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Deciphering the multiple effects of climate warming on the temporal shift of leaf unfolding

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1 **Target journal:** *Nature Climate Change*

2 **Deciphering the multiple effects of climate warming on the temporal**
3 **shift of leaf unfolding**

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15

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

29

30 **Main**

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

44 Temperature has been regarded as the most important environmental factor
45 controlling plant phenology in the extratropics¹⁸. Plants in these temperate and boreal
46 regions generally require a certain number of cold days to break bud dormancy, and
47 subsequently, a certain number of days with warmer conditions (called forcing
48 temperatures) to trigger cell growth and leaf development¹⁹⁻²². Several studies have
49 argued that changes in winter chilling and thermal accumulation caused by climate
50 change explain the divergent shifts of LUD in response to rising temperature^{7,23-26}. In
51 particular, warming during winter can affect leaf unfolding through two distinct
52 effects: it may delay the timing of bud dormancy release^{27,28}, and may increase the
53 thermal requirement for bud break^{20,29}. Both effects induce a delay in LUD. In
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 complete³², 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 Europe³⁴ (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 decade⁷.

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 simultaneously¹⁹. 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 models⁷. We therefore used this model to disentangle the various effects of climate
92 warming on leaf unfolding.

93 **Contributions of winter and spring warming to LUD shifts**

94 Based on *in-situ* observations, the average LUD in Europe advanced by 1.9 (± 2.3 ,
95 standard deviation of the shifts in LUD for all species across all observation sites, SD)
96 and 5.8 (± 2.9) days for the periods 1980–1999 and 2000–2019, respectively,
97 compared to the reference period 1951–1979 (Δ LUD, Fig. 1a & Extended Data Fig.
98 2). Changes in LUD over time were similar across the six broadleaf species analysed,
99 with differences between species in mean advancement of LUD at each site rarely
100 exceeding one day for both periods. Yet, for all six species, there were larger
101 differences in LUD shifts across sites, ranging from an advance of more than 10 days
102 to a delay of more than 2 days (Extended Data Figs. 2 & 3). Generally, advances in
103 LUD occurred more often at sites with stronger warming (e.g. northern Germany),

104 while delays in LUD mostly occurred at sites with temperature declines (e.g. south-
105 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
107 and mean winter temperatures in central Europe was 4.4 (± 1.8), 3.2 (± 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
110 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
113 used in this study³³, highlighting that uncertainties in simulated LUDs might partly be
114 due to uncertainties in observed LUDs. The model explained 65–78% of the
115 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
117 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 (± 2.1)°C
119 (Extended Data Fig. 7c), which is similar to values obtained with experimental data
120 (2.5–9.1°C)³⁷⁻³⁹.

121 According to the Unified model¹⁹ (see Methods for details), bud dormancy is assumed
122 to be released when chilling accumulation meets plants' critical requirements (CHA_0
123 in Fig. S1). The forcing stage starts as soon as this chilling requirement is met, and
124 leaf unfolding occurs when the thermal accumulation during the forcing stage exceeds
125 a given threshold. This threshold, denoted by TA_0 , declines exponentially with the
126 total amount of chilling received during the whole pre-growing season (CHA_{tot} , Fig.
127 S1b), defined as the period from the onset of chilling accumulation to leaf unfolding.
128 Therefore, the temporal shifts in LUD are determined by the time when bud dormancy

