010 and 2000–2019, respectively (Fig. 2d). However, |
| 186 | this slight increase in TA0 was largely compensated by an increase in the forcing rate |
| 187 | (F _{rave} , Fig. 2e) during spring of $8.9(\pm 10.4)$ and $22.9(\pm 13.9)$ % between the reference |
| 188 | period and 1981-2010 and 2000-2019 periods, respectively. Thus, despite being |
| 189 | higher, the plants' thermal requirements were reached within a shorter time interval in |
| 190 | recent decades compared to the reference period, resulting in a significant |
| 191 | advancement of the LUD (Fig. 1). |

192 Explaining the declining sensitivity of LUD to warming

193 Consistent with previous studies conducted in Europe and China^{7,17}, we found a

194 general decline in temperature sensitivity of LUD (S_T), although this decline seems to

have stopped in the last 20 years in central Europe (Extended Data Fig. 9). The

average daily chilling rate during the dormancy stage (Fig. 3, CH_{rave} from d_{c0} to d_{f0})

and the total chilling accumulation during the whole pre-growing season (Fig. 3,

198 CHA_{tot} from d_{c0} to LUD), which together represent the overall impacts of winter

199 chilling on leaf unfolding, explained $33.4(\pm 21.5)\%$ (mean±standard deviation) of the

200 temporal variation in S_T . The average daily forcing rate (F_{rave} from d_{f0} to LUD)

explained $21.0(\pm 20.5)$ % of the temporal variation of S_T, on average (Fig. 4). The three

metrics CH_{rave} , CHA_{tot} , and F_{rave} together accounted for 44.5(±21.0)% of the variation

203 in S_T. Irrespective of the metrics, their explanatory powers varied drastically among

204 observation sites, as demonstrated by the large interquartile and 95% confidence intervals of R² in Fig. 4. This finding suggests that the metrics of controlling S_T might 205 differ across observation sites. Note that the pre-growing season used to calculate S_T 206 207 here (Fig. 4) is defined as the period from d_{c0} to LUD and thus differs from that applied in several previous studies^{7,17,40}, in which the pre-growing season was usually 208 209 defined as the period for which the absolute value of the correlation coefficient between LUD and air temperature was largest (i.e. the period which is most relevant 210 to leaf unfolding, see Methods). Nevertheless, calculating the pre-growing season this 211 212 way provided similar results (Figs. 4 & S7). Changes in winter chilling due to warming have been proposed as the main 213 explanation for the temporal variation in $S_T^{7,17}$. Our results show that the overall 214 215 effect of winter warming on S_T is indeed higher than that of spring warming. Our results further support the hypothesis that winter warming leads to a decline in S_T by 216 reducing the total amount of chilling received by the plants and subsequently 217 increasing the critical forcing requirements for leaf unfolding (Figs. 2, 4 & Eq. 3). 218 However, our findings do not support the hypothesis that winter warming leads to a 219 220 decline in S_T by delaying the timing of dormancy release (d_{f0}). Indeed, although 221 changes in CH_{rave} due to winter warming can induce changes in d_{f0} (Fig. 2), which 222 would explain a decrease in S_T (Fig. 4), we found very limited changes in CH_{rave} and 223 d_{f0}. In fact, at many observation sites, d_{f0} occurred slightly earlier, and not later, in response to the winter warming (Fig. 1). 224

 $\label{eq:second} \ensuremath{\text{225}} \qquad \ensuremath{\text{We}}\xspace \ensuremath{\text{also}}\xspace \ensuremath{\text{draw}}\xspace \ensuremath{\text{also}}\xspace \ensuremath{\text{statemath{\text{mom}}}\xspace \ensuremath{\text{statemath{\text{mom}}}\xspace \ensuremath{\text{mom}}\xspace \ensuremath{\mom}}\xspace \ensuremath{\mom}\xspace \ensuremath{\mom}}\xspace \ensuremath{\mom}\xspace \en$

226 The response function to temperature during bud growth (forcing) was not linear at

227 most sites (Fig. S1a), contrary to the widely used degree-day (defined as the

difference between daily mean temperature and a base temperature, e.g. Fig. S14d).