129 is released (d_{f0}), which in turn depends on the chilling accumulation rate (CH_r , Eq. 1),
130 the thermal accumulation rate (F_r , 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 (± 3.8) and 8.7 (± 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 (± 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
155 explain why the LUDs of some plants show a weak or even delayed shift with climate
156 warming^{7,8,16}. A common hypothesis relies on the premise that warm temperatures in
157 winter delay the timing at which the chilling requirement for dormancy release is met,
158 thus postponing the start of the forcing stage and mitigating the advancement of the
159 LUD. However, our results suggest that the winter warming only marginally changed
160 the timing of dormancy release, especially from 1951–1979 to 1980–1999 (Fig. 1). At
161 most of the observation sites, the optimized response functions to chilling temperature
162 showed an optimum (see the pattern plotted in Fig. S6b), in contrast to the widely
163 used index-chilling days^{20,36} (Fig. S6a), which assumes a uniform effect of chilling
164 temperatures as long as they remain below a certain threshold. Winter temperatures
165 recorded at the observation sites were mostly 3–12°C lower than the local optimal
166 chilling temperature (T_{op} , °C) in the period 1951–1979, and then gradually increased
167 towards T_{op} with time (Fig. 2a). This decreasing difference between winter
168 temperature and optimal chilling temperatures translated into an important increase in
169 the chilling rates during winter (e.g. between days d_{c1} and d_{c2} in Fig. 3). On the
170 contrary, in late autumn and early spring, chilling tended to decrease because the
171 temperature tended to be higher than T_{op} (e.g. before d_{c1} and after d_{c2} in Fig. 3).
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
174 release days (ΔD_{df0}) were not substantially postponed and mostly occurred slightly
175 earlier for the six species investigated (Fig. 1).

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 (± 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(± 0.5) and 1.2(± 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(± 10.4) and 22.9(± 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
195 have stopped in the last 20 years in central Europe (Extended Data Fig. 9). The
196 average daily chilling rate during the dormancy stage (Fig. 3, CH_{rave} from d_{c0} to d_{f0})
197 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(± 21.5)% (mean \pm standard deviation) of the
200 temporal variation in S_T . The average daily forcing rate (F_{rave} from d_{f0} to LUD)
201 explained 21.0(± 20.5)% of the temporal variation of S_T , on average (Fig. 4). The three
202 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
205 intervals of R^2 in Fig. 4. This finding suggests that the metrics of controlling S_T might
206 differ across observation sites. Note that the pre-growing season used to calculate S_T
207 here (Fig. 4) is defined as the period from d_{c0} to LUD and thus differs from that
208 applied in several previous studies^{7,17,40}, in which the pre-growing season was usually
209 defined as the period for which the absolute value of the correlation coefficient
210 between LUD and air temperature was largest (i.e. the period which is most relevant
211 to leaf unfolding, see Methods). Nevertheless, calculating the pre-growing season this
212 way provided similar results (Figs. 4 & S7).

213 Changes in winter chilling due to warming have been proposed as the main
214 explanation for the temporal variation in S_T ^{7,17}. Our results show that the overall
215 effect of winter warming on S_T is indeed higher than that of spring warming. Our
216 results further support the hypothesis that winter warming leads to a decline in S_T by
217 reducing the total amount of chilling received by the plants and subsequently
218 increasing the critical forcing requirements for leaf unfolding (Figs. 2, 4 & Eq. 3).
219 However, our findings do not support the hypothesis that winter warming leads to a
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
224 response to the winter warming (Fig. 1).

225 We also draw attention to another cause of decreasing S_T with progressive warming.
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
228 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
230 temperature moves towards T_{50} (the temperature inducing 50% of optimal growth, the
231 inflection point of the function), but decreases as temperature moves away from T_{50} .
232 Estimates of T_{50} in Europe mostly varied between 8 and 11°C, on average (Fig. S7).
233 While the temperature during the forcing stage was, on average, 0.35(±2.36) °C lower
234 than T_{50} for the period 1951–1979 (Fig. 5), it was 0.08(±2.28) and 1.55(±2.51) °C
235 higher for the periods 1980–1999 and 2000–2019 respectively. Therefore, spring
236 mean temperature moved towards T_{50} from 1951–1979 to 1980–1999, while it moved
237 away from it afterwards; this explains why the effect of warming on accelerating
238 forcing accumulation decreased in the last 20 years while it had increased in the
239 earlier periods (Fig. 1).

240 Although temperature is the dominant factor of spring phenology¹⁸, the various
241 temperature effects on LUD explain less than half of the temporal changes in S_T at
242 many sites (Fig. 4). Other factors may also influence the response of leaf unfolding to
243 climate warming in some species^{5,41,42}. Temperature can vary strongly within a short
244 time (e.g. a few days) and may show large interannual variations contrary to the
245 photoperiodic cue. The latter is often viewed as an insurance against untimely bud
246 break that could lead to fatal consequences (e.g. frost damage) during autumn and
247 winter⁴³. Nonetheless, we found that incorporating photoperiod (see Methods) into the
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
250 been reported as one of the most sensitive species to photoperiod^{44,45}, although there
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
253 exert a strong control on the bud phenology of several specific species⁴⁶⁻⁴⁸. In semi-

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

261 We also recognize that there might be some uncertainties in our results. First, our
262 findings are based on phenological observations from central Europe, and they may
263 not hold true for other regions. Second, temperature data were obtained from gridded
264 databases (see Methods). Although the spatial resolution is high (0.1°) and the
265 temperature was adjusted to the elevation of the sites with a temperature lapse rate,
266 the temperature data still might be different from the actual temperature at the forest
267 canopy. For example, some meteorological phenomena, such as air temperature
268 inversion or the effect of topography on local air circulation and land–atmosphere
269 feedbacks, can hardly be accounted for by a simple lapse rate^{51,52}. Third, although the
270 Unified model integrates most of the up-to-date known causal relationships between
271 temperature and bud development¹⁹, it may still miss some unknown mechanisms
272 affecting bud phenology. Finally, the Unified model was calibrated using observed
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
277 simulation results.

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

292

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299 the PEP725 network for collecting and providing the phenological data.

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.