229 Therefore, the effects of warming on accelerating forcing accumulation increases as temperature moves towards T_{50} (the temperature inducing 50% of optimal growth, the 230 inflection point of the function), but decreases as temperature moves away from T_{50} . 231 232 Estimates of T₅₀ in Europe mostly varied between 8 and 11°C, on average (Fig. S7). While the temperature during the forcing stage was, on average, 0.35(±2.36) °C lower 233 than T_{50} for the period 1951–1979 (Fig. 5), it was $0.08(\pm 2.28)$ and $1.55(\pm 2.51)$ °C 234 higher for the periods 1980–1999 and 2000–2019 respectively. Therefore, spring 235 mean temperature moved towards T₅₀ from 1951–1979 to 1980–1999, while it moved 236 237 away from it afterwards; this explains why the effect of warming on accelerating forcing accumulation decreased in the last 20 years while it had increased in the 238 earlier periods (Fig. 1). 239

Although temperature is the dominant factor of spring phenology¹⁸, the various 240 temperature effects on LUD explain less than half of the temporal changes in S_T at 241 many sites (Fig. 4). Other factors may also influence the response of leaf unfolding to 242 climate warming in some species^{5,41,42}. Temperature can vary strongly within a short 243 time (e.g. a few days) and may show large interannual variations contrary to the 244 245 photoperiodic cue. The latter is often viewed as an insurance against untimely bud break that could lead to fatal consequences (e.g. frost damage) during autumn and 246 winter⁴³. Nonetheless, we found that incorporating photoperiod (see Methods) into the 247 248 Unified model significantly improved the performance of the model in capturing LUD 249 at only a few locations (Extended Data Fig. 10), even for Fagus sylvatica, which has been reported as one of the most sensitive species to photoperiod^{44,45}, although there 250 251 was a very modest decrease of the model error (Extended Data Fig. 10). Besides 252 photoperiod, some studies suggest that frosts in late winter and early spring might exert a strong control on the bud phenology of several specific species⁴⁶⁻⁴⁸. In semi-253

arid and arid regions, bud phenology may also be strongly affected by precipitation⁴⁹, ⁵⁰. Changes in such environmental factors might explain why the predictive power of temperature to explain temporal changes in S_T is not greater (Fig. 4). In addition, we found that the relationships between temperature sensitivity of leaf unfolding and the duration of the forcing stage and the forcing rate might be nonlinear at many sites (e.g. Fig. S8). Using linear regression functions may therefore underestimate the impacts of these variables on the temporal variation of S_T .

We also recognize that there might be some uncertainties in our results. First, our 261 262 findings are based on phenological observations from central Europe, and they may not hold true for other regions. Second, temperature data were obtained from gridded 263 databases (see Methods). Although the spatial resolution is high (0.1°) and the 264 265 temperature was adjusted to the elevation of the sites with a temperature lapse rate, the temperature data still might be different from the actual temperature at the forest 266 canopy. For example, some meteorological phenomena, such as air temperature 267 inversion or the effect of topography on local air circulation and land-atmosphere 268 feedbacks, can hardly be accounted for by a simple lapse rate^{51,52}. Third, although the 269 270 Unified model integrates most of the up-to-date known causal relationships between temperature and bud development¹⁹, it may still miss some unknown mechanisms 271 affecting bud phenology. Finally, the Unified model was calibrated using observed 272 273 LUDs but without information on bud dormancy break date because no observation 274 data of the imperceptible bud development processes for multiple trees at large scale 275 are available yet. More experimental observation on the imperceptible phenological 276 phases will be very helpful to further calibrate model parameters and evaluate the simulation results. 277

278 In this study, we showed that the overall effect of winter warming explained most of the decline in the sensitivity of leaf unfolding to temperature in Europe from 1951 to 279 2019, although not through a delayed dormancy break date. Additionally, we showed 280 281 that spring warming explained part of the decline in the temperature sensitivity of LUD because of a smaller increase in forcing rate per degree of warming in recent 282 decades. Our results reveal the importance of representing the antagonistic effects of 283 chilling and forcing temperatures on bud development, as well as their heterogeneous 284 effectiveness, especially when considering the seasonally uneven climate change^{30,31}. 285 We conclude that temperature sensitivity of leaf unfolding, calculated with a linear 286 regression of LUD over mean pre-season temperature, is not a reliable index to 287 288 project the response of plant phenology to future climate change. We call for further 289 studies based on field observations and controlled condition experiments to deepen our understanding of the mechanisms driving plant phenology in a larger range of 290 climatic conditions. 291

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| 300 | |
| 301 | Author contributions |
| 302 | H.Z. and I.C. designed this study. H.Z. performed the specific simulation and data |
| 303 | analysis. H.Z., P.R. and I.C. wrote most of the manuscript, with substantial |
| 304 | contributions from P.C. and W.Y. All authors reviewed and revised the manuscript. |
| 305 | |
| 306 | Competing interests |
| 307 | The authors declare no competing interests. |
| | |



Figure 1 | Contribution of changes in winter chilling and spring forcing to 311 changes in the LUDs of six tree species in Europe from 1951 to 2019. (a) and (b) 312 show the absolute (Eqs. 6–11 in Methods) and relative (Eqs. 12–14 in Methods) 313 contributions, respectively, of winter chilling and spring forcing to the changes in leaf 314 unfolding date (Δ LUD). The negative and positive values denote an advance and a 315 delay in LUD, respectively. ΔD_{df0} is the change in date when dormancy is released. 316 ΔD_{Fr} is the potential change in the duration of the forcing stage caused by change in 317 spring forcing temperatures. ΔD_{TA0} is the potential shift in LUD caused by change in 318 plants' critical requirement for thermal accumulation. The black dot shows the 319 average change in LUD from 1951-1979 to 1980-1999, and the red dot shows the 320 average change in LUD from 1951-1979 to 2000-2019. Error bar denotes the 321 standard deviation of Δ LUD across observation sites. ** indicates that the changes in 322 LUD are significantly different from zero (p < 0.05 based on one-sample t-test); and 323 for each species, the different letters (a, b) below asterisks means that the changes in 324 LUDs from 1951–1979 to 1980–1999 are significantly different from the changes 325 from 1951–1979 to 2000–2019 (p<0.05 based on the paired-samples t-test). AH: 326 Aesculus hippocastanum; AG: Alnus glutinosa; BP: Betula pendula; FS: Fagus 327 328 sylvatica; FE: Fraxinus excelsior; QR: Quercus robur; All: the average value for all the six species. 329



Figure 2 | Differences between mean winter (December-February), mean spring 332 (March-May) temperatures and the optimal chilling temperature Top (°C), and 333 the relative changes in different chilling and forcing metrics from 1951-1979 to 334 335 1980–1999 and 2000–2019. CHAtot is the total chilling accumulation (c); TA₀ is the critical forcing accumulation required for leaf unfolding (d); and Frave is the average 336 337 daily forcing rate during forcing stage (e). In each violin plot, the red dot refers to the mean value and the balloon represents the probability density distribution of each 338 339 value. Whiskers indicate the interguartile (thick vertical bars) and 95 % confidence intervals (thin vertical bars). The asterisks (**) indicate that the differences between 340 winter/spring temperatures and T_{op} (a,b) and the relative changes in CHA_{tot} (c), TA₀ 341 (d) and F_{rave} (e) are significantly different from 0 (p < 0.05 based on one-sample t-342 test). For each plant species, the violins marked with different letters (i.e. a, b and c 343 below the asterisks) are significantly different (p<0.05 based on the paired-samples t-344 test). AH: Aesculus hippocastanum; AG: Alnus glutinosa; BP: Betula pendula; FS: 345 Fagus sylvatica; FE: Fraxinus excelsior; OR: Quercus robur; All: the average value 346 for all of the six species. 347