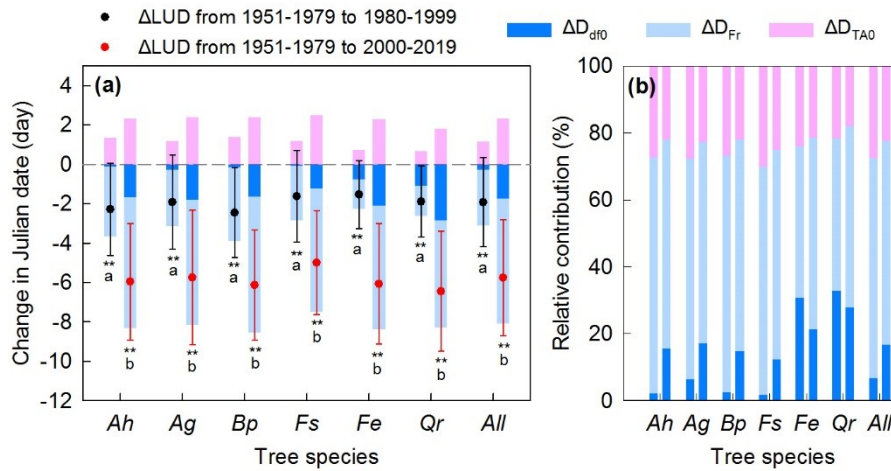
305

306 **Competing interests**

307 The authors declare no competing interests.

308

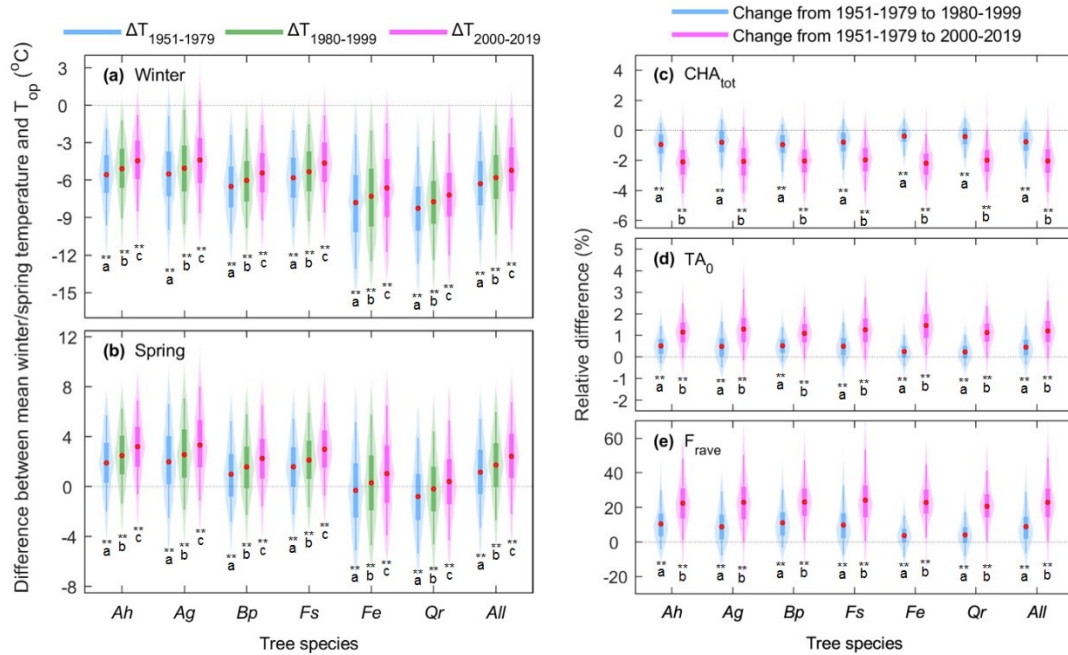
309 **Figure Legends**



310

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

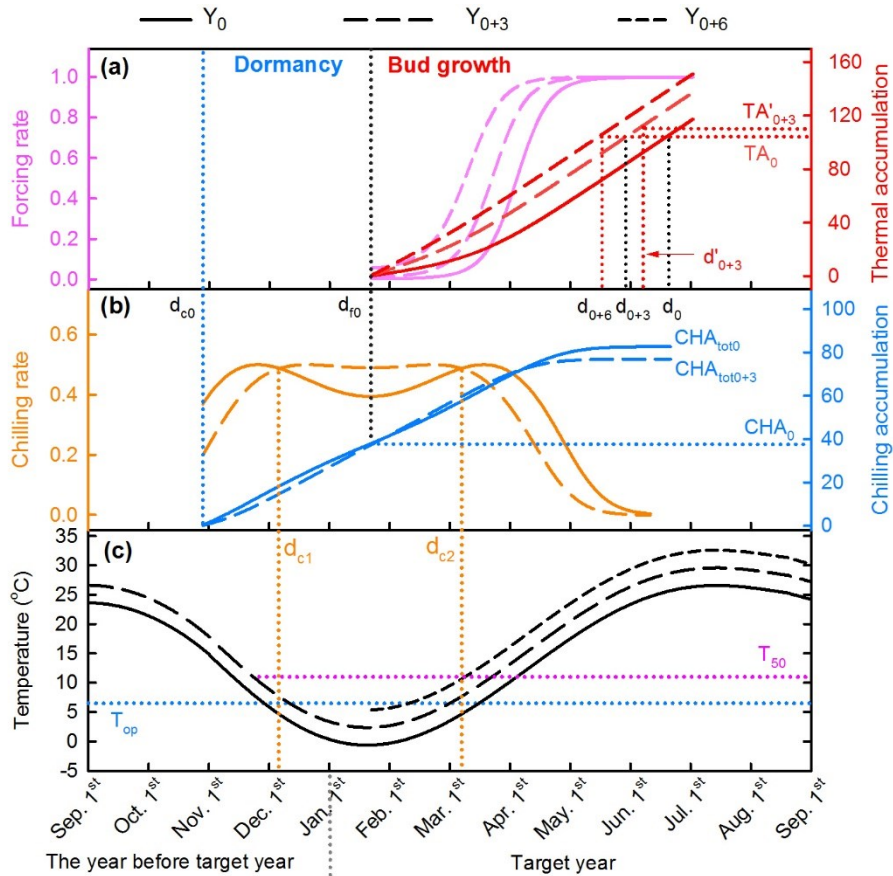
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331