350 Figure 3 | Schematic plot showing the impacts of rising temperatures (+3 and +6 °C) on winter chilling, spring forcing and leaf unfolding date. Top is the 351 optimal chilling temperature (°C, Eq. 1); T_{50} is the mid-response temperature of daily 352 forcing rate (°C, Eq. 2); CHA₀ is the critical chilling requirement for releasing 353 354 dormancy; CHAtot0 and CHAtot+3 are the total chilling accumulation during the reference year (Y_0) and during an hypothetical year with 3 °C warming (Y_{0+3}) ; TA₀ 355 and TA₊₃ are the corresponding critical forcing requirements for leaf unfolding. d_{c0} 356 and d_{f0} are the respective start dates of chilling and forcing accumulation in the 357 reference year (Y_0) . d_0 , d_{0+3} and d_{0+6} are the LUDs in the reference year Y_0 and in the 358 years with +3°C and +6°C warming if the chilling accumulation would have been 359 360 identical to the reference year (CHAtoto). d'0+3 is the LUD in Y0+3 when considering the lower chilling accumulation (CHAtot+3) induced by warming, and which leads to a 361 higher forcing requirements. dc1 and dc2 represent the start and end dates of the period 362 when temperatures in Y_{0+3} are more efficient for the chilling rate (because they are 363 closer to T_{op}) than the temperatures in Y_0 . 364 365



Figure 4 | Coefficients of determination (R²) for the linear regression function 367 between the temperature sensitivity of LUD and different metrics of winter 368 chilling and spring forcing. The metrics are: CH_{rave}, the average daily chilling rate 369 from the start date of chilling accumulation (d_{c0} in Fig. 3) to the start date of forcing 370 accumulation (d_{f0} in Fig. 3); CHA_{tot}, the total chilling accumulation in the whole pre-371 growing season; Frave, the average daily forcing rate during the forcing stage; and DF, 372 the duration of forcing stage (day). In addition, CH_{rave} +CHA_{tot} refers to the regression 373 using both CH_{rave} and CHA_{tot} as independent variables, and CH_{rave} +CHA_{tot} +F_{rave} 374 refers to the regression using CH_{rave}, CHA_{tot} and F_{rave} together as independent 375 variables. In each violin plot, the balloon represents the probability density 376 distribution of each gradient of R². Whiskers indicate the interquartile (thick vertical 377 bars) and 95 % confidence intervals (thin vertical bars). AH: Aesculus hippocastanum; 378 AG: Alnus glutinosa; BP: Betula pendula; FS: Fagus sylvatica; FE: Fraxinus 379 excelsior; QR: Quercus robur; All: the average value for all of the six species. 380





383 Figure 5 | Differences between mean temperature during the forcing stage and the mid-response temperature T₅₀ (°C). ΔT50₁₉₅₁₋₁₉₇₉, ΔT50₁₉₈₀₋₁₉₉₉ and ΔT50₂₀₀₀₋ 384 2019 denote the difference between mean forcing stage temperature and T₅₀ during the 385 periods 1951-1979, 1980-1999 and 2000-2019, respectively. Black and Red dots 386 denotes the mean and median value, respectively. The balloon represents the 387 probability density distribution of each value. Whiskers indicate the interquartile 388 (thick vertical bars) and 95 % confidence intervals (thin vertical bars). The asterisks 389 (**) indicate that the mean temperatures during forcing stage are significantly 390 different from the mid-response temperature T_{50} (*p*<0.05 based on one-sample t-test). 391 392 For each species, the different letters (a, b, c) below asterisks means the mean 393 temperatures during forcing stage are significantly different during the periods 1951-1979, 1980–1999 and 2000–2019 (p<0.05 based on the paired-samples t-test). AH: 394 395 Aesculus hippocastanum; AG: Alnus glutinosa; BP: Betula pendula; FS: Fagus sylvatica; FE: Fraxinus excelsior; QR: Quercus robur; All: the average value for all of 396 397 the six species. 398

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522 Methods

523 Phenological and climatic data. Phenological datasets of LUD for the period 1951–

- 524 2019, as well as the geographical location and elevation for each observation site,
- 525 were obtained from the Pan European Phenology (PEP) network
- 526 (<u>http://www.pep725.eu</u>), an open access repository of *in situ* phenological records for
- 527 multiple plant species across $Europe^{34}$. The LUDs were defined by the BBCH
- 528 (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) code as stage
- 529 11 (first leaf unfold). Specifically, we selected the LUD records of the six most
- observed tree species at 2,944 sites in central Europe (Table S1 and Extended Data
- Fig. 1). For each species, only the sites with phenological observations of at least 40
- 532 years were included in our analysis. The median absolute deviation (MAD)
- method 53,54 was then used to identify and exclude potentially erroneous records of
- LUD. For each species at each site, the MAD was calculated as: MAD = median
- 535 $(|LUD_i median (LUD_1, LUD_2, ..., LUD_n)|)$, where 1, 2, i and n are the 1st, 2nd, ith and
- n^{th} observation years, respectively. Any record deviating by more than three times the
- 537 MAD was considered as an outlier and removed from the original dataset used in this
- study. After MAD pre-treatment, 386,320 records of LUD remained for further
- analysis (Table S1). Distribution of these records across 1951–2019 is given in
- 540 Extended Data Fig. 1b.
- 541 Daily mean air temperature at each site was obtained from the gridded database E-
- 542 OBS (<u>http://ensembles-eu.metoffice.com</u>) at a spatial resolution of 0.1° (approx. 10
- 543 km)⁵⁵. Due to the relatively coarse spatial resolution of the E-OBS database, the
- elevation of some phenological sites may be different greatly from the mean elevation
- of the grid cells (also obtained from the E-OBS database) where they locate,
- 546 especially in mountainous areas. To reach a more accurate quantification of

temperature at each site, the temperature data from E-OBS were adjusted using the difference between the actual elevation at each site (as specified in the PEP database) and the mean elevation of the corresponding grid cell (as specified in E-OBS). The temperature lapse rate is set to -0.64° C per 100 m increase in elevation⁵⁶.

551 The Unified phenology model. Phenological models are generally developed based on distinct assumptions regarding the response of bud growth to spring thermal 552 accumulation and/or winter chilling^{35,36}. For example, the Thermal Time model 553 considers that only forcing temperatures explain the leaf unfolding²². More 554 sophisticated models also consider the effect of chilling temperatures on bud 555 dormancy. For example, the Sequential model assumes that the effect of forcing 556 temperatures cannot be effective unless chilling requirements have already been 557 fulfilled³⁸. In contrast, the Parallel model assumes that forcing temperatures can be 558 active concomitantly with chilling accumulation³⁵. Furthermore, other models, such as 559 the Alternating model, assume that the thermal accumulation required for leaf 560 unfolding declines exponentially with increasing chilling accumulation²⁰. These 561 models are non-nested (within each other) and, therefore, cannot be used to test the 562 effects of the above assumptions on the response of leaf unfolding to chilling and 563 forcing temperatures simultaneously¹⁹. To circumvent these limitations, we applied 564 the Unified phenology model¹⁹ in our study. 565

The Unified model considers two phases of bud development, like the most complex models that have been developed. These phases can overlap in time, as assumed in the Parallel model; the second phase can also depend on the first phase, as assumed in the Alternating model²⁰. Most important, depending on the parameter estimates obtained with the data, these assumptions can show support or not from the observation data and the model can be simplified accordingly, for example in a Sequential model³⁸.

Similarly, the response functions to temperature during chilling and forcing stages can
be simplified in other functions which have been widely used as explained in Fig S6.
Overall, the model used integrates the main assumptions of simpler phenology
models, in particular the Sequential³⁸, Parallel³⁵ and Alternating²⁰ models, which can
be regarded as particular cases of the Unified model. For a complete explanation of
the relationship between the Unified model and earlier simpler models, see the
reference publication by Chuine (2000)¹⁹.