332 **Figure 2 | Differences between mean winter (December-February), mean spring**
 333 **(March-May) temperatures and the optimal chilling temperature T_{op} ($^{\circ}C$), and**
 334 **the relative changes in different chilling and forcing metrics from 1951–1979 to**
 335 **1980–1999 and 2000–2019.** CHA_{tot} is the total chilling accumulation (c); TA_0 is the
 336 critical forcing accumulation required for leaf unfolding (d); and F_{rave} is the average
 337 daily forcing rate during forcing stage (e). In each violin plot, the red dot refers to the
 338 mean value and the balloon represents the probability density distribution of each
 339 value. Whiskers indicate the interquartile (thick vertical bars) and 95 % confidence
 340 intervals (thin vertical bars). The asterisks (**) indicate that the differences between
 341 winter/spring temperatures and T_{op} (a,b) and the relative changes in CHA_{tot} (c), TA_0
 342 (d) and F_{rave} (e) are significantly different from 0 ($p < 0.05$ based on one-sample t-
 343 test). For each plant species, the violins marked with different letters (i.e. a, b and c
 344 below the asterisks) are significantly different ($p < 0.05$ based on the paired-samples t-
 345 test). *AH*: *Aesculus hippocastanum*; *AG*: *Alnus glutinosa*; *BP*: *Betula pendula*; *FS*:
 346 *Fagus sylvatica*; *FE*: *Fraxinus excelsior*; *QR*: *Quercus robur*; *All*: the average value
 347 for all of the six species.

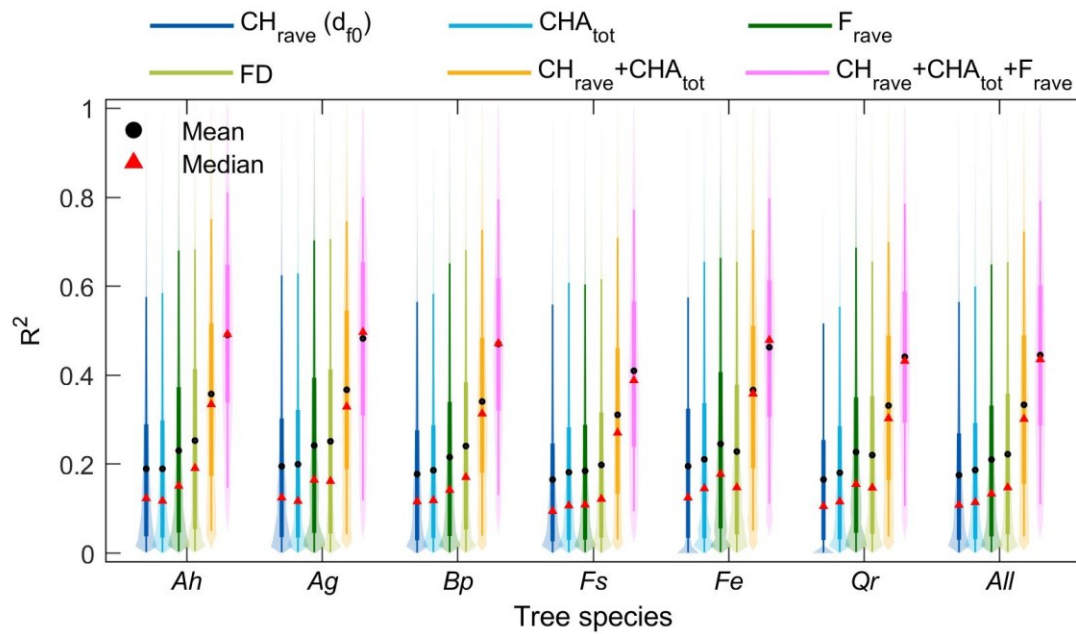
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349

350 **Figure 3 | Schematic plot showing the impacts of rising temperatures (+3 and**
 351 **+6 °C) on winter chilling, spring forcing and leaf unfolding date.** T_{op} is the
 352 optimal chilling temperature (°C, Eq. 1); T_{50} is the mid-response temperature of daily
 353 forcing rate (°C, Eq. 2); CHA_0 is the critical chilling requirement for releasing
 354 dormancy; CHA_{tot0} and CHA_{tot0+3} are the total chilling accumulation during the
 355 reference year (Y_0) and during an hypothetical year with 3 °C warming (Y_{0+3}); TA_0
 356 and TA_{+3} are the corresponding critical forcing requirements for leaf unfolding. d_{c0}
 357 and d_{r0} are the respective start dates of chilling and forcing accumulation in the
 358 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
 359 years with +3°C and +6°C warming if the chilling accumulation would have been
 360 identical to the reference year (CHA_{tot0}). d'_{0+3} is the LUD in Y_{0+3} when considering
 361 the lower chilling accumulation (CHA_{tot0+3}) induced by warming, and which leads to a
 362 higher forcing requirements. d_{c1} and d_{c2} represent the start and end dates of the period
 363 when temperatures in Y_{0+3} are more efficient for the chilling rate (because they are
 364 closer to T_{op}) than the temperatures in Y_0 .