The Unified phenology model¹⁹ allows for a direct estimation of the response of spring phenology to both chilling and forcing temperatures, and of the periods when these temperatures affect the plant phenology. In the Unified model, the daily chilling rate (*CH_r*, unitless) during cold days is calculated using a unimodal function (Fig. S1a) of daily mean air temperature (T, °C):

584
$$CH_r = \frac{1}{e^{c_1(T-T_{op})^2 + c_2(T-T_{op})}}$$
(1)

where T_{op} is the optimal chilling temperature, and c_1 and c_2 are two calibration 585 coefficients (Table S2). With specific values of T_{op} , c_1 and c_2 , Eq. (1) can capture 586 other widely used chilling metrics¹⁹, such as, the chilling days ($CH_r = 1$ if T $\leq 5^{\circ}$ C; 587 $CH_r = 0$ if T > 5°C) (Fig. S6a) and the chilling unit based on the triangular function 588 (Fig. S6b). Bud dormancy is released (d_{i0}) when the accumulation of daily chilling 589 590 rate since a specific day (d_{c0} , the start day of chilling accumulation) exceeds the plants' critical chilling requirement (CHA₀, unitless), i.e. when $\sum_{d_{r0}}^{d_{f0}} CH_r > CHA_0$. 591 Note that d_{t0} also corresponds to the start day of forcing (thermal) accumulation (Fig. 592 593 S1). The daily forcing rate (F_r , unitless) is calculated using a sigmoid function (Fig. S1a) of daily mean air temperature $(T, ^{\circ}C)$: 594

595
$$F_r = \frac{1}{1.0 + e^{c_3(T - T_{50})}}$$
(2)

where T_{50} is the mid-response temperature that induces 50% of optimal growth in forcing rate and is the inflection point of the function; and c_3 is a calibration coefficient. Leaf unfolding occurs when the forcing accumulation $(\sum_{d_{f0}}^{LUD} F_r)$ exceeds a certain thermal requirement (TA_0) which declines exponentially with the total chilling accumulation (CHA_{tot}) during the whole pre-growing season (i.e. period from the start day of chilling accumulation to the LUD) (Fig. S1b in SI):

$$602 TA_0 = c_4 e^{c_5 CHA_{tot}} (3)$$

where c_4 and c_5 are calibration coefficients. Note that, in the Unified model, chilling temperature continues to have an effect on CHA_{tot} after dormancy break and forcing requirement decreases as CHA_{tot} increases.

Parameter estimation and model application. Nine parameters of the Unified 607 model, including the start day of chilling accumulation (d_{c0}) , the critical chilling 608 requirement for releasing bud dormancy (CHA_0) , the optimal chilling temperature 609 (T_{op}) , the mid-response temperature $(T_{50} \text{ in Eq. } 2)$ and the five coefficients c_1 to c_5 in 610 Eqs. 1–3, were optimized for each species at each site using an effective global 611 optimization algorithm-the shuffled complex evolution algorithm (SEC-UA)⁵⁷. Prior 612 values and the range of each parameter to be optimized are listed in Table S2. Root 613 mean square error (RMSE, Eq. 5) between simulated (LUD_{sim}) and observed 614 (LUD_{obs i}) LUD was used as the objective function, and parameter values that 615 minimized the RMSE were regarded as optimal. 616

617
$$RMSE = \sqrt{\left(\frac{\sum_{i=1}^{n} (LUD_{sim_i} - LUD_{obs_i})^2}{n}\right)}$$
(5)

where *n* is the number of records (years) for each species at each site; and *i* is the rankof the observation year.

Using the optimized parameters, the Unified model was then applied to estimate the 620 621 day of bud dormancy release, total chilling accumulation, daily forcing rate and the LUD for each year, species and site. We divided the whole 1951–2019 period into 622 three shorter timespans: 1951–1979 (the reference period), 1980–1999 and 2000– 623 624 2019. Analysis of the time series of LUD, mean winter temperature and mean spring 625 temperature showed that the LUD and temperatures overall were stable in Europe during 1951–1979 (Figs. S9 & S10). In the 1980–1999 period, the spring temperature 626 627 in Europe increased significantly and the LUD advanced quickly, by up to 0.5 day yr⁻ ¹. Then, in 2000–2019, the spring temperature in Europe was stable again overall, 628 629 while winter temperature increased significantly (Figs. S9 & S10). For each of these three timespans, in addition to the average LUD and spring and winter temperatures, 630 631 we calculated the metrics needed to represent winter chilling (i.e. CH_r and CHA_{tot}) 632 and spring forcing (i.e. F_r and TA₀). The changes in each variable for each tree species 633 at each site were then calculated, and the significance of changes was evaluated using the one-sample t-test (i.e. test whether the changes are significantly different from 634 635 zero). The significance of difference between changes from 1951–1979 to both 1980– 1999 and 2000–2019 was evaluated using the paired-sample t-test. 636 637 In the Unified model, the LUD is determined by the time when bud dormancy is released (which itself depends on the rate of chilling accumulation), the rate of forcing 638 accumulation and the amount of forcing (TA₀) required for leaf unfolding (Fig. S1). 639

640 To assess the relative contributions of these three factors to the temporal shifts in

LUD, we expressed their effects in number of days. We first calculated the changes in the date of bud dormancy break (d_{f0} in Fig. S1c) from the period 1951–1979 (d_{f0_1970s}) to periods 1980–1999 (d_{f0_1990s}) and 2000–2019 (d_{f0_2010s}) (Eqs. 6 & 7) for each tree species at each site (ΔD_{df0} , Figs. 2 & Extended Data 2):

645
$$\Delta D_{df0_1990s} = d_{f0_1990s} - d_{f0_1970s}$$
(6)

$$\Delta D_{df0_2010s} = d_{f0_2010s} - d_{f0_1970s}$$
(7)

Second, to estimate the shifts in LUD caused by the increased thermal accumulation 647 $(\Delta D_{TA0} \text{ in Fig. 1})$ required for leaf unfolding due to warming-induced loss of winter 648 chilling, we simulated the LUD for each species at each site for the two more recent 649 timespans (1980–1999 and 2000–2019) by fixing the TA₀ in the Unified model to the 650 average TA₀ corresponding to the reference period. From the reference period to the 651 1980–1999 and 2000–2019 periods, the ΔD_{TA0} was calculated as the difference 652 between the simulated LUDs using the reference TA₀ (LUD_{TA0 1970s}) and those 653 654 calculated based on the actual total winter chilling accumulation for each period using Eq. (3) (i.e. LUD_{TA0 1990s} and LUD_{TA0 2010s}) (Eqs. 8 & 9): 655

656
$$\Delta D_{TA0_{1990s}} = LUD_{TA0_{1990s}} - LUD_{TA0_{1970s}}$$
(8)

657
$$\Delta D_{TA0_{2010s}} = LUD_{TA0_{2010s}} - LUD_{TA0_{1970s}}$$
(9)

Third, the contribution of warming-induced changes in daily forcing rates to shifts in
LUD (
$$\Delta D_{Fr}$$
) was calculated as the change in the duration of the forcing stage (FD, i.e.
the number of days from d_{f0} to LUD) from the reference period 1951–1979 (FD_{1970s})
to the periods 1980–1999 (FD_{1990s}) and 2000–2019 (FD_{2010s}), but excluding the
influence of TA0 changes on this temporal shift (Eqs. 10 & 11):

663
$$\Delta D_{Fr_{1990s}} = FD_{1990s} - FD_{1970s} - \Delta D_{TA0_{1990s}}$$
(10)

664
$$\Delta D_{Fr_2010s} = FD_{2010s} - FD_{1970s} - \Delta D_{TA0_2010s}$$
(11)

Finally, the relative contributions of ΔD_{df0} ($p\Delta D_{df0}$), ΔD_{Fr} ($p\Delta D_{Fr}$) and ΔD_{TA0}

666 $(p\Delta D_{TA0})$ to the shifts in LUD were calculated as follows:

667
$$p\Delta D_{df0} = \left(\frac{|\Delta D_{df0}|}{|\Delta D_{df0}| + |\Delta D_{FD}| + |\Delta D_{TA0}|}\right) \times 100$$
(12)