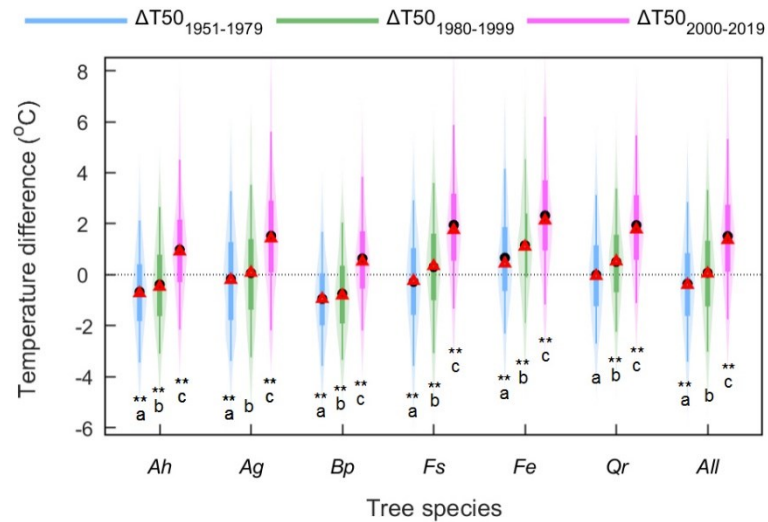
365



366

367 **Figure 4 | Coefficients of determination (R^2) for the linear regression function**
 368 **between the temperature sensitivity of LUD and different metrics of winter**
 369 **chilling and spring forcing.** The metrics are: CH_{rave} , the average daily chilling rate
 370 from the start date of chilling accumulation (d_{c0} in Fig. 3) to the start date of forcing
 371 accumulation (d_{f0} in Fig. 3); CHA_{tot} , the total chilling accumulation in the whole pre-
 372 growing season; F_{rave} , the average daily forcing rate during the forcing stage; and DF,
 373 the duration of forcing stage (day). In addition, $CH_{rave} + CHA_{tot}$ refers to the regression
 374 using both CH_{rave} and CHA_{tot} as independent variables, and $CH_{rave} + CHA_{tot} + F_{rave}$
 375 refers to the regression using CH_{rave} , CHA_{tot} and F_{rave} together as independent
 376 variables. In each violin plot, the balloon represents the probability density
 377 distribution of each gradient of R^2 . Whiskers indicate the interquartile (thick vertical
 378 bars) and 95 % confidence intervals (thin vertical bars). *AH*: *Aesculus hippocastanum*;
 379 *AG*: *Alnus glutinosa*; *BP*: *Betula pendula*; *FS*: *Fagus sylvatica*; *FE*: *Fraxinus*
 380 *excelsior*; *QR*: *Quercus robur*; *All*: the average value for all of the six species.