668
$$p\Delta D_{FD} = \left(\frac{|\Delta D_{FD}|}{|\Delta D_{df0}| + |\Delta D_{FD}| + |\Delta D_{TA0}|}\right) \times 100$$
(13)

669
$$p\Delta D_{TA0} = \left(\frac{|\Delta D_{TA0}|}{|\Delta D_{df0}| + |\Delta D_{FD}| + |\Delta D_{TA0}|}\right) \times 100$$
(14)

Temperature sensitivity of LUD. The temperature sensitivity of LUD (S_T, day °C⁻¹) 670 671 was first calculated for each species at each site based on a linear least square regression analysis of LUD and mean pre-season temperature, defined as the period 672 from the start date of chilling accumulation (d_{c0} in Fig. 3) to the mean LUD. The 673 674 slope of the linear regression line was then used to quantify S_T . In addition, we also calculated, from 1951 to 2019, the S_T when the pre-season for each species at each 675 site is defined as the period (with 5-day steps) for which the absolute value of the 676 correlation coefficient between LUD and air temperature was highest, i.e. the period 677 which is most relevant to leaf unfolding⁷. In this case, we first calculated the mean 678 temperature during each of the 27 periods ranging from 20 to 150 days (i.e. 20, 679 25, ..., 145, 150, each at 5 day intervals) preceding the mean LUD. Pearson's 680 correlation coefficient was calculated between the LUD and the mean temperature for 681 682 each of these 27 periods. The period for which the absolute value of correlation coefficient between LUD and mean air temperature was highest was regarded as the 683 684 optimal pre-season.

To estimate the trend in the temporal change of the temperature sensitivity of LUD, we also conducted a reduced major axis regression for each species at each site with a 15-year moving window from 1951 to 2019, that is, we calculated the temperature sensitivity for each continuous 15 years over the entire record period.

Photoperiod effect. To explore the potential uncertainties resulting from the neglecting the photoperiod in the Unified model, we compared the performance of the default Unified model (described above) against a revised version that represents the photoperiod effect. The comparison was performed using the model's ability to capture capture the observed LUD as a minimum criterion. In the revised model, the daily forcing rate (F_r) was calculated based on both daily mean air temperature (T, °C) and daily photoperiod (P, hours):

696
$$F_r = \frac{1}{1.0 + e^{c_3(T - T_{50})}} \left(\frac{P}{10}\right)^e$$
(15)

where the temperature factor (Eq. 2) is identical to that in the default Unified model. 697 The photoperiod factor $\left(\left(\frac{P}{10}\right)^{e}\right)$ was obtained from Bluemel & Chmielewski (2012)⁵⁸ 698 with e as a model parameter. The methodology for optimizing the free parameters in 699 the revised Unified model was identical to that used in the default Unified model. The 700 range for optimizing the parameter e was set to 0–5 with a prior value of 1.56. The 701 revised Unified model was then applied to Fagus sylvatica, which has been reported 702 to be one of the most sensitive species to photoperiod^{44,45}. The performances of both 703 the default and the revised Unified models in capturing LUDs was evaluated using the 704 RMSE (Eq. 5) and the Akaike information criterion (AIC, Eq. 16), which considers 705 both the goodness of fit and the number of free model parameters (n_{param}) : 706

707
$$AIC = n \times ln\left(\frac{\sum_{i=1}^{n} (LUD_{sim_{i}} - LUD_{obs_{i}})^{2}}{n}\right) + 2n_{param}$$
(16)

where *n* is the number of records (years) for each species at each site; and LUD_{sim_i}

and LUD_{obs_i} are the simulated and observed LUD in the year *i*, respectively.

711 Data availability

- 712 Phenology data are available from the Pan European Phenology (PEP) network
- 713 (<u>http://www.pep725.eu</u>). Climate data can be downloaded from E-OBS site:
- 714 <u>http://ensembles-eu.metoffice.com</u>.
- 715

716 **Code availability**

- 717 The codes of the Unified model and the program (SCE-UA algorithm) used for
- 718 parameterization and data analysis can be found at
- 719 <u>https://github.com/hchzhang/UnifiedModel.git</u>.

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724 Method feferences

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