381



382

383 **Figure 5 | Differences between mean temperature during the forcing stage and**
 384 **the mid-response temperature T_{50} ($^{\circ}\text{C}$).** $\Delta T_{50}_{1951-1979}$, $\Delta T_{50}_{1980-1999}$ and ΔT_{50}_{2000-}
 385 2019 denote the difference between mean forcing stage temperature and T_{50} during the
 386 periods 1951–1979, 1980–1999 and 2000–2019, respectively. Black and Red dots
 387 denotes the mean and median value, respectively. The balloon represents the
 388 probability density distribution of each value. Whiskers indicate the interquartile
 389 (thick vertical bars) and 95 % confidence intervals (thin vertical bars). The asterisks
 390 (**) indicate that the mean temperatures during forcing stage are significantly
 391 different from the mid-response temperature T_{50} ($p < 0.05$ based on one-sample t-test).
 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–
 394 1979, 1980–1999 and 2000–2019 ($p < 0.05$ based on the paired-samples t-test). *AH*:
 395 *Aesculus hippocastanum*; *AG*: *Alnus glutinosa*; *BP*: *Betula pendula*; *FS*: *Fagus*
 396 *sylvatica*; *FE*: *Fraxinus excelsior*; *QR*: *Quercus robur*; *All*: the average value for all of
 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 (<http://www.pep725.eu>), an open access repository of *in situ* phenological records for
527 multiple plant species across Europe³⁴. 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
530 observed tree species at 2,944 sites in central Europe (Table S1 and Extended Data
531 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)
533 method^{53,54} was then used to identify and exclude potentially erroneous records of
534 LUD. For each species at each site, the MAD was calculated as: $MAD = \text{median}$
535 $(|LUD_i - \text{median}(LUD_1, LUD_2, \dots, LUD_n)|)$, where 1, 2, i and n are the 1st, 2nd, ith and
536 nth 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
538 study. After MAD pre-treatment, 386,320 records of LUD remained for further
539 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 (<http://ensembles-eu.metoffice.com>) 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
544 elevation of some phenological sites may be different greatly from the mean elevation
545 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

547 temperature at each site, the temperature data from E-OBS were adjusted using the
548 difference between the actual elevation at each site (as specified in the PEP database)
549 and the mean elevation of the corresponding grid cell (as specified in E-OBS). The
550 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
552 on distinct assumptions regarding the response of bud growth to spring thermal
553 accumulation and/or winter chilling^{35,36}. For example, the Thermal Time model
554 considers that only forcing temperatures explain the leaf unfolding²². More
555 sophisticated models also consider the effect of chilling temperatures on bud
556 dormancy. For example, the Sequential model assumes that the effect of forcing
557 temperatures cannot be effective unless chilling requirements have already been
558 fulfilled³⁸. In contrast, the Parallel model assumes that forcing temperatures can be
559 active concomitantly with chilling accumulation³⁵. Furthermore, other models, such as
560 the Alternating model, assume that the thermal accumulation required for leaf
561 unfolding declines exponentially with increasing chilling accumulation²⁰. These
562 models are non-nested (within each other) and, therefore, cannot be used to test the
563 effects of the above assumptions on the response of leaf unfolding to chilling and
564 forcing temperatures simultaneously¹⁹. To circumvent these limitations, we applied
565 the Unified phenology model¹⁹ in our study.

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

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

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

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

585 where T_{op} is the optimal chilling temperature, and c_1 and c_2 are two calibration
 586 coefficients (Table S2). With specific values of T_{op} , c_1 and c_2 , Eq. (1) can capture
 587 other widely used chilling metrics¹⁹, such as, the chilling days ($CH_r = 1$ if $T \leq 5^\circ\text{C}$;
 588 $CH_r = 0$ if $T > 5^\circ\text{C}$) (Fig. S6a) and the chilling unit based on the triangular function
 589 (Fig. S6b). Bud dormancy is released (d_{f0}) when the accumulation of daily chilling
 590 rate since a specific day (d_{c0} , the start day of chilling accumulation) exceeds the
 591 plants' critical chilling requirement (CHA_0 , unitless), i.e. when $\sum_{d_{c0}}^{d_{f0}} CH_r > CHA_0$.

592 Note that d_{f0} also corresponds to the start day of forcing (thermal) accumulation (Fig.
 593 S1). The daily forcing rate (F_r , unitless) is calculated using a sigmoid function (Fig.
 594 S1a) of daily mean air temperature (T , °C):

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

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

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

603
$$CHA_{tot} = \sum_{d_{co}}^{LUD} CH_r \quad (4)$$

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

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

617
$$RMSE = \sqrt{\left(\frac{\sum_{i=1}^n (LUD_{sim,i} - LUD_{obs,i})^2}{n}\right)} \quad (5)$$

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

620 Using the optimized parameters, the Unified model was then applied to estimate the
 621 day of bud dormancy release, total chilling accumulation, daily forcing rate and the
 622 LUD for each year, species and site. We divided the whole 1951–2019 period into
 623 three shorter timespans: 1951–1979 (the reference period), 1980–1999 and 2000–
 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
 626 during 1951–1979 (Figs. S9 & S10). In the 1980–1999 period, the spring temperature
 627 in Europe increased significantly and the LUD advanced quickly, by up to 0.5 day yr⁻¹.
 628 Then, in 2000–2019, the spring temperature in Europe was stable again overall,
 629 while winter temperature increased significantly (Figs. S9 & S10). For each of these
 630 three timespans, in addition to the average LUD and spring and winter temperatures,
 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
 634 the one-sample t-test (i.e. test whether the changes are significantly different from
 635 zero). The significance of difference between changes from 1951–1979 to both 1980–
 636 1999 and 2000–2019 was evaluated using the paired-sample t-test.

637 In the Unified model, the LUD is determined by the time when bud dormancy is
 638 released (which itself depends on the rate of chilling accumulation), the rate of forcing
 639 accumulation and the amount of forcing (TA₀) required for leaf unfolding (Fig. S1).

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

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

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

$$646 \quad \Delta D_{df0_2010s} = d_{f0_2010s} - d_{f0_1970s} \quad (7)$$

647 Second, to estimate the shifts in LUD caused by the increased thermal accumulation
 648 (ΔD_{TA0} in Fig. 1) required for leaf unfolding due to warming-induced loss of winter
 649 chilling, we simulated the LUD for each species at each site for the two more recent
 650 timespans (1980–1999 and 2000–2019) by fixing the TA_0 in the Unified model to the
 651 average TA_0 corresponding to the reference period. From the reference period to the
 652 1980–1999 and 2000–2019 periods, the ΔD_{TA0} was calculated as the difference
 653 between the simulated LUDs using the reference TA_0 (LUD_{TA0_1970s}) and those
 654 calculated based on the actual total winter chilling accumulation for each period using
 655 Eq. (3) (i.e. LUD_{TA0_1990s} and LUD_{TA0_2010s}) (Eqs. 8 & 9):

$$656 \quad \Delta D_{TA0_1990s} = LUD_{TA0_1990s} - LUD_{TA0_1970s} \quad (8)$$

$$657 \quad \Delta D_{TA0_2010s} = LUD_{TA0_2010s} - LUD_{TA0_1970s} \quad (9)$$

658 Third, the contribution of warming-induced changes in daily forcing rates to shifts in
 659 LUD (ΔD_{Fr}) was calculated as the change in the duration of the forcing stage (FD, i.e.
 660 the number of days from d_{f0} to LUD) from the reference period 1951–1979 (FD_{1970s})
 661 to the periods 1980–1999 (FD_{1990s}) and 2000–2019 (FD_{2010s}), but excluding the
 662 influence of TA_0 changes on this temporal shift (Eqs. 10 & 11):

$$663 \quad \Delta D_{Fr_1990s} = FD_{1990s} - FD_{1970s} - \Delta D_{TA0_1990s} \quad (10)$$

664
$$\Delta D_{Fr_{2010s}} = FD_{2010s} - FD_{1970s} - \Delta D_{TA0_{2010s}} \quad (11)$$

665 Finally, the relative contributions of ΔD_{df0} ($p\Delta D_{df0}$), ΔD_{FD} ($p\Delta D_{FD}$) and ΔD_{TA0}
 666 ($p\Delta D_{TA0}$) to the shifts in LUD were calculated as follows:

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

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

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

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

685 To estimate the trend in the temporal change of the temperature sensitivity of LUD,
 686 we also conducted a reduced major axis regression for each species at each site with a
 687 15-year moving window from 1951 to 2019, that is, we calculated the temperature
 688 sensitivity for each continuous 15 years over the entire record period.

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

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

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

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

708 where n is the number of records (years) for each species at each site; and LUD_{sim_i}
 709 and LUD_{obs_i} are the simulated and observed LUD in the year i , respectively.

710

711 **Data availability**

712 Phenology data are available from the Pan European Phenology (PEP) network

713 (<http://www.pep725.eu>). Climate data can be downloaded from E-OBS site:

714 <http://ensembles-eu.metoffice.com>.

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 <https://github.com/hchzhang/UnifiedModel.git>.

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724 **Method references**

725

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